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TOOTH DIVERSITY IN ARVICOLIDAE (MAMMALIA, RODENTIA): ECOCHOROLOGICAL FACTORS AND SPECIATION TIME

DIVERSITA' DENTARIA NELLE ARVICOLE (MAMMALIA, RODENTIA): FATTORI ECO-COROLOGICI E TEMPO DI SPECIAZIONE

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ABSTRACT

Tooth diversity of palaearctic Arvicolidae seems to be not directly and strictly linked to the environmental characters of the range of relevant populations (according to an intraspecific approach) or species (according to an interspecific approach). A significant correlation was found with the minimal (not with the average) genetic distance, as estimator of evolutionary speciation time. Such correlation was not dependent from any linkage between genetic distance and quantitative similarity of dentary forms. As mainly non-adaptative, the studied characters can be substancially affected by time "entropic" consequences on isolated informational systems.

Key words: Diversity, Rodents, **Tooth** morphology, Speciation time.

RIASSUNTO

La diversità dentaria degli arvicolidi paleartici sembra non essere direttamente e strettamente correlata alle caratteristiche ambientali degli areali di distribuzione delle varie popolazioni (secondo un approccio intraspecifico) o specie (secondo un approccio interspecifico). Una correlazione significativa è stata trovata con la minima (non con la media) distanza genetica, quale stima di tempo evolutivo di speciazione. Tale correlazione non dipende da nessun legame tra la distanza genetica e la similarita quantitativa delle forme dentarie. I caratteri studiati, essenzialmente non adattativi. possono essere influenzati da un aumento "entropico" tipico dei sistemi informazionali isolati.

Parole chiave: Diversità, Roditori, Morfologia dentaria. Tempo di speciazione.

INTRODUCTION

The present work is aimed to analyze tooth diversity of European Arvicolidae and to give a causal explanation of its pattern.

Molars of Arvicolidae Gray, 1821 are caracterized by an open prismatic structure producing the so called "triangles" in occlusion norma (Toschi, 1965; Kowalski & Ruprecht, 1981).

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Within the frame of a quite stable general pattern, such molar shows a number of characters represented by some alternative forms, long codified in the literature (Kratochvil, 1970; Angermann, 1974, 1984; Niethammer & Krapp, 1982).

In the same tooth, two or more such forms can be compatible with each other when belonging to different characters (e.g. fig. 1 B; "agrestis" vs. "radnensis") or they can be alternative when belonging to a single character (e.g. fig. 1A; "simplex" vs. "complex").

Often, such forms are not species-specific, being present almost in all species, althought they are represented with very different percentages. Moreover, forms, considered characteristic of a given taxon (e.g. "oeconomus" M^1) or of some taxa

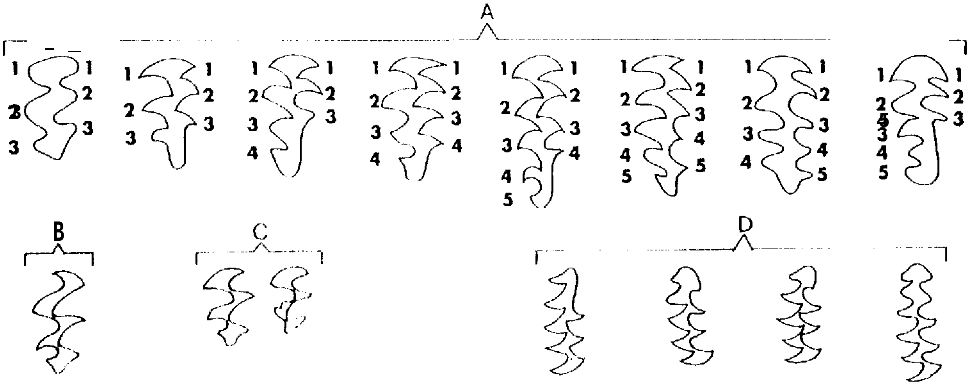

Fig 1 – A: M^3 forms. from the left to the right: "persimplex", "simplex", "typica", "duplicata", "complex", var. 5/5, var. 5/4. var. 3/5; B: M^1 "exsul" form; C: M^2 forms. left "agrestis", right "radnensis"; D: M_1 forms, from the left to the right: "oeconomus", "gud", "nivalis", "maskii".

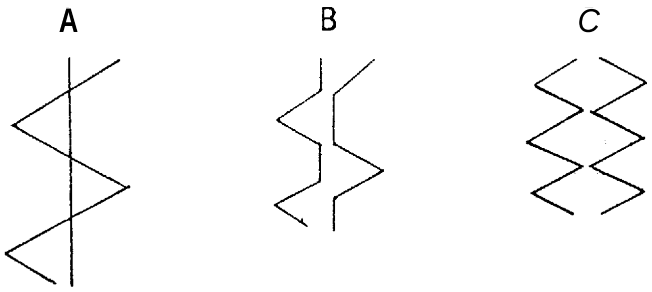

Fig. 2 – Teeth features. a: "open"; h: so called "open", but showing a structure more **linked** to "closed; c: "closed".

having same geographical range (e.g. "ibericus" M^3), were discovered also in other taxa (see Angermann, 1974; 1978; Niethammer & Krapp, 1982). However. tabb. 1-8 clearly shows that the same tooth form frequently can reappear in different taxa, even if not ever with similar relevant frequencies.

In the literature, the characters above described, basically are of two kinds: those linked to the presence or to the absence of one or more particular enamel triangles; those linked to greater or smaller confluence of the nearest triangles ("Characters of confluence").

The characters of presence or absence of particular enamel triangles can be considered mainly qualitative, when the characters of confluence of triangles are clearly linked to quantitative differences in the relevant position of the involved triangles. Nevertheless some AA were able to identify characters very simple as "open" (confluent) vs. "closed" (isolated), bringing about a very strong subjectivity on the intermediate characters (see fig. 2).

For this reason we decided to consider only the qualitative characters in our analysis.

In previous studies, emphasis was devoted mainly to the frequencies of a particular form for each character, for taxonomic and systematic purposes (e.g. Niethammer & Krapp, 1982).

Our present approach is quite different, being focused on the diversification of such characters, irrespective of the prevalence of one or another particular form. Ours then, is an analysis of diversity, not linked to taxonomy, systematic and phylogenetic aspects of the studied taxa.

In such an analysis is needed. obviously, to clump the considered units (in the present instance, the single tooth) in pertaining tooth forms classes and. then to apply an index to compute diversity of the given character in the given tooth-type, in a given taxon or population. Moreover, is needed to calculate averages referred to two or more characters of a given taxonomic unity.

We then correlated the so obtained diversity values with some hypothetical factors, with respect to ecology, chorology and evolution of considered Arvicolidae species.

The **AA** are jointly responsible for this paper, even if each played a different role. Namely L.C. dealt with the general theoretical approach and statistical analysis. G.A. with the systematical, chorological and ecological aspects, C.N. with sorting and first stage of data processing.

MATERIAL AND METHODS

Our data were based only on literature, with respect to European species of the Arvicolidae family, but taking into account all of their Palaearctic range. Moreover we only considered papers giving quantitative and comparable data (see tabies 1-9).

The non homogeneous criteria and nomenclature relating to the different tooth forms resulted in a major problem. The forms "typica". "duplicata", "complex", "var. 5/5", "var. 5/4", "var. 3/5" (fig. 1) referred by some AA to M^3, and considered as

Tab. 1 – **Teeth** forms **percentages** for *Clethrionomys glareolus*. **Data** from **Hagen,** 1958: **1,** 2, 3; **Delany & Bishop, 1960:** 13; **von Lehmann, 1961: 4; Corbet,** 1964: 9, 10, 11, 12, 15; von **Lehmann,** 1964: 5; **Saint Girons,** 1969: 6; **Rey,** 1970: 8; **Rothkopf,** 1970 20; **Saint Girons & Beaucournu, 1970** 7, **14; Sikorski & Bernshtein,** 1984: 16, 17, 18, 19.

		M^3 FORM	
COUNTRIES		"SIMPLEX" (%)	"COMPLEX" (%)
1	GERMANY	36.6	63.4
2	SWITZERLAND	15	85
3	ITALY	85.2	14.8
4	ITALY	18	82
5	ITALY	10	90
6	FRANCE	21	79
7	FRANCE	30	70
8	SPAIN	73	27
9	GREAT BRITAIN	3	97
10	GREAT BRITAIN	75	25
11	GREAT BRITAIN	82.5	17.5
12	GREAT BRITAIN	80	20
13	GREAT BRITAIN	89	11
14	FRANCE	17	83
15	GREAT BRITAIN	90	10
16	EX-USSR	27.1	72.3
17	EX-USSR	37.1	62.9
18	EX-USSR	45.9	54.1
19	EX-USSR	70.4	29.6
20	GERMANY	98	2

Tab. 2 – **Teeth forms percentage** for *Microtus duodecimcostatus*. **Data** from **Niethammer & Krapp,** 1982

FORM		%
M_1	"normalis"	100
M^3	"simplex"	100

forms "complex" by other. Moreover, despite the very rich literature on Arvicolidae, only relatively small percentage of papers was useful for our study.

Taking into account the two shortcomings mentioned above, we decided to pool the questionable forms into a rather small number of forms referred to each character (fig. 1). Only those characters examined on at least two species, and included in the Angermann's (1974) review, were considered. Moreover, in each paper, characters not discussed were considered as not examined, and were not included in the calculation of the diversity indices.

Tab. 3 – Teeth forms percentage for *Microtus nivalis*. Data from Angermann, 1974; Niethammer & Krapp, 1982.

FORM		LOCALITIES		
		ALPS	SPAIN	HIGH TATRA
M^1	"exsul"	3	—	—
M_1	"maskii"	1.58	0	—
	"oeconomus"	0	14.3	—
	"gud"	17.4	71.4	30
	"nivalis"	78.5	14.3	50
	other	2.5	0	20
M^2	"agrestis"	4	—	25
	"radnensis"	2	—	—
	"normal"	94	—	—
M^3	"simplex"	95	—	—
	"complex"	5	—	—

Our approach was a stepwise analysis centered on populations. First we averaged the diversity indices of all teeth. Second we calculated the average diversity of each tooth for all the populations. This was done because of the different number of specimens in each population.

Different tables were compiled for each species, for practical purposes, also in order to avoid many empty cases that would arise in a comprehensive "species/tooth" matrix. Moreover, data were used both for an intra- and interspecific study approach.

The intraspecific approach was aimed at elucidating the overall environmental effects on tooth diversity, in a context characterized by a reduced number of degrees of freedom.

The interspecific approach was aimed at a more specific analysis with respect to the potential factors of diversification.

As potential diversifying factors we considered the following:

1- at intraspecific level, the many ecological parameters that could be important for tooth diversity were weighed jointly, even if indirectly, through a differential analysis among populations. In fact, environmental conditions were indeed much more homogeneous for the individuals of the same population than they were for those of different ones and, therefore, living in biotopes possibly very different each other, also, but not only, due to their relevant geographic distance.

2- at interspecific level, we preferred to consider some features probably important for each species:

Tab. 4 – Teeth forms percentage for *Microtus arvalis*. Data from Zimmermann, 1935: 7, 8, 9, 10, 11, 13, 14, 15, 16, 17, 18, 19, 20. 21, 22, 23; Ognev, 1950: 25, *26;* Heim de Balsac & Lamotte, 1951: 1; Kratochvil, 1970: 4, 6, 12; Dottrens, 1961: 3; Görner, 1973: *5;* Rothkopf, 1970: 27, *28,* 29. 30, 31, 32. 33, 34, 35; Stohl, 1974 24; Niethammer & Winking, 1971: 2.

		M^3 form	
Countries		"Simplex" (%)	"Complex" (%)
1	France	46	54
2	Spain	31	69
3	Switzerland	1	99
4	Czechoslovakia	9	91
5	Germany	5	95
6	Germany	2	98
7	Germany	5	95
8	The Netherlands	17	83
9	Austria	3	97
10	Germany	43	57
11	Pound	5	95
12	Czechoslovakia	2	98
13	Germany	11	89
14	Poland	12	88
15	Poland	30	70
16	Poland	22	78
17	Germany	87	13
18	Poland	70	30
19	Germany	85	15
20	Germany	90	10
21	Germany	60	40
22	Germany	51	49
23	Germany	43	57
24	Hungary	6	94
25	Ex-URSS	20	80
26	Ex-URSS	0	100
27	Germany	5	95
28	Germany	1.5	98.5
29	Germany	3	97
30	Germany	6	94
31	Germany	7	93
32	Germany	14.5	85.5
33	Germany	16	84
34	Germany	19	81
35	Germany	19	81

Tab. 5 – Teeth forms percentage for *Microtus agrestis*. Data from Ognev, 1950: 2, 3. 4; Kratochvil et **al.,** 1956: 7; Bauer & Festics. 1958: 11; Niethammer, 1964: 12; Reichstein & Reise, 1965: 1, 5, 6, 8. 9; Meylan, 1967: 10; Niethammer & Krapp. 1982: 13, 14, 15.

COUNTRIES		M^1 FORM 'EXSUL' (%)
1	FINLAND & NORWAY	68
2	EX-USSR	98
3	EX-USSR	100
4	EX-USSR	50
5	GERMANY	4
6	GERMANY	0.3
7	CZECHOSLOVAKIA	6
8	GREAT BRITAIN	86
9	GREAT BRITAIN	100
10	SWITZERLAND	16
11	FRANCE	6
12	SPAIN	16
13	SWEDEN	50
14	GERMANY	20
15	FRANCE	10

a) anthropophily i. e. linkage with human activity;

b) multi-annual intensity degree of numerical population's fluctuation;

c) habitat more or less corresponding to a wooded environment;

e) the effective areal considered for each species, obtained connecting the peripheric geographical source points;

f-g) average genetical distance (Graf, 1982);

h-i) speciation time estimated, through the genetical distance from the closest different species (Graf, 1982). Some of these parameters, obviously, could not be estimated in a quantitative manner and they were estimated in a relative, ordinal way by ranks (tab. 10).

For this reason, our statistical analysis was performed mainly using non-parametric tests (Sokal & Rohlf, 1981).

To estimate diversity, the Gini (1912) index, considered one of the more reliables among other by a number of AA, was adopted.

The diversity was separately calculated for each compatible character. The obtained values were averaged for each species. Conversely, alternative forms of the same character and tooth were jointly considered in a single computation of diversity.

The affinity of the quantitative relationships among the tooth forms were estimated by Renkonen (1938) index.

Tab. 6 – Teeth forms percentages for *Microtus oeconomus*. Data from Angermann, 1984.

		FORMS						
		M$_1$			M^2		M^3	
	COUNTRIES	"oeconomus"	"gud"	"nivalis"	"radnensis"	normal	"simplex"	"complex"
1	THE NETHERLANDS	85.6	13.1	1.3	7.6	92.4	1.4	98.6
2	AUSTRIA	85.4	11.2	3.4	0.53	99.47	0	100
3	HUNGARY	79.6	14	6.7	0.3	99.7	0	100
4	GERMANY	88.6	11.4	0	0.6	99.4	0.6	99.4
5	GERMANY	74.2	25.8	0	0	100	0	100
6	GERMANY	89	8.8	2.2	0.6	99.4	0	100
7	GERMANY	71.6	21	7.4	3.6	96.4	0	100
8	GERMANY	98.6	1.4	0	0	100	0	100
9	SWEDEN	81.9	15.3	2.8	0	100	0	100
10	NORWAY	52	43.8	4.2	0	100	0	100
11	SWEDEN	91.1	8.9	0	0	100	0	100
12	NORWAY	86.8	7.9	5.3	0	100	0	100
13	ex-URSS	91.7	6.7	1.7	0	100	0	100
14	ex-URSS	94.2	4.2	1.7	0.8	99.2	1.7	99.4
15	ex-URSS	87.5	11.9	0.6	1.55	98.54	0	100
16	ex-URSS	74.6	13.9	11.6	0	100	0	100
17	ex-URSS	56.7	26.9	16.4	0	100	0	100
18	ex-URSS	77.1	20	2.9	0	100	0	100
19	ex-URSS	75	19.6	5.4	0	100	0	100
20	ex-URSS	82.2	16.7	1.1	0.1	99.9	0	100
21	ex-URSS	92.2	6.1	1.7	0.9	99.1	0	100
22	ex-URSS	55.8	15.6	18.6	0	100	0	100
23	ex-URSS	35	62.5	2.5	0	100	0	loo
24	ex-URSS	85.5	8.5	8	0	100	0	100
25	ex-URSS	82.8	9.8	7.4	0	100	0	100
26	ex-URSS	90	5	5	0	100	0	100

Tab. 7 – Teeth forms percentages for *Microtus subterraneus*. Data from Kratochvil, 1970: 3; Angermann, 1974: 4, 5, 6, 7, 8; Krapp & Winking, 1976 1, 2

FORM		GERMANY 1	AUSTRIA 2	CZECHOSLOVAKIA 3	GERMANY 4	GERMANY 5	GERMANY 6	BALKANS 7	ALPS 8
M^1	"exsul"	0	0	0	4	18.5	0	0	5.1
M_1	"maskii"	21.6	13.9	–	50	87	27	83.3	79.5
	"normal"	78.4	86.1	–	50	13	83	16.7	20.5
M^2	"agrestis"	–	–	7.7	59.2	70.3	3.3	36.8	52.2
	"radnensis"	–	–	–	5	7.4	0	0	1.3
	"normal"	–	–	–	35.8	22.3	96.7	63.2	45.5
M^3	"simplex"	2	–	0.8	0	0	32.6	0	0
	"complex"	98	–	99.2	100	100	67.4	100	100

Tab. 8 – Teeth forms percentages for *Microtus savii*. Data from Contoli, 1980. (1) = Belagaio; (2) = Beldiletto; (3) = M. Castello Vibio-Montecastrilli; (4) = Santa Lucia; (5) = Tarquinia; (6) = Tolfa; (7) = Castellaccio di San Gennaro; (8) = Tagliacozzo; (9) = Rende. (data from Contoli, 1980)

					LOCALITIES	(ITALY)				
FORM		(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
M^1	"normal"	85.71	92'	96.71	96.3	85.72	95.55	83.33	69.7	77.27
	"exsul"	0	4	3.22	0	0	0	0	0	0
	"radnensis"	14.29	4	3.22	3.7	14.28	4.45	16.67	30.3	22.73
M_1	"normal"	100	92	92.6	92.6	100	100	96	97.14	83.34
	"maskii"	0	4	7.4	7.4	0	0	4	2.86	8.33
	"oeconomus"	0	4	0	0	0	0	0	0	8.33
M^2	"agrestis"	32.16	16	39.39	7.41	57.14	39.13	38.45	40	24.99
	"radnensis"	7.69	24	57.57	18.52	28.57	19.57	34.62	57.15	29.16
	"normal"	61.54	60	33.30	74.07	42.85	47.83	38.46	22.86	58.33
M^3	"simplex"	100	87.5	80	80.36	85.72	68.36	40.39	87.88	91.67
	"complex"	0	12.5	20	19.64	14.28	31.64	59.61	12.12	8.33

Tab. 9 – Teeth forms percentage for *Microtus multiplex*. Data from Niethammer & Krapp, 1982; Storch & Winking, 1977.

FORM		%
M^2	"agrestis"	11
	"normal"	89

RESULTS

1) Intraspecific approach:

Only for a few species there were data sufficient for such an analysis. For the considered species (*Clethrionomys glareolus, Microtus oeconomus, Microtus subterraneus, Microtus savii)* the different geographic sites of the considered populations do not explain the variance of the diversity values of the various characters studied, according to the Friedman test (tab. 10).

2) Interspecific approach

In this context, we were able to collect sufficient data on the following species *Clethrionomys glareolus, Microtus duodecimcostatus, Microtus nivalis, Microtus arvalis, Microtus agrestis, Microtus oeconomus, Microtus subterraneus, Microtus savii* and *Microtus multiplex*.

The diversity values are reported in tab. 11.

The preference for a wooded habitat (tab. 11, c), the importance of population fluctuations (tab. 11, b) and the dependence on human presence and/or activities (tab. 11, a), showed no significant correlations with tooth diversity, whether they were analyzed singularly or pooled (tab 11, d). No significant correlation was also obtained between the tooth diversity and the actually specific areal surface based on available data (tab. 11, e). The only significant correlation was found with the minimal genetic distance (tab. 11, h,i), considered as long time of speciation.

Such correlations was performed both taking into account the distances referring to the studied species alone ($P = 0.02$, two tails) and those referring to all species considered by Graf (1982) ($P << 0.01$, two tails). On the other hand, comparable results were obtained using the Spearman rank correlation and the linear regression (considering original data: $P < 0.001$, two tails) tests (tab. 11).

The above correlation was not confirmed when we used, instead of the minimal one, the average genetic distance. The latter is, in fact, only partly linked to speciation time. In this case a significant correlation by linear regression was not confirmed by Spearman test (tab. 11). Lastly, we did not detect significant correlations between genetic distance and quantitative similarity of M^3 forms (the only teeth for which enough data were available) in each pair of the considered species (tab. 12).

Tab. 10 — Nonparametric analysis of variance among different monospecitic populations, for the relative frequencies **of** teeth forms. Friedman test: P = n.s. For simbols see text.

POPULATION DIVERSITY

M. subterraneus (data from tab. 7)

	M^1	M_1	M^2 ag/-	M^2 ra/-	M^3
10	3	5	4	4	2.5
11	5	1	2	5	2.5
12	1.5	2.5	1	1.5	5
13	1.5	2.5	3	1.5	2.5
14	4	4	5	3	2.5

$X^2 = 4.24 < \chi^2_{05(4)}$

C. *glareolus* (data and symbols from tab. 2 of Sikorski & Bcrnshtein, 1984)

	M_1: 11	12	13	14	16	M^3: 10	3	617	8
15	3	3.5	4	2	1	1	1	3	3
16	2	1	1	1	2.5	3	3	4	1
17	3	2	3	[illegible]	2.5	3	3	1	2
18	1	3.5	2	4	4	2	2	2	3

$X^2 = 0.93 < \chi^2_{05(3)}$

M. oeconomus (data from Angermann, 1984 and tab. 6)

	M_1	M^2	M^3
1	11	26	8
	12.5	19	25
3	17	18	26
3	7.5	20.5	9.5
5	19	8.5	22.5
6	7.5	20.5	16
7	22	25	19
8	1	8.5	1
9	16	8.5	12.5
10	24	8.5	9.5
11	5	8.5	4
12	10	8.5	6.5
13	3.5	8.5	20
14	2	22	2.5
15	9	24	6.5
16	21	8.5	12.5
17	25	8.5	2.5
18	18	8.5	14
19	20	8.5	21
20	14.5	17	17.5
21	3.5	23	17.5
22	26	8.5	11
23	23	8.5	24
24	12.5	8.5	15
25	14.5	8.5	7
26	6	8.5	22.5

$X^2 = 23.66 < \chi^2_{.05(25)}$

M. savii (data and symbols **from** Contoli, 1980 and tab. 8)

	M' *ex*	M^1 **ra**	M_1	M^2 *ay*	M^2 ra	M^3 sic	M^3 corners
1	4	5.5	2	4	1	1	6
2	9	3	7	2	4	4	1.5
3	8	1	5.5	6.5	8	6	8
4	4	3	5.5	1	2	7	1.5
5	4	5.5	2	9	5.5	5	9
6	4	3	2	6.5	3	8	4.5
7	4	7	4	5	7	9	7
8	4	9	8	8	9	3	3
9	3	8	9	3	5.5	2	4.5

$X^2 = 12.45 < \chi^2_{05(8)}$

Tab. 11 – Numerical values or attributes and relative ranks for the studied species according to the interspecific approach.

	Y		X							
SPECIES	AVERAGE TEETH DIVERSITY		a) LINKAGE WITH HUMAN ACTIVITY		b) FLUCTUATION INTENSITY DEGREE		c) LINKAGE WITH WOODED ENVIRONMENT		d) Σ RR. (a +b +c)	
C. glareolus	.3056	R. = 2	–	1/R. = 1.5	±	1/R. = 4	+	R. = 1	6.5	R. = 1
M. nivalis	.3571	1	–	1.5	–	1	–	6.5	9	2
M. arvalis	.2295	3	+	7.5	+	8	–	6.5	22	8.5
M. savii	.2250	4	+	7.5	±	4	–	6.5	18	6
M. subterraneus	.1769	7	+	7.5	±	4	±	2.5	14	4
M. agrestis	.2037	5	+	7.5	+	8	–	6.5	22	8.5
M. multiplex	,1958	6	±	4	±	4	±	2.5	10.5	3
M. oeconomus	,1068	8	±	4	+	8	–	6.5	18.5	7
M. duodecimcostatus	.0000	9	±	4	±	4	–	6.5	14.5	5
Spearman				n.s.		n.s.		n.s.		n.s.

	X									
SPECIES	e) EFFECTIVE AREAL		f) AVERAGE OF TOTAL GENETIC DISTANCE (GRAF, 1982)		g) AVERAGE GENETIC DISTANCE OF CONSIDERED SPECIES		h) MINIMUM OF TOTAL GENETIC DISTANCE (GRAF, 1982)		i) MINIMUM OF GENETIC DISTANCE OF CONSIDERED SPECIES	
C. glareolus	56	R. = 3	.636	R. = 2	.616	R. = 1	.46	R. = 1	.46	R. = 2
M. nivalis	4	9	.643	1	.618	1	.45	2	.54	1
M. arvalis	88	1.5	.567	3	.507	3	.30	3	.34	3
M. suvii	14	7	.412	6	.378	7	.21	4.5	.21	6
M. subterraneus	23	6	.424	5	.393	5	.21	4.5	.21	6
M. agrestis	88	1.5	.380	9	.343	9	.19	6	.21	6
M. multiplex	11	8	.399	8	.357	8	.18	7	.18	8
M. oeconomus	44	4	.408	7	.398	4	.16	8	.29	4
M. duodecimcostatus	29	5	.430	4	.380	6	.03	9	.03	9
Spearman		n.s.		n.s.		n.s.		P < < .01 (2t)		P = .02 (2t)
Linear regression		n.s.		P < .05 (2c)		P < .05 (2t)		P < .001 (2t)		P < < .01 (2t)

Tab. 12 – Genetic and morphologic distances (M^3) between species. Renkonen index. Spearman test (n.s.).

	TEETH DIFFERENCIES						
	C. gl.	*M. ar.*	*M. ni.*	*M. su.*	*M. sa.*	*M. du.*	*M. oe.*
GENETIC DISTANCES							
C. glareolus	--	26	44.78	45.79	29.98	49.78	50.02
M. arvalis	.70	--	70.78	19.79	55.98	75.78	24.02
M. nivalis	.67	.73	--	90.57	14.8	5	94.8
M. subterraneus	.63	.42	.66	--	75.77	95.57	4.23
M. savii	.62	.48	.25	.22	--	19.8	80
M. duodecimcostatus	.66	.34	.65	.25	.22	--	99.8
M. oeconomus	.46	.42	.58	.36	.35	.38	--

DISCUSSION

This study is to be considered as a preliminary one, due to the difficulties mentioned above. Nevertheless, the results allow some tentative conclusions.

It is well know that many tooth forms tend to be present in different species of Arvicolidae, see the "Vavilov's series" (Angermann, **1974).** Therefore, such forms do not seem strictly linked to the phyletic relationships among the studied species. In fact, we did not detect a significant correlation between genetic distance and quantitative similarity of percentages of various forms of M^3. This means that the prevailing of a tooth forms upon another seem to be more associated with the neutral and stochastic component of the intraspecific evolutionary histories than with the interspecific history of the Arvicolidae family.

The different forms studied do not even seem to be the consequence of direct environmental pressures, **as** indicated by the prevalence of the same forms in species clearly differing in habitat, range and behaviour. But, in some cases, such forms seem to be indirectly correlated to other characters **as,** in primis, body size.

The studied tooth characters seems not affected by environmental influxes of epigenetic type. Such evidences, if from one hand justify the long established use of tooth characters by taxonomists, on the other hand discourage the systematic-evolutionistic use of the dominance of a given form in a given character. Moreover, our results suggests some caution in the use of the above characters in paleontologically based comparisons, because some frequencies variation of the various forms during anagenetic evolutionary times are possible. If the relevant frequencies of tooth forms were more or less directly driven in a substantial manner by adaptative factors, one would expect, during anagenesys, a tendence toward dediversification of tooth characters, due to the prevailing of a single form, namely the more adaptative, with respect to the others. On the contrary, the present results shows a trend toward an increase of diversity in time, after speciation. On the basis of the obtained results, an interpretative hypothesis, obviously to be confirmed by more evidences, **could** be the following: after reproductive isolation, environmental pressure selectively influences adaptative characters, with the consequent variation of the level of heterozygosity. On the other hand , the above pressure has less effect on characters, mainly on non-adaptative ones as those here studied. Therefore, such characters could escape from the adaptative dediversification, being mainly influenced by stochastic variation, as expected in a isolated (in an evolutionistic sense) informational system: this is the case, of a taxon during the anagenesys. The frequence of the above casual variations, based on random mutation and polygenic rearrangement, is linked to time and it is expected to happen, caeteris paribus, mainly in the initially more frequent form, just for simple statistical reasons. This phenomenon could cause, among various forms, an increase of a component of diversity, the evenness.

One of us (L.C.) has long evidenced some analogous aspects of "entropic diversification". Such diversification is mainly due to the time of relevant status of informational and/or energetic isolation. This is both true of ecological (Contoli, 1988) and cultural (Contoli, 1989) functional systems.

It is also possible thht the phenomena outlined in the present paper could be included in this framework and could essentially be related, even though indirectly, to the second principle of thermodynamics.

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