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Multivariate analysis of craniometric characters in European wild cat, Domestic cat, and African wild cat (genus *Felis*)

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Abstract

Studied craniometric characters of Italian populations of domestic and European wild cat (genus *Felis*) including comparison with African wild cat to assess their relevant taxonomical relationships. 135 specimens were submitted to a multivariate analysis of 5 skull's traits.

Principal component analysis shows the same eigenvectors' structure in the three groups. Canonical analysis displays large overlap in the plot of sample scores. This intergradation generate a morphometrical transition among *catus*, *libyca* and *silvestris* phenotypes. The suggested conclusion is that these phenotypes belong to a single polytypical species *Felis silvestris* Schreber, 1777.

Introduction

Systematic and phylogenetic relationships between European wild cat and domestic cat have been subjected to longlasting debates. Most authors have directly compared these two taxa without considering African wild cat, possibly the principal, if not only, form to originate the present domestic population (HALTENORTH 1953; HEMMER 1976; TODD 1978; ROBINSON 1980; CLUTTON-BROCK 1981). Furthermore, morphometric and mor-

phologic traits of the skull, one of the main information sources haven't led to homogeneous conclusions on the case.

HAMILTON (1896) first points out resemblances between the skull of European wild cat and the ones of *F. chaus*, African wild cat and domestic cat. He shows a continuous variation existing between the two wild forms and hybrids of domestic and European wild cats and believes that at present wild cat in Europe is represented by "*Felis catus ferus*, the mixed bred between the wild and domestic cat".

Examining skulls of domestic and European wild cats, DIDIER and RODE (1936) observe only one distinctive morphologic character. They admit that the wild European, the African and the domestic cat descent from the same ancestor and they consider them as separate species.

In a monograph on genus *Felis*, POCOCK (1951) bases his diagnoses on the coat's pattern. Moreover in considering craniometric and craniologic data he admits that constant differences between the skulls of European and African wild cats do not exist and that it is very difficult to distinguish the striped tabby type of domestic cat from African wild cat. Nevertheless he classifies the three forms as separate species.

In his Old world's wild cats monograph HALTENORTH (1953) points out that craniometric data do not show significant mean differences even when populations from distant areas such as Central Europe and Tropical Africa, are compared. He considers the European, African and Asian populations as subspecies of one polytypical species. SUMINSKI (1962) believes that difficulties in determining critical differences between domestic and European wild cats' skulls prove that the present wild cats of Europe would be "des bâtards qui ont environ 63 % de sang de chat sauvage". However he maintains three separate species. SCHAUENBERG (1969) demonstrates that European wild cat and domestic cat can be separated on the basis of cranial index (total length of the skull/neurocranium capacity) and ascribes the two entities to separate species. The same author, subsequently (1977) considering "l'homogénéité parfaite" of European wild cat throughout his range "par opposition à la grande variabilité" of African wild cat, believes that the two entities should belong to distinct species, as African wild cat doesn't present any transitional character towards European wild cat. KRATOCHVIL (1976) confirms this taxonomic distinction.

Recent acquisitions of RAGNI and MARIANI (1981), RAGNI (1984), RAGNI and RANDI (1985) working on historical and univariate morphologic data on Italian wild cat, Sardinian wild cat and domestic cat, point out the affinity of *Felis* forms living in the Italian range. In the present work skulls of Italian populations of domestic and European wild cat have been analyzed, including in the comparison African wild cat. The latter is represented by samples of populations living at the boundaries of domestic cat's most probable derivation range: the Mediterranean group *sarda*, and the Somali-ethiopian one, both included at the present in the *libyca* form (CORBET 1978). Multivariate analysis techniques have been used in order to define interrelationships and variation range of cranial size and shape values in the three forms.

For objectivity sake, in the following discussion the populations will be called phenotype (p.) *silvestris* = European wild cat; p. *libyca* = African wild cat; p. *catus* = domestic cat, according to CORBET (1978) and HEMMER (1978).

Material and methods

Skulls come from public or private Italian collections, or were directly collected by the authors. Museological statements about the skulls were tested with:

- Cranial index (SCHAUENBERG 1969) in *silvestris* and *catus*;
- Coat pattern (POCOCK 1951; HALTENORTH 1953; WEIGEL 1961; RAGNI 1981, 1984) in *silvestris*, *catus* and *libyca*.

When none of the above mentioned tests were possible, the authors preferred not to use the material.

Size and geographic origin of the single samples are the following: *silvestris* (Italy, Sicily) = 49; *libyca* (Sardinian sub sample = 19; Somali-ethiopian subsample = 15) = 34; *catus* (Italy, Sicily, Sardinia) = 52.

On the skull 5 measures were taken: total length of the skull (TL) and zygomatic breadth (ZB), which inform about cranial general dimensions; greatest breadth (BFM) and height (HFM) of the foramen magnum and neurocranium capacity (NC), which turned out to be, after univariate analysis (RAGNI 1984), within the most discriminating metrical characters.

Lengths were measured in mm (DRIESCH 1976), and neurocranium capacity in cm³, according to SCHAUENBERG's procedure (1969).

Two multivariate analysis models were used (MORRISON 1979). Principal Components Analysis (PCA) allows description of the multivariate spatial distribution of observed values, by means of reciprocally orthogonal vectors oriented along the successive maximum variability directions. Each vector's elements (eigenvectors) are the loadings of the single variables in determining the variance percent linked to the vector. Eigenvectors plot represent the association pattern of craniometric characters within each group and is therefore used to compare these patterns among the three groups.

Canonical Analysis (CA) allows to visualize the discrimination among a-priori determined groups, maximizing the between-groups variance versus the within-groups variance. Within a system of orthogonal canonical variates (CV), the distances between-groups are shown by the respective canonical means (centroids) or by the distribution of single individual scores.

Results

Mean TL and NC values of the three forms fall within published data variation range (POCOCK 1951; HALTENORTH 1953; DERENNE and MOUGIN 1976; HEMMER 1976; SCHAUENBERG 1977). We have no references about BFM and HFM. (Discussion of such data in univariate terms will be exposed in a further work).

Variance-covariance S matrices show similar patterns. We therefore suppose they are homogeneous. Patterns of correlation R matrices are similar too. Correlations of TL and ZB with HFM have negative sign in *catus*, but they are not significant, similarly to *silvestris* and *libyca*. Therefore, HFM appears to be the less correlated variable within the considered system (Tab. 1).

Variance percentage explained from each of the first 3 PCs appears to be practically identical in the three groups. PC-I explains about 80 % of the total variance, PC-II about 10 % and PC-III about 5 % (Tab. 2).

The plot of eigenvectors is shown in Fig. 1. PC-I can be interpreted as the main dimensional factor of the system because its heaviest loadings are given by TL, ZB and NC, these variables being positively interrelated. Therefore this first variation direction separates long, wide and large skulls from narrow and small ones. Eigenvectors are practically identical in the three groups.

PC-II can be interpreted as the next dimensional factor in the system, because along this variation direction NC has the highest loading. It therefore separates bulky skulls from small ones. Again eigenvectors are similar in the three groups. These first two PCs altogether express over 90 % of the system's total variance.

PC-III can be interpreted as a shape factor, as its eigenvectors load TL and ZB, but in opposition. It therefore separates skulls according to their shape. Eigenvectors' structure in the three groups is similar for PC-III as well.

CA allows for drafting two CVs, the first explaining about 93 % of total variance between groups, the second explains the remainder 7 %. Only CV-I discriminates significantly groups.

In Fig. 2 the three centroids are well separated along CV-I and partially overlapping along CV-II. Eigenvectors (Tab. 3) show that NC has the highest loading in determining this between-groups discrimination.

Large overlapping areas among the 3 groups are displayed in the canonical plot of sample scores (Fig. 3). Within-group variation in spite of its minimization obtained

Table 1
Descriptive statistics of skull traits

		Phenotype <i>silvestris</i> (n = 49)				
Variables	1 = TL	2 = ZB	3 = BFM	4 = HFM	5 = NC	
$\bar{X} \pm$ S.E.	92.63 \pm 0.84	65.67 \pm 0.61	14.45 \pm 0.10	12.23 \pm 0.14	39.22 \pm 0.48	
S.D.	5.85	4.25	0.70	1.01	3.37	
S. Matrix	1	2	3	4	5	
1	34.28	23.14	1.77	0.62	13.82	
2		18.09	1.32	0.54	9.82	
3			0.49	0.39	1.03	
4				1.03	1.09	
5					11.36	
R. Matrix	1	2	3	4	5	
1	1.00	0.93**	0.43**	0.10	0.70**	
2		1.00	0.44**	0.13	0.68**	
3			1.00	0.55**	0.43**	
4				1.00	0.32*	
5					1.00	
		Phenotype <i>libyca</i> (n = 34)				
Variables	1 = TL	2 = ZB	3 = BFM	4 = HFM	5 = NC	
$\bar{X} \pm$ S.E.	92.87 \pm 1.06	64.47 \pm 0.85	13.79 \pm 0.13	11.73 \pm 0.15	33.21 \pm 0.55	
S.D.	6.18	4.94	0.77	0.87	3.23	
S. Matrix	1	2	3	4	5	
1	38.15	24.18	2.81	1.91	8.78	
2		24.45	1.89	1.20	6.31	
3			0.60	0.35	1.37	
4				0.76	1.29	
5					10.44	
R. Matrix	1	2	3	4	5	
1	1.00	0.79**	0.59**	0.36*	0.44**	
2		1.00	0.49**	0.28	0.39*	
3			1.00	0.52**	0.55**	
4				1.00	0.46**	
5					1.00	
		Phenotype <i>catus</i> (n = 52)				
Variables	1 = TL	2 = ZB	3 = BFM	4 = HFM	5 = NC	
$\bar{X} \pm$ S.E.	90.18 \pm 0.73	64.79 \pm 0.54	13.21 \pm 0.12	10.81 \pm 0.11	28.60 \pm 0.44	
S.D.	5.25	3.90	0.80	0.79	3.17	
S. Matrix	1	2	3	4	5	
1	27.56	17.13	1.51	-0.52	9.98	
2		15.19	0.61	-0.81	5.80	
3			0.65	0.22	1.35	
4				0.62	0.28	
5					10.07	
R. Matrix	1	2	3	4	5	
1	1.00	0.84**	0.36**	-0.12	0.60**	
2		1.00	0.19	-0.26	0.47**	
3			1.00	0.35*	0.53**	
4				1.00	0.11	
5					1.00	

$\bar{X} \pm$ S.E.: arithmetic mean \pm 1 standard error; S.D.: standard deviation; S. Matrix: variance - covariance matrix; R. Matrix: correlation matrix; Variables: 1 = total length of the skull; 2 = zygomatic breadth; 3 = breadth of foramen magnum; 4 = height of foramen magnum; 5 = neurocranium capacity.
* r significance level: 5%; ** r significance level: 1%.

Table 2

Principal Components Analysis
Eigenvalues for the first three principal components

	Eigenvalue	% of trace
Phenotype <i>silvestris</i>	I 57.12	87.55
	II 5.20	7.97
	III 1.68	2.57
Phenotype <i>libyca</i>	I 59.18	79.53
	II 8.19	11.01
	III 6.14	8.25
Phenotype <i>catus</i>	I 43.64	80.67
	II 6.58	12.17
	III 2.91	5.39

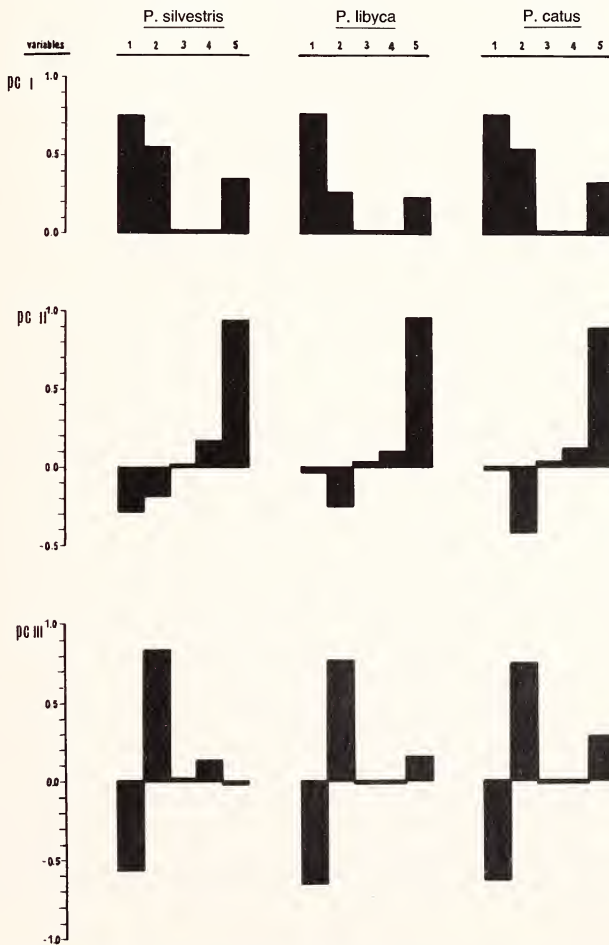


Fig. 1. Principal Components Analysis. Maps of eigenvectors for the Principal Component PC-I, PC-II and PC-III

through CA procedure is wide enough to prevent a sharp individual between-groups discrimination variation. Extension of *catus* variation range is similar to the one of *silvestris* and *libyca*. A similar situation can be observed in body size variability (POCOCK 1951; HALTENORTH 1953; DERENNE 1976; KRATOCHVIL 1975, 1976). Furthermore, substantial homogeneity in the three forms' behaviour (LEYHAUSEN 1979; RAGNI and RANDI 1985) can be added to the previous matters in order to overcome possible perplexities in treating at the same rate wild and domestic entities (CORBET 1978):

Table 3
Canonical Analysis
Eigenvectors

Canonical variate	I	II
Eigenvectors 1	-0.088	0.336
2	-0.034	-0.390
3	0.099	-0.343
4	0.107	0.482
5	0.356	-0.063

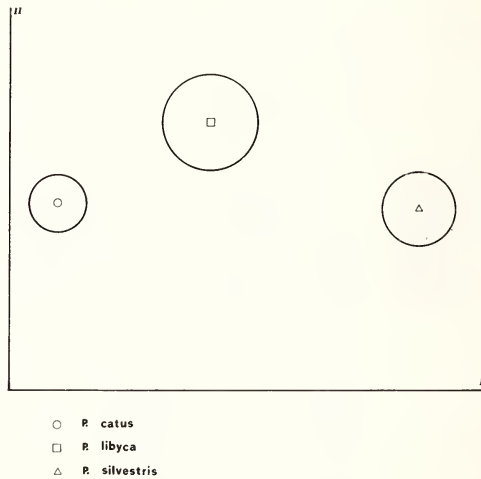


Fig. 2. Canonical Analysis. Canonical Variates (CV) map of centroids with 95% probability level circle. I = first CV explaining 93.71% of discrimination; II = second CV explaining 6.29% of discrimination

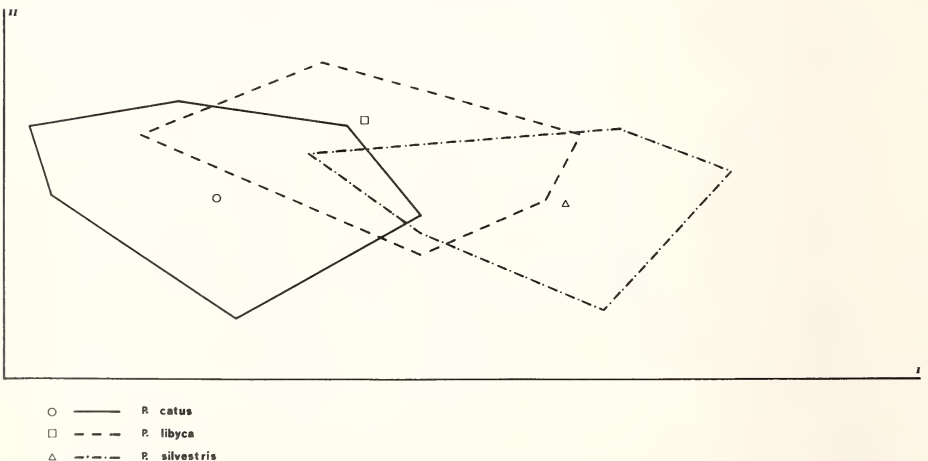


Fig. 3. Canonical Analysis. Canonical Variates map of sample scores

Discussion and conclusions

Specimens belonging to the *silvestris*, *libyca* and *catus* phenotypes, show similar covariations among the craniometric traits we have analyzed.

PCA informs that size as well as shape variations are phenotypically expressed through multivariate patterns which turn out to be similar and perfectly comparable in the three groups. We therefore suggest that a shared system of regulation of cranial morphometric growth (size and shape) can work on *silvestris*, *libyca* and *catus* groups in witness of close phylogenetic relationships and probably small genetic distances.

The centroids of the three groups appear well separated within the canonical variates space. Such a separation reflects the discriminating power of NC in multivariate as well as in univariate dimension. Furthermore it confirms a morphological differentiation among these populations, previously observed in coat's pattern comparison and in the univariate analysis of craniometrical characters (RAGNI and RANDI 1985).

But a wide within-group variation exists, so that CA cannot sharply separate the individuals. This wide intergradation without continuity solution shows that skull size can vary in a continuous way generating a morphometrical transition among the three groups.

Concordant results were obtained by WERDELIN (1981) by testing different linear metric characters with different techniques of skull multivariate analysis on a small *Felis silvestris* (*sensu lato*) sample (22 individuals from Europe and Middle East).

Such an intergradation could be the result of quantitative genetic causes as well as of environmental variations. CA results point out that *catus* and *libyca* phenotypes are more closely related to one another than to *silvestris* phenotype, in perfect accordance with historical data concerning the African origins of domestic cat. Location of the *catus* scores dispersion swamp within the CVs orthogonal axis is congruent with the wellknown domestication effects on skulls of mammals (KLATT 1912; STEPHAN 1951; RÖHRS 1955; HÜCKINGHAUS 1965). These effects are however not enough to separate ancestors (*libyca*) from descendants (*catus*).

Phenotypic distinction between *catus* and *silvestris* becomes indeed a morphometric continuity via African wild cat.

The remarkable geographic distance between considered wild populations and the consequent environmental diversities are not enough to interrupt continuity in character variation. Hypotheses of genetic separation are therefore scarcely supported.

Craniometric variation, the genetic basis of which is unknown, as well as multivariate analysis patterns, which don't allow direct decomposition of total variability in genetic and non-genetic components, operate on a phenotypic level.

From a phylogenetic point of view it is therefore not possible to interpret univocally the above mentioned phenotypic data that show invariance in the patterns, on one hand, and size variance on the other, without continuity solution.

Both morphometric analysis on samples of different geographic provenience and electrophoretic analysis of genetic variation defined by enzyme and protein systems of blood and tissues are necessary, the former allowing improvement of zoogeographic distribution hypothesis, the latter allowing precise measurements of genetic distances between different taxa (both in progress).

The most cautious and objective taxonomic conclusion allowed by the present work is that *catus* phenotype (Italian domestic cat population), *libyca* phenotype (Mediterranean and Tropical African wild cat population) and *silvestris* phenotype (Italian wild cat population) belong to one polytypical species named *Felis silvestris* Schreber, 1777.

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Zusammenfassung

Multivariate Analyse von craniometrischen Merkmalen bei europäischen Wildkatzen, Hauskatzen und afrikanischen Wildkatzen (Genus Felis)

Es wurden einige craniometrische Merkmale italienischer Populationen von Hauskatzen und europäischen Wildkatzen (Genus *Felis*) sowie von afrikanischen Wildkatzen untersucht, um deren taxonomische Beziehungen festzustellen. Insgesamt wurden 135 Individuen einer multivariaten Analyse anhand von 5 Schädelmerkmalen unterzogen. Die Untersuchungen ergaben identische Strukturen der Eigenvektoren in den drei Vergleichsgruppen. Die kanonische Analyse erbrachte weite Überlagerungen in der Verteilung individueller Maße. Daraus ergibt sich ein morphometrischer Übergang zwischen den Phänotypen *catus*, *lybica* und *silvestris*, der den Schluß zuläßt, daß diese Phänotypen einer einzigen polytypischen Art *Felis silvestris* Schreber, 1777 angehören.

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WISSENSCHAFTLICHE KURZMITTEILUNGEN

Is dominance an absolute quality in male Tree shrews (*Tupaia belangeri*)?

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There is always a good chance that one can predict the results of dominance fighting in animals: The stronger individual will be the winner or, if the opponents are comparable in strength, the owner of the territory will win. The question remains to be answered what will happen in experiments in the laboratory, where the opponents are of comparable physical and/or physio-psychological strength and do not have a territory? In the context of physiobehavioral studies in tree shrews, often the question has been raised concerning the consequences of confrontation of two formerly dominant males. To study this situation, we designed a confrontation experiment and analysed the behavior of two males which had proved themselves dominant in former experiments. It is unknown, whether dominance in tree shrews under laboratory conditions is an absolute or relative quality. If it is a relative quality, a hierarchy system should be established between the two animals, and in this situation we would receive the first quantitative description of behavior in subordinate tree shrews.

The behavior of two adult male tree shrews (δ 525, δ 447), which both had reached dominant positions in former confrontation experiments (AUE and FUCHS 1986) was recorded on video tapes on three days over a period of one month during the first three hours of the light phase of an artificial L:D (08.00–20.00 hr). To avoid a territorial advantage for either one of the animals, they were placed together in a cage, which was new for both of them and which was equipped like their home cages. After putting the animals together, behavior was again recorded during the first three hours after beginning of the light phase on confrontation days 1, 2, 3, and 10. On day 19, when both animals were back in their home cages after the seventeen day confrontation period, the behavior of both animals was monitored. The body weight of each animal was recorded daily before, during,

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