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THE *PANTHERA GOMBASZOGENSIS* STORY: THE CONTRIBUTION OF THE CHÂTEAU BRECCIA (SAÔNE-ET-LOIRE, BURGUNDY, FRANCE)



Alain ARGANT¹ & Jacqueline ARGANT¹

ABSTRACT

At present, numerous sites from Europe and Asia have yielded up remains of *Panthera gombaszogensis*. It is without doubt the one Felid most similar to *Panthera onca* but it is an ancestor, not the present day jaguar. Palaeogenetics estimates the divergence between the lion and the jaguar to 2 Myrs. Obviously, jaguars originate from Africa and they spread in Europe between 1.95 et 1.77 Myrs during the time of Olduvai polarity subchron. Recently Hemmer *et al.* (2010) demonstrated that the semi-mandible of Dmanissi (Georgia) corresponds with a new taxon *Panthera onca georgica ssp. nov.*, the earliest known Asian member of the species. This taxon spread out through Asia and got to North America during a glacial period between 0.99 and 0.78 Myrs (between the Jaramillo polarity subchron and the end of the Matuyama magnetochron), and finally reached South America not before the Rancho-labrean. The Château Breccia (Saône-et-Loire, France) has given an abundant paleontological material of *Panthera gombaszogensis* (about 400 remains, with a minimum of 6 individuals). It is the mid Middle Pleistocene European form. The pollen analysis indicates temperate climatic conditions but cooler than today and sometimes even quite cold. The landscape was open with grasses spread over the uplands, while woodlands of pine and fir, but also some broadleaved trees were found in the valley. The Château Breccia largely contributes to the story of *Panthera gombaszogensis*. It demonstrates that the species was at least adapted to a cold temperate climate and to a biotope highly different from that of the today's jaguar. It shows also the replacement of *Panthera gombaszogensis* by *Panthera spelaea fossilis* about 0.6 Myrs ago, after a period of coexistence of these two Felids.

Key-words: Felids, *Panthera gombaszogensis*, Pleistocene, Château Breccia, palaeoenvironment.

RÉSUMÉ

L'HISTOIRE DE *PANTHERA GOMBASZOGENSIS* : CONTRIBUTION DE LA BRÈCHE DE CHÂTEAU (SAÔNE-ET-LOIRE, BOURGOGNE, FRANCE)

De nombreux sites d'Europe et d'Asie ont livré des restes de *Panthera gombaszogensis*. C'est sans doute le Félinid le plus proche de *Panthera onca*, mais il s'agit d'un ancêtre, distinct du jaguar actuel. La divergence entre le lion et le jaguar est estimée par la paléogénétique à 2 Ma. Les jaguars sont clairement originaires d'Afrique et se sont répandus en Europe entre 1,95 et 1,77 Ma, pendant le subchron Oldowai. Récemment, Hemmer *et al.* (2010) ont prouvé que l'hémi-mandibule de Dmanissi (Géorgie) correspond à un nouveau taxon *Panthera onca georgica ssp. nov.*, le premier membre de cette espèce connu en Asie, à l'origine de la dispersion dans tout ce continent, puis du passage en Amérique du nord pendant une période glaciaire entre 0,99 et 0,78 Ma (entre le subchron Jaramillo et la fin du magnétochron Matuyama), sans atteindre l'Amérique du sud avant le Rancho-labréen. La Brèche de Château (Saône-et-Loire, France) a livré un abondant matériel paléontologique de *Panthera gombaszogensis* (environ 400 restes, minimum de 6 individus). C'est la forme européenne du Pléistocène moyen médian. L'analyse pollinique indique des conditions climatiques tempérées mais plus fraîches qu'aujourd'hui et parfois même froides. Le paysage était ouvert avec des herbacées sur les hauteurs, tandis qu'un boisement de pins et sapins, mais aussi de quelques feuillus, occupait la vallée. La Brèche de Château contribue largement à l'histoire de *Panthera gombaszogensis*. Elle apporte la preuve de l'adaptabilité de l'espèce à un climat tempéré froid et son adaptation à un biotope bien différent de la ripisylve de grands cours d'eau qu'on connaît pour le jaguar actuel. Le gisement enregistre également le remplacement, vers 0.6 Ma, de *Panthera gombaszogensis* par *Panthera spelaea fossilis*, après une période de coexistence de ces deux grands félins.

Mots-clés : Félinidés, *Panthera gombaszogensis*, Pléistocène, Brèche de Château, paléoenvironnement.

PREFACE

In relation to spelling, we will respect J. Wagner's clarification (this volume) recommending *Panthera gombaszogensis*.

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1 - INTRODUCTION

The story of *Panthera gombaszogensis* began to become clear in 1971, mainly because of the work of H. Hemmer (i.e. Hemmer & Schütt 1969; Hemmer, 1971, 1972; Hemmer *et al.*, 2003; Hemmer *et al.*, 2001, 2010). The European jaguar has always stirred the imagination of researchers because it has not often been encountered in palaeontological deposits, and because *Panthera onca*, its present-day descendant, lives only in the essentially tropical environments of Central and South America. The Château Breccia, which we have been excavating with teams of diggers since its rediscovery in 1968, is particularly rich in large Felidae: firstly *Panthera gombaszogensis* then *Panthera spelaea fossilis* which replaced it after a period of coexistence (Argant *et al.*, 2007). The European jaguar has been much less unobtrusive here than in other deposits. Indeed, the Château Breccia has been an abundant source of jaguar remains (about 400 items from at least 6 individuals including a “complete” skeleton). In addition, palynological studies have clarified contemporary palaeoenvironmental conditions. The Château Breccia has thus made an important contribution to our knowledge of the evolution of this species.

2 - HISTORY OF THE SPECIES:

The first reference to the species occurred in 1938 when Kretzoi created the species *Leo gombaszogensis* based on isolated teeth from the Gombasek deposit in Slovakia (fig.1). In France, jaguars were first discovered in the Escale cave (Saint-Estève-Janson, Bouches-du-

Rhône), where four individuals were found. M.F Bonifay created a new species she called *Jansofelis vaufreyi* (Bonifay, 1971). H. Hemmer (1972) showed that *Jansofelis vaufreyi* was synonymous with *Panthera gombaszogensis* (Kretzoi, 1938) and distinguished two subspecies *P. gombaszogensis toscana* and *P. gombaszogensis gombaszogensis*. Fossils excavated from 1968 onwards at the Château Breccia, which is the second jaguar-bearing site discovered in France, are attributed to *Panthera gombaszogensis* (Argant, 1980, 1991). Up until today, remains of *Panthera gombaszogensis* have been found in about 50 Eurasian sites (fig. 2).

The origin of jaguars is African and is related to a subspecies of *Panthera* of the Villafranchian period around 1.9 Myr in South Africa: Kromdraai (Barry, 1987). Populations spread across Europe between 1.95 and 1.77 Myr during the time of the Olduvai polarity subchron. Early

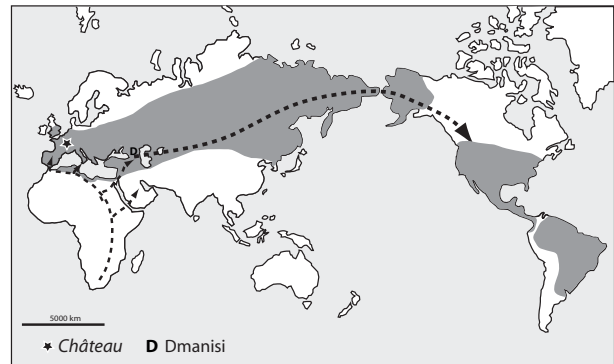


Fig. 2: *Panthera gombaszogensis*, world distribution and possible dispersal routes.

Fig. 2: *Panthera gombaszogensis*, répartition dans le monde et voies de dispersion possibles.

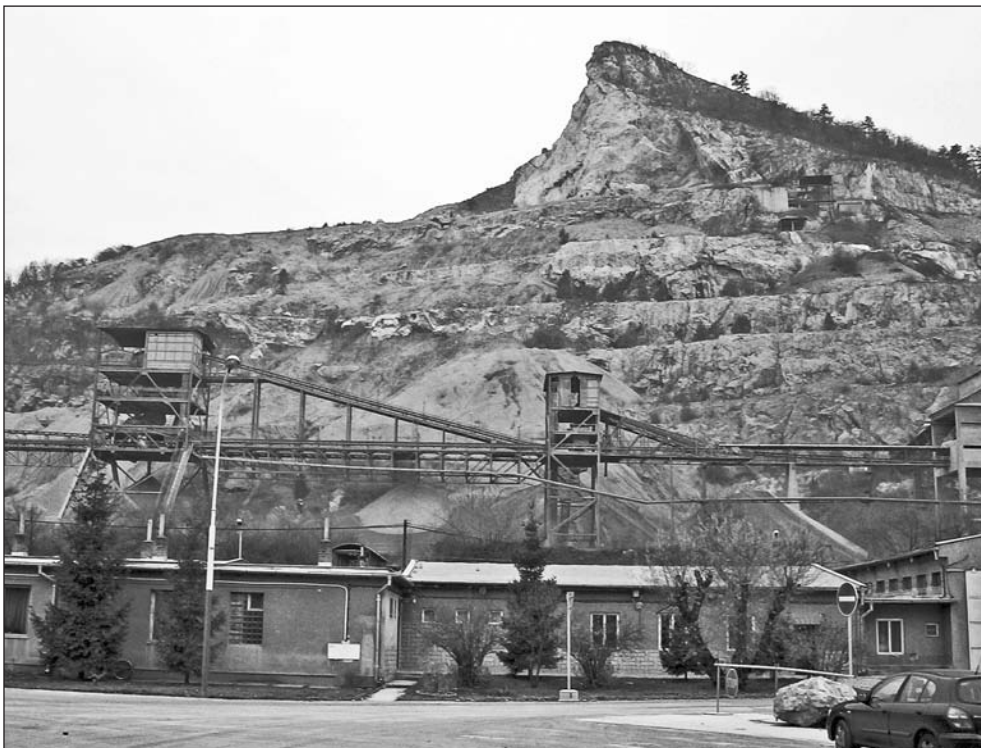


Fig.1: The quarry of Gombasek (Slovakia).

Fig.1 : La carrière de Gombasek (Slovaquie).

Pleistocene European jaguars were first considered as independent species, *P. toscana* (Schaub, 1949) from Italy and *P. schreuderi* (Koenigswald, 1960) from the Netherlands. Later on, they were considered to be conspecific with the final Early Pleistocene to early Middle Pleistocene European taxon *Panthera gombaszogensis* (Kretzoi, 1938) and to represent jaguars (Hemmer, 1971).

Recently, H. Hemmer (Hemmer *et al.*, 2010) has shown that the semi-mandible from Dmanissi (Georgia), dated to about 1.77 Myr, belongs to the new taxon *Panthera onca georgica* ssp. nov., the earliest known Asian member of the species. Transcontinental dispersal probably brought the jaguar to North America during a glacial period between 0.99 and 0.78 Myr (between the Jaramillo polarity subchron and the end of the Matuyama magneto-chron), to finally reach South America not before the Rancholabrean. The lineage connecting *P. onca toscana* via *P. onca georgica* with *P. onca augusta* reflects quite well the geographic distribution of the earliest jaguar palaeopopulations from Europe via western Asia to North America (fig. 3 and 4).

3 - TAXONOMY

Panthera gombaszogensis is without doubt the Felid most similar to *Panthera onca* (Linné, 1758), the present day jaguar. As is often the case, the taxonomic nomenclature has varied over the course of time according to the different ideas of the authors. All are valid so long as the synonymies have been made clear. However it seems to us that the nomenclature *Panthera onca* quite often used following the work of H. Hemmer (2001) should be avoided. *Panthera gombaszogensis* (the palaeontological species) corresponds to the ancestral form of the jaguar, but is not the same as the present-day jaguar (the biological species). When we examine sufficient material, particularly post-cranial, we can see that it has significant differences which identify it as the palaeontological species. In the course of the evolution of the African populations of the genus *Panthera*, the divergence between the “lion” and the “jaguar”, the latter the origin of the species *Panthera gombaszogensis*, is estimated through palaeogenetics to have occurred about 2 Myr (Johnson *et al.*, 2006). We now hold the view that the species in the broad sense of *Panthera gombaszogensis* emerged after the divergence “2 Myr”, but with several subspecies to

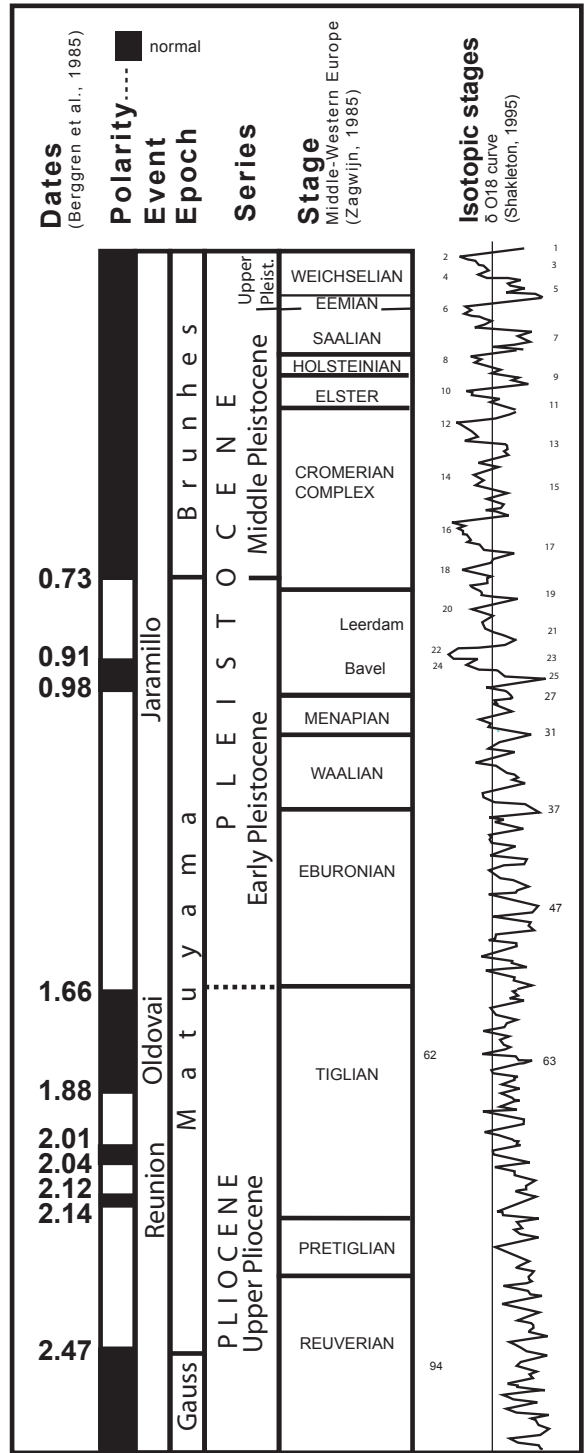


Fig. 3: Chronology of the Quaternary since 2.47 Myr.
Fig. 3 : Chronologie du Quaternaire depuis 2,47 Ma.

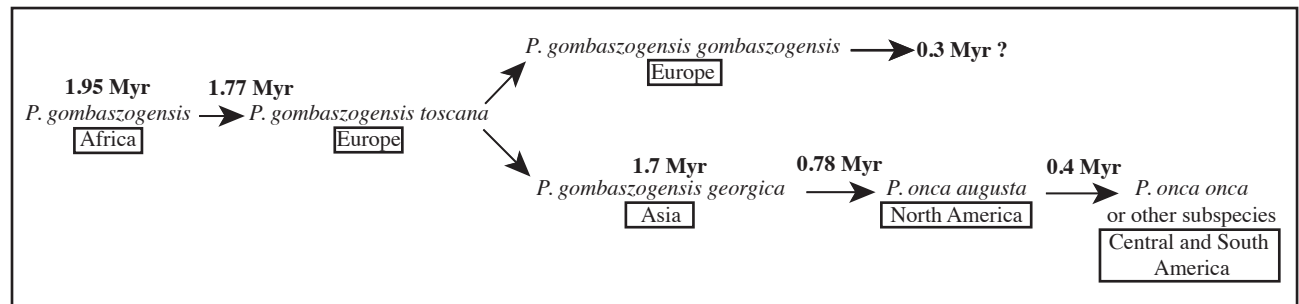


Fig. 4: *Panthera gombaszogensis* story, chronology, after Hemmer, 2010 and Spassov, 2000.
Fig. 4: Histoire de *Panthera gombaszogensis*, chronologie, d'après Hemmer, 2010 and Spassov, 2000.

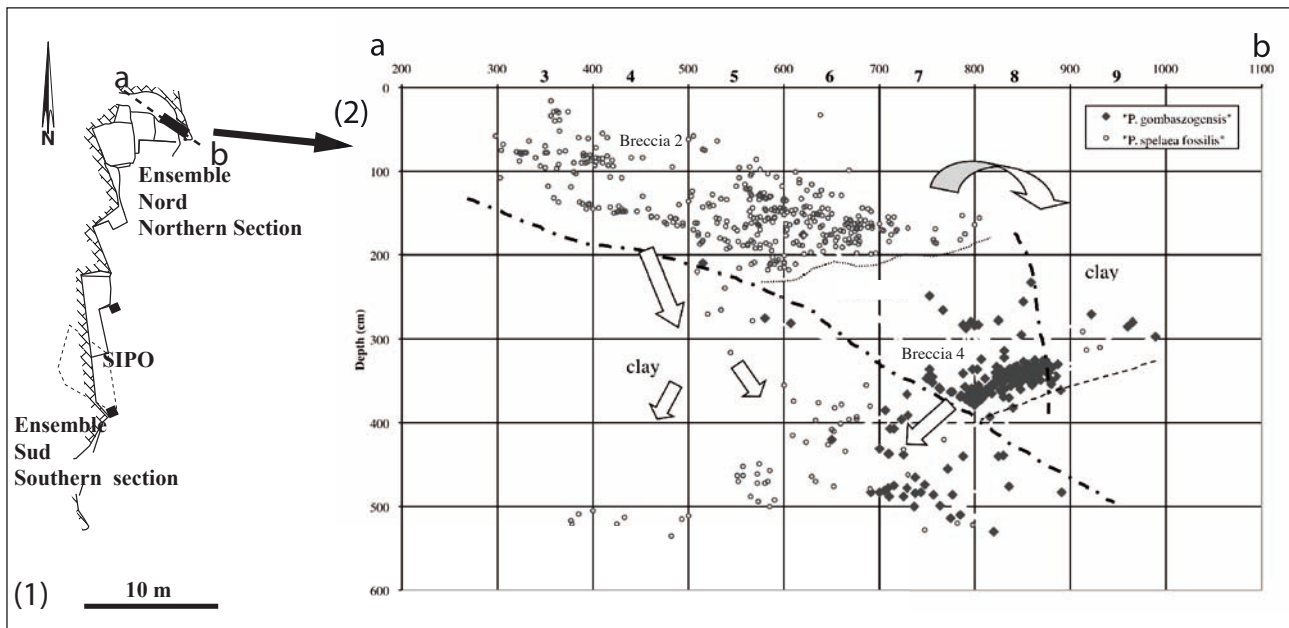


Fig. 5: (1) Distribution of the remains of *Panthera gombaszogensis* in Château (CHA.1-Ensemble Nord). (2) Section "ab": projection on a vertical cross section within C squares alignment. Two layers of bones appear clearly inside breccia: Breccia 2 between 100 and 200 cm depth, with only *Panthera spelaea fossilis* (white dots), Breccia 4 between 300 and 400 cm depth, with only *Panthera gombaszogensis* (black diamonds). The arrows indicate the origine of the clayish excavated material of the quarry also rich in palaeontological material, but reworked.

Fig. 5 : (1) Répartition des restes de *Panthera gombaszogensis* à Château (CHA.1-Ensemble Nord). (2) Coupe selon «ab» : projection sur un plan vertical dans l'axe des carrés C. On distingue nettement deux couches d'ossements dans la brèche : Brèche 2 entre 100 et 200 cm avec seulement *Panthera spelaea fossilis* (cercles), Brèche 4 entre 300 et 400 cm avec seulement *Panthera gombaszogensis* (losanges noirs). Les flèches indiquent l'origine des déblais argileux de la carrière contenant aussi du matériel paléontologique, mais remanié.

be identified if it is possible to validly characterise them, not losing sight of the paucity of the numeric series, at times a little too quickly forgotten. *Panthera gombaszogensis toscana* of the Villafranchian was smaller in size, *Panthera gombaszogensis gombaszogensis* of the Middle Pleistocene was clearly larger in size, *Panthera gombaszogensis georgica* (= *Panthera onca georgica* Hemmer, 2010) had remarkable dental characteristics, *Panthera onca*, the present-day jaguar lives only in America.

4 - PALAEOLOGICAL STUDY OF THE *PANTHERA GOMBASZOGENSIS* OF THE CHÂTEAU BRECCIA (CHA.1)

The palaeontology of the Felidae suffers from several handicaps. The first of these lies in the rarity of palaeontological material. While reasonably numerous, deposits where large Felidae have been found have not provided much material. We are a long way from the sizeable series

that we are able to put together for cave bears for example. It is practically impossible to know in the case of the Felidae if the morphometric variations observed relate to sexual dimorphism, subspecific variations, or simply individual variations. Another factor to take into account is the morphological homogeneity of Felidae skeletal components. With a few fortunate exceptions, it is often the case that too much emphasis is placed on size when determining the species. A third handicap arises from the almost exclusive predominance of dental studies, often based on too few elements to demonstrate variability. Lastly, the rarity of post-cranial skeletal

studies makes it practically impossible to make comparisons between sites.

In this context, the Château Breccia deposit has provided some particularly important material because it is unusually rich in *Panthera gombaszogensis* and in the ancient form of the cave lion *Panthera spelaea fossilis*. The presence of only these two species greatly increases our capacity to reliably and accurately determine the species of finds. So great is the difference in the size of these two Felidae that no hesitation is possible when deciding on the species. *Panthera gombaszogensis*, the size of a large present-day jaguar (about the size of a small African lioness), cannot be confused with the *Panthera spelaea fossilis* of Château, among the first populations arriving in Western Europe in the median Middle Pleistocene, and which is of an especially impressive size.

4.1 - DISTRIBUTION WITHIN THE DEPOSIT

The Château Breccia deposit is found in a very old karstic system dismantled by erosion and then finally by a quarry. Practically nothing remains except a few very fossiliferous breccia fillings corresponding to solifluction flows which filled the lower galleries and fissures of the deep "blind" karst, carrying with them numerous faunal remains and at times complete animal carcasses or body parts still in anatomical connection. The fauna is dominated by *Ursus deningeri*, but the remains of big cats are particularly numerous. *Canis lupus mosbachensis* completes this list of large carnivores. The hardening of the breccia, and the walls of the often narrow fissures helped protect the fossils before their exposure to the

open air partly through erosion but especially as a result of quarrying.

Panthera gombaszogensis is the only species of large Felidae found in Breccia 4 (Ensemble Nord), the most ancient part of the deposit (early Middle Pleistocene). In Breccia 3 its remains are mixed with those of the very large *Panthera spelaea fossilis* (median Middle Pleistocene) dated biochronologically by *Arvicola cantianus* (Jeannot in Argant *et al.*, 2007) and contemporaneous with the German deposit Mosbach 2. In Breccia 2, also in the Ensemble Nord, (median Middle Pleistocene, a little more recent), *Panthera spelaea fossilis* is the only large Felidae found. In the Ensemble Sud, *Panthera gombaszogensis* is found only in the final phase of the filling of the SIPO (Sondage intermédiaire paroi ouest – Intermediate Excavation West Wall), unfortunately without any other elements to provide dating information.

4-2 - MORPHOMETRIC DATA

The main objective of this study is to present the greatest possible quantity of morphometric data, but given the size of this article, it will not be possible to enter into the detail of descriptions or of morphological variations. Nor will it be possible to develop detailed comparisons with material already known in a way that this should be done.

Warning

The measurements in this study are always in mm and this unit does not appear in the tables.

The height of the crown (HC) of a cheek tooth is calculated on the external side in a direct line, and only given in the case of teeth that are not very worn.

Abbreviations

A: measure of the alveolus of a tooth, (A) measure between the alveoli for a series of teeth

* about (after a measure)

Dentition : I = incisive ; C = canine ; P = premolar ; M = molar

P2/ = second upper premolar

P/2 = second lower premolar

prox. ext. = proximal extremity ; dist. ext. = distal extremity

fragt or fgt = fragment

l. or r. = left or right = *droit ou gauche*

inf.; sup. ; ant. ; post. ; med. ; art. = inferior ; superior ; anterior; posterior, median, articular

juv. = juvenile

lat: lateralization (left or right)

mand. = mandible = *mandibule*

min. ; max. = minimum ; maximum

APD = antero-posterior diameter = length or *DAP* = *diamètre antéro-postérieur*

TD = transverse diameter or *DT* = *diamètre transverse*

DPD = dorso-palmar or dorso-plantar diameter = height or *DDP* = *diamètre dorso-palmaire ou dorso-plantaire* = *hauteur*

MD = mesio-distal diameter = length (for a tooth) = *diamètre mésio-distal* = *longueur (pour une dent)*

VL = vestibulo-lingual diameter = width (for a tooth) = *diamètre vestibulo-lingual* = *largeur (pour une dent)*

HC = height of the crown = *hauteur de la couronne*

NR = number of remains (complete or fragments) = *nombre de restes*.

MNI = minimum number of individuals

Mtc, Mtt = metacarpal, metatarsal bone ; Mtt 3 = 3rd metatarsal bone

TN = transfer number (in a table, a figure, a caption)

PFEMA (Plan Félidés d'Enregistrement Morphométrique Argant) = Plan Argant for morphometric record of Felids.

4.2.1 - Skull

We have collected data from a single complete skull (CHA.1-00-F.8-73) and we have several fragments from other individual skulls which give us additional measurements. **Figure 6 and table 1** provide the available measurements.

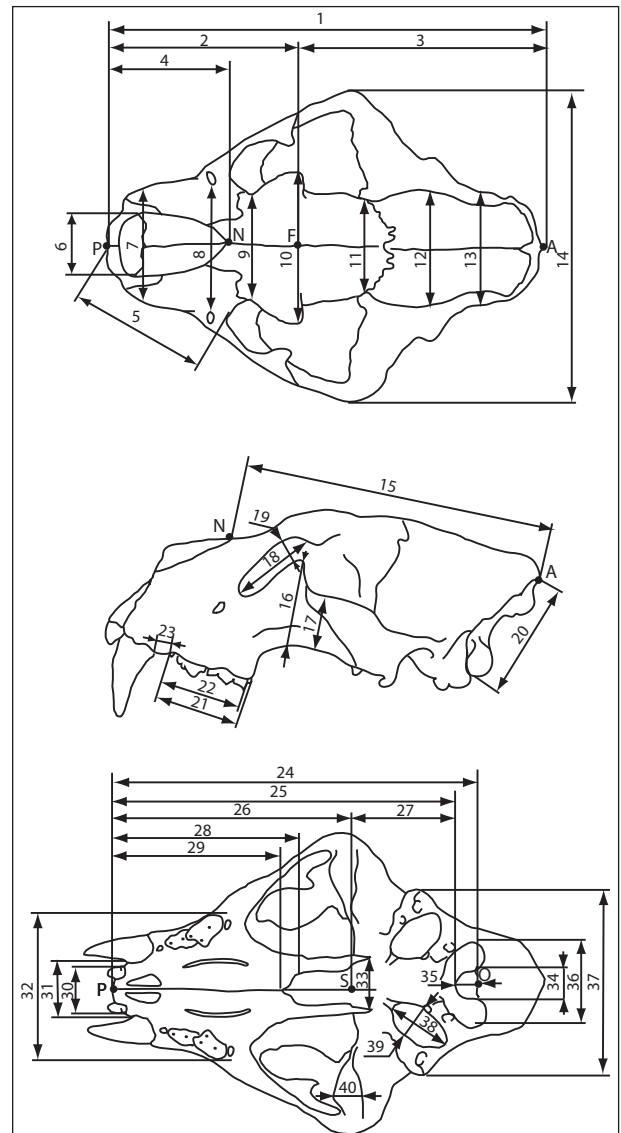


Fig. 6: Measurement of the skull of Felids (PFEMA 10).
Fig. 6: Plan de mesure du crâne des Félidés (PFEMA 10).

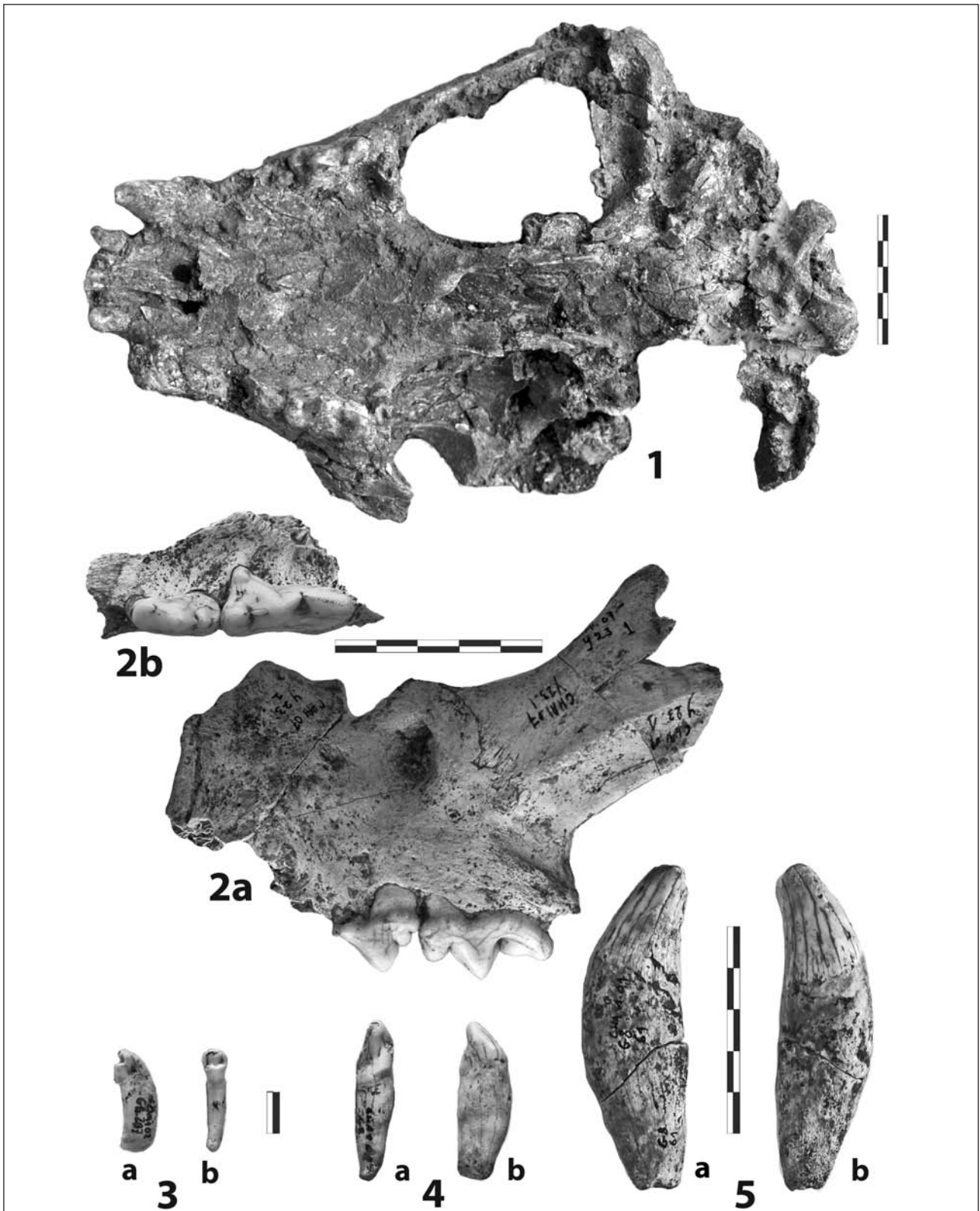


Plate 1: Château, *Panthera gombaszogensis*.

1 - CHA.100-F8-73: "complete" skull, lower view.

2 - CHA.1-07-Y.23-1: **a**- fragment of the upper left maxilla with P3/ and P4/ and part of the zygomatic arch, lateral view; **b**- fragment of the right upper maxilla with P3/ and P4/ of the same individual.

3 - CHA.1-02-G.8-297, right I1/: **a**-; external lateral view; **b**- lingual view

4 - CHA.1-02-G.8-296, right I3/: **a**- lingual view; **b**- internal lateral view.

5 - CHA.1-01-G.8-61, upper left canine: **a**- internal lateral view; **b**- external lateral view.

Planche 1: Château, Panthera gombaszogensis.

1 - CHA.100-F8-73: crâne «complet», vue inférieure.

2 - CHA.1-07-Y.23-1: **a**- fragment de maxillaire supérieur gauche avec P3/ and P4/ et départ de l'arcade zygomatique, vue latérale ; **b**- fragment de maxillaire supérieur droit avec P3/ and P4/ du même individu.

3 - CHA.1-02-G.8-297, I1/ droite : **a**- vue latérale externe ; **b**- vue linguale.

4 - CHA.1-02-G.8-296, I3/ droite: **a**- vue linguale; **b**- vue latérale interne.

5 - CHA.1-01-G.8-61, canine supérieure gauche : **a**- vue latérale interne; **b**- vue latérale externe.

<i>Panthera gombaszogensis</i> Skull		1 CHA.1-00-F8-73		2 CHA.1-07-Y23-1		3 CHA.1-01- G8-118
		left	right	left	right	right
1	Length, prosthion - basion	288.0 *	-	-	-	-
2	Facial length, prosthion - point F	175.0	-	-	-	-
3	Neurocranial length, point F - acrocranium	-	-	-	-	-
4	Viscerocranial length, prosthion - cranion	129.0	-	-	-	-
5	Lateral length of muzzle	111.2	111.4	-	-	-
6	Max breadth of nasal opening	44.3	-	-	-	-
7	Max breadth at the canines	82.1	-	-	-	-
8	Breadth between infraorbital foramens	85.3	-	-	-	-
9	Min breadth at orbits, entorbital-entorbital	60.4	-	-	-	-
10	Frontal breadth, ectorbital-ectorbital	84.2	-	-	-	-
11	Min breadth of neurocranium	58.8 *	-	-	-	-
12	Max breadth of neurocranium at parieto-temporal suture	-	-	-	-	-
13	Max breadth of external occipital process	-	-	-	-	-
14	Bizygomatic breadth, zygion - zygion	180.0 *	-	-	-	-
15	Neurocranial length, nasion - nasion	182.0 *	-	-	-	-
16	Max height of zygomatic arch	-	-	-	-	-
17	Min height of zygomatic arch	36.3	-	35.3	-	-
18	Max length of orbit	59.4	62.0 *	-	-	-
19	Max height of orbit	-	-	-	-	-
20	Height of occipital triangle, acrocranium -basion	-	-	-	-	-
21	Length of cheek teeth, P2/ - M1/ or alveoli	70.3	-	61.0	59.4	66.3 *
22	Length of premolars, P3/ - P4/ ou alveoli	62.6	-	64.3	-	62.5
23	Length of diastema between C - P3/ alveoli	7.4	-	-	-	8.4 *
24	Condylbasal length	282.2	-	-	-	-
25	Total length, prosthion - acrocranium	264.2	-	-	-	-
26	Basifacial length, prosthion-synsphenion	196.7	-	-	-	-
27	Basifacial length, synsphenion - basion	72.2	-	-	-	-
28	Maxi median palatinal length, prosthion-staphylion	137.3	-	-	-	-
29	Min median palatinal length, prosthion-staphylion	128.9	-	-	-	-
30	Length of incisives or alveoli	39.5	-	-	-	-
31	Interne breadth between the roots of canines	44.2	-	-	-	-
32	Max breadth of palate	115.8	-	-	-	-
33	Max breadth at pterygoid process	38.1	-	-	-	-
34	Max breadth of occipital foramen	28.1 *	-	-	-	-
35	Height of occipital foramen, basion-opisthion	22.2 *	-	-	-	-
36	Max breadth at condylus occipitalis	60.4	-	-	-	-
37	Breadth, otion - otion	130.0	-	-	-	-
38	Length of tympanic bulla	36.6	-	-	-	-
39	Breadth of tympanic bulla	25.8	-	-	-	-
40	Max breadth of glenoid fossa (external measure)	22.2	-	-	-	-

Tab. 1: Château (CHA.1), *Panthera gombaszogensis*. Measurements of the skull (PFEMA 10, fig. 6).

Tab. 1 : Château (CHA.1), *Panthera gombaszogensis*. Mesures du crâne (PFEMA 10, fig. 6).

rements. The mark * which follows a measurement indicates only an approximation because of the condition of the remains or because they have been reconstructed on a more solid basis.

The “complete” skull was crushed and the right half of the neurocranium has been flattened so the most important part is missing. The central part has slightly lost its shape. On the left hand side which has been well preserved we can see the teeth as far as occipital condylus. The left hand zygomatic arch is in its original state and is in its

correct position. The occipital part of the back of the skull is missing on the top. The occipital condylus is in place, a little bit turned towards the left but in a continuous line with the section that precedes it.

We were able to open up the ventral, although with great difficulty, and because of the very fragmented state of the bone it was necessary to continually strengthen it with polyurethan varnish. This allowed us to get most of the data we had hoped for with the exception of the right part of the neurocranium which was very damaged

and what remained of the right hand condylus which had shifted. It is possible to observe a complete palate which shows the two long and narrow intact palatal openings and the choanae. The left tympanic bulla, the only remaining one, was destroyed but its position and its edges can still be seen. The left zygomatic arch and the condylus of the left mandible give us the usual measurements.

The teeth are not always there but the basic essentials are:

The incisives: I1/ l. and r. are damaged ; I2/ l. and r. are broken but the roots are still in the alveoli; I3/ l. and r. are very damaged.

The right P2/ was broken. The P3/ l. shows only the empty alveolus and the area around the P3/ r. is completely destroyed. The two P4/ which are important teeth, have been well preserved in their proper place but unfortunately they were embedded in a very hard breccia and when this was removed the enamel of the crown was badly damaged on the internal side.

Molars: the two empty alveoli, in their correct place, of two M1/ l. and r. were able to be measured.

All the observable morphologic characters, whether they be skull bones or teeth, relate to those of *Panthera onca*, the current jaguar. But the skull CHA.1-00-F8-73 appears to be much bigger and more massive with a particularly enlarged palate. Its size is about the same as the skull of a little female lion today.

The morphology of the rear extremity of the palatine at the opening of the choanae gives us interesting data. N. K. Vereschagin (1969) put this morphology into two types, one of the steppe with today's *Panthera leo* – *Panthera spelaea* and on the other hand the shape of the forest with *Panthera tigris* – *Panthera onca*. The skull of the *Panthera gombaszogensis* from Château fits more with the morphology of the steppe shape with the deep and round median indentation (fig.7) of *Panthera spelaea* and *Panthera leo* of today, contrary to what the figure of Vereschagin shows. Conversely, the skull of the today's jaguar that I use by way of comparison, a strong male, shows the same configuration as the *Panthera gombaszogensis* of Château. We think we must conclude that it is not a specific feature contrary to what Vereschagin suggests, but a character which shows how certain communities adapt to particular biotopes. In this case the *Panthera gombaszogensis* of Château conforms to the shapes of open spaces, "steppic", which confirms the pollen analysis of J. Argant.

4.2.2 - Semi-mandible

Four semi-mandibles exist which can give us the essential measurements but none of them is complete. Figure 8 relates to the Pfema 20 measurement plan and the numbers 1 to 16 in the first column refer to measurements in table 2.

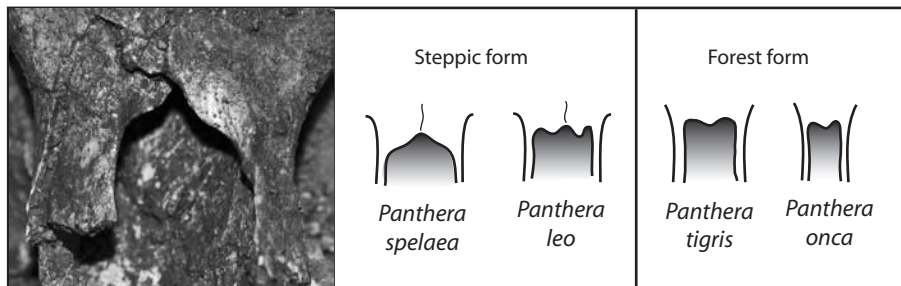


Fig.7: Shape of the choanae of *P. gombaszogensis* (CHA.1-00-F8-73). Comparison with other *Panthera* (after Vereschagin, 1969).
 Fig.7: Formes des choanes de *P. gombaszogensis* (CHA.1-00-F8-73). Comparaison avec d'autres *Panthera* (d'après Vereschagin, 1969).

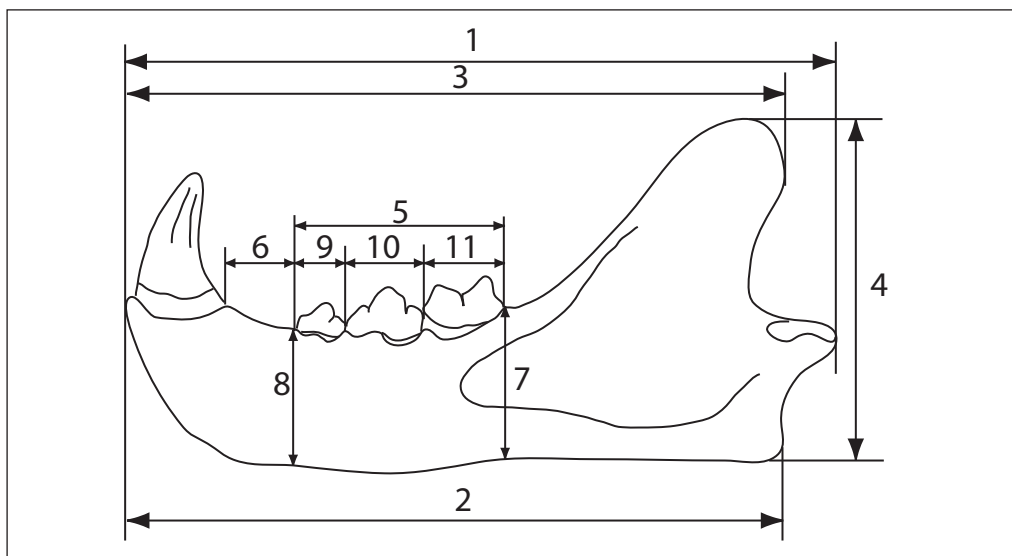


Fig. 8: Measurement of the mandible of Felids (PFEMA 20).
 Fig. 8 : Plan de mesure de la mandibule des Félidés (PFEMA 20).

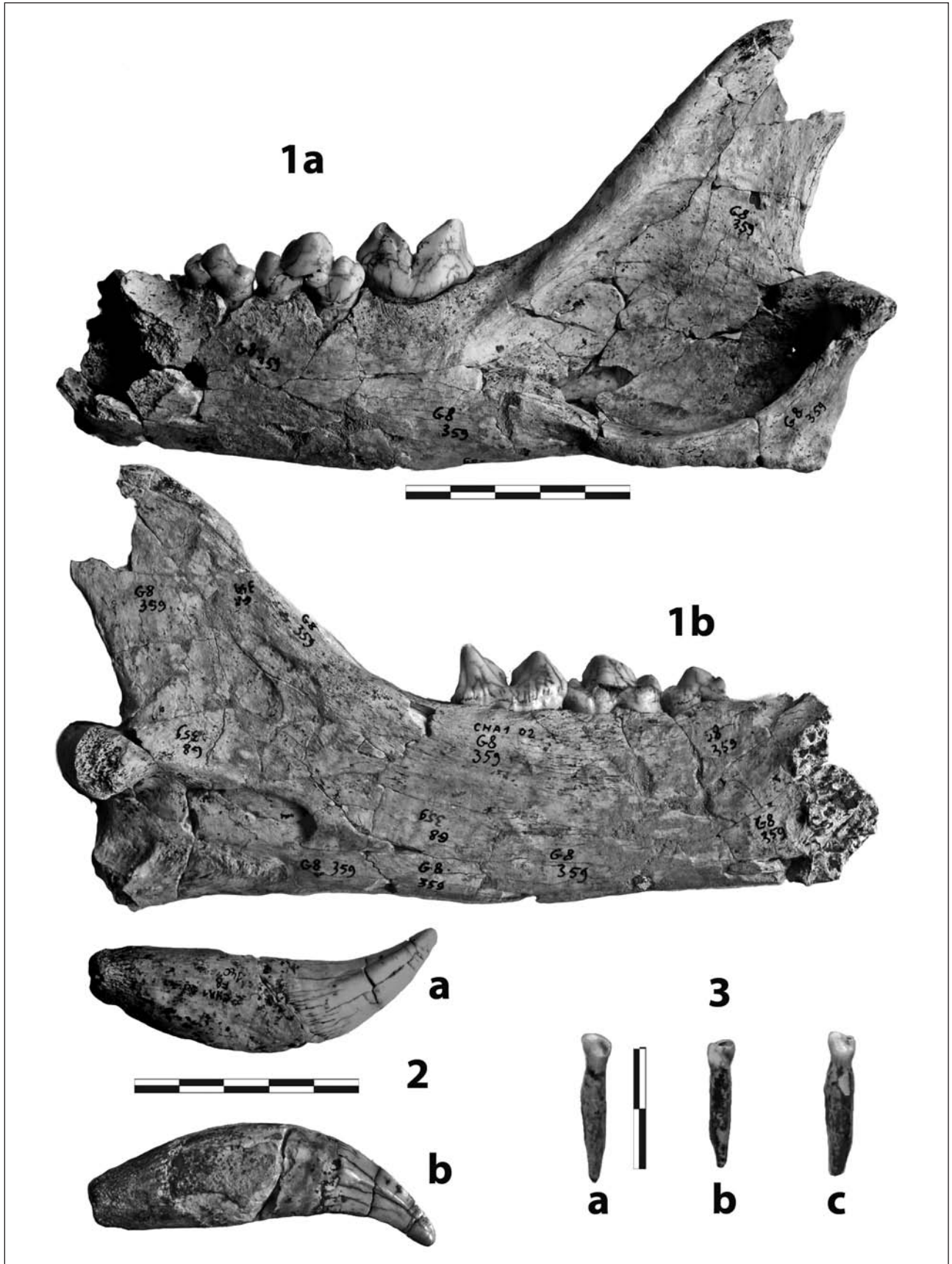


Plate 2: Château, *Panthera gombaszogensis*.

1 - CHA.1-G.8-359: **a**- left semi-mandible: external lateral view; **b**- internal lateral view.

2 - CHA.1-00-F.8-140, lower right canine: **a**- vestibular view; **b**- lingual view.

3 - Lower inciseive 1, lingual view: **a**- CHA.1-F.6, right I/1; **b**- CHA.1-00-F.8-22, left I/1; **c**- CHA1-B.3-6, right I/1.

Planche 2: Château, Panthera gombaszogensis.

1 - CHA.1-G.8-359: **a**- demi mandibule gauche: vue latérale externe; **b**- vue latérale interne.

2 - CHA.1-00-F.8-140, canine inférieure droite : **a**- vue latérale vestibulaire; **b**- vue latérale linguale.

3 - Incisive 1 inférieure, vue linguale: **a**- CHA.1-F.6, I/1 droite; **b**- CHA.1-00-F.8-22, I/1 gauche; **c**- CHA1-B.3-6, I/1 droite.

<i>Panthera gombaszogensis</i> - Mandible							
NT Sample →	1	2	3	4	5	6	7
1	Length infradental - mid condylus	-	-	-	-	-	-
2	Length infradental - angular apophysis	-	-	-	-	-	-
3	Length infradental - coronoid apophysis	-	-	-	-	-	-
4	Height angular process - coronion	99.0	-	-	-	-	-
5	Length of P/3-M/1 or alveoli	62.3	60.8	62.3	65.8	-	-
6	Length of diastema C - P/3 (between alveoli)	14.7	13.3	-	15.3	-	-
7	Horizontal ramus height behind M/1	43.3	37.7	41.6	-	-	-
8	Horizontal ramus height before P/3	39.8	39.3	40.7	39.4	-	-
9	Length of alveoli of P/3	16.1	16.1	16.1	-	-	-
10	Length of alveoli of P/2	23.6	22.4	23.6	24.1	-	-
11	Length of alveoli of M/1	24.9	24.6	24.0	25.3	-	-
12	Breadth at canine	-	-	-	-	-	-
13	Horizontal ramus breadth before P/3	16.6	18.2	18.9	20.0	-	-
14	Horizontal ramus height behind M/1	16.6	17.0	19.4	-	-	-
15	Length of condylus	42.1	-	-	-	-	50.7
16	Breadth of condylus	-	-	-	-	14.7	17.8

Tab. 2 : Château (CHA.1), *Panthera gombaszogensis*. Measurements of the half mandible (PFEMA 20, fig. 8). The numbers (TN) on the horizontal line (1 to 7) indicate the references of the samples mentioned in the text.

Tab. 2 : Château (CHA.1), *Panthera gombaszogensis*. Mesures de la demi-mandibule (PFEMA 20, fig. 8). Les numéros (TN) horizontaux (de 1 à 7) correspondent aux références des pièces indiquées dans le texte.

The numbers on the line (1 to 7) refer to the following samples :

- 1- CHA.1-G.8-359 ; semi-mandible l.
- 2- CHA.1-00-F.8-140 ; semi-mandible r.
- 3- CHA.1-01-G.8-171 ; semi-mandible r.
- 4- CHA.1-01-G.8-100 ; semi-mandible r.
- 5- CHA.1-G.7- fissure S.1; condylus l.
- 6- CHA.1-G.7 ; condylus r.
- 7- CHA.1-G.8-35 ; condylus r.

4.2.3 - Dentition

In tables 3 and 4, the transfer numbers of the first line, from 1 to 7 and even 8 for the lower teeth, indicate the reference inside the site of each measured piece. See the list below:

Upper dentition:

Incisives :

- I1/ : 1- CHA.1-D.5 l. ; 2- CHA.1-02-G.8-297 r. ; 3- CHA.1-00-F.8-73 l. ; 4- CHA.1-00-F.8-73 r.
- I2/ : 1- CHA.1-D.4-51 r.
- I3/ : 1- CHA.1-02-G.8-296 r. ; 2- CHA.1-G.8-108 l. ; 3- CHA.1-00-E.7-78 r. ; 4- CHA.1-01-G.8-118 r. ; 5- CHA.1-02-G.8-302 l. ; 6- CHA.1-00-F.8-73 l. ; 7- CHA.1-00-F.8-73 r.
- Canine: 1- CHA.1-01-G.8-61 l. ; 2- CHA.1-01-G.8-118 r. ; 3- CHA.1-02-G.8-302 l. ; 4- CHA.1-00-F.8-73 l.

Premolars :

- P2/ : 1- CHA.1-07-Y.23-1 alveolus l. ; 2- CHA.1-02-G.8-374 alveolus r. ; 3- CHA.1-01-G.8-118 r. ; 4- CHA.1-02-G.8-302 l.
- P3/ : 1- CHA.1-07-Y.23-1 l. ; 2- CHA.1-07-Y.23-1 r. ; 3- CHA.1-02-G.9-10+E.7-22 l. ; 4- CHA.1-00-G.8-19 l. ; 5- CHA.1-02-G.8-374 r. ; 6- CHA.1-01-G.8-118 r. ; 7- CHA.1-02-G.8-302 l.
- P4/ : 1- CHA.1-07-Y.23-1 l. ; 2- CHA.1-07-Y.23-1 r. ; 3- CHA.1-02-G.8-374 r. ; 4- CHA.1-01-G.8-118 r. ; 5- CHA.1-02-G.8-302 l. ; 6- CHA.1-00-F.8-73 l. ; 7- CHA.1-00-F.8-73 r.

Molars:

- M1/ : 1- CHA.1-07-Y.23-1 l. alveolus; 2- CHA.1-01-G.8-118 r. ; 3- CHA.1-01-G.8-118 l. ; 4- CHA.1-02-G.8-302 l.

Lower dentition:

Incisives :

- I/1: 1- CHA.1-B.3-6 r. ; 2- CHA.1-F.6 r. ; 3- CHA.1-F.8-22 l. ; 4- CHA.1-07-FF.25-3 l. ; 5- CHA.1-01-G.8-107 l.
- I/2: 1- CHA.1-02-G.8-414 l. ; 2- CHA.1-HS l.
- I/3: 1- CHA.1-01-G.8-107 r. ; 2- CHA.1-01-G.8-107 l.
- Canines: 1- CHA.1-01-G.8-102 l. ; 2- CHA.1-00-F.8-140 r. ; 3- CHA.1-01-G.8-110 r. ; 4- CHA.1-02-G.8-359 l. ; 5- CHA.1-01-G.8-100 r.
- Premolars :
- P/3: 1- CHA.1-02-G.8-359 l. ; 2- CHA.1-00-F.8-140 r. ;

Panthera gombaszogensis - Château Breccia																	
UPPER TEETH		1	2	3	4	5	6	7	← TN →		1	2	3	4	5	6	7
		I1/	M.D.	8.5	5.3	6.5	6.4				P3/	MD	20.7	20.5	22.4	22.0	21.9
	V.L.	7.8	5.4	4.2	5.0				V.L.max.	10.5		9.8	11.2	11.2	10.2	10.9	10.8
I2/	M.D.	8.1							V.L. ant.	8.5		8.6	9.6	9.1	8.9	9.5	8.8
	V.L.	5.6							HC	12.0		12.0		12.0	11.9	12.0	12.7
I3/	M.D.	11.8	12.2	12.0	12.1	12.2	12.8	12.6	MD paracone	10.2		10.3	12.0	10.4	11.2	11.0	11.4
	V.L.	9.0	9.5	9.9	9.9	9.0	9.6	9.1	MD tub. acces.	4.5		4.5	4.4	4.6	4.5	4.6	5.0
C	M.D.	21.6	21.7	20.4	19.9				MD ext.	31.2		31.6	30.3	30.4	30.4	32.4	31.9
	V.L.	16.4	16.8	16.3	15.8				MD med.	29.7		29.6	29.8	29.8	29.8	30.8	30.8
	H.C.				39.5				MD int.	30.2		30.1	30.5	30.7	30.9	31.1	32.7
	P.C.	61.8	64.0	60.0	64.4				MD protocone	8.9		8.1	7.7	9.2	7.9	9.6	9.5
P2/	MD	(A) 7.3	(A) 7.1	7.1	8.7				MD paracone	13.1		12.7	12.5	12.6	12.3	12.2	13.2
	V.L.	(A) 6.0	(A) 5.6	5.6	5.9				MD metacone	11.7		12.7	11.8	11.8	12.1	13.0	13.3
	HC	-	-	3.2	5.2				VL ant.	17.1	15.9	16.7	16.6	18.4	15.6	16.4	
M1/	MD	(A) 5.6	5.3	6.0	5.7				VL post.	10.9	10.1	10.1	11.1	10.7	10.0	10.3	
	VL	(A) 11.6	10.2	9.8	10.9				HC paracone	15.4	16.4	15.7	16.4	15.7	16.8	17.9	

Tab. 3: Château (CHA.1), *Panthera gombaszogensis*. Upper teeth. The numbers (TN) on the horizontal line (1 to 7) indicate the references of the samples mentioned in the text.

Tab. 3 : Château (CHA.1), *Panthera gombaszogensis*. Denture supérieure. Les numéros (TN) horizontaux (de 1 à 7) correspondent aux références des pièces indiquées dans le texte.

Panthera gombaszogensis - Château Breccia																			
LOWER TEETH		1	2	3	4	5	6	7	← TN →		1	2	3	4	5	6	7	8	
		I1/	M.D.	6.7	6.7	6.6	7.6	6.2			P4/	MD	24.1	22.5	23.0	22.8	22.7	23.0	24.0
	V.L.	4.6	4.8	4.8	5.3	4.6			V.L. ant.	9.3		8.8	9.7	9.5	9.8	9.9	9.3		
I2/	M.D.	7.2	7.1						V.L. post.max.	10.8		10.1	11.3	11.5	11.1	11.3	10.8		
	V.L.	6.3	5.8						HC	-		14.3	14.2	-	-	13.7	13.8		
I3/	M.D.	6.8	7.2						HT	-		-	-	-	-	-	38.0		
	V.L.	6.8	-						MD paraconid	12.1		12.2	12.4	-	-	11.4	12.6		
C	M.D.	21.1	21.8	19.0	19.0	18.4			MD talonide	7.3		7.1	8.1	-	-	7.8	8.0		
	V.L.	14.5	14.9	14.5	15.7	15.6			MD	24.9		25.0	24.4	24.2	22.9*	24.1	-	25.2	
	H.C.	36.8	36.7	34.7	-	-			VL max.	12.8		12.9	12.2	11.9	11.8	12.0	12.3	12.8	
	P.C.	62.3	61.4	-	57.6	58.3			HC paraconid	15.6		13.2	13.5	12.4	-	-	-	-	
P3/	MD	16.0	16.1	15.5	15.6	16.1	16.3		M1/	HC metaconid		14.1	14.3	-	14.4	13.0	-	-	14.1
	VL post. max.	8.0	8.0	7.7	8.4	8.7	8.5			HC sous sillon		7.0	6.2	7.1	6.7	6.9	7.3	7.8	7.1
	HC	9.2	9.4	9.6	10.2	9.8	9.7			MD paraconid	13.3	13.4	12.4	11.7	-	-	13.4	13.4	
	MD protoconic	8.7	10.0	9.3	8.7	8.7	9.0			MD metaconid	15.2	14.9	14.4	14.2	14.4	-	-	14.8	

Tab. 4: Château (CHA.1), *Panthera gombaszogensis*. Lower teeth. The numbers (TN) on the horizontal line (1 to 7) indicate the references of the samples mentioned in the text. (A)= alveolus.

Tab. 4 : Château (CHA.1), *Panthera gombaszogensis*. Denture inférieure. Les numéros (TN) horizontaux (de 1 à 7) correspondent aux références des pièces indiquées dans le texte. (A) = alvéole.

3- CHA.1-G.6-93 l. ; 4- CHA.1-G.7-105 r. ; 5- CHA.1-01-G.8-102 l. ; 6- CHA.1-01-G.8-171 r.

P/4: 1- CHA.1-02-G.8-359 l. ; 2- CHA.1-00-F.8-140 r. ; 3- CHA.1-01-G.8-171 r. ; 4- CHA.1-G.7-104-fissure l. ; 5- CHA.1-01-G.8-63 l. ; 6- CHA.1-01-G.8-35 r. ; 7- CHA.1-01-G.8-100 r.

Molars :

M/1: 1- CHA.1-02-G.8-359 l. ; 2- CHA.1-01-G.8-35 r. ; 3- CHA.1-00-F.8-140 r. ; 4- CHA.1-G.7-111 l. ; 5- CHA.1-G.7-15+G.7-38 r. ; 6- CHA.1-01-G.8-171 r. ; 7- CHA.1-01-G.8-21 l. ; 8- CHA.1-01-G.8-100 r.

4.2.4 - Post-cranial skeleton

The long bones have undergone intense fragmentation since the time of their accumulation in small upper caves no longer in existence, initially because of the footsteps of other animals, (perhaps) also because of blocks of limestone falling from the ceiling or walls of the cave, and almost certainly during their transport by solifluction flows. The ultimate ordeal was that imposed by the rootlets of trees growing on the site which penetrated the smallest cracks and then grew larger in size over the

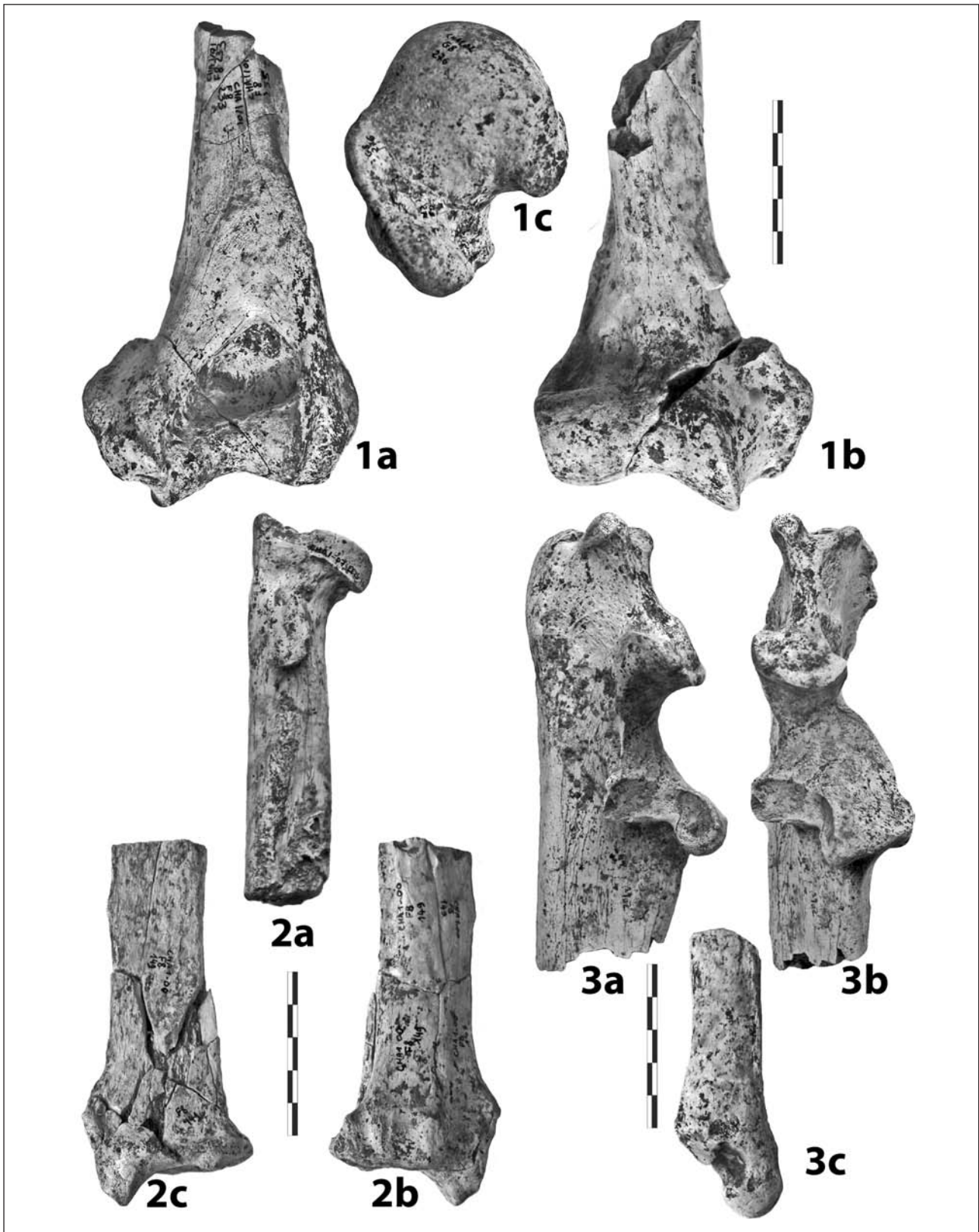


Plate 3: Chateau, *Panthera gombaszogensis*.

1 - Right humerus, CHA.1- F.8-233, distal part: **a-** frontal posterior view; **b-** frontal anterior view; **c-** CHA.1-02-G.8-276, proximal part, upper view.

2 - Radius **a-** CHA.1-07-EE-25-16, left, proximal part, internal lateral view; **b-** CHA.1-00-F.8-149, right, distal part, external lateral view; **c-** the same, internal lateral view.

3 - Right ulna CHA.1- 07-Y.22-149: **a-** proximal part, external lateral view; **b-** dorsal view; **c-** CHA.1-98-6-7-Eb.tr.3, distal part, internal lateral view.

Planche 3: Chateau, Panthera gombaszogensis.

1 - Humérus droit, CHA.1- F.8-233, partie distale : **a-** vue de face, postérieure ; **b-** vue de face, antérieure ; **c-** CHA.1-02-G.8-276, partie proximale vue de dessus.

2 - Radius : **a-** CHA.1-07-EE-25-16, gauche, partie proximale, vue latérale interne ; **b-** CHA.1-00-F.8-149, droit, partie distale, vue latérale externe ; **c-** le même, vue latérale interne.

3 - Cubitus droit : CHA.1- 07-Y.22-149 : **a-** partie proximale, vue latérale interne ; **b-** vue dorsale ; **c-** CHA.1-98-6-7-Eb.tr.3, partie distale, vue latérale externe.

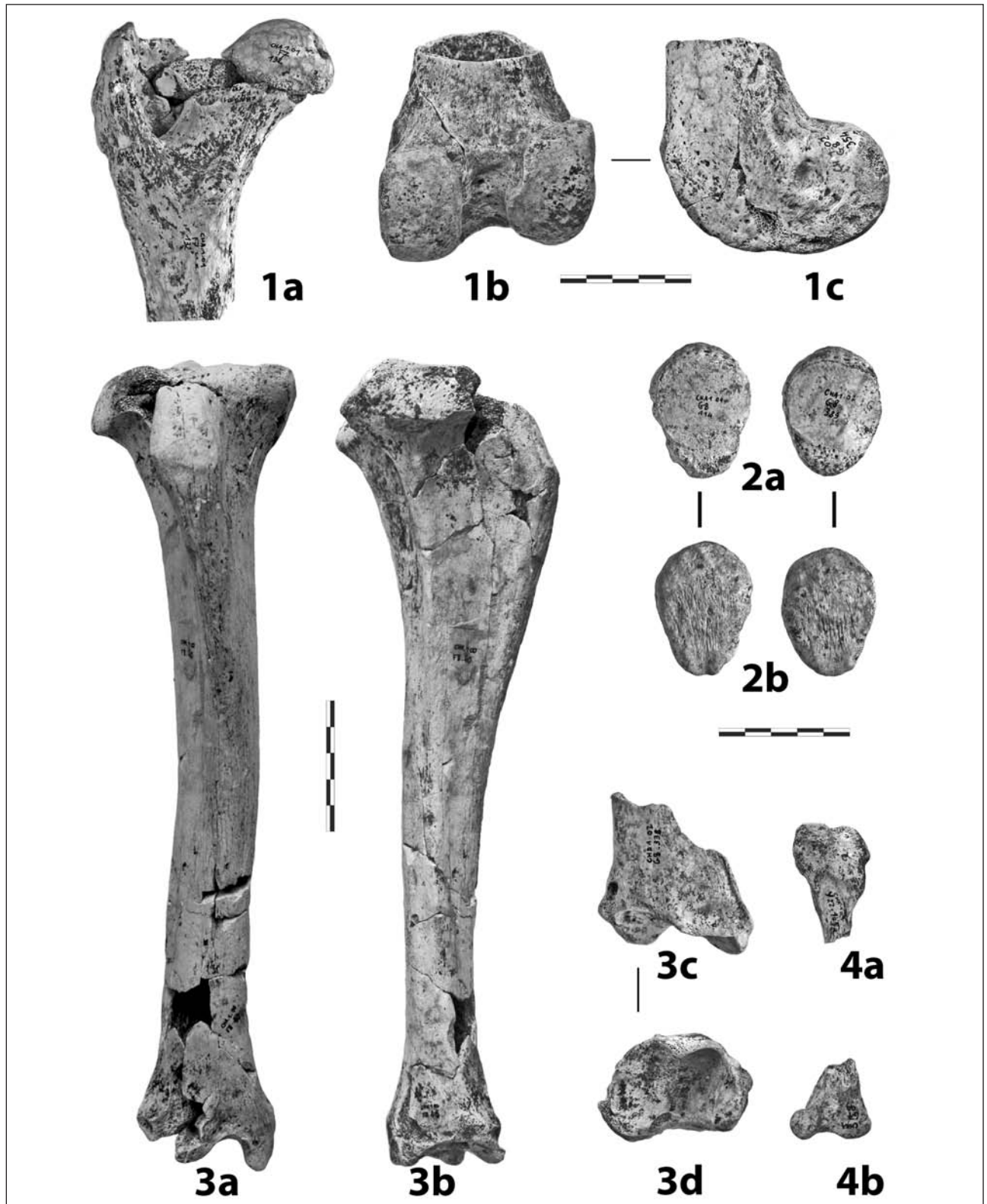


Plate 4: Chateau, *Panthera gombaszogensis*.

1 - **a-** CHA.1-01-F.7-132, left femur, proximal part, lateral posterior view; **b-** CHA.1-02-G.8-354, right femur, posterior view; **c-** the same, internal lateral view.

2 - Patellae of the same individual, CHA.1-01-G.8-114 (right) and CHA.1-01-G.8-389 (left): **a-** internal view (articular); **b-** frontal view.

3 - CHA.1-01-F.8-40, right tibia: **a-** cranial view; **b-** external lateral view; CHA.1-01-G.8-338, left tibia: **c-** distal part, frontal view; **d-** lower view.

4 - Fibula: **a-** CHA.1-07-Y.22-145, right, proximal part, internal view; **b-** CHA.1-G.7-99, distal part, external view.

Planche 4 : Chateau, Panthera gombaszogensis.

1 - **a-** CHA.1-01-F.7-132, fémur gauche, partie proximale, vue latérale postérieure; **b-** CHA.1-02-G.8-354, fémur droit, vue postérieure; **c-** le même, vue latérale interne.

2 - Rotules du même individu, CHA.1-01-G.8-114 (droite) and CHA.1-01-G.8-389 (gauche): **a-** vue interne (articulaire); **b-** vue frontale.

3 - CHA.1-01-F.8-40, tibia droit : **a-** vue crâniale; **b-** vue latérale externe;

CHA.1-01-G.8-338, tibia gauche : **c-** partie distale, vue frontale; **d-** vue inférieure.

4 - Fibula: **a-** CHA.1-07-Y.22-145, droit, partie proximale, vue interne; **b-** CHA.1-G.7-99, partie distale, vue externe.

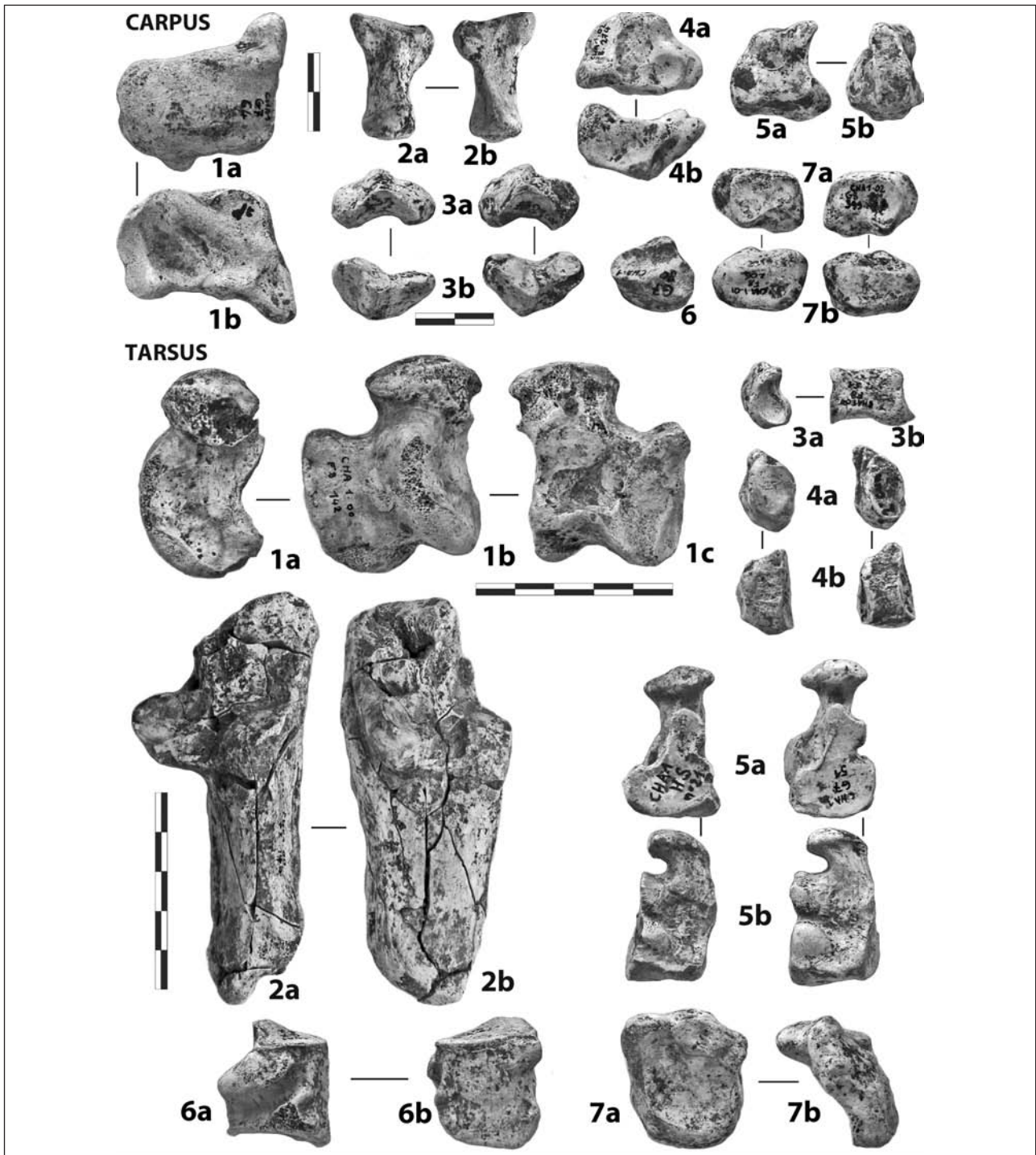


Plate 5 : Chateau, *Panthera gombaszogensis*.

Carpus : 1 - Right scapholunar, CHA.1-G.7-64 : **a**- proximal view; **b**- distal view. - 2 - Left pisiform, CHA.1-01-F8-241 : **a**- anterior view; **b**- posterior view. - 3 - Left trapezium, CHA.1-G.7-69 and CHA.1-02-G.8-227 - **a** - external lateral view; **b**- internal lateral view. - 4 - Right magnum, CHA.1-02-F8-274 : **a**- internal lateral view; **b**- external lateral view. - 5 - Left unciform, CHA.1-G.7 : **a**- external lateral view; **b**- internal lateral view. - 6 - Right trapezoid, CHA.1-G.7-80: proximal view. - 7 - Pyramidal CHA.1-01-F8-206 (left) and CHA.1-02-G.8-399 (right) : **a** / **b**- posterior view; **c** / **d**- anterior view.

Tarsus : 1 - Left astragalus, CHA.1-00-F8-142 : **a**- internal lateral view; **b**- anterior view; **c**- posterior view. - 2 - Right calcaneus, CHA.1-00-F8-146 : **a**- anterior view; **b**- internal lateral view. - 3 - Right cuneiform 1, CHA.1-00-F8-51 : **a**- proximal view; **b**- internal lateral view. - 4 - Left cuneiform 2, CHA.1-01-G.8-105 and CHA.1-00-F8-51 : **a**- proximal view; **b**- internal lateral view. - 5 - Left cuneiform 3, CHA.1-HS-21 and CHA.1-G.5-51 : **a**- distal view; **b**- internal lateral view. - 6 - Right cuboid, CHA.1-G.7-67 : **a**- external lateral view; **b**- anterior view. - 7 - Left navicular, CHA.1-00-F8-145 : **a**- proximal view; **b**- external lateral view. - *Planche 5 : Chateau, Panthera gombaszogensis.*

Planche 5 : Chateau, Panthera gombaszogensis.

Carpe : 1 - Scapholunaire droit, CHA.1-G.7-64 : **a**- vue proximale; **b**- vue distale. - 2 - Pisiforme gauche, CHA.1-01-F8-241 : **a**- vue antérieure; **b**- vue postérieure. - 3 - Trapèzes gauches, CHA.1-G.7-69 et CHA.1-02-G.8-227 - **a** / **b**- vue latérale externe; **c** / **d**- vue latérale interne. - 4 - Magnum droit, CHA.1-02-F8-274 : **a**- vue latérale interne; **b**- vue latérale externe. - 5 - Unciforme gauche, CHA.1-G.7 : **a**- vue latérale externe; **b**- vue latérale interne. - 6 - Trapézoïde droit, CHA.1-G.7-80 : vue proximale. - 7 - Pyramidaux CHA.1-01-F8-206 (gauche) et CHA.1-02-G.8-399 (droit) : **a** / **b**- vue postérieure; **c** / **d**- vue antérieure.

Tarse : 1 - Astragale gauche, CHA.1-00-F8-142 : **a**- vue latérale interne; **b**- vue antérieure; **c**- vue postérieure. - 2 - Calcaneum droit, CHA.1-00-F8-146 : **a**- vue antérieure; **b**- vue latérale interne. - 3 - Cunéiforme 1 droit, CHA.1-00-F8-51 : **a**- vue proximale; **b**- vue latérale interne. - 4 - Cunéiforme 2 gauche, CHA.1-01-G.8-105 et CHA.1-00-F8-51 : **a**- vue proximale; **b**- vue latérale interne. - 5 - Cunéiformes 3 gauches, CHA.1-HS-21 et CHA.1-G.5-51 : **a**- vue distale; **b**- vue latérale interne. - 6 - Cuboïde droit, CHA.1-G.7-67 : **a**- vue latérale externe; **b**- vue antérieure. - 7 - Naviculaire gauche, CHA.1-00-F8-145 : **a**- vue proximale; **b**- vue latérale externe.

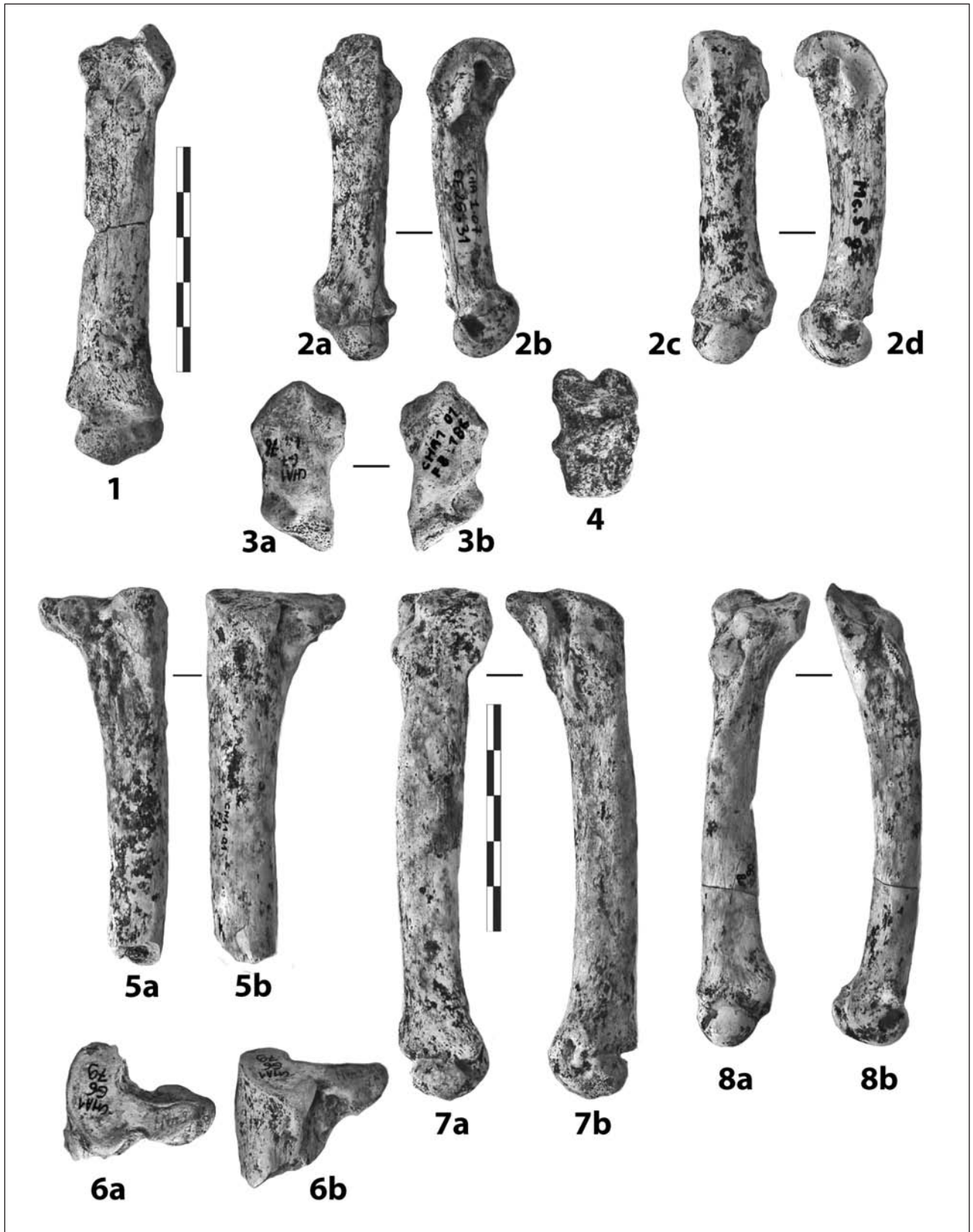


Plate 6: Château, *Panthera gombaszogensis*.

1 - Right metacarpal 3, CHA.1-00-F.8-31, anterior view. – 2 - Metacarpal 5, CHA.1-07-EE-25-31, right, and CHA.1-G.7-124, left: **a** / **c**- vue antérieure; **b** / **d**- vue latérale interne. – 3 - Metacarpal 1, **a**- CHA.1-G.7-79-fissure, gauche, et **b**- CHA.1-01-F.8-186, droit: vue antérieure. – 4 - Phalange 1, right finger 1, CHA.1-F.7-125, anterior view. – 5 - Right metatarsal 3, CHA.1-00-F.8-266: **a**- external lateral view; **b**- internal lateral view. – 6 - Right metatarsal 3, CHA.1-G.6-79, proximal part: **a**- proximal view; **b**- internal lateral view. – 7 - Left metatarsal 4, CHA.1-00-F.8-211: **a**- anterior view; **b**- internal lateral view. – 8 - Left metatarsal 5, CHA.1-00-F.8-90: **a**- anterior view; **b**- internal lateral view.

Planche 6: Château, Panthera gombaszogensis.

1 - Métacarpien 3 droit 3, CHA.1-00-F.8-31, vue antérieure. – 2 - Métacarpien 5, CHA.1-07-EE-25-31, droit, et CHA.1-G.7-124, gauche: **a** / **c**- vue antérieure; **b** / **d**- vue latérale interne. – 3 - Métacarpien 1, **a**- CHA.1-G.7-79-fissure, gauche, et **b**- CHA.1-01-F.8-186, droit: vue antérieure. – 4 - Phalange 1, doigt 1, droit, CHA.1-F.7-125, vue antérieure. – 5 - Métatarsien 3 droit, CHA.1-00-F.8-266: **a**- vue latérale externe; **b**- vue latérale interne. – 6 - Métatarsien 3 droit, CHA.1-G.6-79, extrémité proximale: **a**- vue proximale; **b**- vue latérale interne. – 7 - Métatarsien 4 gauche, CHA.1-00-F.8-211: **a**- vue antérieure; **b**- vue latérale interne. – 8 - Métatarsien 5 gauche, CHA.1-00-F.8-90: **a**- vue antérieure; **b**- vue latérale interne.

course of time, splintering even the most resistant long bones. It is therefore not surprising to notice in table 5 the small number of bones sufficiently well preserved to allow their length to be measured for example. Only the right tibia, CHA.1-F.8-14, well protected in the pothole along with the skull, has reached us intact. It has been possible to validly work out the length of an ulna using several sections of different ulna of equivalent size which

when put together covered the full length of a single ulna. On the other hand, the epiphyses, more massive, have been much more resistant and have provided considerable information for each type of long bone and certainly belong to *Panthera gombaszogensis*.

In table 5, the transfer numbers of the second column (from 1 to 10 max for the ulna) give the reference inside the site of each measured piece. See the list below:

Panthera gombaszogensis - Forelimb and Hindlimb long bones												
TN Measures →	1	2	3	4	5	6	7	8	9	10	11	12
TN Sample ↓	L	prox TD	prox APD	med TD	med APD	dist TD	dist APD	dist art TD	dist art APD			
Humerus	1	-	66.8	85.7	-	-	-	-	-	57.8	59.4	
	2	-	-	-	-	-	79.5	49.3	52.1	-	-	
	3	-	64.9	82.7	-	-	80.6	48.4	55.5	-	56.1	58.1
Radius	1	-	40.1	26.3	29.0	16.8	-	-	-	26.7	-	
	2	-	39.1	27.0	28.6	16.8	-	-	-	26.6	-	
	3	-	-	25.6	-	-	-	-	-	26.7	-	
	4	-	38.6	25.4	-	-	-	-	-	-	-	
	5	-	-	-	29.9	15.2	53.3	32.8	42.4	26.6	-	-
Ulna	1	-	48.0	62.3	-	-	-	-	-	33.0	26.4	20.6
	2	323.0*	-	-	19.0	27.9	-	-	-	-	23.8	22.0
	3	-	-	-	-	-	22.3	29.8	-	-	-	-
	4	-	-	-	-	-	-	-	-	-	24.2	19.5
	5	-	-	-	-	-	-	-	-	-	25.4	19.2
	6	-	-	-	-	-	21.6	27.6	-	-	-	-
	7	-	41.7	-	-	-	-	-	-	29.2	-	-
	8	-	-	55.5	-	-	-	-	-	-	23.7	20.6
	9	-	-	-	0.0	-	19.4	28.0	-	-	-	-
	10	-	-	-	16.0	24.3	-	-	-	-	21.1	20.6
Femur	1	-	83.3	50.7	31.6	28.1	-	-	-	-	70.9	
	2	-	-	-	-	-	73.3	70.1	71.9	-	-	
	3	-	-	-	-	-	-	-	-	38.1	-	
	4	-	-	-	-	-	-	-	-	37.2	-	
	5	-	-	-	-	-	-	-	-	37.8	-	
Tibia	1	295.5	75.3	78.1	29.4	30.9	52.9	35.1	49.0	-	-	
	2	-	-	-	25.1	27.3	-	-	-	-	-	
	3	-	-	-	-	-	53.0	35.8	50.8	-	-	
	4	-	-	-	-	-	56.7	36.1	50.8	-	-	
Fibula	1	-	26.0	17.5	-	-	-	-	-	-	-	
	2	-	24.5	15.2	-	-	-	-	-	-	-	
	3	-	29.3	18.3	-	-	-	-	-	-	-	
	4	-	26.9	-	-	-	-	-	-	-	-	
	5	-	-	-	-	-	29.5	14.4	-	-	-	
TN Measures →	1	2	3	4	5							
Patella	1	51.6	38.2	21.6	35.3	38.5						
	2	-	37.3	23.7	40.2	36.4						
	3	-	37.2	23.3	37.7	36.6						
	4	53.9	38.2	22.5	36.7	37.2						

Tab. 5: Château (CHA.1), *Panthera gombaszogensis*. Forelimb and hindlimb long bones, and patella. The vertical numbers (TN) (maximum 1 to 10) indicate the references of the samples mentioned in the text.

The numbers (TN) on the horizontal line (1 to 12) indicate the measurements taken. For long bones, the numbers from 1 to 9 have always the same meaning. For 10, 11, 12, measurements vary with bones:

- humerus: 10 = prox articular TD; 11 = prox articular APD

- radius: 10 = TD at the neck

- cubitus: 10 = max TD olecranon; 11 = TD anconeus process; 12 = trochlea min. TD

- femur: 10 = TD caput; 11 = distance between greater and lesser trochanters

- For patella: 1 = DPD; 2 = TD; 3 = med APD; 4 = articular DPD; 5 = articular TD.

Tab. 5 : Château (CHA.1), *Panthera gombaszogensis*. Os longs des membres antérieurs et postérieurs, et rotule. Les numéros (TN) verticaux (de 1 à 10 au maximum) correspondent aux références des pièces indiquées dans le texte.

Les numéros (TN) horizontaux (de 1 à 12) correspondent aux mesures prises. Pour les os longs, les numéros de 1 à 9 ont toujours la même signification.

Pour 10, 11, 12, les mesures varient suivant les os :

- humérus : 10 = DT articulaire prox. ; 11 = DAP articulaire prox.

- radius : 10 = DT du col

- cubitus : 10 = DT max olécrane ; 11 = DT processus anconé ; 12 = DT min. incisure trochléaire

- fémur : 10 = DT tête ; 11 = distance grand trochanter-petit trochanter

- Pour la rotule : 1 = DDP ; 2 = DT ; 3 = DAP méd. ; 4 = DDP articulaire ; 5 = DT articulaire.

humerus : 1- CHA.1-G.8-276 r. ; 2- CHA.1-01-F.8-233 r. ; 3- CHA.1-07-EE.25-13+21 l.

radius : 1- CHA.1-00-F.8-25 r. ; 2- CHA.1-07-EE.25-16 l. ; 3- CHA.1-01-F.8-135 r. ; 4- CHA.1-G.6-72 l. ; 5- CHA.1-00-F.8-149 r.

ulna : 1- CHA.1-07-Y.22-149 r. ; 2- CHA.1-00-F.8-24+277 r. ; 3- CHA.1-98-F.6/7+Eb.tr.3 r. ; 4- CHA.1-GAR.1 A l. ; 5- CHA.1-G.7-103-fissure S.E. r. ; 6- CHA.1-F.7-16 l. ; 7- CHA.1-00-F.8-125 l. ; 8- CHA.1-01-F.7-104 r. ; 9- CHA.1-00-F.8-32 l. ; 10- CHA.1-07-EE.25 l.

femur : 1- CHA.1-01-F.7-132 l. ; 2- CHA.1-02-G.8-354 r. ; 3- CHA.1-01-F.8-240 l. ; 4- CHA.1-H.6-10 r. ; 5- CHA.1-G.7-58 r.

patella : 1- CHA.1-02-G.8-389 l. ; 2- CHA.1-01-G.8-173 l. ; 3- CHA.1-01-F.8-204 l. ; 4- CHA.1-01-G.8-114 r.

tibia : 1- CHA.1-00-F.8-40 r. ; 2- CHA.1-01-F.8-263 r. ; 3- CHA.1-01-F.8-229 r. ; 4- CHA.1-02-G.8-338 l.

fibula : 1- CHA.1-01-F.7-110 l. ; 2- CHA.1-01-F.8-218 l. ; 3- CHA.1-07-Y.22-145 r. ; 4- CHA.1-01-F.7-137 r. ; 5- CHA.1-G.7-99 r.

The complete right tibia F.8-40 (tab. 5) allows us to make a comparison. It is definitely a Felid's. It has the same length as that of the today's lioness which we used for comparison but its diaphysis is clearly wider. The median TD vs median APD is :

P. leo (extant female) = 24.3 x 26.7 mm

P. gombaszogensis = 29.4 x 30.9 mm

The tibial crest of *Panthera gombaszogensis* is strongly developed, higher and wider, more turned over, and creates a deeper tibial fossa. The general dip of the upper edge of the bone towards the middle of the diaphysis is thus more pronounced. This is a distinctive characteristic of the jaguar.

As is often the case in deposits, the best preserved bones the short ones, solid and less fragile. The carpus, tarsus, metapodials and particularly the phalanges and sesamoid bones appear well represented and in an excellent state of preservation. Of course these are the most numerous bones in a skeleton. They allow us to measure almost everything (tab. 6 and 7). Morphologically, differences exist between the *Panthera gombaszogensis* from Château, *Panthera spelaea* and living *Panthera leo*, and even with today's *Panthera onca*. These differences are to be spelt out in the future. For example, the metapodial bones of *Panthera gombaszogensis* look shorter and relatively more massive; the carpus and tarsus record variations which reflect slightly different locomotory adaptations.

The different phalanges and the sesamoid bones, very well preserved, are still the more numerous. Table 8 provides a statistical evaluation of their size and details for two individual cases. The first phalanges and the sesamoid bones retained belong to the same individual as the complete skull.

With respect to morphology, we can recognise the characteristics of the large Felidae of the genus *Panthera* as well as a clear closeness to the present-day jaguar. On the other hand, the *Panthera gombaszogensis* from Château is clearly bigger than the extant *Panthera onca* and keeps some primitive characters.

4.3 - "COMPLETE" INDIVIDUAL: ACCORDING TO THE SPATIAL DISTRIBUTION F.8 - G.8.

Breccia 4 in the Ensemble Nord (the most ancient) can reasonably be attributed to the early Middle Pleistocene because it is older than Breccia 3 and 2 which are contemporaneous with Mosbach 2 in Germany (median Middle

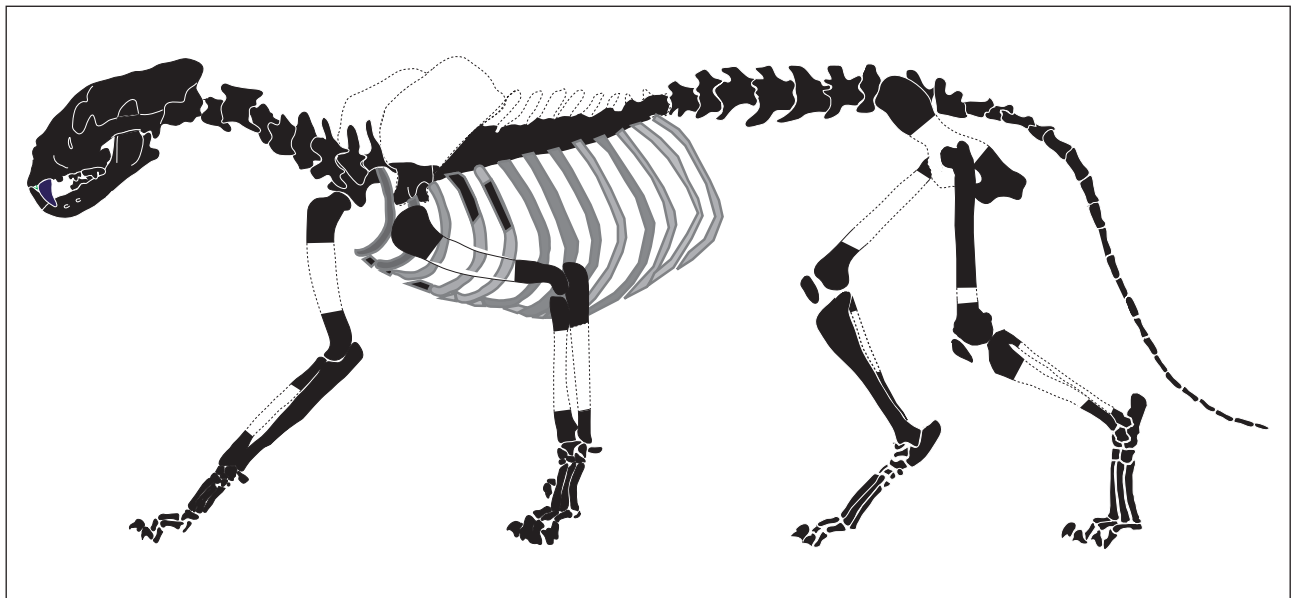


Fig.9: Château (CHA.1). Elements of the complete skeleton of *Panthera gombaszogensis* found in Breccia 4 (after Turner & Antón, 1997, p. 71, figs 3, 27).

Fig.9 : Château (CHA.1). Eléments du squelette complet de *Panthera gombaszogensis* trouvé dans la Brèche 4 (d'après Turner & Antón, 1997, p. 71, figs 3, 27).

<i>Panthera gombaszogensis</i> - Carpus and metacarpals										
TN Measures →		Lat	1	2	3	4	5	6	7	8
Sample ↓										
Scapholunar	CHA.1-G.7-64	r.	26.0	39.7	33.3	40.8	25.3	38.0	24.6	49.1
	CHA.1-02-H.8-43	r.	25.9	-	-	40.2	26.1	37.8	27.0	-
	CHA.1-01-F.8-194	r.	27.3	41.8	33.4	37.4	24.6	28.2	28.5	48.9
	CHA.1-99-I.7-66	l.	-	43.3	33.6	-				
Pyramidal	CHA.1-01-F.8-206	l.	22.9	10.2	15.5					
	CHA.1-G.8-399	r.	24.1	10.0	16.3					
Pisiform	CHA.1-01-F.8-241	l.	22.9	10.2	15.5					
	CHA.1-01-F.8-196	r.	24.1	10.0	16.3					
Unciform	CHA.1-G.7	l.	25.0	19.0	24.7					
Capitatum	CHA.1-02-F.8-274	r.	31.0	23.7	20.6					
Trapezoid	CHA.1-G.7-80	r.	22.0	11.0	18.9					
Trapezium	CHA.1-G.7-69	l.	25.6	14.4	14.5					
	CHA.1-02-G.8-360	r.	25.4	14.1	14.0					
Mtc 1	CHA.1-G.7-78-fissure	l.	39.0	21.7	14.2	15.0	12.1	17.2	15.4	17.9
	CHA.1-02-G.9-11	l.	37.8	21.4	14.4	16.7	12.0	16.4	14.9	17.7
	CHA.1-01-D.5-207	l.	36.4	18.5	12.9	13.5	11.0	16.0	15.0	16.4
	CHA.1-01-F.8-186	r.	38.3	20.1	14.6	14.2	12.3	16.1	14.6	17.4
	CHA.1-01-J.8-15	r.	39.1 *	-	-	14.4	-	17.2	13.6	16.7
Mtc 2	CHA.1-00-F.8-91	r.	79.3	20.1	-	13.3	12.7	19.0	17.4*	16.6
	CHA.1-00-F.8-30	r.	79.0*	20.4	-	13.5	13.9	-	-	-
	CHA.1-00-F.8-167	l.	-	-	-	13.5	13.7	19.9	17.1	18.4
Mtc 3	CHA.1-00-F.7-53+F.8-31	r.	98.9*	23.1*	15.1	13.3	13.0	22.3	19.8*	19.6
	CHA.1-00-F.7-87	r.	92.5	25.7	13.9	14.0	12.4	22.2	17.2	18.0
Mtc 4	CHA.1-00-F.8-29	r.	-	19.1	22.4	13.5	13.0	-	-	-
Mtc 5	CHA.1-G.7-124	l.	73.6	20.7	18.7	12.0	12.3	19.3	17.5	16.8
	CHA.1-00-F.8-100	r.	74.6*	20.0	18.5	12.2	12.2	19.5	17.2	17.3
	CHA.1-HS-169	l.	-	19.6	20.1	12.5	11.6	-	-	-
	CHA.1-07-EE.25-31	r.	70.8	19.0	20.6	11.3	12.6	18.4	17.5	17.2

Tab. 6: Château (CHA.1), *Panthera gombaszogensis*. Carpus and metacarpus. The numbers (TN) on the horizontal line (1 to 8) indicate the measurements taken and vary with bones:

– scapholunar: 1 = DPD; 2 = TD; 3 = APD; 4 = prox articular TD; 5 = prox articular APD; 6 = articular TD dist.; 7 = distal articular APD; 8 = max L (diagonally)

– From pyramidal to trapezium: 1 = APD (length); 2 = TD (width); 3 = DPD (height)

For all metacarpal bones, the numbers (TN) on horizontal line have all the same meaning: 1 = Length; 2 = prox TD; 3 = prox APD; 4 = med TD; 5 = med APD; 6 = dist TD; 7 = dist APD; 7 = dist APD; 8 = dist articular TD.

Tab. 6 : Château (CHA.1), *Panthera gombaszogensis*. Carpe et métacarpe. Les numéros (TN) horizontaux (de 1 à 8) correspondent aux mesures prises et varient suivant les os :

– scapholunaire: 1 = DDP ; 2 = DT ; 3 = DAP ; 4 = DT articulaire prox ; 5 = DAP articulaire prox ; 6 = DT articulaire dist. ; 7 = DAP articulaire distal ; 8 = L max suivant diagonale

– de pyramidal à trapèze : 1 = DAP (longueur) ; 2 = DT (largeur) ; 3 = DDP (hauteur)

Pour tous les métacarpiens, les numéros (NT) horizontaux ont tous la même signification : 1 = Longueur ; 2 = DT prox ; 3 = DAP prox ; 4 = DT méd ; 5 = DAP méd ; 6 = DT dist ; 7 = DAP dist ; 7 = DAP dist ; 8 = DT dist articulaire.

Pleistocene). In Breccia 4 a skull and numerous skeletal elements in continuity or in anatomical proximity were discovered. The position in which these components were found implies that an intact jaguar corpse with its bones still connected by ligaments was transported by water and/or mudflows, then deposited with its head inside and protected by a small pothole which water had hollowed out in the surrounding limestone a long time before. It is obviously of the greatest palaeontological interest to be able to characterise with certainty the same individual. The tables of data provide as far as possible the

metric information which pertain to this individual, but a detailed taphonomic study has not yet been completed and will be the subject of a later publication.

How heavy was the *Panthera gombaszogensis* from the Château Breccia? There are important differences within present-day populations of *Panthera onca*, their body mass being generally between 56 and 96 kg. But the heaviest males can reach 159 kg, just like a lioness. The smallest known males weigh only 36 kg. Important variations are also linked to their geographical location and to their habitat. The jaguars that live in wet tropical forest

<i>Panthera gombaszogensis- Tarsus and metatarsals</i>										
TN Measures →		Lat	1	2	3	4	5	6	7	8
Sample ↓										
Calcaneus	CHA.1-00-F.8-144	l.	96.3	44.6	41.5	-	28.8	73.6	20.6	39.4
	CHA.1-00-F.8-148	r.	99.3	46.8	43.3	-	29.0*	73.2	20.1	40.0
	CHA.1-G.7-20+35	l.	-	-	43.9	26.2	29.0	69.2	18.4	-
	CHA.1-H.3-73	l.	-	45.4	46.2	-	-	-	20.4	39.8
	CHA.1-G.6-24	r.	-	-	46.0	-	-	-	23.3*	-
	CHA.1-G.7-50	l.	-	44.8	-	-	-	-	-	-
	CHA.1-I.6-1	l.	-	-	-	28.5	-	-	-	-
Astragalus	CHA.1-00-F.8-142	l.	49.5	43.5	30.2*	25.5	32.3	23.4	29.2	56.5
	CHA.1-00-F.8-166	r.	49.5	42.4*	30.6*	27.2	-	23.9	30.3*	58.9
	CHA.1-G.6-121	r.	50.2	-	-	26.2	31.3	23.0	-	56.9
	CHA.1-F.7-9	r.	50.9	-	33.0	27.6	-	23.5	31.2	-
Cuboid	CHA.1-HS-15	l.	28.3	26.7*	28.0					
	CHA.1-01-J.8-16	l.	28.1*	-	27.7					
	CHA.1-01-G.8-87	r.	27.7	25.8	26.5					
	CHA.1-G.7-67	r.	28.3	27.2	28.3					
Navicular	CHA.1-00-F.8-145	l.	34.3	31.6	19.6					
	CHA.1-F.7-3	l.	36.3	36.6	20.1					
	CHA.1-01-F.8-249	r.	33.4	31.7	20.6					
Cuneiform 1	CHA.1-01-I.5-1	l.	-	-	14.7					
	CHA.1-00-F.8-51	r.	21.0	10.8	14.5					
	CHA.1-00-F.8-140	l.	-	9.6	15.6					
Cuneiform 2	CHA.1-G.7-79	l.	21.5	11.3	14.0					
	CHA.1-G.8-105	l.	21.2	11.9	14.4					
	CHA.1-01-F.8-222	l.	20.0	11.2	11.8					
	CHA.1-01-G.8-144	r.	22.0	13.0	14.1					
Cuneiform 3	CHA.1-G.7-51	l.	38.1	23.4	20.1	18.0	7.9			
	CHA.1-00-F.8-138	l.	36.7	22.2	19.3	15.9	7.4			
	CHA.1-HS-21	l.	36.8	22.6	19.8	18.8	10.0			
	CHA.1-HS-154	r.	-	24.6	18.4	-	-			
	CHA.1-01-G.8	r.	-	23.5	18.2	-	-			
Mtt 2	CHA.1-00-F.8-141	r.	98.0	17.7	26.5	13.8	12.4	20.0	17.4	17.9
	CHA.1-G.7-56	r.	-	18.9	27.5	-	-	-	-	-
Mtt 3	CHA.1-01-F.7-146	l.	-	22.2*	29.4	16.0	12.6	-	-	-
	CHA.1-00-F.8-15	l.	-	25.0	-	-	-	-	-	-
	CHA.1-01-F.8-266	r.	-	22.6	29.5	15.8	12.5	-	-	-
	CHA.1-G.6-79	r.	-	25.2	32.6	-	-	-	-	-
Mtt 4	CHA.1-01-F.8-211	l.	112.9	21.7	25.1	13.4	13.3	20.2	18.5	17.8
	CHA.1-HS-152	l.	-	21.8	25.5	-	-	-	-	-
	CHA.1-01-F.7-136	r.	112.4	21.6	25.3	13.8	14.0	20.5	18.5	17.9
	CHA.1-02-G.8-269	r.	119.9*	-	-	14.9	15.2	21.0	19.3*	18.7
	CHA.1-HS-153	l.	-	19.9	22.1	-	-	-	-	-
	CHA.1-02-H.8-64	r.	-	22.2	-	15.7	13.4	20.2	19.8	18.3
Mtt 5	CHA.1-00-F.8-89+90	l.	101.4	21.9	17.6	11.3	10.0	17.8	17.1	16.0
	CHA.1-G.7-66	l.	-	-	17.9	-	-	-	-	-
	CHA.1-00-F.8-89	r.	-	20.1	15.5*	10.4	11.3	-	-	-
	CHA.1-02-G.8-220	r.	-	-	-	-	-	17.7	17.6	16.1

Tab. 7: Château (CHA.1), *Panthera gombaszogensis*. Tarsus and metatarsus. The numbers (TN) on the horizontal line (1 to 8) indicate the measurements taken and vary with bones:

- Calcaneus: 1 = Length; 2 = prox TD; 3 = prox APD; 4 = TD tuber calcanei; 5 = APD tuber calcanei; 6 = L manubrium; 7 = min TD diaphysis; 8 = max articular TD

- astragalus: 1 = Length; 2 = prox TD; 3 = prox APD; 4 = TD tuber calcanei; 5 = APD tuber calcanei; 6 = L manubrium; 7 = min TD diaphysis; 8 = max articular TD

- from cuboid to cuneiform 2 : 1 = APD (Length); 2 = TD (width); 3 = DPD (height)

- cuneiform 3 : 1 = APD; 2 = TD; 3 = DPD; 4 = max TD caput; 5 = min TD col.

For all metatarsial bones, the numbers (TN) on horizontal line have all the same meaning: 1 = Length; 2 = prox TD; 3 = prox APD; 4 = med TD; 5 = med APD; 6 = dist TD; 7 = dist APD; 8 = dist articular TD.

Tab. 7 : Château (CHA.1), *Panthera gombaszogensis*. Tarse et métatarses. Les numéros (TN) horizontaux (de 1 à 8) correspondent aux mesures prises et varient suivant les os :

- calcanéum : 1 = Longueur ; 2 = DT prox ; 3 = DAP prox ; 4 = DT tuber calcanei ; 5 = DAP tuber calcanei ; 6 = L manubrium ; 7 = DT min diaphyse ; 8 = DT max articulaire

- astragale : 1 = Longueur ; 2 = DT ; 3 = DAP ; 4 = DAP min ; 5 = DT trochlea ; 6 = DT col ; 7 = DT tête ; 8 = L. diagonale max.

- de cuboïde à cunéiforme 2 : 1 = DAP (Longueur) ; 2 = DT (largeur) ; 3 = DDP (hauteur)

- cunéiforme 3 : 1 = DAP ; 2 = DT ; 3 = DDP ; 4 = DT max tête ; 5 = DT min col.

Pour tous les métatarsiens les numéros (TN) horizontaux ont tous la même signification : 1 = Longueur ; 2 = DT prox ; 3 = DAP prox ; 4 = DT méd ; 5 = DAP méd ; 6 = DT dist ; 7 = DAP dist ; 8 = DT dist articulaire.

CHA.1, <i>Panthera gombaszogensis</i> , phalanges and sesamoid bones									
	TN →	1	2	3	4	5	6	7	8
Phalanx 1	n	8	8	8	8	8	8	8	7
	min	41.6	15.9	14.7	9.6	10.5	15.2	10.7	14.2
	max	50.9	20.4	16.7	16.1	12.7	16.9	12.9	16.8
	mean	47.3	19.1	15.7	13.7	11.1	15.8	12.0	15.7
	σ n	3.4	1.5	0.7	2.0	0.7	0.7	0.7	0.9
Phalanx 1, finger 1		39.00	21.73	13.43	15.46	11.22	17.13	15.99	18.41
Phalanx 2	n	11	9	11	11	11	11	11	11
	min	27.4	14.8	12.5	9.4	8.5	13.2	9.6	13.2
	max	38.3	19.6	17.4	11.6	12.0	16.0	12.2	16.0
	mean	33.62	16.39	15.34	10.51	10.39	14.53	11.09	14.40
	σ n	3.53	1.36	1.41	0.81	1.01	0.91	0.75	0.85
	TN →	1	2	3					
Phalanx 3	n	8	5	8					
	min	11.5	26.9	3.5					
	max	13.5	34.7	3.8					
	mean	12.55	30.19	3.63					
	σ n	0.69	2.91	0.14					
	TN →	1	2	3					
Sesamoid bones	n	10	10	10					
	min	7.2	18.9	9.2					
	max	9.6	23.0	12.1					
	mean	8.41	21.55	11.00					
	σ n	0.73	1.20	0.85					

Tab. 8: Château (CHA.1), *Panthera gombaszogensis*. Phalanges and sesamoid bones. The numbers (TN) on the horizontal line (1 to 8) indicate the measurements taken:

– phalanges 1 and 2: 1 = Length; 2 = prox TD; 3 = prox APD; 4 = med TD; 5 = med APD; 6 = dist TD; 7 = dist APD; 8 = dist articular TD.

– phalanx 3 : 1 = prox TD; 2 = prox APD; 3 = med TD blade

– sesamoid : 1 = articular TD; 2 = APD (Length); 3 = DPD (thickness)

The series of phalanges 1 and the series of sesamoid bones are from the same individual, the one with «complete» skull.

Tab. 8 : Château (CHA.1), Panthera gombaszogensis. Phalanges et sésamoïdes. Les numéros (TN) horizontaux (de 1 à 8) correspondent aux mesures prises.

– phalanges 1 et 2 : 1 = Longueur ; 2 = DT prox ; 3 = DAP prox ; 4 = DT méd ; 5 = DAP méd ; 6 = DT dist ; 7 = DAP dist ; 8 = DT dist articulaire.

– phalange 3 : 1 = DT prox ; 2 = DAP prox ; 3 = DT méd lame

– sésamoïde : 1 = DT articular ; 2 = DAP (Longueur) ; 3 = DDP (épaisseur)

La série des phalanges 1 et la série des sésamoïdes proviennent du même individu, celui du crâne «complet».

areas reach an average body mass of 42 kg for the females and 57 kg for the males, and respectively 76 and 87 kg in the Pantanal plain in Brasil (Medellin *et al.*, 2002). H. Hemmer estimates that the body mass of *Panthera gombaszogensis toscana*, the smaller and older villafranchian subspecies, varies from 70 to 210 kg and from 90 to 120 kg for *Panthera gombaszogensis gombaszogensis*, the average being 140 kg (10 individuals) (Hemmer, 2001). Using the calculations of B. Valkenburgh (1990) in the body mass of Felids based on the skeleton and the teeth, for the M/1: log of body mass = 3,05 x log of length of the M/1 (mean of 7 values) -2,15, we get weights from 95 to 150 kg at the maximum and an average body mass of 130 kg for the *Panthera gombaszogensis* of Château. These results seem coherent.

4.4 - BIOCHRONOLOGY

Felid's lower carnassial is generally a well-studied tooth. **Figure 10** is the diagram of the width vs length distribution of this molar in *P. gombaszogensis toscana*,

P. gombaszogensis gombaszogensis as well as in modern *P. onca*. In this diagram, we have not retained the data from the new fossil felid material from the Plio-Pleistocene site of Tegelen (Netherlands) (O'Reagan & Turner, 2004) because we think that there occur two different species of Felids. Figure 1, p. 1184, shows the external view of a left half-mandible (NGM 103142) which belongs to *Puma pardoides* of big size rather than *Panthera gombaszogensis toscana*. It is very similar to that of *Puma pardoides* from Saint-Vallier (Drôme, France) (Viret, 1954 ; Argant, 2004), excepted the posterior part of the M/1, but the authors indicate that this part of the tooth is damaged. Tegelen probably yielded both *Puma pardoides* and *Panthera gombaszogensis*. Only the biggest form should be *P. gombaszogensis*. Because of the mode of occurrence, its stratigraphic position remains uncertain. The site of Untermassfeld (Germany) also yields such an association during the Early Pleistocene. The distribution of the M/1 of the Felid from Château shows that it is really *P. gombaszogensis gombaszogensis*. The size of the M/1 of *P. gombaszogensis toscana* and of

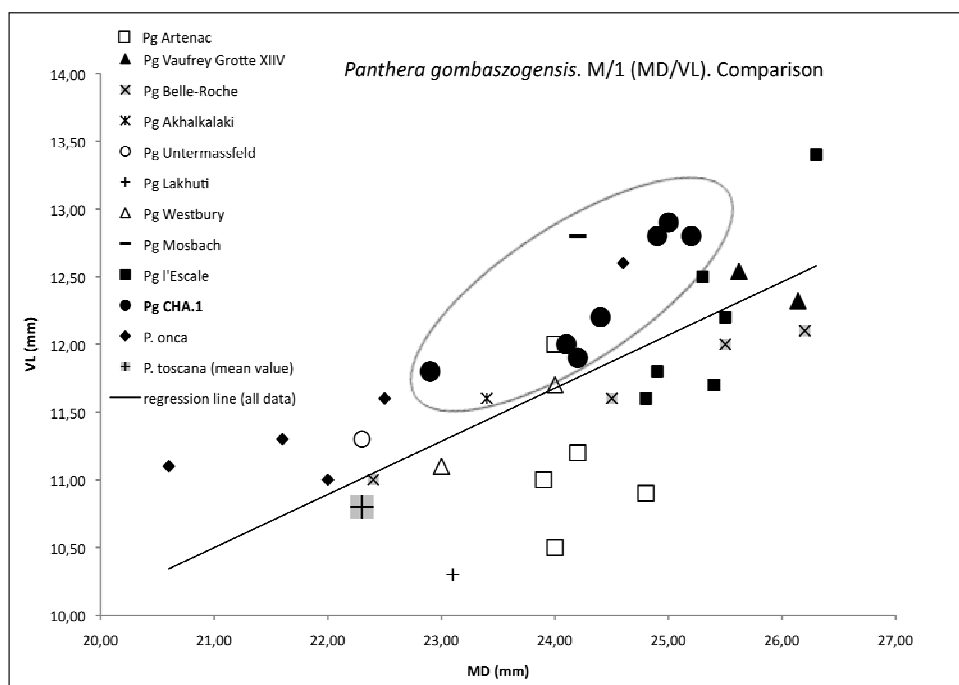


Fig.10: *Panthera gombaszogensis*, scatter diagram for the length and width of the M/1 from various sites. Position of CHA.1.

Fig.10: Panthera gombaszogensis, diagramme de répartition de la longueur et de la largeur de la M/1 de différents sites. Position de CHA.1.

Panthera onca is clearly smaller. The Felid from Château is of average size, which confirms that it belongs to the Middle Pleistocene forms, at the end of their evolution. Referring to present-day jaguars, the forms from open areas tend to be the biggest while those from woodlands tend to be darker and lighter.

5 - PALAEOENVIRONMENTAL CONTRIBUTION OF THE CHÂTEAU BRECCIA

Two samples of the Breccia 4 have been analyzed by J. Argant (Argant *et al.*, 2007) for pollen study (fig. 11):

– CHA.1-01-G.8-21bis has been taken from under a block covering the tooth of a Carnivore. The pollen spectra is based on 300 pollen grains and spores which represent 30 different taxa : 45,4 % of arboreal pollen (AP), 48,8 % of herbs and 5,7 % of fern spores. It reflects a largely open landscape. The dominant tree pollen is that of *Pinus* (27 %), then *Quercus* (10,4 %). We find also *Abies* (2,7 %), and broadleaved trees, essentially *Betula*, *Alnus* and *Juglans*.

The herbs are all heliophilous and mostly represented by Poaceae and Cichorioideae. Ranunculaceae, Brassicaceae and *Plantago* occur among other numerous taxa. This relative diversity implies grassy areas in various ecological niches.

– CHA.1-F.8-158, taken under the complete skull of *Panthera gombaszogensis* (F.8-73) gives us a similar result (341 pollen grains and spores, 25 taxa) in spite of some divergences concerning the amount of fern spores (40 %) probably due to the local presence of these plants on limestone walls.

These spectra indicate a temperate climate but colder than today and sometimes even quite cold. The landscape was open with grasses spread on the uplands, while woodlands of pine and fir, but also of some broadleaved trees such as oak, birch, walnut tree distributed in the valley.

Panthera gombaszogensis has traditionally been considered as a forest dweller, with a preference for locations close to large streams (Hemmer, 2010). This idea, obviously influenced by our knowledge of the present-day jaguar of Central or South America, cannot be generalised without significant qualification.

In the small valley where the Repentir flows today, a small permanent stream about a meter wide has always flowed, in all likelihood throughout the Pleistocene if the width and form of the valley is any indication. About 5 km downstream, the Repentir flows into the Grosne, a small river about 3 m wide at this location. After a journey of about forty kilometres from this point, the Grosne joins the Saône, the only large river in this region. However one does the calculation, the Saône is always at least 30 km away from the Château Breccia. Palynology suggests that the vegetation in the vicinity of the Château Breccia consisted of a concentration of trees on the lowlands and in the valleys, with herbaceous plants and grasses on the uplands and summits. This was not a riparian forest environment.

Panthera gombaszogensis benefitted from favourable conditions at Château: 385 m above sea level, upstream from a small brook valley, with small caves opening towards the south-east at the bottom of low cliffs, and not far from three permanent springs. The area probably

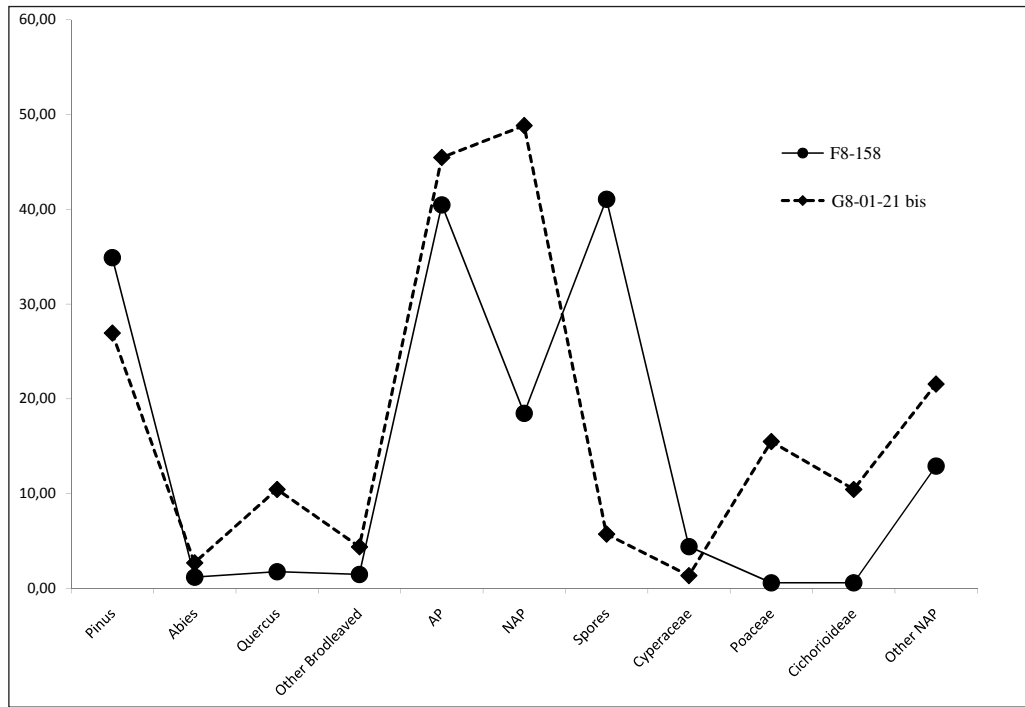


Fig. 11: Château (CHA.1), simplified results of pollen analysis of two samples from Breccia 4.

Fig. 11 : Château (CHA.1), représentation schématique des résultats de l'analyse pollinique de deux échantillons de Brèche 4.

attracted herbivores on their way towards the granite summits (e.g. Mont Gremoi, 555 m asl), the Guye valley (Pontot pass) and the Grosne valley (Les Granges pass).

Over the course of the Early Pleistocene, the Eurasian expansion of *Panthera gombaszogensis* continued as far as North America, via what is now the Bering Strait. The need for a terrestrial passage means that the current stretch of water about 60 m deep could not have been there. The continuity of the two "Beringia" continents can only be explained by a climate cold enough to greatly lower the sea level. *Panthera gombaszogensis* has obviously proved to be capable, at least at a particular time, of adapting to the especially harsh climates of glacial periods. It should not be forgotten that large cats such as the Siberian tiger (for example) are able to withstand very harsh climatic conditions in winter while other populations of the same species are perfectly adapted to tropical conditions. We should therefore refine our first impressions of the palaeoclimatic significance of *Panthera gombaszogensis* and of its ethology. A key feature of the latter is the great adaptive capacity of the carnivores. It is probably the presence of potential prey that has played the decisive role in population dynamics.

6 - CONCLUSION: "THE PANTHERA GOMBASZOGENSIS STORY"

The palaeontological study of jaguars is far from finished but palaeontologists have begun to reconstruct

with some degree of certainty the history of this large feline which underwent a considerable geographic expansion during the course of the Pleistocene, passing from Africa into Europe, then into Asia before finally ending up in Central and South America where its remaining populations live today. There are obviously many points still to be clarified, particularly its very early history, its expansion in Africa, and the time of its disappearance from this continent. There has been spectacular progress in our knowledge of this animal in Eurasia but numerous points remain to be clarified, particularly the precise time and causes of its disappearance. The Château Breccia is making a significant contribution to this history. It confirms the very wide expansion of the species during the Middle Pleistocene including its presence in Burgundy where the evidence suggests it found favourable conditions. The deposit provides proof of the adaptability of the species to a cold temperate climate, much colder than today's climate, and to a biotope quite different to that found in riparian forests bordering large rivers where the jaguar lives today. The Château Breccia also allows us to follow over time the evolution of an association between the large carnivores and other fauna, from the early and median Middle Pleistocene (Ensemble Nord, SIPO) up until the late Middle Pleistocene (Ensemble Sud). It records the disappearance of the jaguar and its replacement, after a period of coexistence, by the very large cave lion, *Panthera spelaea fossilis*. The dating that we are able to put forward for this event corresponds at Château to the late Middle Pleistocene, about 0.6 Myr. But its final extinction in Europe is generally accepted,

not without argument, to have occurred at the end of the second last glaciation (in the course of OIS 6) (D. Janossy, oral comm.). This last point deserves future clarification.

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