Phylogenetische Methoden in der Historischen Linguistik

String Alignment

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The Levenshtein Distance

- also known as *edit distance*
- defines the distance between two strings as the minimal number of *edit operations* to transform one string into the other
- edit operations:
  - deletion
  - insertion
  - replacemant
- example: grm. `mEnS` vs. Cimbrian `menEs`
  1. `mEnS` $\rightarrow$ `menS` (replace)
  2. `menS` $\rightarrow$ `menES` (insert)
  3. `menES` $\rightarrow$ `menEs` (insert)
- $d_L(\texttt{mEnS}, \texttt{menEs}) = 3$

The Levenshtein Distance

- alternative presentation: alignment

m	E	n	–	S
|	|	|	|	|
m	e	n	E	s

- distance for a particular alignment is the number of non-identities
- Levenshtein distance is the number of mismatches for the optimal alignment

Computing the Levenshtein Distance

- recursive definition:
  1. $d_L(\epsilon, \alpha) = d_L(\alpha, \epsilon) = l(\alpha)$
  2. $$d_L(\alpha x, \beta y) = \min \begin{cases} d_L(\alpha, \beta) + \delta(x, y) \\ d_L(\alpha x, \beta) + 1 \\ d_L(\alpha, \beta y) + 1 \end{cases}$$
- apparently requires exponentially growing number of comparisons $\Rightarrow$ computationally not feasible
- but:
  - if $l(\alpha) = n$ and $l(\beta) = m$, there are $n + 1$ substrings of α and $m + 1$ substrings of β
  - hence there are only $(n + 1)(m + 1)$ many different comparisons to be performed
  - computational complexity is polynomial (quadratic in $l(\alpha) + l(\beta)$)

Computing the Levenshtein Distance

- Dynamic Programming

	—	m	E	n	S
—	0	1	2	3	4
m	1				
e	2				
n	3				
E	4				
s	5				

Computing the Levenshtein Distance

- Dynamic Programming

	—	m	E	n	S
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Computing the Levenshtein Distance

- Dynamic Programming

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e	2				
n	3				
E	4				
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- Dynamic Programming

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m	1	0	1		
e	2				
n	3				
E	4				
s	5				

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- Dynamic Programming

	—	m	E	n	S
—	0	1	2	3	4
m	1	0	1	2	
e	2				
n	3				
E	4				
s	5				

Computing the Levenshtein Distance

- Dynamic Programming

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n	3				
E	4				
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e	2	1	1		
n	3				
E	4				
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e	2	1	1	2	3
n	3	2			
E	4				
s	5				

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e	2	1	1	2	3
n	3	2	2		
E	4				
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n	3	2	2	1	
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n	3	2	2	1	2
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E	4	3			
s	5				

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e	2	1	1	2	3
n	3	2	2	1	2
E	4	3	2		
s	5				

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n	3	2	2	1	2
E	4	3	2	2	
s	5				

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n	3	2	2	1	2
E	4	3	2	2	2
s	5	4			

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s	5	4	3		

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E	4	3	2	2	2
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e	2	1	1	2	3
n	3	2	2	1	2
E	4	3	2	2	2
s	5	4	3	3	3

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- Dynamic Programming

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m	1	0	1	2	3
e	2	1	1	2	3
n	3	2	2	1	2
E	4	3	2	2	2
s	5	4	3	3	**3**

- memorizing in each step which of the three cells to the left and above gave rise to the current entry lets us recover the corresponing optimal alignment

Computing the Levenshtein Distance

- Dynamic Programming

	—	m	E	n	S
—	0	1	2	3	4
m	1	0	1	2	3
e	2	1	1	2	3
n	3	2	2	1	2
E	4	3	2	2	2
s	5	4	3	3	3

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n	3	2	2	1	2
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m	1	0	1	2	3
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n	3	2	2	1	2
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- Dynamic Programming

	—	m	E	n	S
—	0	1	2	3	4
m	1	0	1	2	3
e	2	1	1	2	3
n	3	2	2	1	2
E	4	3	2	2	2
s	5	4	3	3	3

m	E	n	—	S
m	e	n	E	s

Computing the Levenshtein Distance

	—	m	E	n	S
—	0	1	2	3	4
m	1	0	1	2	3
e	2	1	1	2	3
n	3	2	2	1	2
E	4	3	2	2	2
s	5	4	3	3	3

m	E	n	—	S
m	e	n	E	s

	—	m	E	n	S
—	0	1	2	3	4
m	1	0	1	2	3
e	2	1	1	2	3
n	3	2	2	1	2
E	4	3	2	2	2
s	5	4	3	3	3

m	E	n	S	—
m	e	n	E	s

Normalization for length

- grm. `mEnS` (*Mensch*, 'person') and Hindi `manuSya` are (partially) cognate
- grm. `ze3n` (*sehen*, 'see') and Hindi `deg` are not cognate
- still

$$\begin{aligned} d_L(\mathtt{mEnS}, \mathtt{manuSya}) &= 4 \\ d_L(\mathtt{ze3n}, \mathtt{deg}) &= 3 \end{aligned}$$

- normalization: dividing Levenshtein distance by length of longer string:

$$\begin{aligned} d_{LD}(\mathtt{mEnS}, \mathtt{manuSya}) &= 4/7 \approx 0.57 \\ d_{LD}(\mathtt{ze3n}, \mathtt{deg}) &= 3/4 = 0.75 \end{aligned}$$

German — Swabian

’I’: 0.5 iX i-	’louse’: 0.0 laus laus	’nose’: 1.0 -naz3 ciNgE	’hear’: 0.6 her3n he--a
’you’: 0.0 du du	’tree’: 0.5 baum b-om	’tooth’: 0.25 chan c-an	’die’: 0.57 Sterb3n StEab--
’we’: 0.67 vir mia	’leaf’: 0.25 blat blad	’knee’: 0.25 kn-i knui	’come’: 0.33 khom3n khom--
’one’: 0.5 ains oi-s	’skin’: 0.0 haut haut	’hand’: 0.5 hant hEnd	’sun’: 0.5 zon3 sonE
’two’: 0.25 cvai cvoi	’blood’: 0.25 blut blud	’breast’: 0.4 brust bXuSt	’star’: 0.2 StErn StEan
’person’: 0.4 mEn-S mEnZE	’bone’: 0.33 knoX3n knoX-E	’liver’: 0.4 leb3r leb-a	’water’: 0.6 vas3r va-za
’fish’: 0.0 fiS fiS	’horn’: 0.25 horn hoan	’drink’: 0.71 triNk3n dXiN--g	’stone’: 0.4 Stain Stoi-
’dog’: 0.25 hunt hund	’eye’: 0.25 aug3 augE	’see’: 0.75 ze3n se--	’fire’: 0.25 foia fuia

German — Swabian

```
'path':   1.0
pfat
-veg

'mountain': 0.5
bErk
bEag

'night':  0.33
nat
nad

'full':   0.0
fol
fol

'new':    0.0
noi
noi

'name':   0.5
nam3
nom-
```

German — English

```
'I':      1.0
iX
Ei

'you':    0.5
du
yu

'we':     0.67
vir
wi-

'one':    0.75
ains
w3n-

'two':    1.0
cvai
--tu

'fish':   0.0
fiS
fiS

'dog':    1.0
hunt
-dag

'louse':  0.0
laus
laus

'tree':   1.0
baum
-tri

'leaf':   0.75
blat
-lif

'blood':  0.5
blut
bl3d

'bone':   0.67
knoX3n
-bo--n

'horn':   0.0
horn
horn

'eye':    1.0
aug3
--Ei

'nose':   0.75
naz3
n-os

'tooth':  1.0
chan
-tu8

'tongue': 0.8
chuN3
-t3N-

'knee':   0.33
kni
-ni

'hand':   0.5
hant
hEnd

'breast': 0.15
brust
brest

'liver':  0.4
leb3r
liv3r

'drink':  0.57
triNk3n
drink--

'see':    1.0
ze3n
--si

'hear':   0.6
her3n
hir--

'die':    1.0
Sterb3n
----dEi

'come':   0.67
khom3n
k---3m

'sun':    0.75
zon3
s3n-

'star':   0.6
StErn
star-

'water':  0.4
vas3r
wat3r

'stone':  0.6
Stain
st-on

'fire':   0.5
foia
fEir

'path':   0.75
pfat
p-E8
```

German — Latin

```
'I':      1.0
-iX
ego

'you':    0.5
du
tu

'we':     1.0
vir
nos

'one':    0.75
ains
unus

'two':    1.0
cvai
-duo

'person': 0.86
---mEnS
persona

'fish':   0.83
---fiS
piskis

'dog':    0.8
hun-t
kanis

'louse':  0.78
-----laus
pedikulus

'tree':   1.0
-baum
arbor

'leaf':   0.8
-blat
folyu

'skin':   0.8
haut--
-kutis

'blood':  1.0
---blut
saNgwis

'bone':   0.83
knoX3n
--o--s

'horn':   0.4
horn-
kornu

'eye':    0.83
-au-g3
okulus

'nose':   0.6
na-z3
nasus

'tooth':  1.0
chan
dens

'tongue': 1.0
-chuN3
liNgwE

'knee':   0.75
-kni
genu

'hand':   0.6
han-t
manus

'breast': 0.83
--brust
pektus-

'liver':  0.6
leb3r
yekur

'drink':  0.86
triNk3n
-bibere

'see':    0.83
--ze3n
widere

'hear':   1.0
-her3n
audire

'die':    0.86
Sterb3n
-mor--i

'come':   1.0
khom3n
wenire

'sun':    0.75
zon3
so-l

'star':   0.8
StErn
stela

'water':  0.8
vas3r
-akwa

'stone':  0.8
Stain
lapis
```

German — Latin

```
'fire':   0.8
-foia
iNnis

'path':   1.0
pfat
viya

'mountain': 1.0
bErk
mons

'night':  0.75
n-at
noks

'full':   1.0
---fol
plenus

'new':    0.6
no--i
nowus

'name':   0.6
nam-3
nomen
```

Evaluation: cognates

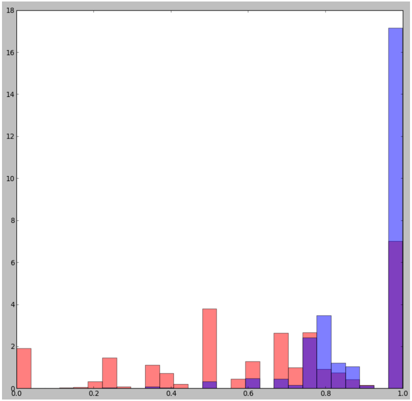
```
0.0
['fiS' 'German_ST' 'fiS' 'English_ST']
0.2
['leb3r' 'German_ST' 'lev3r' 'Dutch_List']
0.2
['leb3r' 'German_ST' 'lev3r' 'Afrikaans']
0.25
['hunt' 'German_ST' 'hont' 'Afrikaans']
0.25
['hunt' 'German_ST' 'hun' 'Kashmiri']
0.25
['hunt' 'German_ST' 'hont' 'Dutch_List']
0.25
['hunt' 'German_ST' 'hun7' 'Danish']
0.4
['leb3r' 'German_ST' 'liv3r' 'English_ST']
0.43
['triNk3n' 'German_ST' 'driNk' 'Afrikaans']
0.5
['leb3r' 'German_ST' 'levEr3' 'Flemish']
0.5
['hant' 'German_ST' 'hEnd' 'Swedish_Up']
0.5
['hant' 'German_ST' 'hEnd' 'English_ST']
0.5
['foia' 'German_ST' 'fir' 'Flemish']
0.5
['blut' 'German_ST' 'bl3d' 'English_ST']
0.5
['hunt' 'German_ST' 'ont' 'Flemish']
```

```
1.0
['aug3' 'German_ST' 'oko' 'BULGARIAN_P']
1.0
['aug3' 'German_ST' 'voka' 'BYELORUSSIAN_P']
1.0
['aug3' 'German_ST' 'oko' 'MACEDONIAN_P']
1.0
['aug3' 'German_ST' 'mati' 'Greek_Mod']
1.0
['aug3' 'German_ST' 'oko' 'Polish']
1.0
['aug3' 'German_ST' 'voka' 'Byelorussian']
1.0
['aug3' 'German_ST' 'oko' 'Czech_E']
1.0
['aug3' 'German_ST' 'yakh' 'Gypsy_Gk']
1.0
['hunt' 'German_ST' 'kau' 'Portuguese_ST']
1.0
['aug3' 'German_ST' 'okyo' 'Italian']
1.0
['aug3' 'German_ST' 'oky' 'Rumanian_List']
1.0
['aug3' 'German_ST' '3y' 'French']
1.0
['hunt' 'German_ST' 'sp3i' 'Afghan']
1.0
['aug3' 'German_ST' 'oko' 'Bulgarian']
1.0
['aug3' 'German_ST' 'oho' 'Spanish']
```

Evaluation: non-cognates

```
0.33
['uL' 'Catalan' 'suL' 'Irish_A' 'EYE']
0.33
['sag' 'Persian_List' 'dag' 'English_ST' 'DOG']
0.33
['sag' 'Tadzik' 'dag' 'English_ST' 'DOG']
0.33
['mau' 'Portuguese_ST' 'Lau' 'Welsh_C' 'HAND']
0.33
['ble' 'Faroese' 'le' 'Singhalese' 'BLOOD']
0.4
['foia' 'German_ST' 'fotya' 'Greek_Mod' 'FIRE']
0.4
['Zuvis' 'Lithuanian_ST' 'vis' 'Dutch_List' 'FISH']
0.4
['lamo' 'Nepali_List' 'largo' 'Spanish' 'LONG']
0.5
['zivs' 'Latvian' 'fis' 'Afrikaans' 'FISH']
0.5
['kan' 'Bengali' 'skuarn' 'Breton_ST' 'EAR']
```

Evaluation



- data from overlap Dyen-Kruskal data base/ASJP
- blue: non-cognates
- red: cognates
- mean normalized distance:
  - cognates: 0.648
  - non-cognates: 0.915

Problems

- binary distinction: match vs. non-match
- frequently genuin sound correspondences in cognates are missed:

c	v	a	i		n	a	**z**	3		-	-	-	**f**	i	S
-	-	**t**	u		n	-	o	**s**		**p**	i	s	k	i	s

- corresponding sounds count as mismatches even if they are aligend correctly

h	a	n	t		h	a	n	t
h	E	n	d		m	a	n	o

- substantial amount of chance similarities

Background: probability theory

- Given two sequences: How likely is it that they are aligned?
- More general question: Given some data, and two competing hypotheses, how likely is it that the first hypothesis is correct?

Bayesian Inference!!!

- given:
  - data: d
  - hypotheses: h_1, h_0
  - model: $P(d|h_1), P(d|h_0)$
- wanted:

$$P(h_1|d) : P(h_0|d)$$

Bayesian inference

- Bayes Theorem:

$$P(h|d) = \frac{P(d|h)P(h)}{\sum_{h'} P(d|h')P(h')}$$

- ergo:

$$\begin{aligned}
P(h_1|d) : P(h_0|d) &= P(d|h_1)P(h_1) : P(d|h_0)P(h_0) \\
P(h_1|d) : P(h_0|d) &= \frac{P(d|h_1)}{P(d|h_0)} \frac{P(h_1)}{P(h_0)} \\
\log(P(h_1|d) : P(h_0|d)) &= \log \frac{P(d|h_1)}{P(d|h_0)} + \log \frac{P(h_1)}{P(h_0)}
\end{aligned}$$

Bayesian inference

- suppose we have many independent data: $\vec{d} = d_1, \ldots, d_n$

$$
\begin{aligned}
P(\vec{d}|h) &= \prod_{i=1}^{n} P(d_i|h) \\
\log P(\vec{d}|h) &= \sum_{i=1}^{n} \log P(d_i|h) \\
\log \frac{P(\vec{d}|h_1)}{P(\vec{d}|h_0)} &= \sum_{i=1}^{n} \log \frac{P(d_i|h_1)}{P(d_i|h_0)} \\
\log(P(h_1|\vec{d}) : P(h_0|\vec{d})) &= \sum_{i=1}^{n} \log \frac{P(d_i|h_1)}{P(d_i|h_0)} + \log \frac{P(h_1)}{P(h_0)}
\end{aligned}
$$

Bayesian inference

- mein argument against using Bayes' rule: the **prior probabilities** $P(h_1), P(h_0)$ are not known
- there are various heuristics, but no generally accepted way to obtain them
- if n is large though, $\log {}^{P(h_1)}/_{P(h_0)}$ doesn't matter very much:[1]

$$\log(P(h_1|\vec{d}) : P(h_0|\vec{d})) \quad \approx \quad \sum_{i=1}^{n} \log \frac{P(d_i|h_1)}{P(d_i|h_0)} = \log(P(\vec{d}|h_1) : P(\vec{d}|h_0))$$

- the quantity $\log(P(\vec{d}|h_1) : P(\vec{d}|h_0))$ is called **log-odds**

[1] Also, if we choose an *uninformative prior* with $P(h_1) = P(h_0)$, we have $\log {}^{P(h_1)}/_{P(h_0)} = 0$ anyway.

Log-odds

- log-odds can take any real value
- a positive value indicates evidence for h_1 and a negative value evidence for h_0
- the higher the absolute value, the stronger is the evidence

Weighted alignment

- suppose our data are two aligned sequences $\vec{x}$, $\vec{y}$
- for the time being, we assume there are no gaps in the alignment
  - h_1: they developed from a common ancestor via substitions
  - h_0: they are unrelated
- additional assumptions (rough approximation in biology, pretty much off the mark in linguistics): substitions in different positions occur independently

The null model

- if $\vec{x}$ and $\vec{y}$ are unrelated, their joint probability equals the product of their individual probabilities
- as a start (quite wrong both in biology and in linguistics): let us assume the strings have no "grammar"; each position is independent from all other positions
- then

$$\begin{aligned} P(\vec{x}, \vec{y}|h_0) &= P(\vec{x}|h_0)P(\vec{y}|h_0) \\ &= \prod_i P(x_i|h_0)P(y_i|h_0) \\ \log P(\vec{x}, \vec{y}|h_0) &= \sum_i \log(P(x_i|h_0) + \log P(y_i|h_0)) \end{aligned}$$

The null model

- suppose $\vec{x}$ and $\vec{y}$ are generated by the same process (reasonable for DNA and protein comparison, false for cross-linguistic word comparison)
- then $P(x_i|h), P(y_i|h)$ are simply the probabilities of occurrence
- q_a: probability that symbol a occurs in a sequence

$$\log P(\vec{x}, \vec{y}|h_0) = \sum_i \log q_{x_i} + \sum_j \log q_{y_j}$$

- q can be estimated from relative frequencies

The alignment model

- suppose $\vec{x}$ and $\vec{y}$ evolved from a common ancestor via independent substitution mutations
- independence between positions:

$$P(\vec{x}, \vec{y}|h_1) = \prod_i P(x_i, y_i|h_2)$$

- $p_{a,b}$: probability that a position in the latest common ancestor of x and y evolved into an a in sequence $\vec{x}$ and into a b in sequence $\vec{y}$

$$\begin{aligned} P(\vec{x}, \vec{y}|h_1) &= \prod_i p_{x_i,y_i} \\ \log P(\vec{x}, \vec{y}|h_1) &= \sum_i \log p_{x_i,y_i} \end{aligned}$$

The log-odds score

- taking things together, we have

$$\log(P(\vec{x}, \vec{y}|h_1) : P(\vec{x}, \vec{y}|h_0)) \quad = \quad \sum_i \log \frac{p_{x_i, y_i}}{q_{x_i} q_{y_i}}$$

- $\log \frac{p_{ab}}{q_a q_b}$: **score** of the alignment of a with b
- assembled in a **substitution matrix**

Substitution matrices

- in bioinformatics, several commonly used substitution matrices for nucleotids and proteins
- based on explicit models of evolution and careful empirical testing
- for nucleotids:

$$\begin{array}{ccccc} & A & G & T & C \\ A & 2 & -5 & -7 & -7 \\ G & -5 & 2 & -7 & -7 \\ T & -7 & -7 & 2 & -5 \\ C & -7 & -7 & -5 & 2 \end{array}$$

Substitution matrices

- for proteins: different matrices for different evolutionary distances
- for instance: BLOSUM50

	A	R	N	D	C	Q	E	G	H	I	L	K	M	F	P	S	T	W	Y	V
A	**5**	−2	−1	−2	−1	−1	−1	0	−2	−1	−2	−1	−1	−3	−1	1	0	−3	−2	0
R	−2	**7**	−1	−2	−4	1	0	−3	0	−4	−3	3	−2	−3	−3	−1	−1	−3	−1	−3
N	−1	−1	**7**	2	−2	0	0	0	1	−3	−4	0	−2	−4	−2	1	0	−4	−2	−3
D	−2	−2	2	**8**	−4	0	2	−1	−1	−4	−4	−1	−4	−5	−1	0	−1	−5	−3	−4
C	−1	−4	−2	−4	**13**	−3	−3	−3	−3	−2	−2	−3	−2	−2	−4	−1	−1	−5	−3	−1
Q	−1	1	0	0	−3	**7**	2	−2	1	−3	−2	2	0	−4	−1	0	−1	−1	−1	−3
E	−1	0	0	2	−3	2	**6**	−3	0	−4	−3	1	−2	−3	−1	−1	−1	−3	−2	−3
G	0	−3	0	−1	−3	−2	−3	**8**	−2	−4	−4	−2	−3	−4	−2	0	−2	−3	−3	−4
H	−2	0	1	−1	−3	1	0	−2	**10**	−4	−3	0	−1	−1	−2	−1	−2	−3	2	−4
I	−1	−4	−3	−4	−2	−3	−4	−4	−4	**5**	2	−3	2	0	−3	−3	−1	−3	−1	4
L	−2	−3	−4	−4	−2	−2	−3	−4	−3	2	**5**	−3	3	1	−4	−3	−1	−2	−1	1
K	−1	3	0	−1	−3	2	1	−2	0	−3	−3	**6**	−2	−4	−1	0	−1	−3	−2	−3
M	−1	−2	−2	−4	−2	0	−2	−3	−1	2	3	−2	**7**	0	−3	−2	−1	−1	0	1
F	−3	−3	−4	−5	−2	−4	−3	−4	−1	0	1	−4	0	**8**	−4	−3	−2	1	4	−1
P	−1	−3	−2	−1	−4	−1	−1	−2	−2	−3	−4	−1	−3	−4	**10**	−1	−1	−4	−3	−3
S	1	−1	1	0	−1	0	−1	0	−1	−3	−3	0	−2	−3	−1	**5**	2	−4	−2	−2
T	0	−1	0	−1	−1	−1	−1	−2	−2	−1	−1	−1	−1	−2	−1	2	**5**	−3	−2	0
W	−3	−3	−4	−5	−5	−1	−3	−3	−3	−3	−2	−3	−1	1	−4	−4	−3	**15**	2	−3
Y	−2	−1	−2	−3	−3	−1	−2	−3	2	−1	−1	−2	0	4	−3	−2	−2	2	**8**	−1
V	0	−3	−3	−4	−1	−3	−3	−4	−4	4	1	−3	1	−1	−3	−2	0	−3	−1	**5**

Substitution matrix for the ASJP data

1. identify large sample of pairs of closely related languages (using expert information or heuristics based on aggregated Levenshtein distance)

```
An.NORTHERN_PHILIPPINES.CENTRAL_BONTOC
An.MESO-PHILIPPINE.NORTHERN_SORSOGON

WF.WESTERN_FLY.IAMEGA
WF.WESTERN_FLY.GAMAEWE

Pan.PANOAN.KASHIBO_BAJO_AGUAYTIA
Pan.PANOAN.KASHIBO_SAN_ALEJANDRO

AA.EASTERN_CUSHITIC.KAMBAATA_2
AA.EASTERN_CUSHITIC.HADIYYA_2

ST.BAI.QILIQIAO_BAI_2
ST.BAI.YUNLONG_BAI

An.SULAWESI.MANDAR
An.OCEANIC.RAGA

An.SULAWESI.TANETE
An.SAMA-BAJAW.BOEPINANG_BAJAU

UA.AZTECAN.NAHUATL_HUEYAPAN_TETELA_DEL_VOLCAN
UA.AZTECAN.NAHUATL_CUENTEPEC_TEMIXCO

An.SOUTHERN_PHILIPPINES.KAGAYANEN
An.NORTHERN_PHILIPPINES.LIMOS_KALINGA

An.MESO-PHILIPPINE.CANIPAAN_PALAWAN
An.NORTHWEST_MALAYO-POLYNESIAN.LAHANAN

NC.BANTOID.LIFONGA
NC.BANTOID.BOMBOMA_2

IE.INDIC.WAD_PAGGA
IE.INDIC.TALAGANG_HINDKO

NC.BANTOID.LINGALA
NC.BANTOID.LIFONGA

An.CENTRAL_MALAYO-POLYNESIAN.BALILEDO
An.CENTRAL_MALAYO-POLYNESIAN.PALUE

AuA.MUNDA.HO
AuA.MUNDA.KORKU

MGe.GE-KAINGANG.KAYAPO
MGe.GE-KAINGANG.APINAYE
```

Substitution matrix for the ASJP data

2. pick a concept and a pair of related languages at random
   - languages: `Pen.MAIDUAN.MAIDU_KONKAU`, `Pen.MAIDUAN.NE_MAIDU`
   - concept: *one*
3. find corresponding words from the two languages:
   - `nisam`, `niSem`
4. do Levenshtein alignment

n	i	s	a	m
n	i	S	e	m

5. for each sound pair, count number of correspondences
   - nn: 1; ii: 1; sS; 1; ae: 1; mm: 1

Substitution matrix for the ASJP data

- steps 2-5 are repeated 100,000 times

```
klem   S3--v   ligini   kulox   Naltir---i   ...
klom   S37on   ji---p   Gulox   Naltirtiri   ...
```

			⋮	⋮	⋮
a	a	56,047			
i	i	33,955	4	8	2
u	u	23,731	4	a	2
n	n	21,363	G	t	2
o	o	19,619	i	!	2
m	m	18,263	G	y	2
t	t	16,975	d	!	2
k	k	16,773	s	G	2
e	e	12,745	Z	5	2
r	r	11,601	G	s	2
l	l	11,377	X	z	2
b	b	8,965	!	k	2
s	s	8,245	q	8	2
d	d	6,829	a	!	2
p	p	6,681	a	!	2
w	w	6,613	!	y	2
N	N	6,275	!	E	2
h	h	5,331	j	G	2
y	y	5,321	G	i	2
3	3	5,255	E	!	2
⋮	⋮	⋮			
			v	S	2

Substitution matrix for the ASJP data

6. determine relative frequency of occurrence of each sound within the entire database

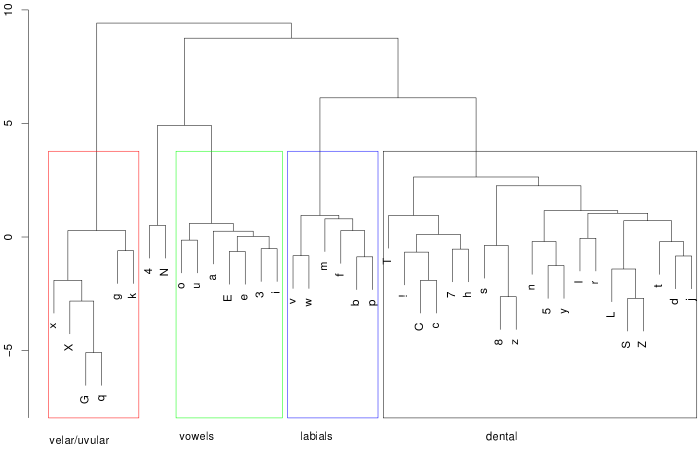
a	0.1479	E	0.0134
i	0.0969	7	0.0124
u	0.0696	C	0.0073
o	0.0626	S	0.0064
n	0.0614	x	0.0062
e	0.0478	c	0.0056
k	0.0478	f	0.0052
m	0.0465	5	0.0049
t	0.0449	v	0.0045
r	0.0346	q	0.0041
l	0.0331	z	0.0035
b	0.0248	j	0.0035
s	0.0243	T	0.0029
w	0.0232	L	0.0027
3	0.0228	X	0.0022
y	0.0222	8	0.0014
d	0.0214	Z	0.0011
h	0.0213	!	0.0009
p	0.0202	4	0.0002
N	0.0201	G	0.0001
g	0.0178		

Substitution matrix for the ASJP data

7. estimate p_{ab} as relative frequency of co-occurrence of a with b, q_a, q_b as individual relative frequencies, and determine substitution scores $\log_2 \frac{p_{ab}}{q_a q_b}$

G	G	11.2348	**Z**	**j**	**4.9386**		o	q	-3.2842
!	!	10.0202	d	d	4.9263		C	a	-3.2893
4	4	9.1480	g	g	4.8958		j	o	-3.2914
8	8	8.0650	b	b	4.8906		a	m	-3.2915
Z	Z	7.9575	s	s	4.8277		E	v	-3.3035
X	X	7.9375	**4**	**5**	**4.7508**		!	w	-3.3079
L	L	7.6276	E	E	4.7143		!	u	-3.3087
z	z	7.2624	w	w	4.6512		5	q	-3.3116
q	q	7.2542	h	h	4.5819		T	o	-3.3158
f	f	6.9117	**G**	**x**	**4.5573**		!	k	-3.3526
v	v	6.8418	**Z**	**z**	**4.4943**		e	z	-3.3763
5	5	6.7731	y	y	4.4637	...	!	s	-3.3788
j	j	6.7587	l	l	4.4037		f	q	-3.3942
T	T	6.6580	**!**	**G**	**4.3760**		N	S	-3.3954
S	S	6.6054	3	3	4.3692		!	b	-3.4077
c	c	6.5989	r	r	4.3061		L	b	-3.4558
C	C	6.2439	**X**	**q**	**4.1200**		T	u	-3.4690
4	**G**	**6.1943**	m	m	4.1087		4	i	-3.5529
x	x	6.1210	t	t	4.1021		5	a	-3.8294
G	**X**	**5.3342**	**G**	**Z**	**4.0429**		C	N	-3.8451
G	**q**	**5.3017**	k	k	3.9046		!	t	-4.2625
7	7	5.2111	**X**	**x**	**3.8116**		!	e	-4.3534
p	p	5.0693	**T**	**Z**	**3.7380**		!	i	-4.3712
N	N	4.9821	**8**	**G**	**3.6993**		!	a	-4.9817

Evaluation



10
5
0
−5
x
X
G
q
g
k
4
N
o
u
a
E
e
3
i
v
w
m
f
b
p
T
!
C
c
7
h
s
8
z
n
5
y
l
r
L
S
Z
t
d
j
velar/uvular
vowels
labials
dental

Gap penalties

- gaps in an alignment correspond either to an insertion or a deletion
- simplified assumption: insertions and deletions are equally likely at all positions; symbols are inserted according to their general frequency of occurrence
- Suppose an item x_i is aligned to a gap. Let α be the probability that an insertion occured since the latest common ancestor, and β the probability of a deletion

$$
\begin{aligned}
P(x_i, -|h_1) &= \alpha q_{x_i} + \beta q_{x_i} \\
P(x_i, -|h_0) &= q_{x_i} \\
\log(P(x_i, -|h_1) : P(x_i, -|h_0)) &= \log(\alpha + \beta) \\
&= -d
\end{aligned}
$$

- i.e., there is a constant term for each gap
- as $\alpha + \beta < 1$, this term is negative, i.e. there a constant **penalty** for each gap

Affine gap penalties

- deletions/insertions frequently apply to entire blocks of symbols (both in biology and linguistics)
- probability of a gap of length n are higher than the product of probabilities of n individual gaps
- penalty e for **extending** a gap is lower than penalty d for **opening** a gap
- g: length of a gap

$$\gamma(g) = -d - (g-1)e$$

- no principled way to derive the values of d and e; have to be fixed via trial and error
- $d = 2.5$ and $e = 1.6$ work quite well for the ASJP data

Weighted alignment

- so far, we assumed that the alignment between $\vec{x}$ and $\vec{y}$ is known
- to assess strength of evidence for h_1 given $\vec{x}, \vec{y}$, we need to consider all alignments between $\vec{x}$ and $\vec{y}$
- enumeration is infeasible, because the number of alignments between two sequences of length n is

$$\binom{2n}{n} = \frac{(2n)!}{(n!)^2} \approx \frac{2^{2^n}}{\sqrt{\pi n}}$$

- computation is nonetheless possible using *Pair Hidden Markov Models* (stay tuned for the next lecture!)
- simpler task: find the most likely alignment and determine its log-odds!

The Needleman-Wunsch algorithm

- almost identical to Levenshtein algorithm, except:
  - matches/mismatches are counted not as 1 and 0, but as log-odds scores of the corresponding symbol pair
  - insertions/deletions are counted as gap penalties
  - by convention, the similarity rather than the distance is counted, i.e. we try to find the alignment that maximizes the score
- let $\vec{x}$ have length n, $\vec{y}$ lenth m, s_{ab} be the log-odds score of a and b, and d/e the gap penalties

The Needleman-Wunsch algorithm

$$
\begin{array}{rcl}
F(0,0) & = & 0 \\
G(0,0) & = & 0 \\
\forall i: & & 0 < i \leq n \\
F(i,0) & = & F(i-1,0) + G(i-1,0)e + (1 - G(i-1,0))d \\
G(i,0) & = & 1 \\
\forall j: & & 0 < j \leq m: \\
F(0,j) & = & F(0,j-1) + G(0,j-1)e + (1 - G(0,j-1))d \\
G(0,j) & = & 1 \\
\forall i,j: & & 0 < i \leq n, 0 < j \leq m \\
F(i,j) & = & \max \left\{ \begin{array}{l} F(i-1,j) + G(i-1,j)e + (1 - G(i-1,j))d \\ F(i,j-1) + G(i,j-1) + (1 - G(i,j-1))d \\ F(i-1,j-1) + s_{x_i y_j} \end{array} \right. \\
G(i,j) & = & 0 \text{ if } \arg\max \left\{ \begin{array}{l} F(i-1,j) + G(i-1,j)e + (1 - G(i-1,j))d \\ F(i,j-1) + G(i,j-1)e + (1 - G(i,j-1))d \\ F(i-1,j-1) + s_{x_i y_j} \end{array} \right\} = 3 \\
 & & 1 \text{ else}
\end{array}
$$

Computing the weighted alignment score

- Dynamic Programming

	–	m	E	n	S
–	0	-2.5	-4.1	-5.7	-7.3
m	-2.5				
e	-4.1				
n	-5.7				
E	-7.3				
s	-8.9				

Computing the weighted alignment score

- Dynamic Programming

	–	m	E	n	S
–	0	−2.5	−4.1	−5.7	−7.3
m	−2.5				
e	−4.1				
n	−5.7				
E	−7.3				
s	−8.9				

Computing the weighted alignment score

- Dynamic Programming

	–	m	E	n	S
–	0	−2.5	−4.1	−5.7	−7.3
m	−2.5				
e	−4.1				
n	−5.7				
E	−7.3				
s	−8.9				

Computing the weighted alignment score

- Dynamic Programming

	–	m	E	n	S
–	0	-2.5	-4.1	-5.7	-7.3
m	-2.5	4.13			
e	-4.1				
n	-5.7				
E	-7.3				
s	-8.9				

Computing the weighted alignment score

- Dynamic Programming

	–	m	E	n	S
–	0	−2.5	−4.1	−5.7	−7.3
m	−2.5	4.13			
e	−4.1				
n	−5.7				
E	−7.3				
s	−8.9				

Computing the weighted alignment score

- Dynamic Programming

	–	m	E	n	S
–	0	−2.5	−4.1	−5.7	−7.3
m	−2.5	4.13			
e	−4.1				
n	−5.7				
E	−7.3				
s	−8.9				

Computing the weighted alignment score

- Dynamic Programming

	–	m	E	n	S
–	0	−2.5	−4.1	−5.7	−7.3
m	−2.5	4.13	1.53		
e	−4.1				
n	−5.7				
E	−7.3				
s	−8.9				

Computing the weighted alignment score

- Dynamic Programming

	—	m	E	n	S
—	0	−2.5	−4.1	−5.7	−7.3
m	−2.5	4.13	1.53	0.03	
e	−4.1				
n	−5.7				
E	−7.3				
s	−8.9				

Computing the weighted alignment score

- Dynamic Programming

	–	m	E	n	S
–	0	−2.5	−4.1	−5.7	−7.3
m	−2.5	4.13	1.53	0.03	−1.47
e	−4.1				
n	−5.7				
E	−7.3				
s	−8.9				

Computing the weighted alignment score

- Dynamic Programming

	–	m	E	n	S
–	0	−2.5	−4.1	−5.7	−7.3
m	−2.5	4.13	1.53	0.03	−1.47
e	−4.1	1.53			
n	−5.7				
E	−7.3				
s	−8.9				

Computing the weighted alignment score

- Dynamic Programming

	–	m	E	n	S
–	0	−2.5	−4.1	−5.7	−7.3
m	−2.5	4.13	1.53	0.03	−1.47
e	−4.1	1.53	5.65		
n	−5.7				
E	−7.3				
s	−8.9				

Computing the weighted alignment score

- Dynamic Programming

	–	m	E	n	S
–	0	−2.5	−4.1	−5.7	−7.3
m	−2.5	4.13	1.53	0.03	−1.47
e	−4.1	1.53	5.65	3.05	
n	−5.7				
E	−7.3				
s	−8.9				

Computing the weighted alignment score

- Dynamic Programming

	–	m	E	n	S
–	0	−2.5	−4.1	−5.7	−7.3
m	−2.5	4.13	1.53	0.03	−1.47
e	−4.1	1.53	5.65	3.05	1.55
n	−5.7				
E	−7.3				
s	−8.9				

Computing the weighted alignment score

- Dynamic Programming

	–	m	E	n	S
–	0	−2.5	−4.1	−5.7	−7.3
m	−2.5	4.13	1.53	0.03	−1.47
e	−4.1	1.53	5.65	3.05	1.55
n	−5.7	0.03			
E	−7.3				
s	−8.9				

Computing the weighted alignment score

- Dynamic Programming

	–	m	E	n	S
–	0	−2.5	−4.1	−5.7	−7.3
m	−2.5	4.13	1.53	0.03	−1.47
e	−4.1	1.53	5.65	3.05	1.55
n	−5.7	0.03	3.05		
E	−7.3				
s	−8.9				

Computing the weighted alignment score

- Dynamic Programming

	–	m	E	n	S
–	0	−2.5	−4.1	−5.7	−7.3
m	−2.5	4.13	1.53	0.03	−1.47
e	−4.1	1.53	5.65	3.05	1.55
n	−5.7	0.03	3.05	9.2	
E	−7.3				
s	−8.9				

Computing the weighted alignment score

- Dynamic Programming

	–	m	E	n	S
–	0	−2.5	−4.1	−5.7	−7.3
m	−2.5	4.13	1.53	0.03	−1.47
e	−4.1	1.53	5.65	3.05	1.55
n	−5.7	0.03	3.05	9.2	6.6
E	−7.3				
s	−8.9				

Computing the weighted alignment score

- Dynamic Programming

	–	m	E	n	S
–	0	−2.5	−4.1	−5.7	−7.3
m	−2.5	4.13	1.53	0.03	−1.47
e	−4.1	1.53	5.65	3.05	1.55
n	−5.7	0.03	3.05	9.2	6.6
E	−7.3	−1.47			
s	−8.9				

Computing the weighted alignment score

- Dynamic Programming

	–	m	E	n	S
–	0	−2.5	−4.1	−5.7	−7.3
m	−2.5	4.13	1.53	0.03	−1.47
e	−4.1	1.53	5.65	3.05	1.55
n	−5.7	0.03	3.05	9.2	6.6
E	−7.3	−1.47	4.75		
s	−8.9				

Computing the weighted alignment score

- Dynamic Programming

	–	m	E	n	S
–	0	−2.5	−4.1	−5.7	−7.3
m	−2.5	4.13	1.53	0.03	−1.47
e	−4.1	1.53	5.65	3.05	1.55
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n	−5.7	0.03	3.05	9.2	6.6
E	−7.3	−1.47	4.75	6.6	7.62
s	−8.9				

Computing the weighted alignment score

- Dynamic Programming

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E	−7.3	−1.47	4.75	6.6	7.62
s	−8.9	−2.97	2.15		

Computing the weighted alignment score

- Dynamic Programming

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m	−2.5	4.13	1.53	0.03	−1.47
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s	−8.9	−2.97	2.15	5.1	

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E	−7.3	−1.47	4.75	6.6	7.62
s	−8.9	−2.97	2.15	5.1	8.84

Computing the weighted alignment score

- Dynamic Programming

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- memorizing in each step which of the three cells to the left and above gave rise to the current entry lets us recover the corresponding optimal alignment

Computing the weighted alignment score

- Dynamic Programming

	–	m	E	n	S
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m	−2.5	4.13	1.53	0.03	−1.47
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s	−8.9	−2.97	2.15	5.1	8.84

- memorizing in each step which of the three cells to the left and above gave rise to the current entry lets us recover the corresponing optimal alignment

Evaluation

- scores:
  - s_{dt}: 0.27
  - s_{aE}: 0.19
  - s_{hm}: -1.76
  - s_{to}: -2.78
- $d_{NW}(hant, hEnd) = 8.59$
- $d_{NW}(hant, mano) = 1.40$

Evaluation

left: Levenshtein alignment; right: Needleman-Wunsch alignment

-iX ego	iX- ego	-blat folyu	b-lat folyu	han-t manus	han-t manus
du tu	du tu	haut-- -kutis	haut-- k-utis	--brust pektus-	b--rust pektus-
vir nos	vir nos	---blut saNgwis	---blut saNgwis	leb3r yekur	leb3r yekur
ains unus	ain-s -unus	knoX3n --o--s	knoX3n --os--	triNk3n -bibere	triNk3n- -bi-bere
cvai -duo	cvai duo-	horn- kornu	horn- kornu	--ze3n widere	--ze3n widere
---mEnS persona	mEnS--- persona	-au-g3 okulus	a-ug3- okulus	-her3n audire	--her3n audire-
---fiS piskis	fiS--- piskis	na-z3 nasus	naz3- nasus	Sterb3n -mor--i	Sterb3n -mor-i-
hun-t kanis	hun-t kanis	chan dens	chan- d-ens	khom3n wenire	khom3n--- w---enire
-----laus pedikulus	------laus pedikul-us	-chuN3 liNgwE	chuN--3 -liNgwE	zon3 so-l	zon3 sol-
-baum arbor	--baum arb-or	-kni genu	k-ni genu	StErn stela	StErn stela

Evaluation

```
vas3r       --vas3r
-akwa       akwa---

Stain       Sta-in
lapis       -lapis

-foia       fo-ia
iNnis       iNnis

pfat        p-fat
viya        viya-

bErk        bErk
mons        mons

n-at        na-t
noks        noks

---fol      fol----
plenus      p-lenus

no--i       no-i-
nowus       nowus

nam-3       nam3-
nomen       nomen
```

German — Swabian

’I’: 0.3
iX
i

’you’: 8.26
du
du

’we’: -1.09
vir
mia

’one’: 4.63
ains
ois

’two’: 16.0
cvai
cvoi

’person’: 12.61
mEnS
mEnZE

’fish’: 16.35
fiS
fiS

’dog’: 11.76
hunt
hund

’louse’: 15.01
laus
laus

’tree’: 6.57
baum
bom

’leaf’: 11.92
blat
blad

’skin’: 14.42
haut
haut

’blood’: 12.88
blut
blud

’bone’: 16.88
knoX3n
knoXE

’horn’: 8.75
horn
hoan

’tooth’: 10.03
chan
can

’tongue’: 9.8
chuN3
cuN

’knee’: 7.77
kni
knui

’hand’: 8.6
hant
hEnd

’breast’: 14.81
brust
bXuSt

’liver’: 10.01
leb3r
leba

’drink’: 4.99
triNk3n
dXiNg

’see’: 0.63
ze3n
se

’hear’: 2.74
her3n
hea

’die’: 10.16
Sterb3n
StEab

’come’: 11.84
khom3n
khom

’sun’: 8.79
zon3
sonE

’star’: 16.16
StErn
StEan

’water’: 7.8
vas3r
vaza

’stone’: 10.36
Stain
Stoi

’fire’: 12.43
foia
fuia

’path’: -2.57
pfat
veg

German — English

'I': -2.3 iX Ei	'tree': -7.83 baum tri	'tongue':-0.63 chuN3 t3N	'die': -7.7 Sterb3n dEi
'you': 2.34 du yu	'leaf': -0.47 blat lif	'knee': 3.86 kni ni	'come': 1.22 khom3n k3m
'we': 2.21 vir wi	'blood': 9.46 blut bl3d	'hand': 8.6 hant hEnd	'sun': 1.95 zon3 s3n
'one': -2.3 ains w3n	'bone': -1.36 knoX3n bon	'breast': 16.93 brust brest	'star': 8.2 StErn star
'two': -5.25 cvai tu	'horn': 15.73 horn horn	'liver': 14.65 leb3r liv3r	'water': 12.06 vas3r wat3r
'fish': 16.35 fiS fiS	'eye': -4.1 aug3 Ei	'drink': 7.48 triNk3n drink	'stone': 6.75 Stain ston
'dog': -7.46 hunt dag	'nose': 1.63 naz3 nos	'see': -3.04 ze3n si	'fire': 6.79 foia fEir
'louse': 15.01 laus laus	'tooth': -6.23 chan tu8	'hear': 4.61 her3n hir	'path': 4.02 pfat pE8

German — Latin

'I': -3.87
iX
ego

'you': 3.62
du
tu

'we': -5.06
vir
nos

'one': 2.39
ains
unus

'two': -5.51
cvai
duo

'person':-4.66
mEnS
persona

'fish': 0.29
fiS
piskis

'dog': -2.27
hunt
kanis

'louse': -0.08
laus
pedikulus

'tree': -3.85
baum
arbor

'leaf': -3.57
blat
folyu

'skin': -0.25
haut
kutis

'blood': -9.18
blut
saNgwis

'bone': -5.72
knoX3n
os

'horn': 7.55
horn
kornu

'eye': -3.87
aug3
okulus

'nose': 4.49
naz3
nasus

'tooth': -2.78
chan
dens

'tongue':-3.4
chuN3
liNgwE

'knee': 0.8
kni
genu

'hand': 0.73
hant
manus

'breast': 1.39
brust
pektus

'liver': 5.37
leb3r
yekur

'drink': -9.22
triNk3n
bibere

'see': -4.15
ze3n
widere

'hear': -4.24
her3n
audire

'die': -6.12
Sterb3n
mori

'come': -9.25
khom3n
wenire

'sun': 0.97
zon3
sol

'star': 5.72
StErn
stela

'water': -5.4
vas3r
akwa

'stone': -3.26
Stain
lapis

Multiple sequence alignment

- Needleman-Wunsch and pair-HMMs only do pairwise alignment
- desirable: aligning all sequences of a taxon into one matrix
  - necessary for character-based phylogenetic inference
  - improves the quality of the alignment

Multiple sequence alignment

- example: 'one'
  - PIE: oinos
  - Bosian: yedan
  - Kashubian: yEdEn
  - optimal pairwise alignments:

o	i	n	o	s	o	i	n	o	s	y	e	d	a	n
y	e	d	a	n	y	E	d	E	n	y	E	d	E	n

- optimal multiple alignment (maximizing sum of pairwise similarities per column):

y	E	d	E	n	-	-
-	o	-	i	n	o	s
y	e	d	a	n	-	-

- alignment of all 'n's is etymologically correct

Multiple sequence alignment

- in principle, the Needleman-Wunsch algorithm can be generalized to aligning k sequences
- however, aligning k sequences of length n has complexity $\mathcal{O}(n^{k^2}) \Rightarrow$ computationally intractable
- two strategies
  - heuristic search
  - progressive alignment

Progressive sequence alignment

- start with a **guide tree** (using some heuristics like pairwise alignment + Neighbor Joining)
- working bottom-up, at each internal node, do pairwise alignment of the block alignments at the daugher node
- complexity is $\mathcal{O}(n^2k^3) \Rightarrow$ computationally feasible