

Plancton du lac Léman (XXV) : année 1999

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Objektyp: **Article**

Zeitschrift: **Archives des sciences et compte rendu des séances de la Société**

Band (Jahr): **55 (2002)**

Heft 1

PDF erstellt am: **22.07.2024**

Persistenter Link: <https://doi.org/10.5169/seals-740289>

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Archs Sci. Genève	Vol. 54	Fasc. 1	pp. 15-50	Mai 2001
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PLANCTON DU LAC LÉMAN (XXV).- ANNÉE 1999

PAR

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(Ms. reçu le 18 décembre 2000, accepté le 9 janvier 2001)

ABSTRACT

Plankton of Lake Geneva (XXV).- Year 1999. - During the whole year 1999 samples of water have been collected twice each month in Lake Geneva between Hermance and Coppet. Qualitative and quantitative data have been recorded: dry weight, number of phytoplankton organisms per liter, diversity index, chlorophyll content, turbidity and transparency. The organisms of the net plankton and the pumped water were listed. The results showing the seasonal changes are discussed and compared to those of the previous year.

Abréviations: Phytopl., Phytoplankton; Zoopl., Zooplankton; Temp., Température; PS, Poids de matière sèche; D, Dominant; TA, Très abondant; A, Abondant; PR, Pas rare; PA, Peu abondant; I, Isolé.

MATÉRIEL ET MÉTHODES

Nous avons effectué 23 prélèvements d'eau dans le Petit-Lac, entre Hermance et Coppet, à raison de deux par mois, pendant l'année 1999, afin de poursuivre nos travaux sur le plancton du Léman (NAEF *et al.*, 1999). Nos méthodes de prélèvement consistaient comme pour les années précédentes (NAEF & MARTIN, 1994) en:

- un échantillon récolté au filet horizontalement en surface (ouverture de maille 80 µm)
- un échantillon récolté au filet verticalement de 50 m à la surface (ouverture de maille 200 µm)
- les échantillons d'eau brute suivants prélevés à la pompe à 1 m:

10 litres pour déterminer le poids de matière sèche, 10 litres pour l'observation des organismes après sédimentation, 1 litre pour effectuer les comptages du phytoplankton, 5 litres pour faire les dosages de chlorophylle, 3 x 1 litre à 10 minutes d'intervalle pour la détermination de la turbidité, 3 x 50 ml à 10 minutes d'intervalle pour le dosage du carbone organique total.

Les comptages ont été faits au microscope inversé selon la méthode d'UTERMÖHL (1958) adaptée par BURKARD (non publié) au laboratoire du Service de l'Eau, SIG, Genève. Les mesures de turbidité, obtenues par néphélométrie, ont été effectuées par Y. Bersier dans ce même laboratoire.

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With $y =$ any tetrapod taxon except $g_urodela$ and $j_ophidia$, we have $\Delta^*(dipnoi,y1) = 18.5 = \Delta^*(dipnoi,y2) \gg \Delta^*(y2,y1) \{-2 \text{ to } 11\}$. In these cases, we are in the presence of ultrametric-like trichotomies with $dipnoi$ being the external taxon.

Otherwise, when the taxa $g_urodela$ or $j_ophidia$ are involved, we have:

$$\Delta^*(dipnoi,urodela) = 19.5 \gg \Delta^*(dipnoi,y) = 18.5 \gg \Delta^*(urodela,y) \{13 \text{ to } 14\};$$

$$\Delta^*(dipnoi,ophidia) = 21.5 \gg \Delta^*(dipnoi,y) = 18.5 \gg \Delta^*(ophidia,y) \{6 \text{ to } 17\};$$

$$\Delta^*(dipnoi,ophidia) = 21.5 \gg \Delta^*(dipnoi,urodela) = 19.5 \gg \Delta^*(ophidia,urodela) = 18.$$

In these three non-ultrametric cases, the $dipnoi$ taxon still appears as the external one in all triads formed from within the Actinopterygii-normalised Protetrapoda subset. (...) We can now proceed with the phyletic reconstruction by considering the f_dipnoi taxon as an outgroup to the Tetrapoda ingroup.

Iteration 5.

Median-normalise on the f_dipnoi taxon (median = 10) the Tetrapoda sub-matrix of original Δ :

Δ		g	h	i	j	k	l	m	n
o=dipnoi	diff	5	3	0	0	0	-1	-5	-3
f_dipnoi	0	5	7	10	10	10	11	15	13
g_urodela	5		4	8	9	7	8	12	10
h_anura	3			8	11	7	8	12	10
i_sauria	0				3	3	4	8	6
j_ophidia	0					6	7	11	9
k_chelonia	0						3	7	5
l_crocodylia	-1							4	6
m_aves	-5								8

Tetrapoda Δ^* median-normalised on the f_dipnoi taxon :

Δ^*		g	h	i	j	k	l	m	n
o=dipnoi	diff	5	3	0	0	0	-1	-5	-3
f_dipnoi	0	10	10	10	10	10	10	10	10
g_urodela	5		12	13	14	12	12	12	12
h_anura	3			11	14	10	10	10	10
i_sauria	0				3	3	3	3	3
j_ophidia	0					6	6	6	6
k_chelonia	0						2	2	2
l_crocodylia	-1							-2	2
m_aves	-5								0

We find ourselves in a situation somewhat akin to the one in iteration 3.

From this normalised matrix, we can evidently focus on the **Amphibia** taxa, $g_urodela$ and h_anura . Let us call **Amniota** all the remaining taxa, and call **Squamata** the i_sauria and $j_ophidia$ taxa.

Let us first consider all the tetrapoda triads involving two amniota taxa and either one of the two amphibian taxa.

$\Delta^*(\text{amphibian} ; \text{amniot2}) = \{10 \text{ to } 14\}$ is either equal or superior to $\Delta^*(\text{amphibian}; \text{amniot1}) = \{10 \text{ to } 13\} \gg \Delta^*(\text{amniot2}; \text{amniot1}) \{-2 \text{ to } 6\}$.

10 (the smallest of the normalised dissimilarities involving urodela or anura) \gg 6 (the largest of the other normalised dissimilarities), hence *both* urodela and anura are external taxon in all the triads that imply two amniots. Accordingly, both taxa urodela and anura are outgroup candidates within the Tetrapoda subset.

Is one of these two taxa a better outgroup candidate than the other? To answer this, we must study more closely all the tetrapoda triads involving both amphibians.

$\Delta^*(\text{urodela, any non-squamatan amniot}) = 12 = \Delta^*(\text{urodela, anura}) \gg \Delta^*(\text{anura, any non-squamatan amniot}) = 10$. These triads form ultrametric-like trichotomies, with urodela external to anura and any non-squamatan amniot.

$\Delta^*(\text{urodela, sauria}) = 13 > \Delta^*(\text{urodela, anura}) = 12 > \Delta^*(\text{anura, sauria}) = 11$. In this triad, urodela again appears as external to anura and sauria. (...)

$\Delta^*(\text{urodela, ophidia}) = 14 = \Delta^*(\text{anura, ophidia}) \gg \Delta^*(\text{urodela, anura}) = 12$. In this triad, we also get an ultrametric-like trichotomy, but here is the sole case where an amniot taxon, the ophidia, is external to the two amphibians, rather than the urodela taxon being external to the anura and the amniots. (...)

We can see how a single incompatibility within a triadic analysis is enough to make us cautious.

So now we have a choice.

A. Either we consider that these triads involving both urodela and anura point to urodela being an outgroup to the other tetrapods, and we discard the last, incompatible triadic result, where urodela and anura seem to form together a clade, as being an inconsequential singularity.

B. Or we consider that this is not a clear-cut case - not only because of the peculiar triad with ophidia, but also because in each of these three triads the three normalised dissimilarities involved (12 to 10, 13 to 11, and 14 to 12) could be considered as practically identical to each other (maximum two units of difference) relatively to the normalised dissimilarities between amniots (-2 to 6).

In the latter case, the taxa urodela and anura would be treated as two distinct outgroups to the Amniota ingroup, and the taxa urodela, anura and Amniota would form an *unresolved trichotomy* in our rooted dendrogram.

Path B. is the path we decide to follow, in accordance with the cautious rule of strict rather than majority consensus.

Iteration 6.

Median-normalise on both taxa g_urodela and h_anura (median = 9) the Amniota sub-matrix of original Δ :

Δ		i	j	k	l	m	n
o=Amphibia	diff	1	-1	2	1	-3	-1
urodela+anura	0	8	10	7	8	12	10
i_sauria	1		3	3	4	8	6
j_ophidia	-1			6	7	11	9
k_chelonia	2				3	7	5
l_crocodylia	1					4	6
m_aves	-3						8

Amniota Δ^* median-normalised on both taxa g_urodela and h_anura :

Δ^*		i	j	k	l	m	n
o=Amphibia	diff	1	-1	2	1	-3	-1
urodela+anura	0	9	9	9	9	9	9
i_sauria	1		3	6	6	6	6
j_ophidia	-1			7	7	7	7
k_chelonia	2				6	6	6
l_crocodylia	1					2	6
m_aves	-3						4

When we do all the 20 triads, we notice that each non-squamatan amniote is external to the (i_sauria,j_ophidia) couple: $\Delta^*(\text{non-squamatan amniote, ophidia}) = 7 > \Delta^*(\text{non-squamatan amniote, sauria}) = 6 \gg \Delta^*(\text{ophidia, sauria}) = 3$, and the four non-squamatan amniote taxa (including k_chelonia) form together a cluster of four interconnected points (...). The taxa i_sauria and j_ophidia thus form a **Squamata** clade outgroup to the four remaining taxa.

Iteration 7.

Median-normalise on the (g_urodela,h_anura) clade (median = 6.5) the non-squamatan Amniota sub-matrix of original Δ :

Δ^*		k	l	m	n
o=Squamata	diff	2	1	-3	-1
(urodela,anura)	0	4.5	5.5	9.5	7.5
k_chelonia	2		3	7	5
l_crocodylia	1			4	6
m_aves	-3				8

Non-squamatan Amniota Δ^* median-normalised on the Squamata clade :

Δ^*		k	l	m	n
o=Squamata	diff	2	1	-3	-1
(urodela,anura)	0	6.5	6.5	6.5	6.5
k_chelonia	2		6	6	6
l_crocodylia	1			2	6
m_aves	-3				4

Except for the unresolved trichotomy (k-chelonia,l-crocodylia,n-Mammalia), the three other triads are ultra-metric and point to the taxon k-chelonia being an outgroup to the three remaining taxa l-crocodylia, m_aves and n_Mammalia.

Iteration 8.

Median-normalise on the k_chelonia taxon (median = 5) the sub-matrix of original Δ for the three remaining taxa :

Δ		l	m	n
o=chelonia	diff	2	-2	-0
k_chelonia	0	3	7	5
l_crocodylia	2		4	6
m_aves	-2			8

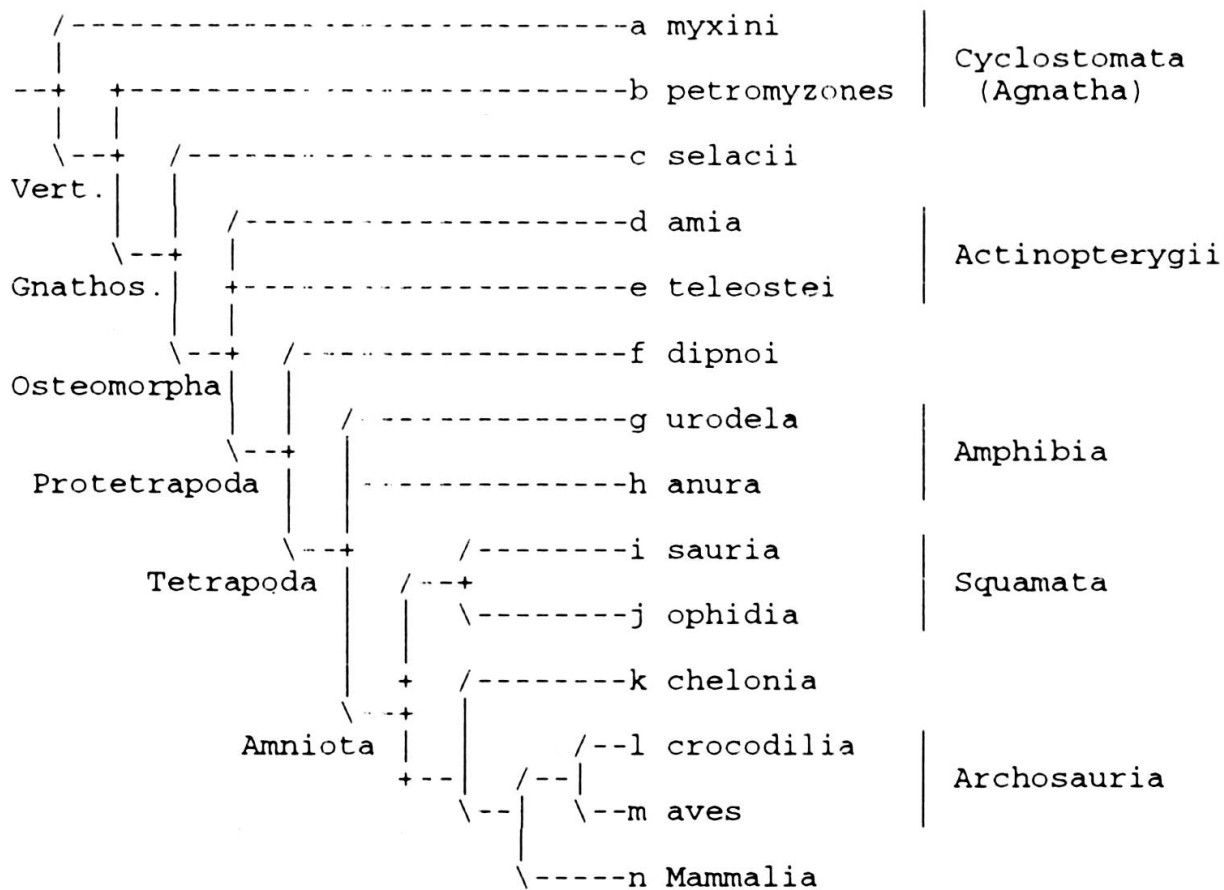
Resulting normalised matrix Δ^* :

Δ^*		l	m	n
o=chelonia	diff	2	-2	-0
k_chelonia	0	5	5	5
l_crocodilia	2		4	8
m_aves	-2			6

We finally get Δ^* (crocodilia,Mammalia) = 8 >> Δ^* (aves,Mammalia) = 6 >>

Δ^* (crocodilia,aves) = 4, thus the Mammalia taxon is external to the Archosauria clade formed by the birds and the crocodilians (...).

The final step is to reconstruct the Anâtaxis rooted dendrogram, and it looks much more like the cladogram than the phenogram :



In terms of homoplasies, the Anâtaxis dendrogram is just as parsimonious as the cladogram.

It must be remembered that the Anâtaxis tree reconstitution process allowed for resolving the {g_urodela, h_anura, Amniota} trichotomy, by positioning the urodela as outgroup to the other tetrapods, but out of caution we settled for an unresolved trichotomy.

We have demonstrated through a relatively complex example how the Anâtaxis method can reconstruct a truly phylogenetic tree, taking into account both homoplasy and

lineage-dependent heterogeneity of transformation rates, while operating on the semi-matrix of dissimilarities between taxa rather than on the matrix of the states of characters.

RÉSUMÉ

LA MÉTHODE PHYLOGÉNÉTIQUE ANÂTAXIS. 2. UN EXEMPLE - RECONSTITUTION D'UN DENDROGRAMME COMPLET

La méthode de taxonomie numérique phénétique est appliquée à la semi-matrice de dissimilitudes (entre taxons terminaux) dérivée d'une matrice des états de caractères à laquelle la méthode de maximum de parcimonie cladistique avait été appliquée au préalable. Cet exemple semi-théorique présentant des cas d'homoplasie et une hétérogénéité interlignées des vitesses de transformation, le phénogramme et le cladogramme présentent des différences phylétiques notables. La nouvelle méthode de reconstruction phylogénétique Anâtaxis est alors appliquée à la même semi-matrice de dissimilitudes, et reconstruit rapidement un dendrogramme pratiquement identique au cladogramme.

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