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Une nouvelle sous-espèce de loup (*Canis lupus maximus* nov. subsp.) dans le Pléistocène supérieur d'Europe occidentale

*A new subspecies of wolf (*Canis lupus maximus *nov. subsp.) from the upper Pleistocene of Western Europe*

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RÉSUMÉ

L'histoire évolutive de la lignée menant aux loups actuels (*Canis lupus sensu largo*) est caractérisée par des changements dans la taille corporelle des individus. Ces modifications avaient contribué à la reconnaissance d'un chronocline utilisé en biochronologie, mais dont la résolution chronologique demeurait imprécise. De nouvelles analyses morphométriques conduites sur les restes d'individus pléistocènes du Sud de la France, ont abouti à la définition d'une nouvelle sous-espèce de loup, *Canis lupus maximus* nov. subsp. présente en Europe occidentale à la fin du Pléistocène supérieur. Cette nouvelle sous-espèce se caractérise par des individus de stature nettement plus imposante que celle de l'ensemble des individus fossiles et actuels. La diagnose est fondée sur les données biométriques recueillies sur les restes de loups de la grotte de Jaurens (Nespouls, Corrèze). Une discussion d'ordre paléoenvironnemental concernant la dispersion de cette sous-espèce est également proposée.

Keywords:
Evolution
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Quaternary
Canis lupus
Body size
Morphometry

ABSTRACT

The evolutionary history of the extant wolf (*Canis lupus sensu largo*) and its ancestors is characterised by changes in body size. A chronocline has been established based on these changes, but its temporal resolution is poorly defined. New morphometric analyses conducted on Late Pleistocene remains from southern France have permitted the diagnosis of a new subspecies of wolf, *Canis lupus maximus* nov. subsp. This new subspecies is statistically larger than all other known fossil and extant wolves from Western Europe. The diagnosis is based on biometric data collected on wolf remains from Jaurens cave (Nespouls, Corrèze, France). The paleoenvironmental context of the biogeographic range of this subspecies is discussed.

Abridged English version

Introduction

The lineage leading to extant Eurasian wolves (*Canis lupus sensu largo*) expanded in Western Europe during

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the second half of the Middle Pleistocene. The earliest occurrence of this species comes from Lunel-Viel (Hérault, France). Based on *Canis* remains from this site, Bonifay (1971) described a subspecies (*Canis lupus lunellensis*) very similar to extant wolves but with a significantly smaller body size (Bonifay, 1971; Boudadi-Maligne, 2010). Studies of the evolution of the lineage have shown that wolf body size has followed a steady increase from their first appearance up to the so-called "Würm maximum" (Argant, 1991; Bonifay, 1971; Brugal, 1981; Cardoso, 1993; Hadjouis, 1982; Patou, 1984; Suire, 1969; Valensi, 1994). Although the maximum growth phase is not clearly defined, this trend has aroused great interest in research on biochronology.

Materials and methods

In order to give a more detailed analysis of this evolutionary trend, the results of biometric analysis based on the remains of over 200 wolves covering a time period from the second half of the Middle Pleistocene (from eight sites) to the present are given in Table 1. The fossil series was chosen to limit the chronological gaps in the Pleistocene period and according to the number of *Canis* remains. Smaller series, on which statistical analyses are limited, were excluded from our study. Extant wild wolves from Portugal and Bulgaria, mature (*sensu* Buchalczyk and Okarma, 1993) and of known sex, were used as a reference group. They express the current variability of western European populations. All skeletal and dental parts were described and measured. Data collected on extant populations of known size and gender were analyzed to establish correlations between biometric data and size (meaning body mass and total body length). To analyze the biometric data, statistical analyses (using PAST v.1.57© 2006 Hammer & Harper and Gilles Escarguel SIST v.1.0© 2008) were performed. In addition to the classical statistical tests, a modified index of variability (VSI* index) was used. This index takes into account not only the standard deviation of the reference population but overlap between the two groups analyzed (Escarguel, 2008). These analyses allow us to determine whether or not populations could be differentiated and, if so, which data could explain these distinctions.

Systematic paleontology

Order CARNIVORA Bowdich, 1821
Family CANIDAE Fischer, 1817
Genus *Canis* Linnaeus, 1758
Species *Canis lupus* Linnaeus, 1758
Canis lupus maximus nov. subsp.

Type locality: Jaurens cave, Nespouls, Corrèze, France.

Holotype: FSL 300422 (Fig. 2-A); skull of an old male, housed in the collection of the University Claude-Bernard in Lyon. This skull was discovered during excavations led by C. Guérin between 1968 and 1972.

Paratypes: Maxillae (FSL 300423, Fig. 2-B; FSL 300424; FSL 300426; FSL 300427; FSL 300428); incisive bone (FSL 300425); mandibles (FSL 300443; FSL 300444, Fig. 2-C; FSL 300445, Fig. 2-D; FSL 300451; FSL 300453; FSL 300454; FSL 300455; FSL 300458); atlas (FSL 300476); humerus (FSL 300482); radius (FSL 300484; FSL 300485); femur (FSL 455811, Fig. 2-E); tibia (FSL 300510; FSL 455812); calcaneus (FSL 300511); talus (FSL 300515) housed in the collection of the University Claude-Bernard in Lyon.

Diagnosis: All skeletal elements are characterized by size that is statistically larger than all other known wolves (Tables 2 and 3). The dimensions of the long bones are about 10% larger in Jaurens than in extant European populations and 12% larger than in *Canis lupus santenaisiensis*. The same conclusions apply to the short bones. For example, the third metacarpal and the calcaneus are on average 7% larger in wolves from Jaurens cave than extant wolves and *C.l. santenaisiensis*. Compared to *C.l. lunellensis*, the bones of the Jaurens wolves are, on average, 20% longer. Similarly, the mesiodistal diameter of the lower carnassial is

Tableau 1
Liste des gisements fossiles et populations actuelles étudiés. Sont figurés les lieux de conservation des collections (MNP : Muséum National de Préhistoire, les Eyzies ; LAMPEA, Aix-en-Provence ; MNHL : Muséum d'Histoire naturelle de Lyon ; MPO : Musée de Préhistoire d'Orgnac ; UCBL : université Claude-Bernard, Lyon ; PACEA : laboratoire de Préhistoire de l'université Bordeaux 1 ; MHNG : Muséum d'Histoire naturelle de Genève ; IPA : Institut portugais d'archéologie ; MNHNS : Muséum National d'Histoire naturelle de Sofia, Bulgarie), l'âge des dépôts analysés, le nombre minimum de loups analysés (NMI) et le nombre de restes (NR) étudiés.

Table 1 Fossil sites and modern populations studied. Places where studied collections are stored are also mentioned (MNP: National Prehistory Museum; LAMPEA, Aix-en-Provence; MNHL: Natural History Museum Lyon; MPO: Prehistory Museum of Orgnac; UCBL: Claude-Bernard University, Lyon; PACEA: Prehistory laboratory from Bordeaux 1 University; MHNG: Natural History Museum of Geneva; IPA: Portuguese Archaeological Institute; MNHNS: National Natural History Museum of Sofia, Bulgaria). Chronological range, minimal number of individuals (NMI) and number of studied remains (NR) are specified.

Période	Site, département	Conservation	Chronologie (BP)	NMI	NR
Pléistocène moyen	Lunel-Viel I, Hérault	MNP	~400–350 ka	18	218
	Igue des Rameaux, Tarn-et-Garonne	LAMPEA	OIS 10–11	74	1025
	Aven I La Fage, Corrèze	MHNL	OIS 7 (185–245 ka)	7	202
	Coudoulous I, Lot	LAMPEA	OIS 7 (185–245 ka)	13	623
Pléistocène supérieur	Aven de l'Arquet, Ardèche	MPO	OIS 3 (40 ka)	24	917
	Jaurens, Corrèze	UCBL	OIS 3 (31 ka)	11	151
	Maldidier, Dordogne	PACEA	OIS 3 (29 ka)	3	156
	Igue du Gral, Lot	MHNG	OIS 2 (19 ka)	8	602
Holocène					
Canis lupus signatus	Portugal	IPA		20	–
Canis lupus lupus	Bulgarie	MNHNS		40	–