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THE ANÂTAXIS PHYLOGENETIC METHOD. 2. AN EXAMPLE - RECONSTITUTING A WHOLE DENDROGRAM

BY

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ABSTRACT

The Anâtaxis phylogenetic method. 2. An example - reconstituting a whole dendrogram. - The WPGMA numerical taxonomy phenetics method is applied to the semi-matrix of dissimilarities (between terminal taxa) derived from a matrix of characters states to which a cladistic maximum parsimony method had also been applied. Because this semi-theoretical case displays homoplasy and lineage-dependent heterogeneity of transformation rates, the phenogram and the cladogram thus produced are phyletically quite different. The new phylogenetic method Anâtaxis is then applied to the same semi-matrix of dissimilarities, and it rapidly reconstitutes a dendrogram which is congruent with the cladogram.

Key-words: Cladistic Maximum Parsimony, Dissimilarity matrix, Evolutionary tree, Heterogeneity of transformation rates, Homoplasy, Numerical Taxonomy Phenetics, Outgroup-based method, Phylogenetic method, Splitting method.

We wish to phyletically study a number of taxa selected from within the **Craniata** phylum, more precisely we want to resolve the phyletic relationships within the **Vertebrata** sub-phylum. Accordingly, we use the **myxini taxon**, which is craniate but non-vertebrate, **as starting outgroup**.

caractères

taxons	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
a_myxini	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	+	+	+	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0
b_petromyzones	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	+	+	+	+	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0
c_selacii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	+	+	+	+	0	0	+	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0
d_amia	0	0	0	0	0	0	0	0	0	0	0	0	0	+	+	+	+	+	0	0	0	+	0	0	0	?	0	0	0	0	0	0	0	0	0	0
e_teleostei	0	0	0	0	0	0	0	0	0	0	0	0	0	+	+	+	+	+	0	+	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0
f_dipnoi	0	0	0	0	0	+	?	0	+	+	?	?	?	+	+	+	+	+	0	0	?	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0
g_urodela	0	0	0	0	0	+	+	+	+	+	+	+	+	+	+	+	+	+	0	0	0	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0
h_anura	0	0	0	0	+	+	+	+	+	+	+	+	+	+	+	+	+	+	0	0	0	0	+	+	0	0	0	0	0	0	0	0	0	0	0	0
i_sauria	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	0	0	0	0	0	0	+	+	0	0	0	0	0	0	0	0	0	0
j_ophidia	+	+	+	+	0	0	0	+	+	+	+	+	+	+	+	+	+	+	0	0	0	0	0	0	+	+	0	0	0	0	0	0	0	0	0	0
k_chelonia	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	0	0	0	0	0	0	0	0	+	0	0	0	0	0	0	0	0	0
l_crocodilia	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	0	0	0	0	0	0	0	0	0	+	+	0	0	0	0	0	0	0
m_aves	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	0	0	0	0	0	0	0	0	0	+	+	+	+	+	+	0	0	0
n_chiroptera	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	+	+	+	+
o_felidae	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	+	+	+	+
p_marsupialia	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	+	+	+	+

This is an *ad hoc* matrix, with characters and taxa chosen for demonstration purposes, and with no pretense at producing a taxonomically or systematically valid phyletic tree. Rather, this matrix was designed to include the main pitfalls associated in a phyletic reconstruction, and to demonstrate the validity and effectiveness of the Anâtaxis method. The characters are binary (presence/absence) morphological ones, and their definition might be obtained through the author.

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With a Cladistic Maximum Parsimony (CMP) method (SWOFFORD, 1993), i.e. by looking for the tree that minimalises the sum of dissimilarities between all pairs of adjacent nodes, and with a post hoc rooting (R) done within the branch leading to the a_myxini node, we obtain the following phylogram, i.e. a cladogram in which the length of each branch is proportional to the dissimilarity between the two nodes which this branch connects (for the DelTran option, the transformations of characters 7 and 11-13 are done one branch later, in the Tetrapoda branch). The total length of this cladistically most parsimonious tree is 39 steps (all the steps are indicated above or below each branch), with a total of 5 homoplasies.

```
  /a myxini          |
  |                  | Agnatha (Cyclostomata)
--R  /b petromyzones |
  | |
  \--+      /---c selacii
  16+|      | 21+
Vert.|      |   /---d amia       |
     \------+   | 22+            | Actinopterygii
     15+,19+|   +---e teleostei |
 Gnathostom.|   | 20+
            \---+                      /f dipnoi
             14+|   Protetrapoda      |
    Osteomorphi |     6+,9+,10+,      |   /---g urodela       |
                \---------------------+   | 22+               | Amphibia (Batrachia)
                     7+,11+,12+,13+   |   |   /------h anura |
                     (if AccTran)     |8+ |   |23+,24+
                                      \---+   |            25+,26+/i sauria   |
                                  Tetrapoda |   |            /------+ 5°,6°,7°  |Squamata
                                            |5+ |            |      \---------j |
                                            \---+            | 27+      ophidia
                                     Eutetrapoda |           +---k chelonia
                                                 |           |
                                                 |   Amniota | 28+, /l crocodilia |Archo-
                                                 \-----------+------+ 30+,31+,32+,|sauria
                                                  1+,2+,3+,4+ | 29+  \-----------m|
                                                              |         33+     aves
                                                              | 33+,      /n chiroptera
                                                              |34+,35+,36+|
                                                              \-----------+o felidae
                                                                Mammalia  |
                                                                          \p marsupialia
```

Now here is a phenogram, i.e. a tree produced by a Numerical Taxonomic Phenetics -NTP- method (SNEATH & SOKAL, 1973). It is the product of an application, on the Δ matrix of dissimilarities between pairs of taxa, of the clustering algorithm **WPGMA** (Weighted-Pair Group Method with Arithmetic averages) - and again, with a post hoc rooting (R) done within the branch leading to a_myxini.

The phenogram differs strongly from the cladogram, because, as a product of an NTP method, it is very sensitive to the lineage-dependent heterogeneity of evolutionary rates, and does not take into account homoplasy. Because of the high number of autapomorphies within the m_aves branch, the birds have been rejected to a basal position within the Amniota phenon; this adds two homoplasies to the tree. Because of the high number of autapomorphies within the Amniota branch, it has been rejected to a basal position relative to the f_dipnoi taxon and the Amphibia; this adds two homoplasies to the tree. And because of the high number of autapomorphies within the branch leading to the f_dipnoi and Tetrapoda, the remaining fish are found assembled together within a Pisces phenon; this adds one homoplasy to the tree.

```
/-------------------------------------a myxini        | Agnatha      |
|                                                     | (Cyclo-      |
|    /--------------------------------b petromyzones  |  stomata)    |
|    |                                                                |
R    |         /-----------------------c selacii                (Pisces_v.s.)
|    |   Pisces|                                                     |
|    |    /----+                  /----d amia       |                |
\----+    |    \------------------+                 | Actinopterygii |
Vert.|    |                       \----e teleostei  |                |
     |    |
     |    |                  /---------f dipnoi
     |    |     Amphibia_l.s.|
     \----+    /-------------+    /----g urodela |
  Gnatho- |    |             \----+               | Amphibia (Batrachia)
  stomata |    |                  \----h anura    |
          |    |
          |    |                  /----i sauria      |
          |    |                  |                  |
          |    |                  +----j ophidia     |
          |    |             /----+                  | Reptilia
          \----r             |    +----k chelonia    |
 Tetrapoda_l.s.|             |    |                  |
               |   Reptimamm.|    \----l crocodilia  |
               |    /--------+
               |    |        |    /----n chiroptera   |
               |    |        |    |                   |
               |    |        \----+----o felidae      | Mammalia
               \----+             |                   |
            Amniota|             \----p marsupialia   |
                   |
                   \------------------m aves
```

Thus, with five more homoplasies, the phenogram is five steps longer than the cladogram. It would be ideal to have a method based on an analysis of the matrix of dissimilarities between taxa rather than on the matrix of the states of characters, thus being much quicker than CMP methods, but that nevertheless would not be subject to the phyletic artefacts typical of NTP methods.

The Anâtaxis method aims to do precisely that (BITTAR, 2002). Let us apply it to this problem. To simplify the demonstration, we do not present here the way Anâtaxis solves the problem of homoplasy - we leave three dots between parentheses (...) when such a problem occurs.

In a preliminary step, their three dissimilarities being equal to 0, the three mammalian taxa are joined together in a n_Mammalia taxon.

Iteration 1.

With indices o for myxini and i for any vertebrate, median-normalise on the a_myxini taxon (median = 15.5) the Vertebrata Δ sub-matrix:

(in bold) $\mathbf{diff_{oi}} = \text{med}(\Delta_{oi}) - \Delta_{oi}$

Δ		b	c	d	e	f	g	h	i	j	k	l	m	n
o=myxini	diff	**14**	**11**	**10**	**10**	**5.5**	**2**	**0**	**-3**	**0**	**-3**	**-4**	**-8**	**-6**
a_myxini	**0**	1.5	4.5	5.5	5.5	10	13.5	15.5	18.5	15.5	18.5	19.5	23.5	21.5
b_petromyzones	**14**		3.5	4.5	4.5	9	12.5	14.5	17.5	14.5	17.5	18.5	22.5	20.5
c_selacii	**11**			3.5	3.5	7	11.5	13.5	16.5	13.5	16.5	17.5	21.5	19.5
d_amia	**10**				2.5	7	8.5	12.5	15.5	12.5	15.5	16.5	20.5	18.5
e_teleostei	**10**					7	10.5	12.5	15.5	12.5	15.5	16.5	20.5	18.5
f_dipnoi	**5.5**						5	7	10	10	10	11	15	13
g_urodela	**2**							4	8	9	7	8	12	10
h_anura	**0**								8	11	7	8	12	10
i_sauria	**-3**									3	3	4	8	6
j_ophidia	**0**										6	7	11	9
k_chelonia	**-3**											3	7	5
l_crocodilia	**-4**												4	6
m_aves	**-8**													8

Vertebrata Δ* sub-matrix median-normalised on taxon myxini,
with $\Delta_{ij}^* = \Delta_{ij} + \text{diff}_{oi} + \text{diff}_{oj}$:

Δ*		b	c	d	e	f	g	h	i	j	k	l	m	n
o=myxini	diff	*14*	*11*	*10*	*10*	*5.5*	*2*	*0*	*-3*	*0*	*-3*	*-4*	*-8*	*-6*
a_myxini	*0*	15.5	15.5	15.5	15.5	15.5	15.5	15.5	15.5	15.5	15.5	15.5	15.5	15.5
b_petromyzones	*14*		28.5	28.5	28.5	28.5	28.5	28.5	28.5	28.5	28.5	28.5	28.5	28.5
c_selacii	*11*			24.5	24.5	23.5	24.5	24.5	24.5	24.5	24.5	24.5	24.5	24.5
d_amia	*10*				22.5	22.5	20.5	22.5	22.5	22.5	22.5	22.5	22.5	22.5
e_teleostei	*10*					22.5	22.5	22.5	22.5	22.5	22.5	22.5	22.5	22.5
f_dipnoi	*5.5*						12.5	12.5	12.5	15.5	12.5	12.5	12.5	12.5
g_urodela	*2*							6	7	11	6	6	6	6
h_anura	*0*								5	11	4	4	4	4
i_sauria	*-3*									0	-3	-3	-3	-3
j_ophidia	*0*										3	3	3	3
k_chelonia	*-3*											-4	-4	-4
l_crocodilia	*-4*												-8	-4
m_aves	*-8*													-6

It is straightforward to define the sub-outgroup. Let us call **Gnathostomata** the non-lamprey vertebrates and gnathostomeX any member of this taxon. When analysing all the triads formed within the myxini-normalised Vertebrata ingroup, we notice that ALWAYS Δ*(petromyzones;gnathostome1) = 28.5 = Δ*(petromyzones;gnathostome2) >> Δ*(gnathostome2;gnathostome1) {-8 to 24.5}: all the triads involving petromyzones are ultrametric-like, and the lampreys taxon appears as the external one in all these triads.

Thus, within the Vertebrata subset, the b_petromyzones taxon is outgroup to the Gnathostomata ingroup.

Iteration 2.

Median-normalise on the b_petromyzones taxon (median = 14.5) the Gnathostomata sub-matrix of original Δ :

Δ		c	d	e	f	g	h	i	j	k	l	m	n
o=petromyzones	diff	**11**	**10**	**10**	**5.5**	**2**	**0**	**-3**	**0**	**-3**	**-4**	**-8**	**-6**
b_petromyzones	**0**	3.5	4.5	4.5	9	12.5	14.5	17.5	14.5	17.5	18.5	22.5	20.5
c_selacii	**11**		3.5	3.5	7	11.5	13.5	16.5	13.5	16.5	17.5	21.5	19.5
d_amia	**10**			2.5	7	8.5	12.5	15.5	12.5	15.5	16.5	20.5	18.5
e_teleostei	**10**				7	10.5	12.5	15.5	12.5	15.5	16.5	20.5	18.5
f_dipnoi	**5.5**					5	7	10	10	10	11	15	13
g_urodela	**2**						4	8	9	7	8	12	10
h_anura	**0**							8	11	7	8	12	10
i_sauria	**-3**								3	3	4	8	6
j_ophidia	**0**									6	7	11	9
k_chelonia	**-3**										3	7	5
l_crocodilia	**-4**											4	6
m_aves	**-8**												8

Gnathostomata Δ* median-normalised on taxon b_petromyzones :

Δ*		c	d	e	f	g	h	i	j	k	l	m	n
o=petromyzones	diff	*11*	*10*	*10*	*5.5*	*2*	*0*	*-3*	*0*	*-3*	*-4*	*-8*	*-6*
b_petromyzones	*0*	14.5	14.5	14.5	14.5	14.5	14.5	14.5	14.5	14.5	14.5	14.5	14.5
c_selacii	*11*		24.5	24.5	23.5	24.5	24.5	24.5	24.5	24.5	24.5	24.5	24.5
d_amia	*10*			22.5	22.5	20.5	22.5	22.5	22.5	22.5	22.5	22.5	22.5
e_teleostei	*10*				22.5	22.5	22.5	22.5	22.5	22.5	22.5	22.5	22.5
f_dipnoi	*5.5*					12.5	12.5	12.5	15.5	12.5	12.5	12.5	12.5
g_urodela	*2*						6	7	11	6	6	6	6
h_anura	*0*							5	11	4	4	4	4
i_sauria	*-3*								0	-3	-3	-3	-3
j_ophidia	*0*									3	3	3	3
k_chelonia	*-3*										-4	-4	-4
l_crocodilia	*-4*											-8	-4
m_aves	*-8*												-6

Let us call **Osteomorphi** the non-selacii gnathostomes. We notice the clear-cut candidacy of the selacii taxon as the next sub-outgroup: with the exception of when the f_dipnoi taxon is involved, there is an ultrametric-like triadic relationship, Δ*(selacii; non-dipnoi osteomorph1) = 24.5 = Δ*(selacii ; non-dipnoi osteomorph2) >> Δ*(non-dipnoi osteomorph2; non-dipnoi osteomorph1) {-8 to 22.5}.

Otherwise, when the f_dipnoi taxon is involved, we have Δ*(selacii; non-dipnoi osteomorph) = 24.5 > Δ*(selacii; dipnoi) = 23.5 >> Δ*(non-dipnoi osteomorph; dipnoi) {12.5 to 22.5}. (...)

The c_selacii taxon appears as the external one in all triads formed from within the lampreys-normalised Gnathostomata subset. Thus, within this subset, the taxon c_selacii is outgroup to the Osteomorphi ingroup.

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