Remarks on the skull morphology of *Canis lupaster* Hemprich and Herenberg, 1832 from the collection of the Natural History Museum "G. Doria" of Genoa, Italy

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Abstract - *Canis lupaster* is a canid that lives in North Africa. In the past, this species was considered a subspecies of golden jackal (*Canis aureus*), a subspecies of wolf (*Canis lupus*), or a separated species. Since 2011 genetic data have demonstrated that *C. lupaster* is not a golden jackal and that it is more closely related to wolf lineage. The recent interest on *C. lupaster* lead to the publication of some papers on this topic, but the vast majority concerned genetic data. In this paper a morphological approach is presented. Twelve specimens, collected in Libya between 1926 and 1931 and now stored in the Natural History Museum of Genoa, are described here. *C. lupaster* is compared with the African golden jackal and with the wolf. MANOVA, PCA and discriminant analysis were performed. *C. lupaster* show many differences and is well separated both from wolf and from African golden jackal. Measures and ratios, that allow to rapidly recognise among these species, were identified. These ratios could be a useful tool for field researchers to quickly identify the correct species.

Key words: *Canis lupaster*, *Canis anthus,* African golden jackal, wolf, skull morphology, Libya.

Riassunto - Osservazioni sulla morfologia del cranio di *Canis lupaster* Hemprich and Herenberg 1832 dalla collezione del Museo di Storia Naturale "G. Doria" di Genova, Italia.

Canis lupaster è un canide che vive in Nord Africa. In passato questa specie è stata considerata come una sottospecie dello sciacallo dorato (*Canis aureus*), come sottospecie del lupo (*Canis lupus*), o come specie separata. Dal 2011 dati genetici hanno dimostrato che *C. lupaster* non è uno sciacallo dorato e che è più affine alla genealogia del lupo. Il recente interesse su *C. lupaster* ha provocato la pubblicazione di alcuni articoli sull'argomento, tutti di taglio genetico. In questo lavoro viene presentato un approccio morfologico. Dodici esemplari, catturati in Libia tra il 1926 e il 1931 e ora conservati presso il Museo di Storia Naturale di Genova, sono qui descritti. *C. lupaster* è stato comparato con lo sciacallo dorato africano e con il lupo. Sono state eseguite MANOVA, PCA e analisi discriminante. *C. lupaster* mostra molte differenze ed è ben distinto sia dal lupo che dallo sciacallo dorato africano. Sono state individuate misure e rapporti che permettono di distinguere tra queste tre specie. Questi rapporti potrebbero essere utili per i ricercatori sul campo per identificare rapidamente la specie corretta.

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INTRODUCTION

Canis lupaster Hemprich and Herenberg 1832 (Fig. 1) is a canid that lives in North Africa (Gaubert *et al.,* 2012). The taxonomic position of *C. lupaster* has changed many times in the last centuries. Initially *C. lupaster* was described as true species by Hemprich and Herenberg (1832), and this position was shared by other authors (Beaux, 1927; Zammarano, 1930; Flower, 1932). After that *C. lupaster* was considered as a subspecies of *Canis aureus* because the distribution and the body-size is closer to *C. aureus* (Anderson & Winton, 1902; Schwarz, 1926a, 1926b; Ellerman & Morrison-Scott, 1951; Setzer, 1961). Despite this, some authors considered this species as separated from *C. aureus* on the basis of ethological observations (Flower, 1932; Hoogstraal, 1964; Hufnagl, 1972).

In 1831 Sykes discovered the Indian wolf *Canis lupus pallipes* and the similarity with *C. lupaster* was noted in the following years (Anderson, 1902). Ferguson (1981) suggests that *C. lupaster* should be considered as subspecies of *C. lupus* from a morphological point of view. Measurements of the skull length, mandible and carnassial of *C. lupaster* overlap the lower limits of *C. lupus arabs* and show a distinct gap with those of *C. aureus* (Ferguson, 1981), and according to the Bergmann's rule, *C. lupaster* is probably a small wolf rather than a giant jackal (Ferguson, 1981).

Genetic analyses have revealed that *C. lupaster* is not a golden jackal (Rueness *et al.,* 2011) and it is more similar to the *Canis lupus* lineage. Gaubert *et al.* (2012) found four distinct lineages of wolf: *C. lupus/familiaris* (Holarctic wolves and dogs), *C. l. chanco* (Himalayan wolf), *C. l. pallipes* (Indian wolf) and *C. l. lupaster* (African wolf). The lineage of *C. l. lupaster* is relatively ancient, with a time to most recent common ancestor estimated at 288k years ago (Gaubert *et al.,* 2012). However, despite phenotypical and ethological differences, *C. lupaster* mtDNA was detected in African *C. aureus*, suggesting a hybridization (Gaubert *et al.,* 2012). At the moment *C. lupaster* is considered a separated species thanks to genetic on mitochondrial and genomic DNA (Koepfli *et al.* 2015; Rueness *et al.,* 2015; Urios *et al.,* 2015), phenotypic (Gaubert *et al.,* 2012) and morphologic data (Spassov & Stoyanov, 2014).

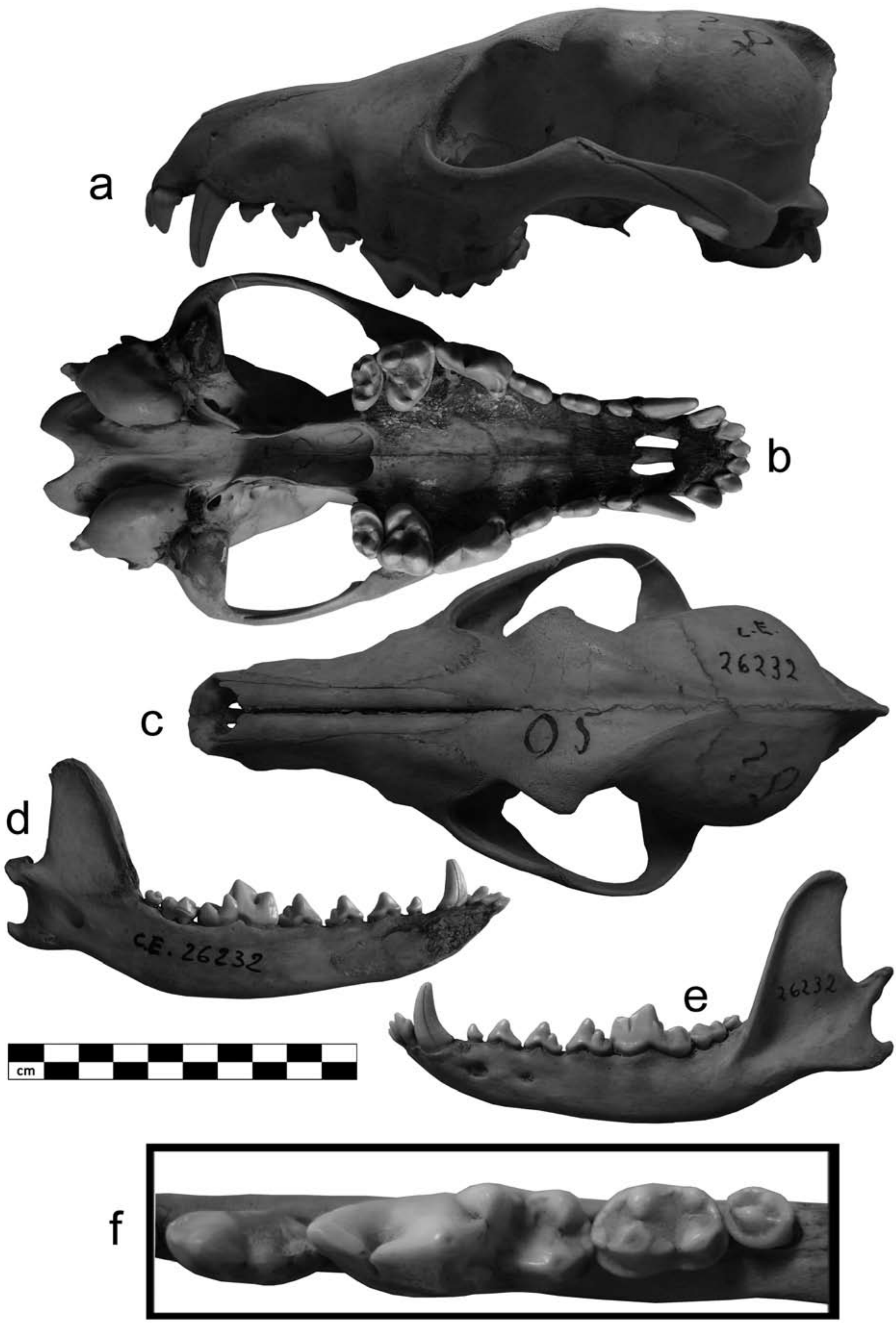


Fig. 1 - Specimen MSNG 26232. a) skull in left lateral view; b) skull in ventral view; c) skull in dorsal view; d) left hemimandible in lingual view; e) left hemimandible in labial view; f) occlusal view of P4-M3.

Koepfli *et al.* (2015) separate European *Canis aureus* from African *Canis aureus*; this latter, following Cuvier, is called *Canis anthus*. Cuvier used the name *C. anthus* to describe an African golden jackal from Senegal as different from Eurasian golden jackal. In the opinion of Koepfli *et al.* (2015) the name *C. aureus* could be referred only to Eurasian specimen while the African specimens must be considered as *C. anthus.* In the paper of Koeplki *et al.* (2015) an exhaustive analysis on different populations of African golden jackal however is absent. In the work of Van Valkenburgh & Wayne (1994) the specimens from different populations of "African golden jackal" are considered all together but the authors recognise that the population of North Africa (*C. lupaster*) is quite different. In the supplementary material Koepfli *et al.* (2015) cite the work of Rueness *et al.* (2015) but a comparison is made only between Eurasian golden jackal and African wolf (*C. lupaster*), while comparison between African golden jackal (*C. anthus*) and African wolf (*C. lupaster*) is lacking. Gaubert *et al.* (2012) compared *C. lupaster* with East African golden jackal and they found significant differences; Gaubert *et al.* (2012) also reported some differences between Eurasian and African jackals, although they didn't separate the two species.

In this work I follow Koepfli *et al.* (2015) considering the "African golden jackal" as *C. anthus* but I suggest that *C. lupaster* must be considered as a different taxonomic unit; this opinion is based on genetic evidence reported in literature (Rueness *et al.* 2011; Gaubert *et al.* 2012) and on morphological differences reported below in this paper.

The taxonomic status of *C. lupaster* is important to establish adequate conservation measures on wild populations. While papers on genetic data are increasing, no recent papers on skeletal morphology are available. Aim of this paper is to identify new morphological and morphometric features that allow to easily distinguish *C. lupaster* both from *C. lupus* and "African golden jackal". On a morphological point of view some typical features of *C. lupaster* are expected to be find because the separation from wolf lineage is relatively ancient and, on counterpart, some convergence with *C. anthus* due to environmental conditions are expected to be find.

MATERIALS AND METHODS

The specimens of *C. lupaster* in exam are stored in Natural History Museum "G. Doria" of Genoa (MSNG). In the collection are present 12 skulls; male and female are equally represented. Ten of the specimens are collected in Cyrenaica (Libya) between 1926 and 1931 and two are from captivity. The specimens MSNG 26228, MSNG 26229, MSNG 26230, MSNG 26231, MSNG 26232, MSNG 26233, MSNG 26449 are collected at oasis of Giarabub in 1926-1927 by C. Confalonieri. The specimens MSNG 31630, MSNG 31632, MSNG 31635 are collected at Es Sahabi, oasis of Cufra, in 1931 by marquis Patrizi. The specimen MSNG 32184 was a gift to Circo Mannucci by Captain Vassallo in 1933. The specimen MSNG 34260 was a gift of B. and S. Sonnenberger to the Zoo of Nervi (Genoa), where has lived between 1932 and 1937. The skins of nine of these specimens are stored in the Natural History Museum "G. Doria" of Genoa.

A comparison of the skull of *C. lupaster* with African golden jackals and European wolf is here presented.

Data on recent *C. lupus* from the Apennine area were taken from Bertè (2013) and include 115 individuals (52 males and 63 females) belonging to the Italian subspecies *C. lupus italicus* (Nowak & Federoff, 2002; Boitani *et al.,* 2003). The specimens considered here are stored at ISPRA, Department of Zoology of Sapienza, University of Rome (DZR), the Natural History Museum "G. Doria" of Genoa (MSNG), the Natural History Museum of Milan (MSNM) and the Regional Natural History Museum of Turin (MRSNT).

The "African golden jackal" specimens are stored at the Natural History Museum "G. Doria" of Genoa and Natural History Museum of Milan. These specimens were collected in African localities (5 from Eritrea, 4 from Somalia, 1 from Tunisia, 1 from Algeria, 1 from Libya) and, following Koepfli *et al.* (2015), now they must be considered as *C. anthus.*

Morphometric data were taken with a standard calliper. The measures, taken following Von den Driesch (1976), are length and breadth of each tooth, the greatest breadth of P^4, the talonid length of M_1, and those listed and described in Tab. 1. The measures are reported in Tabs. 2 and 3.

All the statistical analyses are performed with the software PAST version 2.08 (Hammer *et al.,* 2001). A Principal Component Analysis (PCA) was performed to visualise variance in skull and mandible measures across samples using Principal Component vectors. Skull and related mandible were analysed together. A Multivariate Analysis of Variance (MANOVA) was also performed. Wilk's lambda value is reported. If the MANOVA shows significant overall difference between groups, the analysis can proceed by pairwise comparisons. Bonferroni correction for multiple test is applied and P values (multiplied by the number of pairwise comparisons) are reported. ANOVA is performed only on PC1. If ANOVA shows significant difference of the means (low P), a "post-hoc" pairwise comparisons is used, based on Tukey's HSD (Honestly Significant Difference) test. Sample sizes do not have to be equal for the version of Tukey's test used. A discriminant analysis was also performed on the data to confirming or rejecting the hypothesis that two species are morphologically distinct. A confusion matrix was produced; it is a table with the true class in rows and the predicted class in columns. The diagonal elements represent correctly classified combinations, while the cross-diagonal elements represent misclassified combinations. On this data the producer accuracy (PA) was calculated as the percentage of correctly classified values in a given class on the total number of values in that class, and the user accuracy (UA) as the percentage of correctly classified values in a given class divided by the number of values classified for that class; the overall accuracy (OA) was calculated as an average value following the formula: (true positives + true negatives)/(true positives + true negatives + false positives + false negatives).

Tab. 1 - List and description of the measures taken on the skull and mandible.

Abbreviation	**Description**
TL	Total length - akrokranion-prosthion
CL	Condylobasal length - aboral border of the occipital condiles-prosthion
BL	Basal length - basal-prosthion
UNL	Upper neurocranium length - akrokranion-frontal midpoint
VcL	Viscerocranium length - nasion-prosthion
FL	Facial length - frontal midpoint-prosthion
GLN	Greatest length of the nasals - nasion-rhinion
SL	Snout length - oral border of the orbits-prosthion
MPL	Median palatal length - staphylion-prosthion
PL	Palatal length - median point intersection choanae-prosthion
LhP	Length of the horizontal part of the palatine - staphylion-palatinoorale
LCR	Length of the cheektooth row - measured along the alveoli on the buccal side
LMR	Length of the molar row
LPR	Length of the premolar row
GdAB	Greatest diameter auditory bulla
Gmb	Greatest mastoid breadth - otion-otion
BdeAM	Breadth dorsal to the external auditory meatus
GBOC	Greatest breadth occipital condili
GbbPp	Greatest breadth of the bases of the paraoccipital processes
GBFM	Greatest breadth of the foramen magnum
HFM	Height of the foramen magnum - basion-opisthion
GNB	Greatest neurocranium breadth - euryon-euryon
ZB	Zygomatic breadth - zygion-zygion
LBS	Least breadth of skull - breadth at postorbital constrinction
FB	Frontal breadth - ectorbitale-ectorbitale
LbbO	Least breadth between the orbits - entorbitale-entorbitale
GPB	Greatest palatal breadth - across outer borders of the alveoli
LPB	Least palatal breadth - behind the canines
BCA	Breadth at the canine alveoli
GiHO	Greatest inner height of the orbit
SH	Skull height
Hot	Height of the occipital triangle - akrokranion-basion
HTO	Height from toothrow to orbit
DJ	Depth of jugal
Tlm	Total length - condyle process-infradentale
Lapi	Length: angular process-infradentale
Lii	Length: indentation between condyle process and angular process- infradentale
Lcpc	Length: condyle process-aboral border canine alveoli
Lic	Length: indentation between condyle process and angular process-aboral border canine alveolus
Lapc	Length angular process-aboral border canine alveolus
Lmr	Length of the molar row
L C-M3	Length from canine to M3
L P1-M3	Length from P1 to M3
L P1-M2	Length from P1 to M2
L P2-M3	Length from P2 to M3
L P1-P4	Length from P1 to P4
L P2-P4	Length from P2 to P4
La M1	Length of the carnassial alveolus
Hm P1	Heigth of the mandible behind P1
Hm P2P3	Heigth of the mandible between P2 and P3
Hm M1	Heigth of the mandible behind M1
GT M1	Greatest thickness of the body of jaw below M1
HVR	Heigth of the vertical ramus - basal point angular process-coronion

Tab. 2 - Measures taken on skull and mandible.

N	MSNG 26231	MSNG 26232	MSNG 26233	MSNG 31632	MSNG 31635	MSNG 34260	MSNG 26228	MSNG 26229	MSNG 26230	MSNG 26449	MSNG 31630	MSNG 32184
Sex	F	F	F	F	F	F	M	M	M	M	M	M
TL	158.0	170.1	167.0	171.0	167.5	155.3	183.0	154.6	173.0	178.0	171.0	180.5
CL	146.8	154.3	155.0		152.0	146.0	155.3	144.7	155.4	158.0		162.0
BL	139.5	146.6	147.4		145.0	138.7	171.6	136.7	149.0	149.0	141.6	153.0
UNL	76.0	75.6	76.0	74.0	70.4	75.0	83.0	76.2	78.5	81.0	74.0	79.5
VcL	69.0	74.3	69.0	77.4	77.0	69.0	78.0	72.3	73.3	77.0	79.0	81.0
FL	89.0	93.5	91.0	97.4	97.0	92.0	100.0	84.6	94.7	97.0	97.0	101.0
GLN	50.0	56.3		57.4	56.0	50.8	56.3	55.3	51.2	58.2	60.0	59.5
SL	64.5	68.6	67.9	70.0	70.4	67.4	74.0	62.5	70.4	71.3	69.6	73.7
MPL	76.6	80.6	79.0	81.2	79.6	76.0	84.0	76.6	79.7	82.0	77.3	87.2
PL	74.8	80.0	77.0	80.7	78.7	75.0	83.6	75.5	78.6	80.7	77.0	85.5
LhP	27.0	29.0	29.6	28.0	26.0	25.0	29.2	28.0	28.7	27.7	27.3	29.7
LCR	56.0	60.0	58.0	59.8	59.3	55.8	65.0	54.5	59.0	59.8	58.6	61.0
LMR	16.3	17.7	16.8	17.0	17.2	17.4	18.5	18.0	16.0	17.0	16.8	18.7
LPR	41.2	46.0	44.2	45.8	45.4	40.6	49.2	39.4	46.0	45.0	43.3	42.7
GdAB	22.4	22.5	23.2	23.8	21.0	20.0	22.6	20.3	21.0	22.2	21.0	23.0
Gmb	51.3	56.0	55.1	54.0	54.0	51.6	55.5	51.5	53.3	56.9	52.3	53.6
BdeAM	48.0	50.6	50.3	50.3	49.8	48.6	52.3	48.7	47.9	52.7	51.2	51.6
GBOC	27.4	29.9	28.7		30.0	29.3	31.5	27.6	25.8	30.2		31.7
GbbPp	39.3	41.6	40.6		39.6	39.0	42.5	37.5	39.0	43.2	38.3	43.0
GBFM	15.8	17.0	16.0		17.2	14.7	17.4	15.0	14.7	16.7	17.5	12.0
HFM	13.2	12.7	14.0		13.3	13.2	12.6	12.3	13.5	14.3	12.0	13.1
GNB	51.3	53.0	53.0	54.5	53.5	49.7	53.0	52.0	50.6	52.0	53.3	54.7
ZB	84.4	86.0		86.6	86.4	80.3	92.0	86.0	87.5	89.8	85.5	88.5
LBS	31.8	30.5	33.0	31.0	32.3	27.0	31.7	28.0	35.8	35.2	49.8	31.2
FB	43.2	41.8	40.7	43.3	41.3	41.8	44.5	40.0	46.8	47.0	41.6	42.8
LbbO	28.2	28.7	30.0	26.9	28.3	29.2	31.0	27.2	33.4	34.0	28.9	26.0
GPB	47.4	48.7	51.0	51.3	49.8	49.5	53.5	51.7	50.3	50.4	49.7	52.0
LPB	23.0	24.4	23.2	25.4	24.5	23.3	27.8	25.6	25.0	27.4	24.7	24.0
BCA	25.9	26.3	24.8	27.4	27.0	25.7	30.5	27.7	27.4	27.0	25.7	26.8
GiHO	28.0	28.7	28.3	29.0	28.0	27.0	28.3	26.3	27.0	28.0	29.4	29.0
SH	44.9	48.0	47.3		44.3	45.4	47.0	43.4	49.0	47.2	43.0	49.0
Hot	36.4	41.0	38.5		37.3	35.7	38.5	35.0	38.4	41.4	36.0	37.6
Tlm	110.6	118.9	115.0	118.6	118.5	113.0	125.7	110.8	116.8	122.2	112.6	123.3
Lapi	112.5	120.0	115.5	120.7	120.0	114.2	126.8	110.8	117.0	120.6	113.4	124.7
Lii	107.2	114.9	111.2	114.0	113.6	108.2	121.4	106.4	111.8	115.7	108.5	119.2
Lcpc	99.0	103.7	102.0	115.5	105.0	99.4	111.2	98.0	104.2	109.5	98.0	109.6
Lic	94.0	100.4	98.3	101.0	101.0	94.4	107.0	94.0	99.0	102.8	94.0	105.4
Lapc	99.5	104.5	103.0	106.5	106.5	101.1	113.3	98.5	104.0	105.6	99.0	110.3
Lmr	31.2	32.6	35.0	33.3	33.0	30.3	35.0	36.0	31.6	34.7	33.6	33.8
L C-M3	67.0	71.6	72.0	72.8	73.2	66.0	76.0	67.3	69.7	73.9	70.0	75.3
L P1-M3	62.0	68.0	68.2	67.0	66.6		72.0	63.0	64.6	68.2	65.0	69.7
L P1-M2	58.6	64.0	63.7	62.8	63.2		68.5	58.9	61.4	63.6	61.4	66.5
L P2-M3	57.5	62.7	63.5	61.2	61.4		68.0	58.0	59.8	64.6	61.2	65.7
L P1-P4	32.5	36.4	34.0	34.0	35.3		38.2	30.3	34.0	35.2	32.2	36.4
L P2-P4	27.7	31.0	29.1	28.6	29.4		34.0	27.0	29.5	30.6	28.0	32.3
La M1	18.0	19.2	20.2	19.5	20.0	18.0	20.4	21.2	19.0	19.5	18.7	18.7
Hm P1	13.2	14.0	14.2	14.0	14.7	12.7	17.6	16.1	16.8	14.0	14.0	17.0
Hm P2P3	12.0	14.6	13.6	14.0	14.2	12.8	16.3	15.0	16.4	14.8	14.0	15.3
Hm M1	16.3	16.2	14.7	16.0	17.2	15.0	19.3	15.4	18.1	19.4	16.0	16.3
GT M1	7.0	6.8	7.2	8.1	8.2	7.5	9.1	8.6	8.0	7.2	7.9	7.5
HVR	44.0	47.8	43.3	45.0	45.0	40.4	47.4	43.4	45.0	45.5	43.0	47

Tab. 3 - Measures of the teeth of *C. lupaster*.

N	MSNG 26231		MSNG 26232		MSNG 26233		MSNG 31632		MSNG 31635		MSNG 34260		MSNG 26229		MSNG 26230		MSNG 26449		MSNG 31630		MSNG 32184	
Side	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L
C L		7.3	7.8	7.9	8.3	8.0	8.0	8.2	8.7		7.6	7.6	8.0	8.0	8.0	8.1	8.3		8.3	8.1	8.7	8.6
C B		4.7	4.5	4.4	4.7	4.8	4.8	4.7	4.8		4.0	3.9	5.0	5.3	4.6	4.7	5.0		4.8	4.9	5.0	5.1
P1 L	4.7	4.7	5.5	5.5	4.8	5.0	5.2	5.2			4.8	4.7	5.0	5.2	5.0	4.8			5.4	5.4	5.2	5.0
P1 B	3.3	3.3	3.4	3.4	3.3	3.4	3.4	3.4			3.3	3.2	3.3	3.4	3.4	3.4			3.7	3.8	3.8	3.7
P2 L	7.9	8.2	9.5	9.6	9.3	9.1	9.0	9.3			8.6		9.4	9.4	9.7	9.3	9.5	9.3	9.1	9.4	9.3	9.5
P2 B	3.6	3.5	3.8	3.9	3.6	3.4	3.8	4.0			3.6		4.3	4.3	4.0	3.9	3.7	3.8	4.2	4.0	4.1	4.0
P3 L	9.8	10.0	10.8	11.0	10.8	11.0	10.7	11.0		9.7	9.7	9.8	10.5	10.8	10.0	10.0			10.7	10.5	11.3	11.4
P3 B	4.0	4.0	4.1	4.0	4.0	4.0	4.6	4.6		3.7	4.0	4.0	5.0	4.7	4.3	4.3			4.3	4.5	4.7	4.7
P4 L	16.6	16.7	18.3	18.3	17.7	18.0	18.2	18.3	18.5	18.3	15.6	15.7	18.3	18.3	17.0	17.0	18.0	18.7	17.7	17.7	18.0	18.0
P4 B	6.7	6.7	6.8	6.8	6.8	6.7	7.2	7.2	7.4	7.3	6.3	6.2	7.4	7.3	6.6	6.7	6.4	6.3	7.0	7.0	7.4	7.3
GB P4	8.7	8.5	8.6	8.7	9.0	9.1	9.1	8.5	8.8	9.0	8.0	7.7	10.0	9.7	9.0	9.2	8.6	8.6	9.0	9.0	9.0	8.8
M1 L	11.7	11.6	12.4	12.2	12.2	12.5		11.0	12.3	12.3	12.0	12.0	14.0	13.8	11.6	11.5	12.7	12.7	12.0	12.3	12.3	12.3
M1 B	13.3	13.5	14.0	14.6	14.3	14.7		14.6	14.0	14.2	13.2	12.8	15.0	15.4	14.5	14.6	15.7	15.7	15.2	15.8	15.2	15.7
M2 L	7.3	7.2	7.4	7.6	7.5		7.5		7.5	7.4	7.2	7.0	8.2	8.0	7.0	6.7	7.6	8.0	7.7	7.6	8.3	8.0
M2 B	10.0	10.4	11.0	12.0	10.7		11.0		10.3	11.0	9.4	9.4	12.0	11.7	11.0	11.2	12.4	13.0	11.0	11.5	11.6	11.4
C L	7.0	7.1	8.4	8.2	7.4	7.3	7.6	7.8	8.2	8.4	7.4	7.6	8.5	8.6	8.0	8.0	8.0	8.2	8.0	8.2	8.0	8.3
C B	4.8	4.8	5.8	5.6	5.2	5.1	5.4	5.0	5.2	5.2	4.7	4.5	6.0	5.8	6.0	5.5	5.6	5.4	5.4	5.3	5.7	5.6
P1 L	4.1	4.0	3.8	4.1	3.8	3.7	4.4	4.0		3.7			3.8	3.7	4.0	4.2	3.6		3.7		4.3	4.2
P1 B	3.0	2.7	3.0	3.0	3.1	3.0	3.0	3.0		3.0			3.0	3.0	3.0	3.0	2.8		3.2		3.2	3.1
P2 L	6.8	6.7	9.0	8.7	8.3	8.2	8.3	8.4	8.7	8.6			8.0	8.4	8.1	8.0	8.3	8.4	8.4	8.2	8.1	8.3
P2 B	3.6	3.5	3.7	4.0	3.7	3.5	4.0	4.0	4.4	4.3			4.3	4.3	3.6	4.0	4.0	4.0	4.2	4.2	4.0	4.1
P3 L	8.3	8.0	9.5	9.5	9.2	9.2	10.0	9.8	10.0		8.7	8.5	9.5	9.5	9.0	9.0	9.5	9.5	9.7	9.6	10.0	9.7
P3 B	3.8	3.8	4.0	4.2	4.0	4.0	4.5	4.5	4.6		4.2	4.0	4.3	4.3	4.3	4.5	4.3	4.2	4.2	4.2	4.4	4.4
P4 L	10.2	10.0	11.3	11.5	11.3	11.6	11.0	11.1	11.5	11.7	10.2	10.0	11.4	11.0	10.8	11.0	11.8	11.8	10.3	10.4	11.3	11.3
P4 B	4.7	4.7	5.0	5.2	5.0	5.0	5.6	5.7	5.6	5.5	4.8	4.8	5.4	5.3	5.0	5.3	5.2	5.3	5.0	5.1	5.2	5.0
M1 L	18.5	18.3	19.6	19.7	20.5	20.4	20.0	20.0	20.7	20.7	18.0	18.0	22.1	21.6	19.2	19.4	20.6	20.0	20.5	20.3	20.0	19.3
M1 B	7.0	7.1	7.2	7.2	7.7	7.7	8.1	8.0	8.0	8.0	6.6	6.7	8.0	8.0	7.6	7.4	7.4	7.6	7.7	8.0	7.7	8.0
Trl	6.0	5.7	6.1	6.3	6.4	6.5	6.6	6.5	6.6	6.6	6.0	5.6	6.3	6.6	6.7	6.3	7.2	5.6	6.5	6.4	6.7	6.3
M2 L	8.3	8.4	9.0	9.3	10.2	9.8	9.0	9.0	8.4	8.6	8.4	8.4	10.4	10.0	8.7	8.7	10.0	10.2	10.2	9.8	10.5	10.0
M2 B	6.0	6.0	6.5	6.3	6.7	6.5	6.7	6.7	7.0	7.0	5.6	5.7	7.0	6.8	6.8	6.8	6.8	7.0	6.0	6.6	7.0	6.6
M3 L	4.2	4.4	4.2	4.6		5.0		4.3			4.0	4.0	4.2	4.8							4.8	4.7
M3 B	4.0	4.0	4.0	4.2		4.6		4.3			3.6	3.6	5.0	4.7							4.5	4.6

A series of box plots with selected craniodental measurements and the derived ratios were generated, thus providing a visual representation of how much *C. lupaster* differs from the other taxa for some key morphological features.

RESULTS

Morphological description

Considering the mean values, as previously noted by Ferguson (1981), *C. lupaster* is smaller than *C. lupus* but bigger than *C. anthus*. Body size is not the only difference, as morphological differences on skull and teeth can also be observed.

The shape of the nasal bones is reported in literature as a diagnostic character to separate wolf from golden jackal (Boitani, 2003); the nasal bones of *C. lupaster* are graph shaped as in Eurasian *C. aureus* and in *C. anthus*, while in *C. lupus* are V shaped. In *C. lupaster* the nasal bones are as long as the maxillary bones while in *C. anthus* they are shorter and in *C. lupus* they are longer. The forehead is low, and the angle between nasals and frontals is flat, while it is more evident in *C. aureus*. The palate is shorter than in *C. lupus* and *C. aureus*, ending in proximity of the mesial border of M^2. A marked restriction of the palate width between P^3 and P^2 is present in *C. anthus* but not in *C. lupus* and *C. lupaster*. The sagittal crest is as low as in *C. aureus*, but this character could be due to an allometric development in small sized canids (Sardella *et al.*, 2014). The pterigoid-palatine crest in distal portion is narrower than in mesial portion.

In *C. lupus* and *C. aureus* P^2 and P^3 have a secondary cusp and the distal cingulum is modified in an accessory cusp while in *C. lupaster* the accessory cusp is absent.

The upper carnassial is less thick than in *C. lupus* (Fig. 2). The paracone of M^1 of *C. lupaster* is bigger than the metacone, as in *C. lupus*, while in *C. aureus* they are equal. In *C. lupaster* the protocone and the metaconule of M^1 are much developed. M^1 of *C. lupaster* has the protocone

Fig. 2 - Teeth comparison; a1: upper teeth of *C. lupus*; a2) lower teeth of *C lupus*; b1) upper teeth of *C. lupaster*; b2) lower teeth of *C lupaster*; c1) upper teeth of *C. anthus*; c2) lower teeth of *C. anthus*.

mesially located; the metaconulo is small; the ipocone is well developed and clearly delineated; the basin is absent; the paraconule is large; the parastyle is even marked. M^2 of *C. lupaster* has a big protocone, while the metaconule is absent or vestigial.

The mandible of *C. lupaster* is intermediate between those of *C. lupus* and *C. anthus*. The teeth of *C. lupaster* are less wide than those of *C. lupus* but are more robust than that of *C. aureus* (Fig. 2).

The P_2 has a secondary cusp and the distal cingulum modified in an accessory cusp; in *C. lupus* another cusp is present. In the P_3 are present two secondary cusps well developed, as in *C. lupus*; the P_3 of *C. lupaster* is less large than that of *C. lupus*, but it is larger than the P_3 of *C. anthus* is.

The trigonid of M_1 is quite narrow and the big metaconid results prominent; the hypoconid is thick; the entoconid is visible. The M_2 of *C. lupaster* has four cusps, and is more similar at *C. anthus* than at *C. lupus*; in *C. lupus* the entoconid of M_2 is often absent or very reduced, while *C. anthus* shows a little entoconid located on the ridge of the cingulum; in occlusal view is quadrangular shaped (Fig. 1f). M_3 of *C. lupaster* has only a central cusp as *C. lupus*, while in *C. anthus* are often present two cusps.

Dental disease

The specimens stored at Natural History Museum "G. Doria" of Genoa show a relative high percentage of dental disease. Various degrees of dental wear can be observed: MSNG 26231 shows little wear of the carnassial teeth and of the molars, MSNG 26230 has advanced wear of the teeth, with loss of many cusps, MSNG 31632 shows a more advanced wear. The specimen MSNG 26228 (Fig. 3) show advanced degree of dental wear. A dental abscess on right M^1 probably caused a parodontal disease (Stillou *et al.,* 2010) and a oronasal fistula (DuPont & DeBowes, 2009).

Morphometric description

The MANOVA analysis performed on skull and mandible shows that the differences between mean are significant (Wilk's lambda: 0.0002138; P: 9.553E-159). The confusion matrix shows that all predicted groups are coincident with given groups and the specimens corrected classified are 100%. A discriminant analysis, performed to test the differences between *C. lupaster* and *C. anthus* and *C. lupus*, is significant (P=1.68E-43). The PCA performed on skull and mandible shows similar differences (Fig. 4a). The species considered are well separated and distinct. The first component PC1 (vertical axis) accounts for 86.1% of the total variance, and has is loadings for TL. The second component (on the horizontal axis) explains 4.5% and is mainly influenced by LhP. ANOVA analysis on PC1 and PC2 has significant result (Tukey's pairwise test P=8.761E-06).

The MANOVA analysis performed on upper and lower teeth shows that the differences between mean are significant (Wilk's lambda: 0.05184; P: 4.388E-136). The confusion matrix shows that just a specimen is classified as *C. lupaster* instead of *C. anthus* and viceversa. No errors of attribution are made with *C. lupus*. The OA value is 90.7. The three groups are well separated (Fig. 4b). A discriminant analysis, performed to test the differences between *C. lupaster* and *C. anthus* and *C. lupus*, is significant (P=1.68E-43). Another PCA is performed on upper and lower teeth: PC1 explains the 84.4% of the total variance and is mainly influenced by the length of the lower M_1; PC2 explain the 2.68% of the variance and depends on the length of the upper canine. Considering only teeth *C. lupaster* and *C. anthus* are quite similar. ANOVA performed on PC1 and PC2 has significant result (Tukey's pairwise test P=8.761E-06).

No sexual dimorphism is found considering carnassial teeth size, a common body size estimator (Van

Valkenburgh, 1990). Sexual dimorphism is noticeable measuring the total length of the skull (TL). While *C. anthus* does not show sexual dimorphism for this character, *C. lupus* shows a similar degree of differentiation (Fig. 5a). The ratio LPR/LMR allows to clearly separate *C. anthus* from *C. lupus* and *C. lupaster* (Fig.5b). This difference is probably due to the diet of these animals, *i.e.* from the carnivorous diet of wolf to the more omnivorous diet of the golden jackal. Considering the palate, the ratio GPB/BCA allows to separate *C. lupaster* from the others species considered (Fig. 5c). The palatal shape of *C. lupaster* shows difference in proportion. Considering the skull length, for example the ratio TL/CL (Fig. 5d), a little difference is observable, due to the difference in the position of the condyles.

DISCUSSION AND CONCLUSIONS

The taxonomic position of the golden jackal in Africa is more complex than previously supposed. Since 2011 genetic researches had suggested that some taxonomic classifications must be reconsidered (Rueness *et al.,* 2011). Furthermore the African golden jackal has enough genetic differences to be considered apart from Eurasian golden jackal: following Koepfli *et al.* (2015) the Eurasian populations belong to *C. aureus* and the African populations belong to *C. anthus.* Some authors, using genetic data, recognise two lineages: *C. lupaster* and the "African golden jackal" (Gaubert *et al.,* 2012). Also morphological differences were observed in the past between *C. lupaster* and the "African golden jackal", but not recognised as taxonomic level (Van Valkenburgh & Wayne, 1994). This work propose the first morphological analysis on this specific

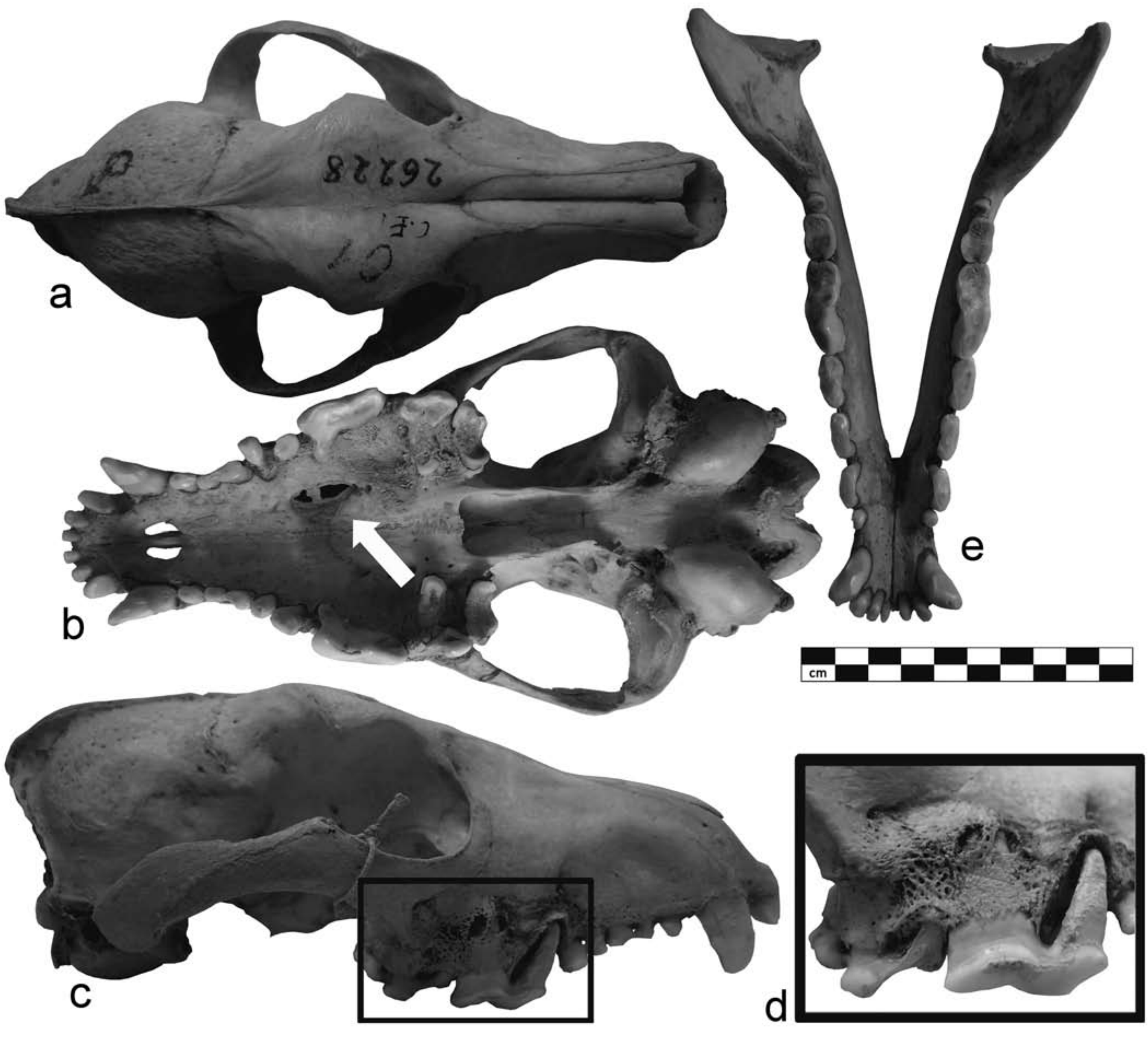
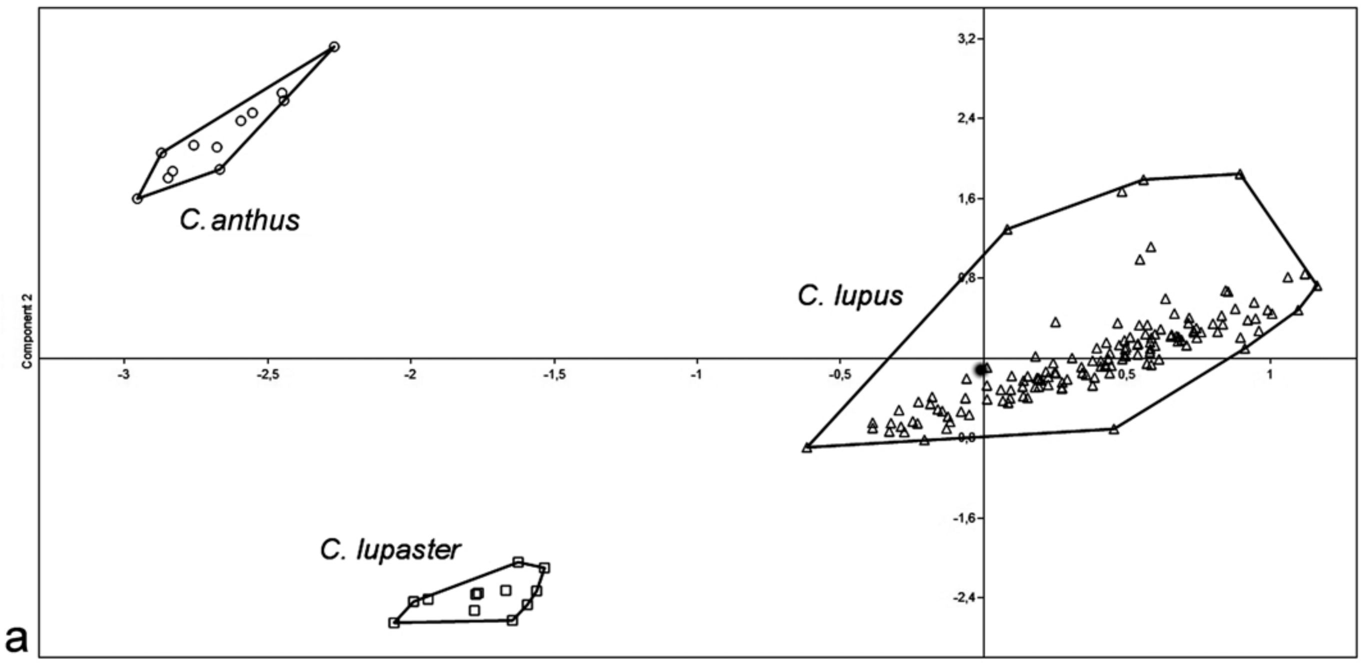


Fig. 3 - Specimen MSNG 26228; a) skull in dorsal view; b) skull in ventral view, oronasal fistula indicated from white arrow; c) skull in right lateral view; d) detail of the right upper carnassial; e) mandible in occlusal view.

topic before the paper of Ferguson (1981). The specimens stored at Natural History Museum "G. Doria" of Genoa, despite the small sample size, show a coherent and homogeneous set of characters that suggest the possibility to identify some features to separate the two species. The present analysis show that *C. lupaster* and *C. anthus* differ in many ratios and proportions and they don't differ only in body-size.

Morphometric analysis applied in this study confirms the results of the genetic data. *C. lupaster* has some characters in common with *C. lupus* and others with *C. anthus* but a multivariate analysis reveals that is well separate from the other species considered. Some of the features that remember *C. anthus,* such as the lack of a developed sagittal crest, are due to scale factors and must be considered as convergence. Future analyses on a bigger sample will be necessary to observe the variability degree of these characters in a population.

The Italian museums are full of specimens, most of them collected during colonial period, which can be very useful to answer modern question. The discussion about the taxonomic status of *C. lupaster* in the last years is



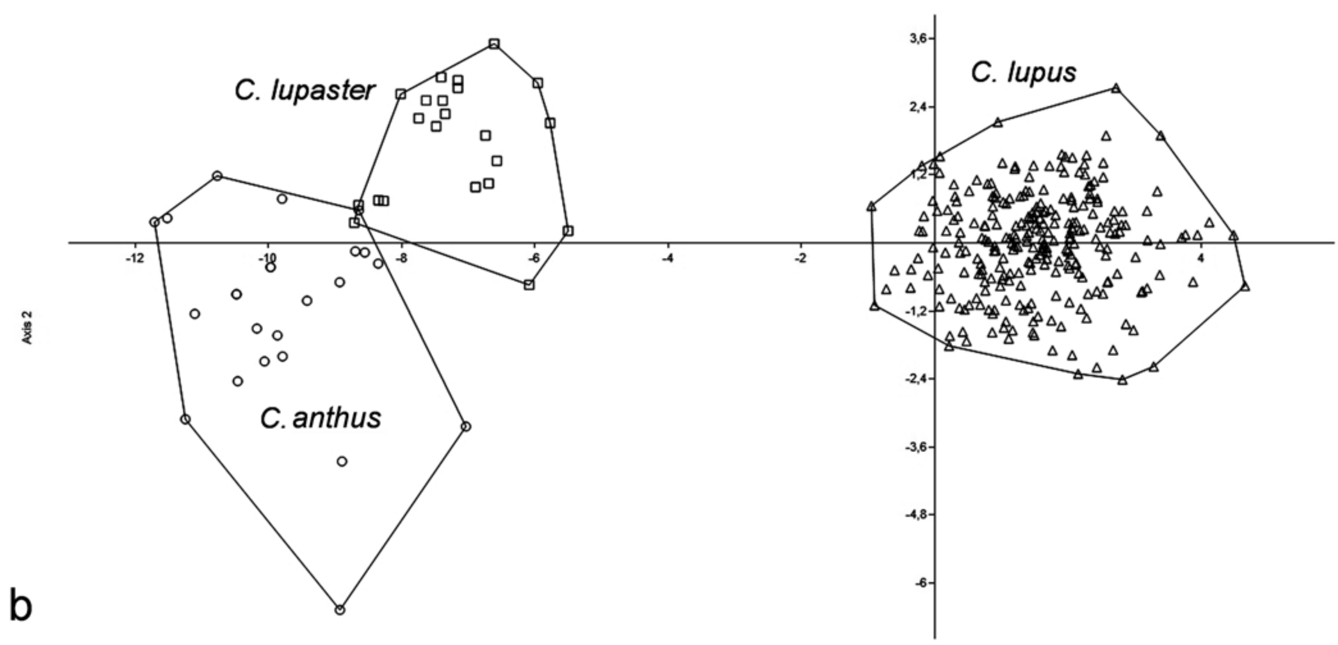


Fig. 4 - Multivariate analysis; triangle) *C. lupus*; square) *C. lupaster*; circle) *C. anthus*; a) PCA on skull and mandible; b) MANOVA on upper and lower teeth.

remarkable. Many studies suggest that the biodiversity of African canids is probably more rich than previously supposed. A correct taxonomy is important to plan conservation actions and help threatened species and this paper would be a little help in order to improve our knowledge.

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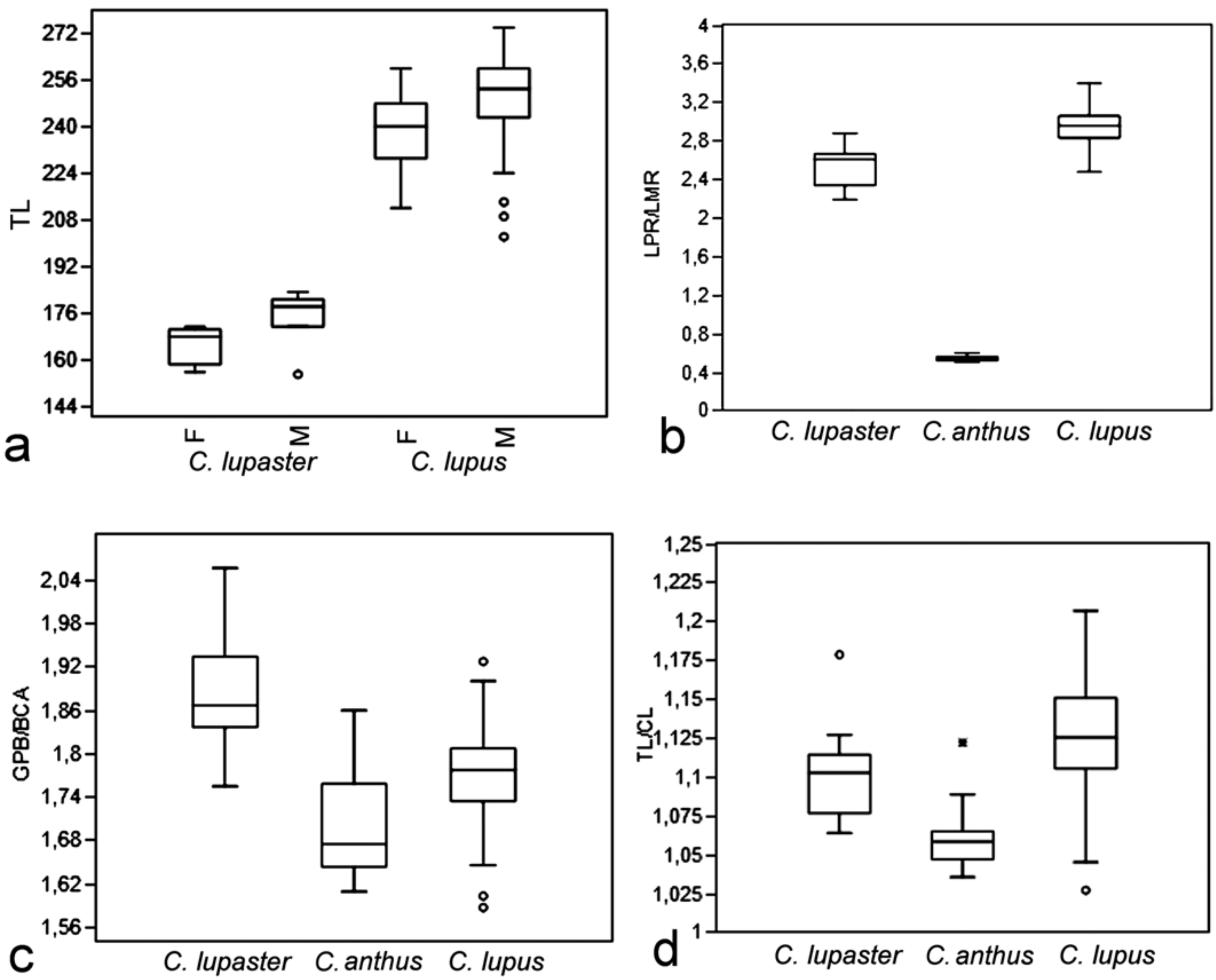

Fig. 5 - Box plots of selected absolute measurements and ratios; a) comparison of total length (TL) of *C. lupaster* and *C. lupus* male and female; b) ratio between length of premolars an length of molars (LPR/LMR); c) ratio between the great palatal breadth and the breadth measured at canine alveoli (GPB/BCA; d) ratio between total length and condilobasal length (TL/CL).

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