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Sexual dimorphism and interpopulational variability in the lower carnassial of the cave bear, *Ursus spelaeus* Ros-Hein

Dimorfismo sexual y la variabilidad interpoblacional de la carnicera inferior del oso de las cavernas, *Ursus spelaeus* Ros-Hein

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A morphometric study on the lower carnassial (M_1 of *Ursus spelaeus* from three european populations has been carried out. Multivariate statistic methods have been used for this purpose. It has been proved that the variability caused by the sexual dimorphism interferes to an important degree in the suposed interpopulational differences. Once the intrapopulational variability has been put aside, significative differences between the analized populations have been found. These differences are well-marked in the degree of development of the cusps, and specially in the metaconid.

Key words: *Ursus spelaeus*, lower carnassial, sexual dimorphism, interpopulational variability, multivariate analysis.

En este trabajo se realiza un estudio morfométrico de la carnicera inferior (M_1) de *Ursus spelaeus* de tres poblaciones europeas, mediante métodos de estadística multivariante. Se comprueba cómo la variabilidad producida por el dimorfismo sexual enmascara en gran medida las posibles diferencias interpoblacionales. Una vez eludida esa variabilidad intrapoblacional, se han encontrado diferencias significativas entre las poblaciones analizadas, especialmente marcadas en el desarrollo de las cúspides, y principalmente en el metacónido.

Palabras clave: *Ursus spelaeus*, carnicera inferior, dimorfismo sexual, variabilidad interpoblacional, análisis multivariante.

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INTRODUCTION

The sexual dimorphism displayed in the Cave Bear has been studied by various authors (EHRENBVERG, 1955; KURTEN, 1955). Kurtén advised the sexing of the bone sample before embarking on a comparative study of different deposits, given that sexual dimorphism concealed or even falsified possible interpopulational variation. However, the sexing method he suggested is not applicable to the whole skeleton. In fact, it is only reliable with skulls or jaws, and their respective dental sets, which conserve their corresponding canine.

This is a considerable problem when studying isolated specimens, especially in the case of the cheek teeth. Later authors such as TORRES (1984) have remarked upon the high percentage of overlapping which exists in the metric values of dental remains of both sexes, thus making sexing impossible.

Consequently, in our opinion, metric comparisons between different populations lose all their value, as one cannot distinguish between differences produced by a real eco-geographic variation, and those arising from the existence of a different sex ratio in each deposit. Even in the case of larger sized samples, the sex ratio is not always comparable in each deposit (KURTEN, 1955; 1958).

Because of this, we have tried a new method based on multivariate statistic. Using the latter, we have managed to avoid the variability produced by sex dimorphism and to concentrate on the real interpopulational differences.

Multivariate statistics is a tool which is being used more and more in the field of vertebrate morphometry. However, very seldom has it been applied to macromammal fossils. Some studies such as those of WERDELIN (1983) on lynx have produced some very interesting results. The principal limitation of studies of this kind lies in the very nature of the fossils themselves: In the case of vertebrates, the bones are very seldom discovered whole, in good condition, or in sufficient number to make the results statistically significant.

The deposits of *Ursus spelaeus* are unusual in that there is an abundance of bone remains. In those cases where they have also been well preserved, we have no difficulty in applying the technique of multivariate statistics.

MATERIAL AND METHODOLOGY

For this study we have used metric measurements of the lower carnassial of three populations of *Ursus spelaeus*, namely: ATLANTICA, from the Eirós Cave (Galicia, NW Iberian Peninsular); CANTABRICA, from the Ekain Cave (Basque Country, N Iberian Peninsular) and BLACK SEA, from the Odessa caves (Ukrania). The location of these deposits is shown in Figure 1.

The three populations have been dated using various methods (C14, U/Th), giving approximate ages between 26,000 and 28,000 years B.P. (ALTUNA, 1984; GRANDAL, 1993; KURTEN, 1969). Consequently, they can be considered as practically contemporary.

After gathering metric data from the specimen studied (See Fig. 2 and Table 1), two types of analysis were carried out: Analysis of Principal Components and Discriminant Analysis.

1. A discriminant analysis was carried out on the metric dataset (no sexing).

2. An analysis of principal components was carried out on the same dataset.

3. Subsequently, a further discriminant analysis was carried out using the data matrix obtained from the analysis of principal components.

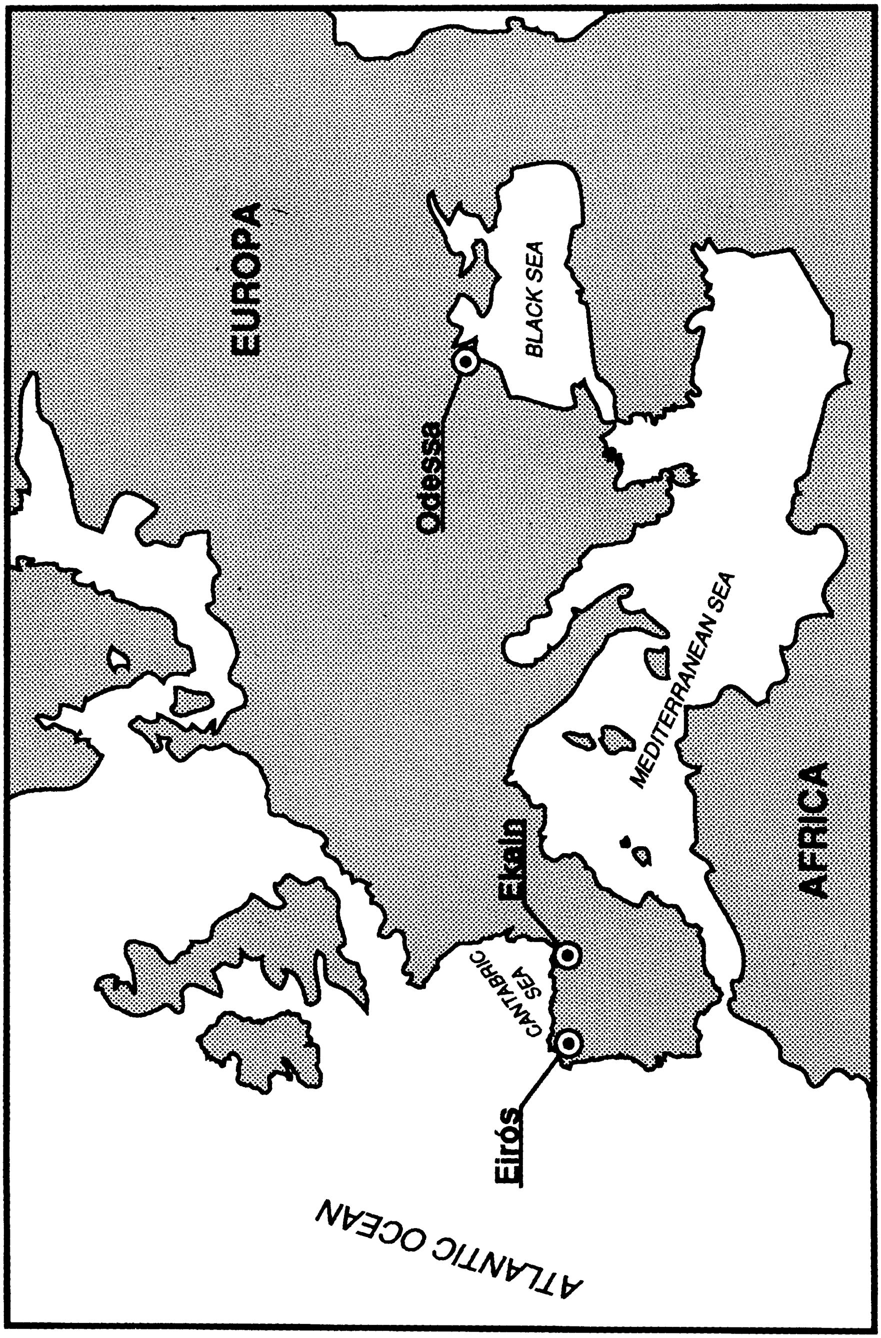

Figure 1. Situation Map.

TABLE 1. Metric data of the lower carnassial of the three populations studied. (All measurements in milimeters).

	ATLANTICA (n=35)			CANTABRICA (n=39)			BLACK SEA (n=30)		
	$\overline{X}$	s	vi-vs	$\overline{X}$	s	vi-vs	$\overline{X}$	s	vi-vs
1	31.4	1.30	28.0-33.1	30.4	1.67	27.1-33.8	31.5	1.46	28.7-34.2
2	19.1	0.82	17.4-20.7	18.6	1.31	13.4-21.2	17.8	1.18	15.3-19.7
3	5.5	0.76	3.9- 7.0	5.8	0.58	4.4- 7.1	5.9	0.50	4.7- 7.2
4	13.8	0.92	11.1-15.1	13.7	1.13	10.0-17.8	13.7	1.10	11.4-16.5
5	12.0	0.83	10.5-13.6	11.6	1.09	9.4-13.7	11.9	1.06	9.5-14.0
6	11.3	1.22	8.9-14.2	10.9	1.61	7.4-14.7	10.9	1.08	9.0-13.4
7	10.4	1.21	8.2-12.9	9.2	0.74	7.9-11.2	9.4	0.64	8.2-10.8
8	11.8	0.82	10.2-13.8	12.2	0.93	10.5-14.7	12.5	0.85	11.3-14.2
9	14.8	0.71	13.3-16.1	14.4	0.94	13.0-17.0	15.3	0.86	13.8-17.2
10	11.2	0.63	9.3-12.6	11.6	0.83	10.2-13.3	11.8	0.72	10.7-13.0
11	10.3	0.82	8.3-11.6	9.7	0.86	7.9-11.9	9.7	0.82	7.9-11.0
12	7.3	0.60	6.0- 8.5	7.0	0.74	5.7- 9.0	7.2	0.76	5.5- 8.5
13	10.0	0.81	7.9-11.7	9.3	0.84	7.7-11.0	9.2	0.90	7.6-11.1
14	14.3	0.76	12.6-15.5	14.1	0.87	11.9-15.9	15.0	1.12	11.5-17.2
15	9.2	0.67	7.5-10.9	8.8	0.79	6.7-10.6	9.5	0.69	8.6-11.7
16	12.0	0.72	10.8-13.7	11.9	0.74	10.7-14.4	12.4	1.01	9.6-14.8
17	8.9	0.69	7.3-10.1	8.8	0.82	6.8-11.0	9.2	0.59	8.3-10.1
18	8.8	0.71	7.3-10.6	9.1	0.72	8.0-11.7	9.7	0.84	8.1-12.6
19	10.2	0.78	8.4-11.8	10.2	0.72	9.1-12.4	10.7	0.89	8.6-12.5

RESULTS

Tables 2 and 3 show the results of the stepwise discriminant analysis carried out on the matrix of metric data of the lower carnassial of the three populations studied. One can observe a certain homogeneity in the behaviour of the variables in the initial variance analysis. The value of Wilks'Lambda, which indicates the power of discrimination of the canonical discriminant functions obtained, is medium (0.322). The reclassifications of the cases conform fairly well to the populations studied. Figure 3 shows a projection of the cases along the plane defined by the two canonical discriminant functions obtained. The three populations become separated but they do not appear to be precisely delimited.

The principal component analysis carried out on this same matrix of data allows

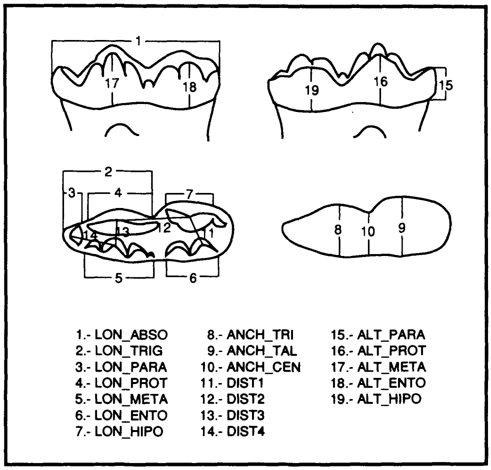

Figure 2. Lower Carnassial Measurements.

TABLE 2.

UNIVARIATE F TESTS

VARIABLE	F	P
LON_ABSO	0.447	0.641
LON_TRIG	0.824	0.442
LON_PARA	0.577	0.563
LON_PROT	0.587	0.558
LON_META	0.466	0.629
LON_ENTO	0.640	0.529
LON_HIPO	0.728	0.485
ANCH_TRI	0.493	0.612
ANCH_TAL	0.348	0.707
ANCH_CEN	0.544	0.582
DIST1	0.657	0.520
DIST2	0.475	0.623
DIST3	0.763	0.469
DIST4	0.333	0.718
ALT_PARA	0.314	0.731
ALT_PROT	0.428	0.653
ALT_META	0.412	0.663
ALT_ENTO	0.368	0.693
ALT_HIPO	0.394	0.675

MULTIVARIATE TEST STATISTICS

WILKS' LAMBDA = 0.322

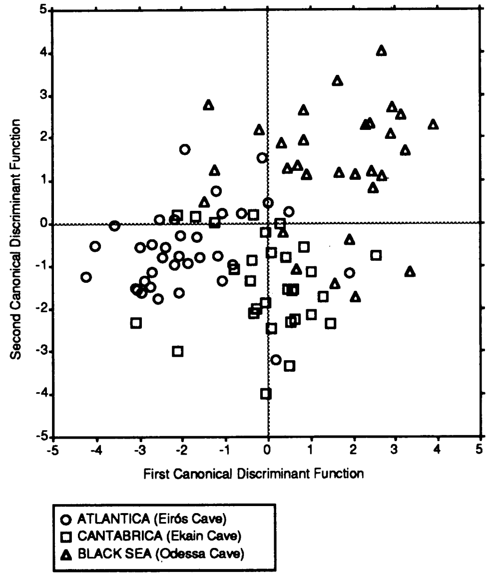

Figure 3. Lower Carnassial (M_1).

TABLE 3. Populations (rows) by Predict (columns).

reclassifications	ATLANTICA	CANTABRICA	BLACK SEA	TOTAL
ATLANTICA	26	7	2	35
CANTABRICA	4	29	6	39
BLACK SEA	4	3	23	30
TOTAL	34	39	31	104

us to obtain a clearer vision of the behaviour or the variables (Table 4). PC I, which explains 41 % of the total variance, is a general component (PIMENTEL, 1979), positively correlated with all the original variables. As is becoming common practice in morphometry, we examine a component which explains the differences in the size of the specimen studied.

PC II correlates positively with those variables concerning the length of the cusps (not their height) and the distances bet-

TABLE 4. Principal component analysis. Component Loadings.

CPs	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	XVII	XVIII	XIX
LON_ABSO	0.905	0.184	0.158	0.013	0.070	0.045	0.042	0.090	0.040	-0.027	0.007	-0.018	0.084	-0.171	0.086	-0.040	-0.074	0.118	-0.192
ANCH_TAL	0.823	-0.211	-0.173	0.275	0.019	-0.100	0.010	0.023	0.069	0.031	-0.032	0.120	0.149	-0.253	0.114	0.022	0.017	0.151	0.137
ANCH_TRI	0.812	-0.294	0.033	-0.046	0.138	-0.121	-0.134	-0.129	0.104	0.111	-0.045	0.188	-0.117	0.012	0.106	-0.052	-0.255	-0.173	0.016
ALT_PARA	0.786	-0.057	0.250	-0.035	-0.078	-0.165	0.138	0.138	-0.025	-0.179	0.263	-0.225	0.055	-0.028	0.105	-0.230	0.076	-0.131	0.018
ALT_HIPO	0.729	-0.344	-0.101	0.065	-0.200	0.184	-0.056	0.125	-0.072	-0.218	0.002	0.104	-0.319	-0.160	-0.066	0.195	0.076	-0.058	-0.032
ANCH_CEN	0.705	-0.367	0.039	0.067	0.364	-0.094	-0.081	-0.098	0.011	0.193	-0.221	0.119	0.042	0.025	-0.270	-0.069	0.154	-0.001	-0.033
ALT_META	0.701	-0.245	-0.297	-0.068	-0.272	0.150	0.055	-0.158	-0.266	0.051	0.083	-0.247	0.114	-0.088	-0.206	0.029	-0.157	0.042	0.023
ALT_ENTO	0.686	-0.478	-0.225	0.030	-0.068	0.079	0.084	0.019	0.106	0.187	0.037	-0.179	0.089	0.220	0.194	0.224	0.083	-0.003	-0.024
LON_PARA	0.600	-0.147	0.324	0.096	0.111	0.495	0.134	0.156	-0.264	-0.248	0.102	0.024	-0.109	0.196	0.033	-0.073	0.020	0.064	0.033
DIST4	0.596	0.115	0.452	-0.348	-0.182	-0.225	0.066	0.291	0.002	0.011	0.244	-0.061	0.176	-0.020	-0.106	0.070	0.000	-0.148	0.026
ALT_PROT	0.583	-0.288	0.288	-0.057	-0.361	0.327	-0.318	-0.106	0.138	0.067	0.169	-0.081	-0.105	0.188	-0.016	-0.162	0.026	0.098	-0.006
DIST1	0.568	0.420	-0.126	0.272	-0.351	-0.266	0.144	-0.051	0.236	-0.201	-0.053	-0.129	-0.095	0.164	-0.122	0.064	-0.123	0.081	0.029
LON_META	0.550	0.298	-0.067	-0.304	-0.433	0.286	-0.054	0.106	0.305	-0.140	-0.178	0.194	0.152	0.110	-0.079	0.071	0.001	0.019	0.014
DIST3	0.544	0.439	0.126	0.307	-0.037	0.058	-0.233	-0.487	-0.081	-0.187	0.106	-0.003	0.148	-0.002	0.044	0.054	0.098	-0.126	-0.014
LON_ENTO	0.518	0.335	-0.556	0.142	0.053	0.175	-0.017	0.160	0.159	0.119	0.389	0.089	-0.064	-0.063	-0.024	-0.124	0.078	-0.022	0.014
LON_TRIG	0.452	0.618	0.260	-0.160	0.018	0.254	-0.106	-0.018	0.045	0.250	-0.142	-0.271	-0.255	-0.116	0.025	0.048	0.051	0.004	0.041
LON_PROT	0.404	0.246	0.333	-0.516	0.290	0.161	-0.415	0.001	-0.286	-0.062	-0.037	0.092	0.014	0.053	0.086	0.026	0.007	0.100	0.021
DIST2	0.493	0.161	-0.008	-0.377	-0.066	-0.156	0.615	-0.352	-0.061	0.080	0.053	0.175	-0.088	0.021	0.038	-0.025	0.055	0.029	0.003
LON_HIPO	0.434	0.487	-0.009	0.417	- 0.248	0.213	0.041	0.230	-0.316	0.267	-0.115	0.157	0.029	0.161	-0.002	0.024	-0.039	-0.029	-0.010

PERCENT OF TOTAL VARIANCE EXPLAINED

I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	XVII	XVIII	XIX
41.086	11.067	6.240	5.872	4.852	4.604	4.334	3.518	2.957	2.570	2.435	2.256	1.876	1.770	1.293	1.156	0.931	0.842	0.340

ween them. It may be seen as a component related to the form of the cusps and the degree of convergence between their vertices.

PC III appears, to a certain extent, to explain the morphology of the trigonid. PC IV, in turn, that of the talonid. PC V correlates positively with the variables which are related to the shape of the specimen: widths, length of the trigonid, length of the paraconid... PC VI concerns the cusps once more, correlating positively with their length and height.

Interpretation of the PCs becomes more difficult as the percentages of variance analyzed become smaller. Nevertheless, we will focus on the PC XIII for reasons which will become clear later on. The latter correlates positively with all the variables related to the metaconid: length, height and distances from the paraconid and protoconid.

In the third analysis, the data matrix obtained from the principal component analysis was used as a basis. For this analysis we have ignored the PC I, the one which explained a higher percentage of variance and which, moreover, was the one which explained the differences in size of the sample studied.

Leaving out this component we have tried to eliminate any influence that sex dimorphism might have on the metric characterization of the populations in question (CAMPBELL & KITCHENER, 1980).

The results of this analysis are shown in Tables 5 and 6. We can observe a more heterogeneous behaviour in the variables, un-

TABLE 5.

UNIVARIATE F TESTS

VARIABLE	F	P
FACTOR 2	46.264	0.000
FACTOR 3	0.199	0.820
FACTOR 4	3.818	0.025
FACTOR 5	4.129	0.019
FACTOR 6	10.026	0.000
FACTOR 7	1.359	0.262
FACTOR 8	4.510	0.013
FACTOR 9	0.367	0.694
FACTOR 10	0.698	0.500
FACTOR 11	0.800	0.452
FACTOR 12	0.505	0.605
FACTOR 13	15.645	0.000
FACTOR 14	2.449	0.091
FACTOR 15	1.269	0.285
FACTOR 16	0.130	0.878
FACTOR 17	0.898	0.410
FACTOR 18	0.631	0.534
FACTOR 19	0.143	0.867

MULTIVARIATE TEST STATISTICS

WILKS' LAMBDA = 0.124

TABLE 6. Populations (rows) by Predict (columns).

reclassifications	ATLANTICA	CANTABRICA	BLACK SEA	TOTAL
ATLANTICA	31	3	1	35
CANTABRICA	0	36	3	39
BLACK SEA	0	2	28	30
TOTAL	31	41	32	104

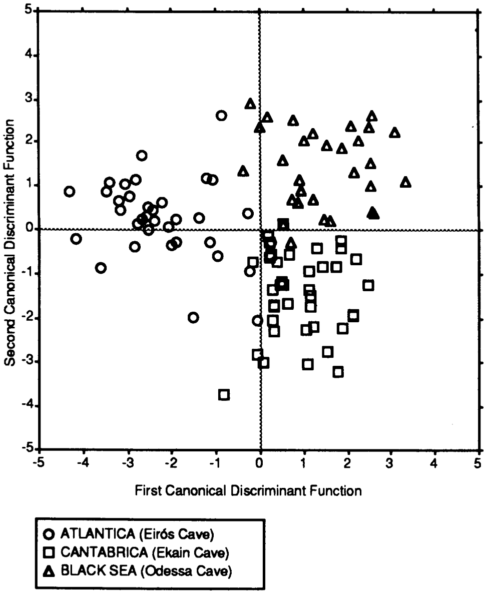

Figure 4. Lower Carnassial (M_1).

derlining factors 2, 6 and 13 which reach high F values and nil probabilities. They are in fact the factors corresponding to those PCs most related to the cusps, both in shape and relative size; PC XIII was directly related to the metaconid, which appears to acquire a special value in interpopulational studies.

The value of Wilks'Lambda is lower (0.124), indicating a higher discriminant power than in the previous analysis. The reclassifications of the cases conform much more to their respective populations. In Figure 4 we see a projection of the cases along the plane defined by the two canonical discriminant functions obtained. The populations are better defined, with hardly and interference between cases from different locations.

CONCLUSIONS

The lower carnassial shows a high morphologic change along the evolutionary line of the ursidae. Starting from *Ursavus*, the structure of the cusps becomes progresively complicated. This process is specially marked on the metaconid. This cusp has a very low development in *Ursavus*, but becomes more and more prominent to such a point that it becomes an entity itself. This is the case of *Ursus etruscus*, where the metaconid is a single cusp perfectly delimited by a well-marked furrow (TORRES, 1988).

The morphology of the cusp becomes more complicated in *Ursus deningeri* and *Ursus spelaeus*, where it appears splitted into two or three cusps, very often accompained by some small accessory cusps.

The differentiation and size increase of the metaconid are higher than those suffered by the others cusps of the tooth, already well developped in the earliest stages of the evolutive line of the Ursidae. This fact must be the reason why the metaconid acquires a special importance in the interpopulational studies, as it has been shown in this paper.

The differences observed between the three populations studied cannot be attributed in this case to temporal variations between populations. The explanation could be different evolutive degree reached by each population, or also because of a process of genetic derive caused by the isolation of them. On the whole, they appear to vary according to a criterion of the geògraphical distance between the sites studied.

It has been proved once more how the sexual dimorphism of *Ursus spelaeus* interferes to an important degree with the metric characterization of the populations; interpopulational study is considerably improved when we disregard the differences in size which exist in each population.

Moreover, and once these size differences are put aside, it is the morphology of the cusps (their vertical development and the degree of convergence between their vertices) which best characterizes each population.

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