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Cranial morphometrics of the Apennine brown bear (*Ursus arctos marsicanus*) and preliminary notes on the relationships with other southern European populations

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Abstract

The geographic variation of seven southern European populations of *Ursus arctos* was investigated through multivariate morphometrics of the skull. Univariate and multivariate analyses were run on 63 cranial and dental measurements recorded on 50 specimens from the Apennines, the Alps, and the Transcaucasus, and on 14 specimens of the fossil *Ursus spelaeus*. Detailed analyses of sexual dimorphism, age structure, and ranges of variation have been carried out on the Apennines population, which morphological variation has been little explored. Subsets of characters were selected to allow comparison with data derived from literature for populations from the Pyrenees, the Rhodopi-Rila-Pirin, the Balkans, and the Caucasus. Analyses clearly indicate that the Apennine bear is morphologically distinct from both a western (Alps, Pyrenees, Balkans, and Rhodopi) and an eastern contingent (Caucasus and Transcaucasus), therefore suggesting that the Apennine population should be reconsidered as a separate taxon, namely *Ursus arctos marsicanus*. These preliminary results suggest caution in restocking conservation actions.

Keywords: Ursus arctos, *Apennine bear, multivariate morphometrics, geographic variation*

Introduction

The brown bear *Ursus arctos* Linné, 1758 is the most widespread species of the family Ursidae occurring across the Holartic. Like other large carnivores, this species still occurs in Europe, but it is forced to live in highly fragmented and human-dominated landscapes. Today, surviving brown bear populations are low in numbers and highly fragmented in southern, central and western Europe. More specifically, the range of western European populations is limited to isolated mountain areas (Cowan 1972; Corbet 1978; Servheen 1990; Soerensen 1991; Kudaktin and Chestin 1993), and the survival of the majority of them is at risk. One important priority in conservation is the release of animals to restock non-viable populations and to favor connections with other populations (Swenson et al. 2000). However, any transfer of individuals should only operate in a clear systematic and genetic framework (Taberlet & Buvet 1994; Felizola Diniz-Filho & Pires De Campos Telles 2002).

The fragmentation of the formal range and the high variability of the brown bear led in fact to the description of many subspecies (see, for example, Miller 1912; Hall 1981; Ellerman & Morrison-Scott 1966, as reported by Pasitschniak-Arts 1993), but in the most recent checklists all subspecies are considered synonyms (see for example Wozencraft 1993). Genetic variation throughout the distribution range of the species has been recently investigated by different authors, mainly through nuclear and mitochondrial DNA sequence comparisons (Goldman et al. 1989; Taberlet & Buvet 1992, 1994; Hartl & Hell 1994; Randi et al. 1994; Kohn et al. 1995; Chestin & Mikeshina 1998). The morphological variation of Central Asian and eastern European populations has been described by Kudaktin and Chestin (1983), Rösler (1984), and by Chestin and Mikeshina (1998), while there is a very little information regarding the western European populations, i.e. Alpine, Apennine, and

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Pyrenean. In fact, the last extensive work was carried out by Couturier (1954).

The Apennine brown bear occurs in a small isolated mountain area of the Italian Central Apennines. It is a critically endangered population and its relationships with the other European populations of *U. arctos* have been a continuous cause of scientific debate. Altobello (1921) described the Apennine brown bear as a distinct subspecies, i.e. *U. a. marsicanus*. But the description was based on few characters examined on one female and two juveniles, and all subsequent authors have since rejected it, or at least considered it as doubtful (Toschi 1965). Only Conti (1954), who examined the skull of one adult male, suggested that the Apennine population should be reconsidered as a distinct taxon. This hypothesis was reinforced through the analysis of a wider sample by one of the authors (Vigna Taglianti et al. 1984; Vigna Taglianti 1988, 2003). Therefore, the aim of this study was to better clarify the morphological relationships of the Apennine bears with the Alpine and other southern European populations through a multivariate morphometric approach.

Materials and methods

A total of 63 measurements were recorded by means of a precision caliper (accurate to the nearest 0.1 mm) on the skull, the teeth and the mandible following Von den Driesch (1976). Details on characters are reported in Figure 1 and Table I. Measurements were recorded on 50 specimens of *U. arctos*, including 35 specimens (15 males, 20 females) from the Apennines, 8 specimens (4 males, 4 females) from the Alps and 7 specimens (4 males, 3 females) from the Transcaucasus. The same measurements were also recorded on 14 specimens of *Ursus spelaeus* Rosenmüller and Heinroth, 1784, from Central Italy (Grotta di Equi, Tuscany), considered as a reference group. Data on another 83 specimens from the Pyrenees ($n=16$), Caucasus ($n=12$); Rhodopi Mountains ($n=26$), and Balkans ($n=29$) were taken from literature (Couturier 1954; Vanev 1990).

Localities, sample sizes and source of materials are reported in Figure 2 and Table II.

Specimens were ascribed to three age classes: adult (over 6 years old, according to Rausch 1963), subadult (2–6 years old) and juvenile (less then 2

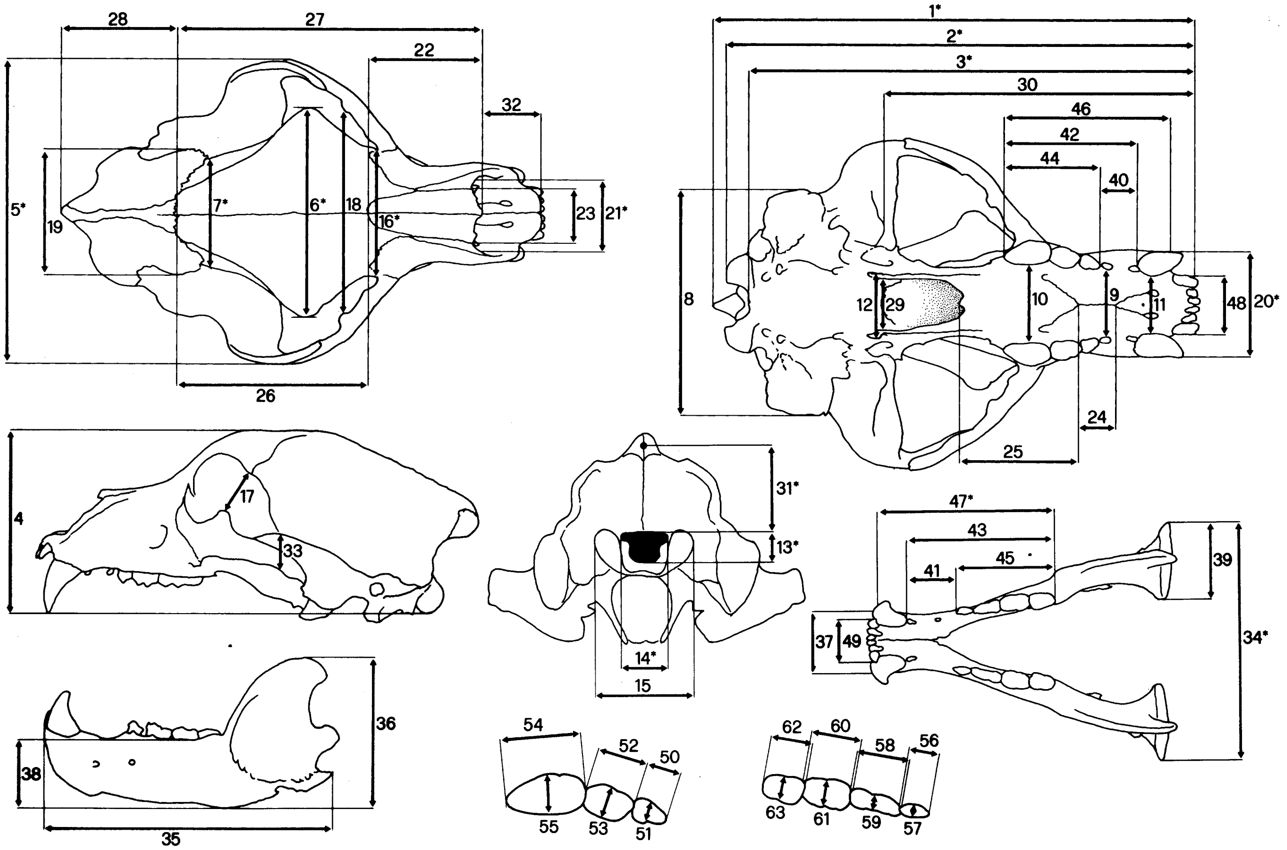

Figure 1. Characters recorded on the skull, the mandible and the teeth of each specimen. See Table I for details.

Table I. Description of the 63 characters measured. Asterisks indicate measurements in common with both Couturier (1954) and Vanev (1990), used for comparisons among all samples. Those in parentheses were exclusively recorded by the authors on the populations from the Alps and the Apennines (see text).

Code	Character description	Code	Character description
1*	Total length of skull	33	Height of zygomatic apophysis at the temporo-molar suture
2*	CB, Condilo basal length	34*	Maximum width of the mandible, recorded between external tips of condyles
3*	Basilar length	35	Length of the mandible
4	Maximum height of skull	36	Max height of the mandible
5*	Bi-zygomatic length	37	Distance between the external margins of canine alveoli of the mandibles
6*	Distance between the ecto-orbitary apophyses	38	Height of the mandible at the level of posterior margin of M$_2$ alveolus
7*	Post-orbitary constriction width, at suture between squamosals	39	Width of the mandible condyle
8	Bi-mastoideal width	40	Length of diastema between superior canine and Pm^4
9	Distance between the internal margins of Pm^4 alveoles	41	Length of diastema between inferior canine and Pm$_4$
10	Width of internal margins of palatine bones, recorded at the M^3 alveoles	42	Distance between posterior edge of superior canine alveolus and posterior edge of M^2 alveole
11	Distance between internal boundaries of superior canines	43	Length of the inferior teeth row, excluding the incisives
12	Maximum distance between pterigoidean apophyses at palato-pterygoideal sutures (recorded along the external boundaries)	44	Distance between the anterior margin of Pm^4 and the posterior margin of M^2
13*	Vertical diameter of foramen occipitalis	45	Distance between the anterior margin of Pm$_4$ and the posterior margin of M$_3$
14*	Transverse diameter of foramen occipitalis	46	Distance between anterior edge of superior canine alveole and posterior edge of M^2 aleveole
15	Maximum distance between external boundaries of occipital codyles	47	Distance between anterior edge of inferior canine and posterior edge of M$_3$
16*	Interorbitary constriction width	48	Length of the superior incisive row (at the coronal level)
17	Distance between free boundaries of superior and inferior post-orbitary apophysis	49	Length of the inferior incisive row (at the coronal level)
18	Distance between inferior post-orbitary apophyses	(50)	Length of Pm^4
19	Maximum width of neurocranium (at the temporo-pariatl sutures)	(51)	Width of Pm^4
20*	Maximum distance between external boundaries of canine alveoles	(52)	Length of M^1
21*	Transverse diameter of nasal fossae	(53)	Width of M^1
22	Maximum length of nasal bones	(54)	Length of M^2
23	Width of anterior margin of nasal bones	(55)	Width of M^2
24	Length of the intermaxillar suture	(56)	Length of Pm$_4$
25	Length of interpalatine suture	(57)	Width of Pm$_4$
26	Length of interfrontal suture	(58)	Length of M$_1$
27	Distance between the anterior tip of nasal suture and the posterior tip of frontal suture	(59)	Width of M$_1$
28	Distance from the fronto-parietal suture and the superior tip of occipital	(60)	Length of M$_2$
29	Width of the sphenoidal fossa at palatal–pterigoidean suture	(61)	Width of M$_2$
30	Distance between the margin of the incisives row and the edge of the temporal condyle	(62)	Length of M$_3$
31*	Distance between external protuberance of occipital and superior edge of foramen occipitalis	(63)	Width of M$_3$
32	Length of nasal fossa		

years old), following the indications reported on the collection labels.

A square scatter matrix of all measurements was first produced using the STATISTICA program (StatSoft, Inc., version 6.0, 1984–2001) in order to detect measurement errors and misclassifications of sex and age rapidly. Univariate and multivariate analyses of variance were run on the Apennine data set to evaluate the influence of age and sex on morphological variation. Principal component scores were evaluated to detect any size factor and to correct the data following the method described by

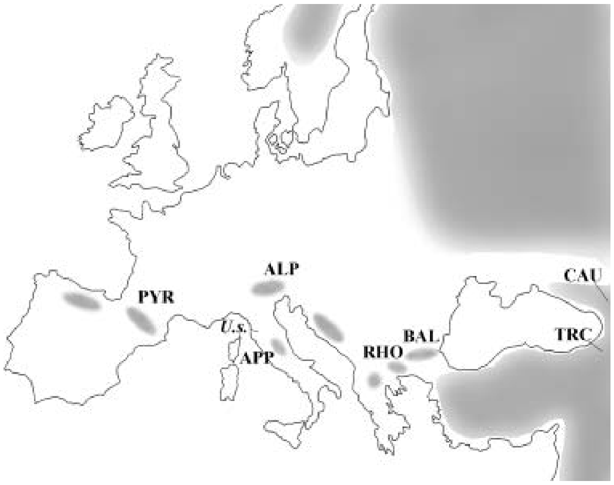

Figure 2. Samples location superimposed to the distribution of *Ursus arctos* in Europe. ALP: Alps; APP: Apennines; BAL: Balkans; CAU: Caucasus; PYR: Pyrenees; RHO: Rhodopi, Rila, and Pyrin Mts; TRC: Transcaucasus; U.s.: *Ursus spelaeus* from Grotta degli Equi (Tuscany, Italy). See Table II for details.

Burnaby (1966, as discussed in Rohlf & Bookstein 1988), Thorpe (1983), and Marcus (1990). A multivariate canonical analysis was performed on the 'size-independent' matrix for comparisons among the western European samples, i.e. from the Alps, the Apennines and the Pyrenees. Pairwise comparisons through the Tukey LSD test were performed for characters showing the largest differences among groups. A geometric morphometric data set (Bookstein 1991; Rohlf & Marcus 1993) was then created to visualize the main shape differences between the Apennine and the Alpine skulls. Cartesian coordinates of 31 landmarks were recorded on the dorsal projection of the digital image of an adult male from the Alps and and adult male from the Apennines, by using the program tpsDig (Rohlf 2002b). Coordinates were then translated, rotated, scaled to unit centroid size and superimposed through the General Procustes Analysis (Rohlf & Slice 1990), by using the program tpsSuper (Rohlf 2002b). A thin plate spline deformation grid was produced with the same program in order to visualize the differences in shape between the two skulls.

Finally, a subset of 13 common characters (see Table I) was selected for comparison with data reported from literature on other mountain populations from southern Europe, i.e. Balkans, Rila-Rhodopi, and Caucasus (Vanev 1990).

Analyses were performed only considering the adult males. Mahalanobis distances resulting from canonical variate analysis run on all extant samples and the fossil *U. spelaeus* were used to produce a UPGMA dendrogram of relationships among populations (Sneath & Sokal 2001), using the NTSYS program (Rohlf 2002a).

Results

Variation of the Apennine population

MANOVA for the whole set of characters computed on adult specimens shows significant differences between the two sexes (Wilks' Lambda $F=320.8$, $P=0.043$). The univariate analyses reveals that

Table II. List of samples.

Species	Population	Code	Source of material	Males	Female	Total
U. arctos	Alps (Italy)	ALP	Museo Storia Naturale della Venezia Tridentina and Museo Civico di Storia Naturale 'G. Doria', Genova	4	4	8
U. arctos	Apennines (Italy)	APP	Centro Studi Ecologici Appenninici—Parco Nazionale d'Abruzzo	15	20	35
U. arctos	Transcaucasus (Russia, Georgia, Armenia, Azerbaidjan, Siria, Iran)	TRC	Museum of Zoology of the University of Amsterdam and Muséum d'Histoire Naturelle de Paris	4	3	7
Ursus spelaeus	Tuscany (Italy)	*U.s.*	Museo di Geologia e Paleontologia Università di Firenze	10	4	14
			Total	43	31	64
Data derived from literature						
U. arctos	Pyrenees (Spain)	PYR	Couturier (1954)	8	8	16
U. arctos	Balkans (Bulgary)	BAL	Vanev (1990)	20	9	29
U. arctos	Rhodopi-Rila-Pirin Mts (Bulgary)	RHO	Vanev (1990)	17	9	26
U. arctos	Caucasus (Russia)	CAU	Vanev (1990)	10	2	12
			Total	55	28	83

males are significantly larger than females in 41 out of the 63 measurements considered (F statistics always significant at $P<0.05$). The only exception were the dental features (characters 50–63), among which only the length of M^1 was found to be significantly larger in males (variable 52: $F=6.5$, $P=0.020$). The scatter plot of the first and second principal component scores (Figure 3) shows that males and females are clearly distinct along the first principal component axis (61.87% variance explained), whose coefficients are all of the same sign and magnitude, confirming that size is the main factor affecting sexual dimorphism. As a matter of fact, significance of canonical variate analysis between sexes is lost when PC1 scores are excluded ($F=0.334$, $P<0.93$, vs. $F=5.348$, $P<0.002$ when PC1 is included). It is worth noting that the same results were obtained for the Alpine and the Pyrenean samples, thus allowing the pooling of males and females in successive ‘size-independent’ comparisons between the western European samples.

Multivariate analysis of variance run separately for males and females did not show any significant difference between age classes (Wilks’ Lambda $F_{\text{FEMALES}}=7.34$, $P=0.126$; $F_{\text{MALES}}=7.34$, $P=0.126$). Nevertheless, univariate analyses run separately for each variable for the female sample, including 5 juveniles, 3 sub adults, and 12 adults revealed that 7 characters differ significantly among age classes. These characters include the transverse diameter of nasal fossae (variable 21, $F=5.36$, $P=0.046$), the distance between the margin of the incisive row and the inferior boundary of the temporal condyle (variable 30, $F=5.63$, $P=0.021$), the length of the diastema between canines and premolars (variables 40 and 41, $F=7.16$, $P=0.006$, and $F=6.55$, $P=0.011$, respectively) and the distance between the the inferior canine and M_3 (variable 47, $F=4.40$, $P=0.037$). Variation of these most significant characters is directly related to age, with mean values always increasing from juveniles to adults (Multiple $R=0.571$, $P=0.032$). Figure 4 shows variation of the two most correlated variables (variables 21 and 30, $r=0.868$) for the three age classes in males and females.

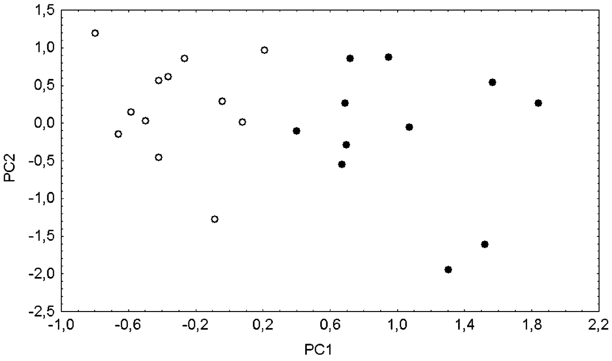

Figure 3. Scatter plot of the first two principal component scores computed on the adult specimens of the Apennine sample; open circles=males; filled circles=females.

Relationships among the western European populations

Figure 5 shows the scatter plot of the first and the second canonical variate scores (79.9% and 20% of total variance explained, respectively) for the samples from the Alps, the Apennines and the Pyrenees (for which data are derived from Couturier 1954), obtained from the pooled (males and females) ‘size-independent’ matrix of $(n-1)$ principal component scores. The three populations are well differentiated (Wilks’ Lambda $F=15.183$, $P<0.0001$), with the Alpine and the Pyrenean populations partially overlapping along the first canonical axis. Results from MANOVA run on all characters to evaluate the effect of sample locality on morphological variation indicate that the differences among the western European populations are mainly related to the variation of the orbital region (variables 6, 7, 16, 17, 18 and 24), the occipital bones (variables 14 and 15) and the mandible (variable 36). The dental features which show significant differences between the Alpine and the Apennine bears (these data are not available for the Pyrenean sample) include the diastema between the upper and lower canines and Pm, (variables 40 and 41), and the size of Pm^4 (variables 50 and 51). More specifically, the characters most relevant to the separation of the Apennine population from the Alps-Pyrenees cluster

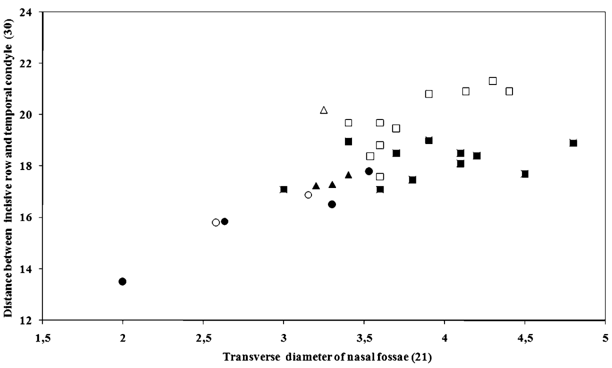

Figure 4. Scatter plot of characters 21 (transverse diameter of nasal fossae) and 30 (distance between the margin of the incisive row and the edge of the temporal condyle) for the Apennine sample. Males and females are shown as open and filled symbols, respectively; circles=juveniles; triangles=sub adults; squares= adults.

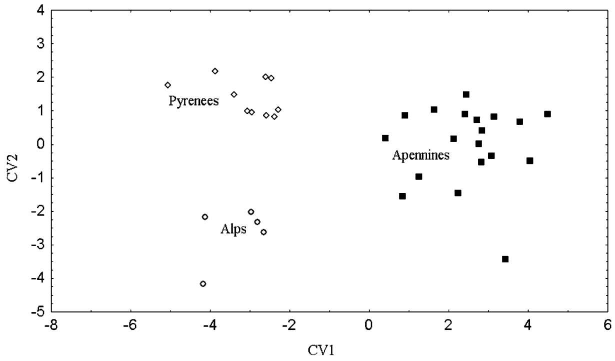

Figure 5. Scatter plot of the first and the second canonical variate scores for the three Western European populations, i.e Alps, Pyrenees, and Apennines, derived from the 'size-independent' matrix (see text).

are the ecto-orbital apophyses (variable 6), the post-orbitary constriction width (variable 7), and the ecto-orbital constriction (variable 16). The large Pm^4 is also typical. The variation ranges of these most diagnostic characters in males and females of Appennine bears are reported in Table III. The Apennine bears are characterized by a greater distance between the ecto-orbital apophyses and by larger ecto-orbital and post-orbital constrictions (variables 7 and 16). Furthermore the PM^4 (variables 50 and 51) is much larger in the Apennine than in the Alpine bears (data on the dental features are lacking for the Pyrenean population). Differences in shape between the Alpine and Apennine skulls are summarized and visualized through the deformation grid in Figure 6. The deformation grid confirms that the main shape differences are located in the middle region of the skull, with an expansion of the ecto-orbital and the postorbital apophyses in the Apennine bear along with a slight shortening of the rostrum and a minor narrowing and elongation of the occipital area.

Relationships between western and eastern populations

As sexual dimorphism in the eastern populations revealed to be not only determined by a size factor, pooling of sexes through the exclusion of the first principal component scores was not possible. Therefore multivariate comparisons among the western and eastern populations were performed on the adult males only. Mahalanobis distances and *F* statistics computed from canonical variate scores on the subset of 13 variables common to both the eastern and the western samples (see Table I) indicate that the Apennine population is significantly different from all other European populations, while the Alpine do not differ significantly from any other than the Apennine bears (Table IV). Relationships among all extant populations are summarized in the UPGMA dendrogram shown in Figure 7. The dendrogram was derived from Mahalanobis distances on a sample including the fossil *U. spelaeus* as the reference group. The phenogram confirms the isolation of the Apennine bears, while the other European samples are grouped into two major clusters. One cluster comprises all the central southern European samples, i.e. the Alps, Pyrenees, Rhodopi, and Balkans, while the second includes the eastern populations from the Caucasus and Transcaucasus. This eastern contigent is mostly differentiated along the second canonical axis, whose coefficients vector indicate a relevant influence of the width of the rostrum (var 20 – distance between canine alveoles), and the height of the occipital region (var 31 – distance between the external protuberance of the occipital and superior edge of

Table III. Mean, standard deviation, maximum and minimum values, of the most diagnostic characters of the Apennine bears. Data are reported for males (M, $n=12$) and females (F, $n=12$) separately. Character codes are those reported in Table II and Figure 2.

Character	Sex	Mean (cm)	Minimum (cm)	Maximum (cm)	DS
6	M	13.18	11.40	15.50	1.22
	F	10.77	10.20	11.90	0.53
7	M	7.14	6.46	7.60	0.33
	F	6.97	6.70	7.30	0.18
16	M	8.30	7.54	9.10	0.52
	F	7.25	6.60	7.80	0.34
40	M	2.32	1.20	2.90	0.44
	F	2.51	1.90	3.40	0.40
41	M	3.27	2.70	4.00	0.49
	F	3.14	2.77	4.15	0.41
50	M	1.30	1.22	1.37	0.05
	F	1.23	1.10	1.40	0.11
51	M	1.01	0.90	1.07	0.06
	F	0.89	0.80	0.95	0.05

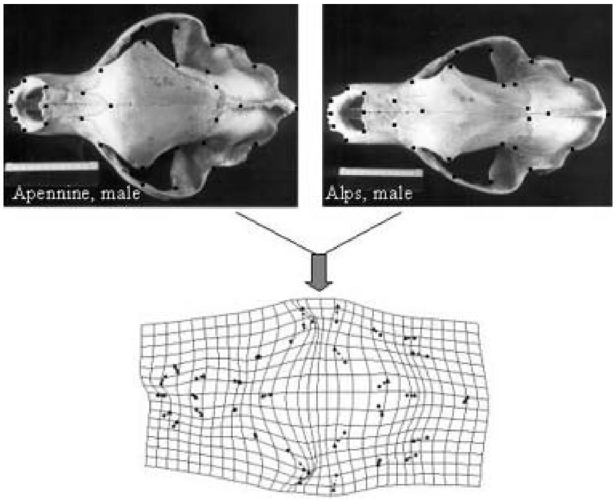

Figure 6. Above: pictures of the dorsal skull of an Alpine (left) and Apennine (right) adult male with landmarks (black dots) used to produce the aligned configurations for a geometric superimposition through GPA (Rohlf & Slice, 1990). Below: thin plate spline deformation grid derived from the superimposition of the two configurations through tpsSplin (Rohlf 2002). Regions of deformations indicate the main shape differences between the two skulls.

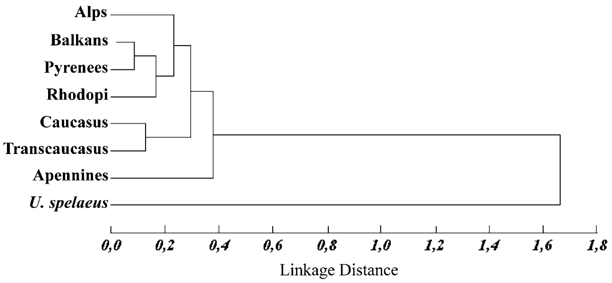

Figure 7. UPGMA dendrogram derived from Mahalanobis distances on canonical variate scores of all samples, including *Ursus spalaeus* as the reference group.

the foramen occipitalis). More specifically, the skull of the eastern European bears shows a slender rostrum and a higher occipital region compared to the western European bears.

Discussion

This first morphometric comparison among seven southern European populations of *Ursus arctos* suggests a closer relationship between the eastern European bears from Caucasus and Transcaucasus compared to a western European contingent, including the bears from the Alps, the Pyrenees, the Balkans and the Rhodopi-Rila mountains. The populations included in this latter cluster show a small degree of morphological divergence, which do not support any separation at subspecific level.

Among the western European bears, size represents an important aspect of non-geographic variation, and it appears to be an important factor in both sexual dimorphism and age growth. By contrast, the eastern bears show more integrated size and shape patterns related to age and sexual dimorphism. These differences could reflect a deviation in allometric patterns which are likely to be due to an early isolation of the western from the eastern European stocks. However, allometric growth patterns need to be further investigated to elucidate the relationships among and within these groups. Furthermore, the eastern European bears show some peculiarities in cranial shape, such as a slender rostrum and a higher occipital region. But the high variability found in the brown bears from the Caucasus by Chestin and Mikeshina (1998) suggests caution in any inference regarding the morphological differentiation in the cranial features of a western and an eastern European cluster. In fact, future studies should be carried out on a much wider sample.

The Italian population from the Apennines represents the only highly diverging population, as it is morphometrically isolated when compared to both the western and the eastern contingent, including the Italian population from the Alps. Interestingly, the morphometric differentiation of the Apennine bears is mainly related to differences in the shape of the skull which cannot be considered as a simple variation in size.

Table IV. Mahalanobis distances (below diagonal), and F statistics (above diagonal) computed on canonical variate scores on the seven populations analyzed. *=$P<0.01$; **=$P<0.001$; ***=$P<0.0001$. For populations codes see Table I.

	ALP	BAL	CAU	APP	PYR	RHO	TRC
ALP	–	1.27	2.34	2.93*	1.19	1.50	1.90
BAL	12.47	–	3.29**	5.81***	3.38**	3.89**	2.28
CAU	25.21	9.65	–	6.30***	3.05*	3.58**	1.64
APP	30.47	14.96	22.36	–	4.85***	9.17***	3.82**
PYR	13.50	11.80	13.63	19.94	–	2.61*	1.80
RHO	15.08	8.678	11.48	26.16	9.82	–	27.9**
TRC	27.81	15.60	12.87	28.53	15.12	27.95	–

The uniqueness of the Apennine bears has already been noticed by Altobello (1921), who suggested considering it a separate subspecies, namely *U. arctos marsicanus*. Our results clearly indicate that the Apennine population represents a differentiated taxon, characterized by a unique and characteristic skull among the European brown bears. The diagnostic features of this subspecies include the expansion of the ecto-orbital apophyses, the narrow postorbital constriction, the short rostrum, and the short diastema between canines and molars. The large Pm^4 is also typical. Recent analyses of mtDNA variation have revealed a common origin of all the western European populations of *U. arctos*, including the Apennine bears (Randi et al. 1994; Taberlet & Buvet 1994). We suggest that despite this common origin, the Apennine brown bear underwent a strong morphological divergence, which was possibly due to an early isolation of a small population, or as a consequence of a bottleneck. An absence of gene flow with the neighboring populations from the Alps and genetic drive may have played a role in this rapid morphological divergence, which was probably amplified by adaptations to local conditions. As a consequence we suggest that the subspecies *U. a. marsicanus* should be revalued following Altobello (1921), Conti (1954), and Vigna Taglianti (2003).

The reconsideration and acceptance of the Appennine population as a distinct taxon will have a strong effect on any action to be undertaken for the conservation of the species in Italy. As was also recently stressed by Randi (2003), there should be distinct conservation management for the Alpine and Apennine brown bear populations, and the Apennine brown bears should be managed as an Evolutionary Significant Unit (ESU, Conner & Hartl 2004).

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