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The cave lion *Panthera* (*Leo*) *spelaea* and its evolution: *Panthera spelaea intermedia* nov. subspecies

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Abstract: The ancient form of the cave lion, *Panthera* (*Leo*) *spelaea fossilis* reported in Eurasia from the median Middle Pleistocene and the more recent one, *P. (Leo) spelaea spelaea* which became extinct at the last Tardiglacial (MIS 2), can be clearly distinguished by their size, but the distinction between the intermediate forms becomes more difficult. The Igue des Rameaux site (Southwestern France) yields an abundant population of cave lions related to upper Middle Pleistocene (MIS 10 to MIS 6) which allows us to characterize a standard population of one of these intermediate forms which we call *Panthera (Leo) spelaea intermedia*. It is clearly different from *P. spelaea fossilis* because of its smaller size. But the distinction between this population and the more recent ones is more uncertain because of very variable size of the cave lions during this time span. For the best characterisation of *Panthera spelaea intermedia* the morphology is used and criteria of distinction established, but the chronology provides also a major indication. A small sized form from the upper Middle Pleistocene suggests *P. s. intermedia*, while the small sized forms of the Upper Pleistocene correspond to the more recent *P. s. spelaea*. The population of the Igue des Rameaux represents a new reference point for comparisons between the fossil series of *Panthera spelaea* of Western Europe.

Key words: *Panthera spelaea*, evolution, Middle Pleistocene, Late Pleistocene, Igue-des-Rameaux, *Panthera spelaea intermedia nov.* ssp.

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I. INTRODUCTION

The main trends in the evolution of the cave lion have been known for a long time (SCHÜTT 1969; SCHÜTT & HEMMER 1978; ARGANT 1991, 2010; SABOL 2011; MARCISZAK et al. 2014). They come up against a major obstacle, the knowledge of the intermediate forms between the ancient ones *Panthera spelaea fossilis*, characterized by their very big size, and the more recent *Panthera spelaea spelaea* decreasing progressively to the size of an extant lion. Between these two relatively certain evolutionary stages the situation is more complicated. The rarity of material in the deposits constitutes a second obstacle, especially when, as in the case of the cave lion, it is insufficient to provide a statistically valid series. Furthermore, the material for comparison is very often poorly dated, without any precise stratigraphical context, particularly for the periods out of the range of ^{14}C. The Igue-des-Rameaux deposit (Saint-Antonin-Noble-Val, Tarn-et-Garonne, France) has all the requirements to make it the benchmark for this intermediate period, because of its abundance of relatively well-dated palaeontological material.

II. CONVENTIONS

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

Abbreviations:

* approximately
APD = antero-posterior diameter = length
C = character
DPD = dorso-palmar or dorso-plantar diameter = height
HC = height of the crown
HT = total height (crown + root)
I3/ = upper incisor
L = left
M/1 = first lower molar
MD = mesio-distal diameter
min. = minimum; max. = maximum
MNI = minimum number of individuals
Mtc = metacarpal bone (ex.: Mtc.5)
NR = number of remains (complete or fragments)
P4/ = fourth upper premolar
PFEMA = Argant Plan for Morphometric Recording of Felids
prox. = proximal; dist. = distal
R = right
TD = transverse diameter
U = empirical scale of wear, a descriptive tool without mathematical meaning: U= 0, no wear; U= 1, visible but small; U= 2, average wear of the crown, enamel sometimes missing; U=3, severe wear but relief still visible; U= 4, crown almost worn out; U= 5, the wear table belongs to the root. A number with one decimal place only indicates an intermediate stage.
VL = vestibulo-lingual diameter.

III. *PANTHERA SPELAEA* SPECIES AND ITS EVOLUTION

Fig. 1.

In carrying out a study, the palaeontologist is observing the results of a chain of events beginning at the birth of an animal but which are observable only through the fossil re-

mains that the animal has left behind. What he discovers depends on multiple factors of varying but always decisive importance, but we can never know all the elements involved. The genetics of the species is obviously the major factor, dependent on the dynamics of the population, on chance meetings between males and females and occasional genetic mutations. Climatic variations, the existence or absence of refuge zones in difficult times, the animals' location, and the effects of new food supplies can all play an important role, of which we remain unaware most of the time. Adaption needed to survive under new conditions or the effects of migration to more favourable environments can also play an important role.

These evolutions are recorded in the skeletal remains of animals, according to their genetics of course, but also according to their adaptation to the natural environment. That depends on their body mass and their dominant physical characteristics as determined by their hunting techniques and the physical environment around them. It is therefore not surprising that we observe individual, geographical, climatic or chronological variations within the same species.

In palaeontology, the species corresponds to a type, first defined by an author and subsequently validated. It is not the same as a biologic species, which is defined according to different criteria, inaccessible in the case of extinct species. The type for the cave lion was originally *Felis spelaea*, named by GOLDFUSS based on material from Gailenruth in Germany (GOLDFUSS 1810). The name *Panthera (Leo) spelaea* (GOLDFUSS) (DIETRICH 1968), now widely used, necessarily corresponds to a species in the broad sense, covering all the variations that are usually very difficult to identify and of which we are most often unaware. Although the situation is better known today for the Upper Pleistocene species, it is still difficult to clarify for the more ancient periods of the Middle Pleistocene out of range of ^{14}C dating and ancient mt-DNA analysis.

The origin of the genus *Panthera* is probably in Africa at about 3.5 Ma at Laetoli (Tanzania). The first African fossils with clear lion characteristics occur in Oldovai – Upper Bed I (1.7-1.87 Ma), Kobi Fora Okote (1.39-1.64 Ma), Olduvai – Upper Bed II (1.2-1.4 Ma), and Omo Shungara (East Africa) (1.12 -1.39 Ma). The almost complete hemimandible from Olduvai – Upper Bed II clearly presents the first developed apomorphic lion tooth characteristics (LEAKEY 1965; PETTER 1973; HEMMER 2011).

Later the cave lion spread from Africa throughout Eurasia and even into North America. It is recorded at Hummal (El Kowm, Syria) at about 1 Ma (ELSUEDE & REYNAUD SAVIOZ 2017). In Europe, the oldest cave lions known are those from Isernia-la-Pineta in Italy (0.7 Ma; SALA 1990) and Pakefield in England (0.75-0.68 Ma; LEWIS et al. 2010). The *Panthera spelaea fossilis* (VON REICHENAU, 1906) from the Château Breccia (Saône-et-Loire, France) belongs to the most ancient forms of the Mid Middle Pleistocene like those of Mosbach and Mauer in Germany (about 0.6 Ma; ARGANT et al. 2007).

Its extinction occurred everywhere in Eurasia at the end of the last Tardiglacial period. The last specimens known are found at 12,248 ± 66 BP in the Parisian Basin (Le Closeau, Rueil-Malmaison, Hauts-de-Seine; BODU & BÉMILLI 2000; BODU et MEVEL 2008), at about 11,150 BP in the South West of France (Duruthy rock shelter, Landes; DELPECH 1983). In Germany the last cave lion dates to about 12,375 BP (Zigeunerfels Cave; STUART & LISTER 2011), in western Beringia to about 12,450 BP (Lena River STP, BARNETT et al. 2009) and to about 11,925 BP in eastern Beringia (Fairbanks Creek; BARNETT et al.

2009). The American lion became extinct later around 10,370 BP (Lost Chicken Creek; KURTÉN & ANDERSON 1980).

For the recent periods, developments in knowledge are evolving rapidly. The numerous ^{14}C-AMS datings and mt-DNA analyses allow us to follow the gradual evolution of European and Siberian lions during the Late Pleistocene. Mitochondrial DNA points to a split of the cave lion (*Panthera spelaea*) and the American lion (*Panthera atrox*) during the Late Middle Pleistocene between 489,000 and 194,000 BP. Phylogenetics analysis shows that *Panthera spelaea* is most closely related to the extant lions from Africa and Asia, but appears to be highly distinct from its living relatives. The cave lion lineages became extinct without mitochondrial descendants (BURGER et al. 2004). This confirms the name *Panthera* (*Leo*) *spelaea* which has been used by numerous palaeontologists for a long time.

Fig. 1. World distribution of the Pleistocene lions.

IV. IGUE DES RAMEAUX: CONTEXT, FAUNA AND CHRONOLOGY

(Fig. 2, Fig. 3)

The cave system of Igue-des-Rameaux in the South-West of France (Tarn-et-Garonne) belongs to a still partly active karstic network situated on the edge of a limestone plateau (Causse) overlooking the Aveyron River. The fossiliferous zone is divided into two independent sections, upstream and downstream, separated by a large stalagmitic concretion. The stratigraphy is complex and the filling has been affected by drainage at the midpoint, occurring later than the filling and partly disturbing the deposits. Taken as a whole, the upstream part constitutes Unit 5 (Layers 50 to 55) while the downstream part constitutes Unit 6 (Layers 60 to 63) (ROUZAUD et al. 1990; ROUZAUD 1997). Situated above on a stalag-

mitic floor (Layer 4) is Unit 3, a fossiliferous layer containing fauna which is more ancient. Units 5 and 6 have provided very abundant and diverse palaeontological material (herbivores, carnivores, lagomorphs, rodents, insectivores, birds, chiroptera, reptiles) (e.g., ROUZAUD et al. 1990; JEANNET 2005; BOUDADI-MALIGNE 2010; JEANNET & MEIN 2016), dominated by carnivores in the downstream sector and by herbivores in the upstream sector. Also important to mention is the presence of a small series of lithic artefacts (n = 76) in Unit 5. Based on the raw materials used and on the methods employed to shape the tools, they can be related to the lithic material from the lower to ancient middle Palaeolithic from Coudoulous I, Vaufrey and La Borde (JAUBERT in ROUZAUD et al. 1990; BRUGAL & JAUBERT 1991).

Several specific studies allow us to clarify the taphonomy of the site (FOSSE 1994; BRUGAL et al. 1997; COUMONT 2006; 2009), its palaeontological and palaeobiological contexts (CROITOR et al. 2008; BOUDADI-MALIGNE 2010, 2012; JEANNET & MEIN 2016; UZUNIDIS 2017), as well as provide a biochronological framework.

The carnivores particularly abundant in Unit 6 are represented by large populations of lions (present study) and wolves and hyaenas. Not less than 74 individual wolves are present, mainly females, but also males, adults (e. 53%), young adults (e. 18%), and lesser numbers of young or old. They have been identified as a chrono-subspecies *Canis lupus lunellensis*, an animal of small size that also occurs at Lunel-Viel (Hérault), La Fage (Corrèze) and Coudoulous I (Lot, lower unit). This subspecies is typical of the second half of the middle Pleistocene in Western Europe. The cave hyaena *Crocuta crocuta spelea* is represented by around 35 individuals including particularly large animals bigger than those from the Upper Pleistocene. This population is distinctive, dominated by prime-adults (57 %), then adults (25 %) with few young or old adults. Many coprolites are present, initially attributed to this species. However, the absence of young subjects, the composition of the population, and the low levels of activity on herbivore bones (e.g. horse), do not support the hypothesis that this site was a den s.s. for this species.

The upstream section contains numerous herbivore remains among which the horse (*Equus caballus*) is the dominant species. There are some differences between units (UZUNIDIS 2017): the horses of Unit 6 (less abundant) have more archaic characteristics (caballin index of metapodial bones, senonian crititeria on upper teeth) than those of Unit 5. The latter are a little more slender than those in the downstream section. Nevertheless the two groups are quite similar and all are attributed to the same species, well known from the middle Pleistocene, *E. caballus mosbaschensis*. The differences observed reflect a slightly different timing between the two accumulations.

A taphonomic analysis of the remains of herbivores and wolves has allowed us to assess the integrity of the units and the possible connections between them. Articular reconstructions, and dental and skeletal matching were systematically used to reveal connections, and while these were found to be frequent within each unit, none was found between these two units, which confirms their independence. These data lead us to envisage a filling in two stages *a minima*, both within the middle Pleistocene:

The presence of "ancient" taxa such as *Haploidoceros mediterraneus, Hyaena prisca, Arvicola cantiana* (high SDQ index, JEANNET 2005) (Unit 3) would indicate a first episode related to a middle stage of the middle Pleistocene, perhaps to the Holsteinian inter-

glacial (?) or MIS 11 (ca. 430-360 ka). These two first taxa are also present at Lunel-Viel 1 (BONIFAY 1967; BONIFAY & BRUGAL 1999) attributed to the "Mindel-Riss", but may be a little more recent (beginning of Riss). Furthermore, these species seem to endure, sporadically, until the beginning of the upper Pleistocene in Iberia (SANZ et al. 2014; BRUGAL et al. 2012);

The evolutionary stage of the wolves and horses, as well as the biometric data from the hyaena and the lion (present study) in Units 5 and 6, would suggest a slightly more recent stage. The faunal association is on the whole temperate (ROUZAUD et al. 1990) and indicates an interglacial or interstadial phase. The more probable hypothesis would be MIS 9 (ca. 330-300 ka), without, however, ruling out either a more ancient period (MIS 11-10) or a more recent one (MIS 9-7). Some racemization tests on horses' teeth from Unit 5 (analysis T. DE TORRES) would tend to support an older period (end of MIS 11). However, in other respects Unit 5 seems to be slightly later than Unit 6.

Some uncertainty therefore remains on the age of these deposits, partly because of our lack of knowledge about the evolutionary dynamics of large mammals, but also because of the scarcity of sites for this period. However, it is possible to attribute the filling of Igue des Rameaux to several periods, not necessarily far apart from each other (e.g. between Units 5 and 6), to the median middle or upper Pleistocene between MIS 11 and 7.

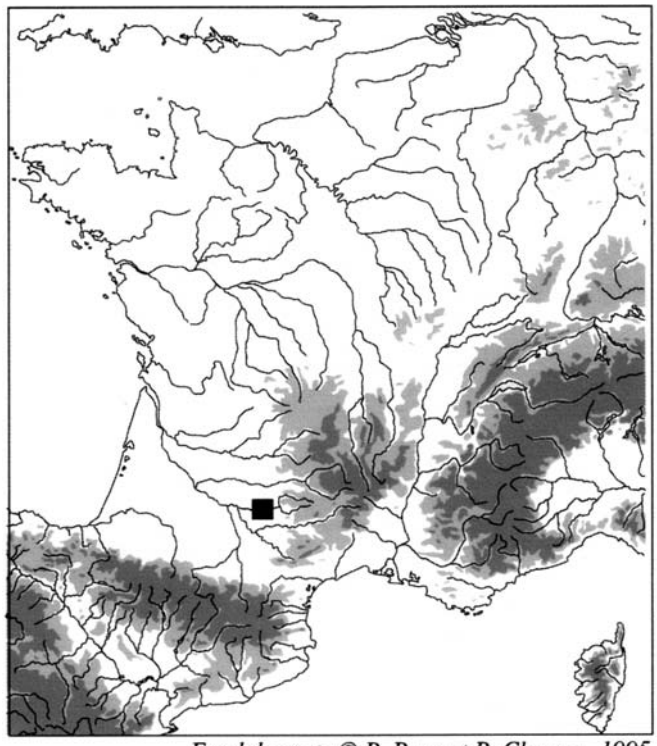


Fig. 2. Location map of the Igue des Rameaux cave at Saint-Antonin-Noble-Val, Tarn-et-Garonne, France (black square).

The origin of the accumulations in Igue des Rameaux has been the subject of several hypotheses, of which, for Unit 5, the most likely is the accidental fall of herbivores into the pothole (complete bones, extent of skeletal representation and connections, young adults – especially in the case of horses). The presence of a diverse collection of carnivores consisting of a great many individuals in Unit 6, raises some questions. The skeletal elements are most often complete (many skull remains, mandibles with teeth) and belong mainly to adults, although juveniles are also present, particularly of lions. There are relatively few marks of predators on the bones of herbivores, or of carnivores themselves. The topogra-

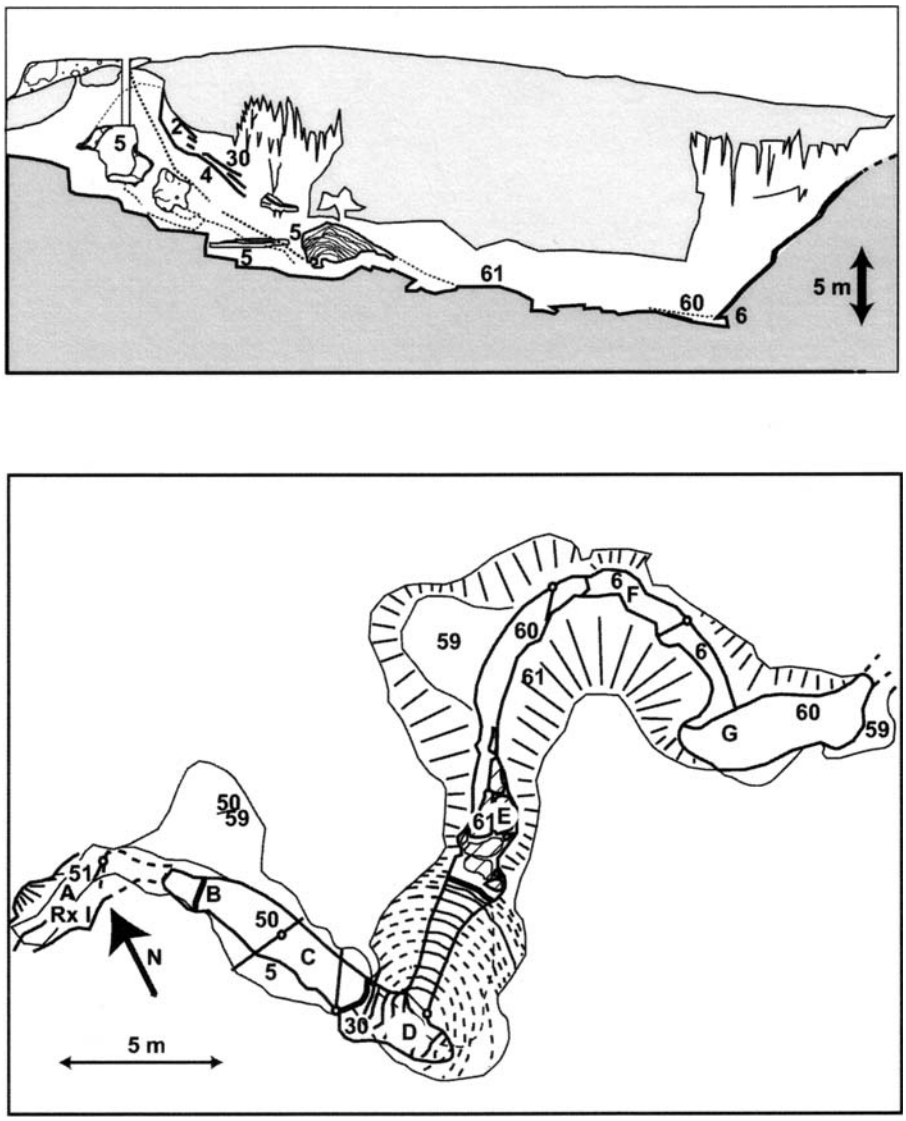


Fig. 3. Cross section and plan of the Igue-des-Rameaux cave.

phy of the cave is a key to understanding these accumulations. In the upstream sector (Unit 5), the dominant vertical component supports the hypothesis of a natural trap ("avens pièges", BRUGAL & JAUBERT 1991). In the downstream sector (Unit 6) the situation is different and a more horizontal entrance seems plausible, probably towards the bottom of the gallery now blocked by a thick stalagmitic concretion. Given such easier access, we can postulate that the cave has been occupied temporarily, voluntarily and repeatedly by many carnivores (including several populations of the same species), and their great number (in MNI) would be a consequence of the length of time over which the remains accumulated. Its function as a den for wolves and hyeanas seems not to have been validated, although it could have been a nursery for lions.

V. THE POPULATION OF *PANTHERA SPELAEA* OF IGUE DES RAMEAUX

M a t e r i a l. The material from Igue des Rameaux is well fossilized, at times slightly abraded from rolling, and beige to grey-beige in colour. While there are no complete skulls, there are large skull fragments. The mandibles are well preserved and there are lots of juvenile remains with numerous examples of milk/deciduous teeth in the process of being replaced by permanent teeth. All parts of the skeleton are represented. The abundance of the remains, their good state of preservation, and the very large number of very young and young individuals make this a rare and remarkable collection.

N u m b e r o f r e m a i n s e s t a b l i s h e d. NR *Panthera spelaea* = 1786. The count is always difficult. Numerous fragmented remains located in a clearly separate group have been counted as a single unit. There are also some isolated fragments which constitute a unit, but they are rare.

M i n i m u m n u m b e r o f i n d i v i d u a l s. MNI = 30 individuals based on 21 M/1 and 9 D/3 (juveniles) after taking account of possible left-right matches from the same individual.

P o p u l a t i o n. Studying the stages of dental eruption enables us to define with some precision the age of lions (SMUTS et al. 1978). The numerous hemimandibles at Igue des Rameaux, often with milk teeth in place and permanent teeth in course of eruption, lend themselves well to this exercise. Of course the cave lion is not the African lion but it is reasonable to assume that this parameter is constant within the genus. Out of 24 individuals, Fig. 4 shows the predominance of "cubs" (2-10 months), "juveniles" (14- 24 months) and "young adults" (2-4 years). Adults (5-9 years) and old adults (9-14 years) are in the minority and seniles with particularly worn teeth are not represented at all. The high levels of mortality among the younger age groups supports the idea that their place of birth was close by and that the topography of their environment represented a real trap for the least experienced animals, leading to relatively high rates of juvenile mortality, which is typical of carnivores.

It will not be possible to present all the data within this article. Only core metric data will be used to define the population of *Panthera spelaea* at Igue des Rameaux. More detailed morphometric data will be used when making comparisons with other European sites.

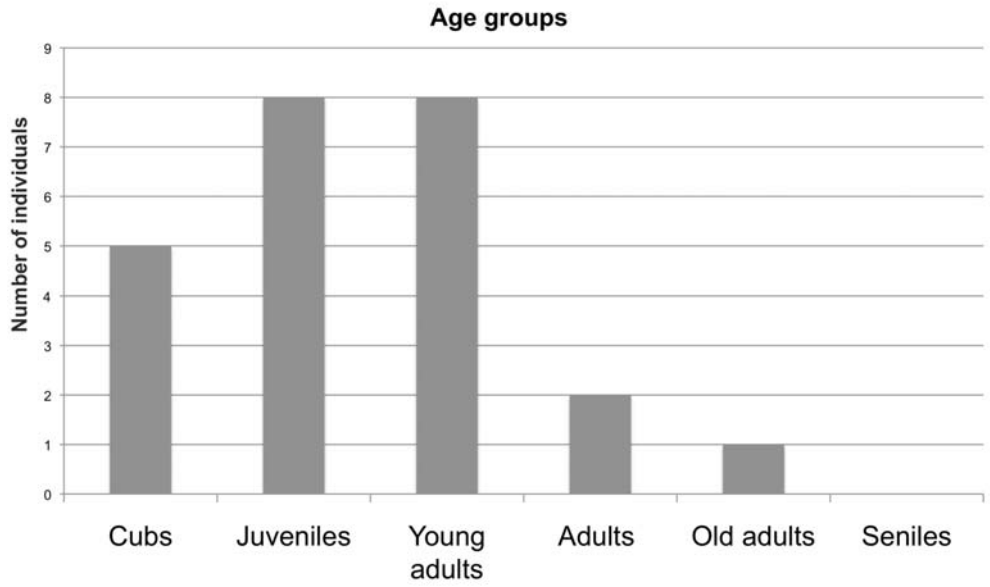


Fig. 4. *Panthera spelaea intermedia*, Igue-des-Rameaux, graph of population and age groups.
Cubs (2-10 months); Juveniles (10-24 months); Young adults (2-5 years); Adults (5-9 years); Old adults (9-14 years); Seniles (14 years).

The homogeneity of the population and therefore the assurance of its chronological position are the only features which allow us to validly use this population as a benchmark in the evolution of *Panthera spelaea*. The scatter diagram MD/VL of the upper canines (see Fig. 11) has been used to test this homogeneity. All these canines originate in Unit 6, mainly from Layer 60 (3 upper C), then Layer 62 (15 upper C) and lastly from Layer 63 (3 upper C). One exception is a small canine from Unit 5 (Layer 53). They all demonstrate a high level of homogeneity of the population, except however for two upper canines from Layer 63, Rx-G2N-C.63-179 (l) and Rx-G2N-C.63-213 (r), which are strongly discordant. These two teeth are clearly from the same individual, a young, very large male, with completely empty canines, free from wear and with a posterior edge still slightly notched (to the touch) as on newly erupted canines not yet smoothed by use. The left hemimandible (Rx90-G1N-c.62-151) surely belongs to the same individual. It has all the characteristics described above and its dimensions match perfectly. However, it comes from Layer 62 not 63. The situation has therefore become much more complicated because this lion is clearly different from the others in the group which have high levels of homogeneity, but to which it is linked by the co-location of this hemimandible. Two hypotheses can be put forward. The first of these is the possibility, as in any large population, of finding an individual much larger than normal. The second is the possible presence of an individual which is not contemporaneous with Layer 62, but which belongs to Layer 63 (Unit 6), a layer underlying and older than Layer 62. The co-location could have come about as a result of a slight reworking of the zone of contact between the two layers, a classic occurrence in a karstic environment. The second hypothesis enables us to attribute this individual to the large an-

cestral forms of *Panthera spelaea fossilis*. The latter disappeared at the end of the Holsteinian interglacial (MIS 11). Layer 63, the oldest layer at the bottom of the cave, could possibly belong to this last phase, a hypothesis which is consistent with the datings put forward for Igue des Rameaux. However, because of the doubt and as a precaution, we have excluded this very large individual from the data used to compare *Panthera spelaea intermedia* from Igue des Rameaux with the other sub-species.

Upper teeth: see Table 1.

Table 1

Panthera spelaea intermedia, Igue-des-Rameaux, upper teeth

Igue des Rameaux			1	2	3	4
Upper teeth			n	mean	Δ	sd
I	I 1/	MD	7	6.0	5.4-7.1	0.6
		VL	7	8.4	7.2-9.2	0.5
		HC	7	9.2	7.6-10.0	1.0
	I 2/	MD	7	6.8	6.3-7.3	1.1
		VL	7	9.5	8.8-10.0	1.0
		HC	7	10.8	9.6-12.0	1.2
	I 3/	MD	16	11.5	9.7-14.1	1.1
		VL	16	13.7	12.5-15.6	1.0
		HC	11	18.8	17.2-20.9	1.2
C	C sup.	MD	22	26.2	22.6-34.4	3.2
		VL	22	19.1	16.3-25.0	2.4
		HC	20	51.6	45.6-61.8	4.2
PM	P2/	MD	2	8.9	8.7-9.2	–
		VL	2	6.8	6.8-6.7	–
		HC	–	–	–	–
	P3/	MD	18	26.8	24.3-30.9	1.5
		VL	16	13.7	12.4-15.5	0.8
		HC	12	15.7	13.6-17.6	1.0
	P4/	MD	19	38.3	35.2-42.8	1.9
		VL	18	19.3	18.1-22.5	1.3
		HC	19	21.1	19.6-23.1	0.9
M	M 1/	MD	3	6.0	5.1-6.7	0.6
		VL	3	11.7	10.3-14.3	2.2
		HC	–	–	–	–

Lower teeth: see Table 2.

Table 2

Panthera spelaea intermedia, Igue-des-Rameaux, lower teeth

Igue des Rameaux			1	2	3	4
Lower teeth			n	mean	Δ	sd
I	I /1	MD	6	4.7	4.1-5.5	0.6
		VL	6	5.7	4.5-6.2	0.6
		HC	6	6.4	5.9-7.0	0.4
	I/2	MD	7	6.3	6.0-7.1	0.4
		VL	7	7.3	6.7-8.0	0.4
		HC	7	8.2	7.2-9.0	0.8
	I /3	MD	8	7.6	7.1-8.1	0.3
		VL	7	8.7	8.0-9.4	0.5
		HC	8	11.4	10.5-12.9	0.9
C	C inf.	MD	19	25.2	21.6-31.9	2.8
		VL	19	17.8	15.6-24.1	2.1
		HC	17	43.4	37.0-54.8	4.4
PM	P/3	MD	19	18.8	16.8-22.9	1.7
		VL	16	18.3	9.3-12.3	0.8
		HC	17	10.9	10.4-12.7	0.6
	P/4	MD	21	27.6	25.2-31.8	1.4
		VL	19	13.8	12.4-15.7	0.7
		HC	20	17.5	15.0-20.2	1.0
M	M/1	MD	21	29.0	27.3-31.8	1.3
		VL	20	14.7	13.5-16.8	1.0
		HC	19	17.7	15.9-19.7	1.0

Postcranial material: see Table 3.

VI. COMPARISONS AND DIAGNOSIS OF *PANTHERA SPELAEA INTERMEDIA*

The elements used for comparison seem to be numerous. However, they are much less numerous when we look for large series, and they become rare when we focus on sites with homogeneous and well-dated populations. The main sites used for comparisons of the population of *Panthera spelaea intermedia* at Igue des Rameaux (chronological frame selected, Fig. 5) are:

Table 3

Panthera spelaea intermedia, Igue-des-Rameaux, anterior and posterior limbs

Igue des Rameaux			1	2	3	4
TN	Post cranial skeleton		n	mean	Ä	sd
1	Humerus	L	5	342.8	336.2-348.3	5.4
		med. TD	9	29.5	27.8-31.3	0.8
		med. APD	9	48.1	44.1-53.7	1.3
		distal TD	8	85.8	79.3-90.2	3.4
2	Radius	L	6	306.9	301.0-311.7	4.8
		med. TD	10	32.8	30.7-34.2	1.0
		med. APD	10	19.4	17.3-21.2	1.0
		distal TD	6	61.9	57.7-66.0	3.2
3	Cubitus	L	5	376.2	366.6-383.5	6.4
		med. TD	11	21.5	20.3-23.6	1.2
		med. APD	11	32.4	30.5-34.7	1.2
		distal TD	5	20.7	18.4-22.3	1.7
4	Femur	L	3	390.7	382.9-395.0	6.7
		med. TD	11	34.4	31.7-36.4	1.7
		med. APD	11	31.4	29.3-35.1	1.7
		distal TD	5	81.8	80.5-83.0	1.1
5	Tibia	L	7	338.9	330.0-346.3	6.7
		med. TD	12	31.1	28.6-34.2	1.9
		med. APD	12	36.3	34.3-39.5	1.8
		distal TD	8	58.9	51.5-64.6	4.6
6	Fibula	L	–	–	–	–
		med. TD	4	8.0	7.7-8.2	0.2
		med. APD	4	9.8	8.1-11.2	1.4
		distal TD	2	16.7	15.1-18.3	–
7	Calcaneum	L	7	120.2	113.7-124.7	4.5
		dist. TD	7	50.5	46.3-55.0	3.5
		dist. APD	7	49.8	47.3-52.6	2.3
		tuber calc. TD	7	32.6	31.0-34.4	1.4

VI.1. SITES

Median Middle Pleistocene: ***Panthera spelaea fossilis***

1 – Azé (Saône-et-Loire, France): Excavations Azé 1 (Upper cave). Azé 1-1: J. COMBIER, 1968-1970, Late Middle Pleistocene et Azé 1-3, A. J. ARGANT, 1982-1985, dating by biochronology of bears, Late Middle Pleistocene – 160,000 years assumed for Azé 1-3

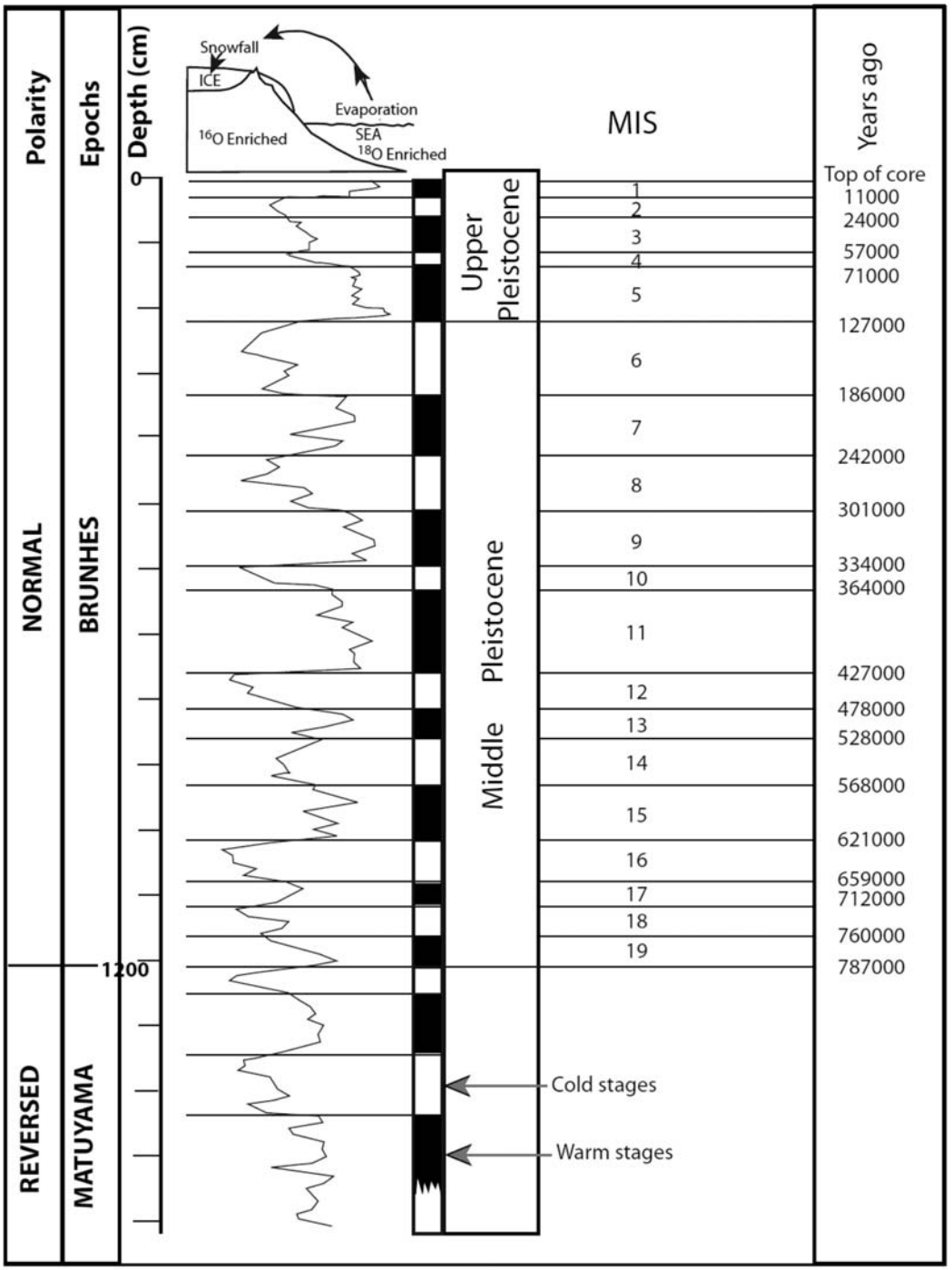


Fig. 5. Selected stratigraphical framework (after GAMBLE 1999).

(ARGANT 1991) – but it seems necessary to increase the age of the site, the large skull of the lion of Azé corresponds to the ancient forms of *Panthera spelaea fossilis* by its morphological characters (SOTNIKOVA & NIKOLSKIY 2006), Holsteinian possible, MIS 11. Personal mesurements (A. A).

2 – Château Breccia (Saône-et-Loire, France): Excavations A. J. ARGANT (1968-2012), personal measurements (A. A), dating of Ensemble Nord (EN) by biochronology of *Arvicola cantiana* (ARGANT et al. 2007): good matching with Mosbach (Allemagne), dating to around 600 ka, MIS 14 or 16.

3 – Belle-Roche (Sprimont, Belgique): Excavations J. M. CORDY; KLECZKO (1999), around 500 ka (RENSON et al. 1999).

4 – Caune de l'Arago (Tautavel, France): CRÉGUT (1979); MOIGNE et al. (2006); TESTU (2006), dating: MIS 12 and MIS 14, ESR level III 520 ± 70 ka à 540 ± 60.

5 – Isernia (Italy): SALA (1990), Cromerian III, dating to around 600 ka, between 783 and 500 ka.

6 – Lunel-Viel (Hérault, France): BONIFAY (1971), dating to Holsteinian («Mindel-Riss»),

7 – Mauer (Germany): interglacial at the beginning of Middle Pleistocene, Cromerian III possible, locus typicus of *Panthera spelaea fossilis* (REICHENAU, 1906), MIS 15 or MIS 13: BAHAIN et al. (2015).

8 – Moggasterhöhle (Germany): GROISS (1992), *Panthera spelaea fossilis.*

9 – Mosbach 2 (Germany): personal measurements (A. A), dating to around 600 ka, MIS 14 or 16.

10 – Petralona (Greece): KURTÉN & POULIANOS (1981), Cromerian.

11 – Sima de los Huesos (Atapuerca, Spain): GARCIA (2003), dating TIMS minimum 350 ka, par ESR 530 ka (BISCHOFF et al. 2003).

12 – Stranska Skala (Czech Republic): THENIUS (1972), dating – Cromerian complex, upper part.

13 – Vertesszöllös 2 (Hungary): HANKÓ (2007), WOLSAN (1993), Elster, Holstein.

14 – Biœnik Cave (Poland): MARCISZAK & STEFANIAK (2010), Middle Pleistocene MIS 8-(9?), *Panthera spelaea fossilis* (layer 18-19).

Late Middle Pleistocene: *Panthera spelaea intermedia*

1 – Igue-des-Rameaux (Saint-Antonin-Noble-Val, Tarn-et-Garonne, France): Excavations F. ROUZAUD, 1985-1989 – personal measurements (A. A) – dating c.60, 62: MIS 9 or MIS 7.

2 – La Fage (Noailles, Corrèze, France): BALLESIO (1975) – dating to MIS 7, 185-245 ka (MOURER-CHAUVIRÉ et al. 2003).

3 – Orgnac III (Ardèche, France): JEANNET (1981); TESTU (2006), dating to 345 ka by U/Th, 337 to 372 ka by ESR (COMBIER 2005).

4 – Romain-la-Roche (France): personal measurements (A. A), dating of the end of Saalian MIS 6, 160 ka, ESR/U-Th method (BAHAIN et al. 2010).

Upper Pleistocene: *Panthera spelaea spelaea*

1 – Baré d'Onnion (Haute-Savoie, France): personal measurements (A. A) – dating on a lion (tooth): 34,600 ± 1100 BP Lyon 3093.

2 – Châteaubourg (Ardèche, France): personal measurements (A. A) – dating from Early Upper Pleistocene, date 14C - AMS greater than 43,500 BP Beta-294651, MIS 4, (PAUTRET-HOMERVILLE et al. 2011).

3 – Gailenreuth - Zoolithen Höhle (Germany): *locus typicus* of *Panthera spelaea* (GOLDFUSS 1810), dating to 47,600 ± 900 OxA-14863 (BARNETT et al. 2009).

4 – Gissey-sur-Ouche (Côte d'Or, France): personal measurements (A. A).

5 – Gondenans-les-Moulins (Doubs, France): personal measurements (A. A) – (MHNBasel), DIDIER 1942, dating from Early Upper Pleistocene, MIS 4.

6 – Jaurens (Nespouls, Corrèze, France): personal measurements (A. A), dating to 32,630 ± 2900 BP Lyon 1938 and 29,300 ± 1400 BP Lyon 359, MIS 3 (BALLESIO 1980).

R. BALLESIO had formerly found two different forms of cave lions at Jaurens, one of considerable size and the other one really small (cf. small current lioness), for which he had adopted the name *Panthera* (*Leo*) *spelaea cloueti* (FILHOL, 1891). This distinction could correspond either to a particularly marked sexual dimorphism (TURNER, 1984, p.3, fig.1), to non-contemporaneous lions with different morphotypes or to the coexistence of two distinct populations, and even to the presence of the African lion along with the cave lion. Three samples have been recently dated by ^{14}C-AMS: the first is of the large form *Panthera spelaea spelaea* (A.215), the second is smaller (A.216) but not as small as *Panthera spelaea cloueti,* and the third is of the very small size (A.214). These datings provide a satisfactory response:

Panthera spelaea spelaea: A.215, FSL 300-902, Lyon-14098 (GrM), 40,000 BP

Panthera spelaea "cloueti": A.216, FSL 300-924, Lyon-14099 (GrM), 40,000 BP

Panthera spelaea cloueti: A.214, FSL 300-214, Lyon-14097 (GrM), 33,080 ± 150 BP, (35,964 – 34,623 cal BC).

There are two forms of lions from two distinct periods at Jaurens. A.215 and A.216 correspond to the sexual dimorphism of the more ancient form of *Panthera spelaea spelaea* dated to more than 40,000 years BP and the small lion *P. spelaea cloueti* dates to 33,080 years, which is the age formerly known for the main site of Jaurens.

7 – L'Arquet (Ardèche, France): personal measurements (A. A) – dating to Upper Pleistocene, MIS 3, around 40 ka (BRUGAL & BOUDADI-MALIGNE 2011).

8 – La Soute (France): personal measurements (A. A) – (MHN La Rochelle), dating from Upper Pleistocene.

9 – Le Closeau (Hauts-de-Seine, France): personal measurements (A. A) – dating on the lion (Mtc.5), 12,248 ± 66 BP AA-41842 (BODU & BÉMILLI 2000; BODU & MEVEL 2008).

10 – Pont-du-Château (Puy-de-Dôme, France): BOUCHUD 1963, dating from Upper Pleistocene. Not to be confused with the Château Breccia (Saône-et-Loire, France) dating from the Median Middle Pleistocene, see BARYCKA 2008, error, p. 80, tab.12.

11 – Prélétang (Presles, Isère, France): personal measurements (A.A) – dating: Early Upper Pleistocene, MIS 4.

12 – Siegdorf (Traunstein, Germany): GROSS 1992, dated on the lion, 47,180 ± 1190 (KIA 14406) ROSENDAHL & DARGA 2004.

13 – Wierzchowska Górna (Kraków, Częstochowa, Poland): WOJTUSIAK 1953; TURNER 1984; BARYCKA 2008 – dating to 38,650 ± 600 BP OxA-10087 on bone, (BARNETT et al. 2009). This large population is far from being homogeneous. The scatter diagram of M/1 (TURNER 1984, p.3, fig.1) shows it clearly. BARYCKA (2008) considers the presence of *Panthera spelaea fossilis* for a small part of this ancient collection and of *Panthera spelaea spelaea* for the major part but without giving any arguments.

VI.2. CHARACTERISTICS OF PRESERVED BONES

Hemimandible

Fig. 6, Fig. 7, Table 4, Table 5, Plate 1, Plate 2

Table 4 brings together the data, metric and morphological, selected according to the PFEMA.20, recording plan usually used (A.A). In Table 5 the morphological features C.1 and C.6 (see Fig. 6) have been subjectively assessed with the results labelled as: 0 – absence of the characteristic; 1 – presence (11= weak; 12= average; 13= strong). The third feature, C.7, is the angle of the upper edge of the ramus with the lower edge of the mandible body as measured from the main horizontal axis in order to be not too dependent on particular cases of the morphology of the base of the mandible which can vary from one individual to another. In some cases, the C.7 characteristic has been determined from published photos. C.3 corresponds to the chin foramina. The Fig. 7 provides both the typology used in the tables and indications given by the site. It is probably an individual character that in the future, perhaps can indicate a "genetic proximity", quite possible at the Igue des Rameaux where the youth of the individuals probably reflects the proximity of their place of birth.

Two well preserved hemimandibles of *P. spelaea* from Igue des Rameaux, considered as characteristic (Table 5), have been compared to hemimandibles of *Panthera spelaea fossilis* on the one hand and of *Panthera spelaea spelaea* on the other. Table 5 clearly shows the differences between the lion from Igue des Rameaux and the ancient forms of the Median Middle Pleistocene, *Panthera spelaea fossilis.* These differences are in size and massiveness, in the size of muscle attachments (C.1 and C.6), and in the shape of the ramus of the mandible which is wide and rather triangular at its base in the ancient forms but more narrow, a little less steeply angled (C.7), more elongated and with parallel sides in the case of *Panthera spelaea intermedia.* These variations clearly go beyond the range of allometry (BENOÎT 2010). The comparison becomes more difficult with the recent forms, *Panthera spelaea spelaea.* The size of the latter is much more variable and doesn't always confirm the distinction between the two subspecies. However, the muscle attachments are less pronounced on the masseteric fossa, which does not extend as far forward under the rear of the M/1, is less deeply concave, and without marked narrowing of its anterior part. The most recent forms of *Panthera spelaea spelaea* can be clearly distinguished by their slenderness.

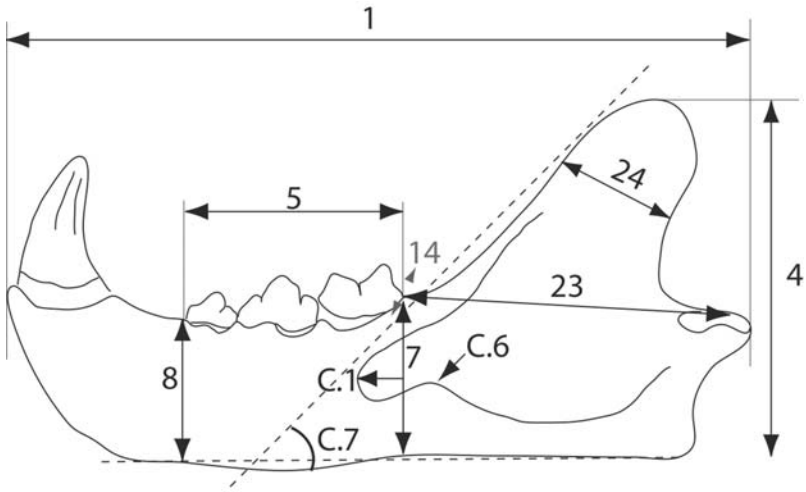


Fig. 6. Measurements of the hemimandible (PFEMA 20). 1 – Length infradental - mid condylus; 2 – Length infradental-angular apophysis; 3 – Length infradental-coronoid apophysis; 4 – Heigth angular process-coronion; 5 – Length of P/3-M/1 or alveoli; 6 – Length of diastema C-P/3 (between alveoli); 7 – Horizontal ramus height behind M/1; 8 – Horizontal ramus height before P/3; 9 – Length of alveoli of P/3; 10 – Length of alveoli of P/2; 11 – Length of alveoli of M/1; 12* – Breadth at canine; 13* – Horizontal ramus breadth before P/3; 14* – Horizontal ramus breadth behind M/1; 15* – Length of condylus; 16* – Breadth of condylus; 23 – Distance from behind M/1 to middle of condylus; 24 – Width at the middle of the ramus. The measures with * are not indicated on the scheme but appear in Table 4. The morphological characteristics refer to PFEMA 20: C.1 = Maximum engagement of the masseteric fossa under the M/1; C.6 = Narrowing of the masseteric fossa; C.7 = Angle between the ramus and the horizontal branch (in degrees).

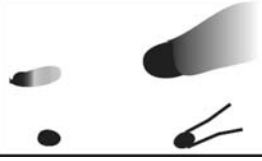
Type	Figure	Number of holes	IgRx n= 15	Comments
A		2	5	id. Azé (Argant, 1988)
B		3 aligned	2	
C		3 in triangular pattern	4	
D		4 in parallel lines	4	particular case?

Fig. 7. *Panthera spelaea*, typology of the foramina (PFEMA 20), position of the chin holes schematised on a left hemimandible.

Table 4

Panthera spelaea intermedia, Igue-des-Rameaux, hemimandible, morphometric data. Specimen numbers in grey: measurements of juvenile mandibles at different stages, showing either milk teeth or the exit of permanent teeth. * – approximately

Igue des Rameaux	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15								
Mandible	Length infradental-mid condylus	Length infradental-angular apophysis	Length infradental-coronoid apophysis	Height angular process-coronion	Length P/3-M/1 or alveoli (A)	Length diastema C-P/3 (between alv.)	Horiz. ramus height behind M/1	Horiz. ramus height before P/3	Length alveoli P/3	Length alveoli P/2	Length. alveoli M/1	Breadth at C.	Horiz. ramus breadth before P/3	Horiz. ramus breadth behind M/1	Length of condylus	Lat.	C.1	C.2 Straight/Curve	C.3	C.4	C.5	C.6	C.7 angle (°)
Rx89-G1M-c.62-11	–	–	–	–	77.47	30.08	52.01	50.10	19.23	27.65	31.59	30.80	24.21	25.00	–	R	5.0	S	B	0	–	–	–
Rx90-G1M-c.62-281	235.00	–	–	–	76.87	30.69	52.14	50.29	18.71	28.00	30.87	35.22	22.33	25.40	>44.7	L	0.0	S	A	0	A	11	–
Rx88-F3-4M-c.62-20	236.20	226.40	–	–	73.69	29.07	47.57	46.17	18.5 (A)	25.6 (A)	30.1 (A)	30.28	20.54	22.62	>45.0	R	5.3	S	D	0	–	11	45
Rx88-F2-M-c.62-20	–	–	–	–	73.09	–	47.52	46.46	17.68	26.88	28.99	–	20.98	21.50	–	L	5.8	S	B	11	–	12	40
Rx87-D2-M-c.53-108	–	–	–	–	–	–	45.39	–	18.08	26.01	27.73	–	–	22.10	–	R	10.0	S	D	–	–	11	40
Rx90-F5M-c.62-54	222.5*	–	231.30	–	72.26	24.14	51.64	45.42	16.17	26.81	28.75	31.2*	22.50	27.20	45.3*	L	8.0	C	D	13	–	–	40
Rx90-F4N-c.62-58	220.90	218.60	228.00	95.80	72.90	24.70	45.30	42.5	18.50	28.90	27.80	26.50	19.10	20.20	>33.8	L	0.0	S	D	0	–	12	30
Rx88-F3-4N-c.6220-4	235.40	225.50	>225.6	–	73.51	27.30	47.90	46.20	17.50	27.40	29.20	34.40	20.70	23.20	>44.8	R	8.7	S	D	0	A	12	30
Rx90-F4M-c.63-392	–	–	–	–	73.45	28.20	50.40	43.30	16.90	26.90	28.90	29.10	21.00	21.60	–	R	7.4	S	A	11	–	12	–
Rx90-G1N-c.63-294	–	–	–	–	–	–	45.80	–	–	29.20	28.30	–	–	19.60	–	R	0.0	S	–	–	–	11	–
Rx90-G1N-c.62-153	–	–	–	–	80.70	–	–	–	23.20	29.30	31.70	–	–	–	–	R	–	–	–	–	–	–	–
Rx87-D2-N-c.54-110	–	–	–	–	69.7*	–	–	–	16.70	25.40	28.00	–	–	–	–	R	–	–	–	–	–	–	–
Rx-sect. D	–	–	–	–	71.30	–	47.60	–	18.37	26.22	27.88	–	18.78	>23.2	–	L	–	–	–	–	–	–	–
Rx89-F4M-c.62-69	–	–	–	–	67.32	–	41.13	38.3*	19.57	25.8*	28.57	22.8*	18.70	17.8*	–	R	6.3	S	A	0	–	12	–
Rx89-F3M-c.62-153	–	–	–	–	–	–	–	40.39	19.2*	25.7*	–	24.85	17.25	17.7*	–	L	–	S	A	0	–	–	–
Rx89-G3N-c.62-93	–	–	–	–	67.94	20.06	43.42	48.61	–	29.38	29.11	–	–	19.01	–	L	–	–	–	–	–	–	–
Rx89-G5M-c.60	–	–	–	–	–	–	30.02	–	–	–	–	–	–	–	–	R	–	–	–	–	–	–	–
Rx89-F3N-c.62	–	–	–	–	68.21	–	36.0*	37.1*	17.8*	25.8*	27.46	–	16.8*	–	–	L	5.0	–	–	–	–	–	–
Rx89-F3N-c.62-52	–	–	–	–	32.13	14.23	26.90	29.10	–	–	–	–	–	–	–	R	0.0	–	–	–	–	–	–
Rx89-G2M-c.62-36	178.7	>167.0	182.24	82.7*	64.33	25.25	40.09	40.33	15.49	18.82	28.59	24.32	17.13	18.54	–	L	0.0	S	B	0	–	11	45
Rx89-F3M-c.62-141	177.59	165.00	–	–	65.84	21.5*	40.54	39.99	–	–	27.49	25.15	17.32	17.58	>34.1	R	–	S	A	11	–	11	40
Rx90-G1N-c.62-151	–	–	–	–	–	–	42.96	–	–	31.71	31.64	30.57	28.1*	21.07	–	L	–	–	C	–	–	–	–
Rx88-F1-3N-c.62	89.55	85.66	>88.46	>33.1	19.64	8.59	22.25	21.06	–	–	–	13.48	9.10	9.09	>12.9	R	–	S	–	11	–	–	–
Rx91-F3	–	–	–	–	–	8.60	24.26	24.38	–	–	–	15.57	11.50	13.40	–	R	–	S	A	11	–	-	–

Table 5

Panthera spelaea intermedia, Igue-des-Rameaux, hemimandible, comparison

	Panthera spelaea - Hemimandible														
	Site	Reference	1	4	5	6	7	8	14	23	24	24/23	C.1	C.6	C.7
P. spelaea intermedia	Igue des Rameaux	F3-4M-c.62-20	236.2	–	73.5	29.1	47.6	46.2	22.6	–	–	–	–	11	40
	Igue des Rameaux	F4-N-c62-58	220.9	95.8	72.9	24.7	45.3	42.5	20.2	87.2	33.5	38.4%	–	11	40
	Romain la Roche	FEL.04-ind.2	275.0	136.3	81.0	37.6	55.6	49.3	25.7	–	–	39%	11	11	44
Panthera spelaea fossilis	Château (CHA.1)	D4-99	280.0	137.5	84.7	32.0	62.0	54.0	30.0	122.4	48.4	39.5%	13	13	40
	Moggaster Höhle		281.0	–	84.7		64.7	60.9	–	–	–	–	12	12	–
	Mosbach 2	(Mus. Darmstadt)	266.0	–	82.0		67.0	53.0	–	–	–	–	13	13	42
	Azé 1-3	K14-6	285.4	141.6	84.5	33.3	60.1	58.0	30.8	127.8	48.5	37.9%	13	13	46
Panthera spelaea spelaea	Jaurens		258.5	128.0	79.5	24.0	54.8	52.3	24.1	59.0	22.0	37.5%		11	40
	Siegdorf		263.0	132.0	82.0		55.0	51.5	–	–	–	–	12	0	46
	Pont-du-Château		282.0	123.5	71.0	21.0	52.0	47.0	–	–	–	–	11	0	42
	Wierzchowska Górna	ISEZ MF/320/6710	246.0	–	75.0	21.0	53.0	51.0	–	–	–	–	11	0	46
	Gondenans-les-Moulins	GLM 4x1951	271.0	126.0	78.8	33.6	61.3	62.5	–	–	–	–	–	–	–
	Igric Höhle	V.60.1785	227.6	121.5	70.3	24.0	50.0	50.0	–	–	–	–	0	0	50

M/1

Fig. 8, Fig. 9, Table 6, Table 7.

The first lower molar is indicative of the evolution of the species (SCHÜTT 1969; SCHÜTT & HEMMER 1978). Three morphological features have been selected:

– C.1: the development of the talonid at the rear of the crown, strong within ancient forms *Panthera spelaea fossilis,* weak on the contrary within the typical forms of *Panthera spelaea spelaea*,

– C.2: the presence of a protuberance in vestibulo-median position at the base of the crown, well developed within the ancient forms, very small or non-existent within the more recent ones,

– C.3: occasionally and only within *Panthera spelaea fossilis*, presence of a groove at the top of this protuberance.

These features, listed in Table 6, do not occur in every case. An intermediate stage appears on *Panthera spelaea intermedia* from Igue des Rameaux where C.1 is always present,

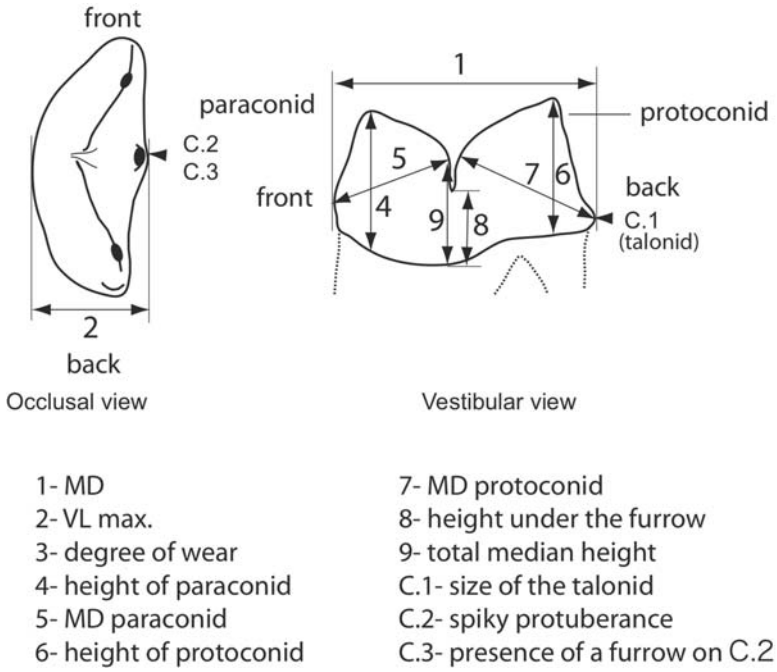


Fig. 8. *Panthera spelaea*, measurements of M/1 (PFEMA. 27).

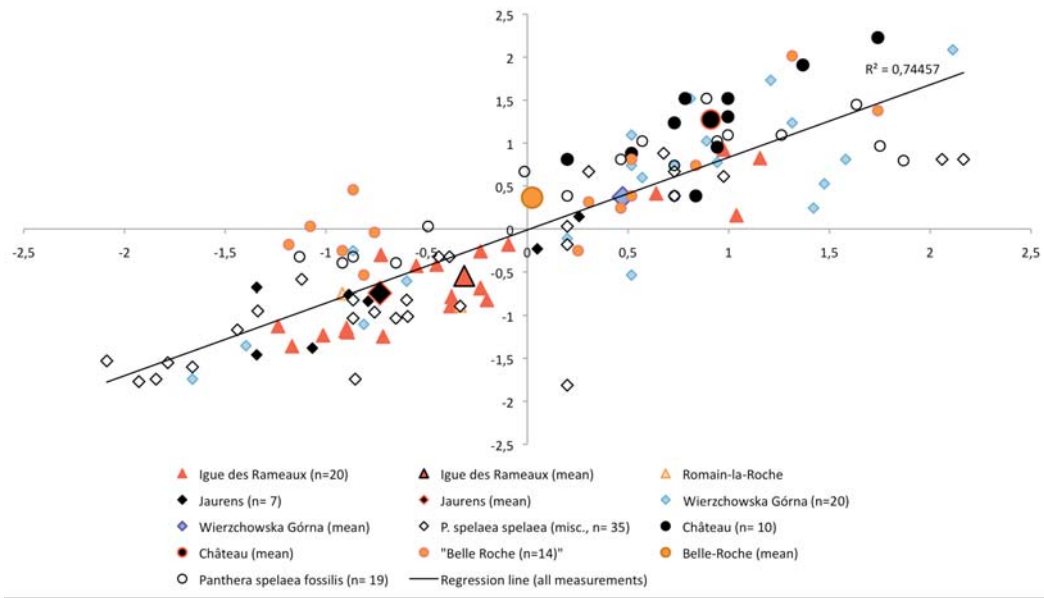


Fig. 9. *Panthera spelaea intermedia*, Igue des Rameaux, M/1, scatter diagram (standardized values), comparison.

Table 6

Panthera spelaea intermedia, Igue-des-Rameaux, M/1, morphometric data. ★ – same individual; C.1 – size of talonid ; C.2 – spiky protuberance; C. 3 – presence of a furrrow on C.2; 0 – absence; 1 – presence: 11 – weak; 12 – average; 13 – strong. * – approximately

Igue des Rameaux	1	2	3	4	5	6	7	8	9				
M/1	MD	VL	U	HC paraconid	MD paraconid	HC protoconid	MD protoconid	Height under furrow	Total median height	C.1	C.2	C.3	Lat.
Rx88-F3 4M-c.62-20	29.19	14.49	–	18.44	17.22	15.97	17.05	10.28	13.1	11	11	0	R
Rx88-F2 M-c.6220	28.90	14.35	0.0	17.28	16.85	16.37	17.05	10.33	13.1	11	11	0	L
Rx89-G1 M-c.62-11	31.60	15.68	0.0	16.97	16.81	16.74	18.87	9.59	14.2	12	12	0	R
Rx87-D2 M53-108	27.70	13.72	0.5	15.85	15.17	–	16.46	7.64	11.6	11	11	0	R
Rx90-G1 M-c.62-281	30.80	16.04	0.3	18.77	15.56	16.78	18.46	10.14	14.7	12	12	0	L
Rx89-G30 c.60 ★	29.50	15.20	0.1	16.92	16.70	17.50	17.50	9.37	15.90	11	12	0	R
Rx90-G1 N-c.62-232	28.60	14.85	0.0	18.29	16.34	17.09	17.29	9.55	14.70	11	12	0	L
Rx89-G30 c.60 ★	29.20	15.09	0.1	18.2	16.75	16.27	17.26	9.28	15.90	11	12	0	L
Rx89-F3 N-c.62	27.40	13.54	0.0	17.92	16.34	16.71	16.66	9.17	14.30	11	11	0	L
Rx89-F4 M-c.62-69	28.80	14.87	0.0	18.79	15.98	18.22	17.85	9.87	14.80	11	11	0	R
Rx90-F4 N-c.62-58	28.30	13.70	0.0	17.81	15.61	16.52	17.16	8.28	13.18	12	11	0	L
Rx88-F3 4N-c.6220-4	29.25	14.30	0.0	17.98	18.05	17.32	17.13	11.86	13.20	12	11	0	R
Rx90-F4 M-c.63-392	28.91	14.20	1.5	16.59	15.2*	14.70	13.7*	7.05	13.18	11	0	0	R
Rx90-G1 N-c.63-294	27.95	13.77	0.0	17.14	16.22	16.92	17.20	8.43	13.35	11	0	0	R
Rx90-G1 N-c.62-153	31.46	16.76	0.0	19.70	19.31	18.0	19.16	11.62	16.80	12	0	0	R
Rx87-D2 N-c.54-110	27.94	13.8*	0.0	–	16.23	16.15	17.17	8.26	13.4*	12	–	0	L
Rx89-G2 M-c.62-36	28.26	15.03	0.0	16.44	16.05	15.54	17.64	8.00	13.37	13	11	0	L
Rx89-F3 M-c.62-141	27.30	13.87	0.0	17.80	16.28	16.35	16.98	8.94	12.63	12	11	0	L
Rx90-G1 N-c.62-151	31.80	16.62	0.0	18.81	18.77	18.79	19.83	11.32	16.57	12	0	0	L
Ig.Rx-sect.D	27.93	13.79	0.0	16.94	15.80	15.54	16.03	7.19	11.81	13	0	0	L

Table 7

Panthera spelaea intermedia, Igue-des-Rameaux, M/1, characteristics and comparison

Lower molar	n	Site	C.1					C.2					C.3			
			0	11	12	13	n	0	11	12	13	n	0	11	12	13
Panthera spelaea spelaea	5	Jaurens		5			5	5				5	5			
	7	L'Arquet		7			7	7					7			
Panthera spelaea intermedia	20	Igue des Rameaux		11	7	2	18	4	13	1		18	0			
	1	Romain-la-Roche		1			1	0				1	0			
	1	La Fage		1			1	1				1	1			
Panthera spelaea fossilis	12	Château			3	9	10	3	6	1		10	5	5		
	4	Mosbach				4	2			1	1	–				

either relatively slight (11 cases out of 20), or well (7 cases) to even very well (2 cases) marked. The protuberance C.2 is absent in 4 cases out of 18 possible observations, it appears but slightly in 13 cases and strongly one time. No groove is observed on this protuberance contrary to ancient forms. The M/1 also allows the distinction to be made when statistically reliable series exist. The cave lion will never yield series as ideal as cave bears do, but valuable conclusions can be drawn from at least six samples provided that they come from a coherent group with a well established chronology. The talon (character C.1) is statistically less developed with *Panthera spelaea intermedia* of Igue des Rameaux than with *Panthera spelaea fossilis.* In the same time the protuberance in the middle of the lingual side of the crown (character C.2) remains absent with the typical forms of the cave lion *Panthera spelaea spelaea.*

Upper and lower canines

Fig. 10, Fig. 11, Table 8, Table 9

Two very large specimens of canines in each series have been excluded in order to have homogeneous data (see page 68). Because of their large size, the canines of the males are clearly distinct from that of the females and the diagrams of standardized values (MD/VL, Figs 10 and 11) confirm the differences in dimensions between *Panthera spelaea intermedia* and *Panthera spelaea fossilis*.

P4/

Fig. 12, Fig. 13, Fig. 14, Table 10

The distribution of the P4/ of the three subspecies of *Panthera spelaea* (Fig. 13) is similar to that obtained in the latter diagrams: distinction from the large ancestral forms and relationship with the small Upper Pleistocene forms of *Panthera spelaea spelaea*, always with populations of large size occuring at some periods for the typical forms of the cave lion.

Table 8

Panthera spelaea intermedia, Igue-des-Rameaux, lower canine, morphometric data. ☆, ★ – same individual; C.1 – 2 external furrows (0 – absence ; 1 – presence); C.2 – Internal furrows; C.3 – posterior crest; C.4 – postero-external wear due to friction between lower and upper C; C.5 – antero-internal wear due to friction between lower C and I3/. * – approximately

Igue des Rameaux	1	2	3	4	5	6						
Lower C	MD	VL	HC (middle external face)	HT	PC	U	C.1	C.2	C.3	C.4	C.5	Lat. Right /Left
Rx88-F34M-c.62-20	25.47	18.41	42.19	–	71.00	0.1	1	0	1	1	0	R
Rx90-F5M-c.62-54	22.87	15.68	41.5*	93.4*	63.62	1.5	–	0	0	1	1	L
Rx89-G1M-c.62-11	26.08	17.96	44.38	–	78.54	0.0	1	0	1	0	0	R
Rx87-D2M-c.53-108	21.58	15.56	37.01	85.51	–	0.0	1	0	1	0	0	R
Rx90-G1M-c.62-281	26.37	17.96	45.00	–	78.00	0.0	1	0	1	1	0	L
Rx86-D2M-	22.83	15.98	37.35	86.54	65.91	0.2	1	0	1	1	0	L
Rx89-F4N-c.62-04	25.46	17.73	41.39	89.85	72.66	0.0	1	0	1	0	0	L
Rx89-G30-c.60 ★	24.69	17.17	42.72	96.7*	72.28	0.0	1	0	1	1	0	R
Rx89-G30-c.60 ★	24.75	17.13	42.86	96.17	70.62	0.0	1	0	1	1	0	L
Rx89-F2N-c.62	22.86	16.00	42.34	–	64.79	0.0	1	0	1	0	0	L
Rx89-G3N-c.62	22.44	15.80	41.55	–	69.74	0.0	0	0	1	0	0	R
Rx89-G3N-c.62 ☆	–	–	–	–	–	0.0	–	–	–	–	–	L
Rx89-G3M-c.60 ☆	–	–	–	–	–	0.0	–	–	–	–	–	R
Rx89-G3N-c.62-93	25.93	17.6*	–	–	–	0.0	–	–	–	–	–	L
Rx89-F4M-c.62-69	22.43	17.46	43.84	–	–	0.0	1	0	1	0	0	R
Rx88-F2M-c.62-20	25.88	18.51	43.83	93.19	73.50	0.0	1	0	1	1	0	L
Rx90-F4N-c.62-58	25.37	18.77	42.34	–	82.23	0.0	1	0	1	1	0	L
Rx88-F34N-c.6220-4	25.94	18.79	42.53	–	76.08	0.0	1	–	1	1	–	R
Rx90-F4M-c.63-392	23.84	15.83	>37.28	–	67.60	1.5	1	0	1	1	1	R

The Simpson's diagram (Fig. 14) is based on the ratio between the three reference populations (Château Breccia, Igue des Rameaux, Jaurens) and the mean dimensions of the P4/ of *Panthera spelaea spelaea* (SCHÜTT & HEMMER 1978). It clearly confirms the distinction between *Panthera spelaea fossilis* and *Panthera spelaea intermedia* and provides two interesting details: a slight difference between the recent forms and the lion from Igue des Rameaux, and a variation of the width of the premolar in its posterior part corresponding to the metacone which seems widened on *Panthera spelaea spelaea.* But caution is necessary because Jaurens yields only four P4/. In any case, there is nearly no relief on the internal

Table 9

Panthera spelaea intermedia, Igue-des-Rameaux, upper canine, morphometric data. ★,☆, ✪, ♣, ✚, ♢ – same individual. * – approximately

Igue des Rameaux	1	2	3	4	5	6					
Upper C	MD	VL	HC (middle external face)	HT	PC	U	C.1	C.2	C.3	C.4	Lat.
Rx88-E8 N-c.60	28.35	20.10	52.63	118.4	78.60	0.0	1	1	1	1	R
Rx87-D2 M-c.53	22.99	17.28	45.56	100.14	–	0.5	1	1	1	0	R
Rx89-F2 N-c.62 ★	24.16	17.93	49.6*	110.92	71.28	0.3	1	1	0	1	R
Rx88-F2 LM-c.622 ★	24.17	17.75	–	–	70.30	–	–	1	0	1	L
Rx89-F2 M-c.62-63	23.88	17.4*	47.8*	–	–	0.0	1	1	1	0	R
Rx90-G3 N-c.63-100 ☆	–	–	–	–	–	0.0	–	–	–	–	L
Rx90-F4 N-c.62-108 ☆	24.93	18.63	51.52	–	70.29	0.0	1	1	1	–	R
Rx90-E14-c.60 ✪	24.66	18.30	49.19	–	72.08	0.0	1	1	1	0	L
Rx90-F1N-c.62 ✪	24.05	17.36	50.95	–	67.66	0.0	1	1	1	0	R
Rx90-G1 N-c.63-213	34.41	24.55	61.80	–	95.0*	0.0	1	1	1	0	R
Rx90-G2 N-c.63-174 ♣	23.19	17.76	47.57	108.99	67.2*	0.2	1	1	1	1	L
Rx90-G2 N-c.62-89 ♣	22.56	16.8*	46.7*	107.41	65.2*	0.3	1	1	1	1	R
Rx90-F4 N-c.62-95	27.28	16.34	49.73	109.28	77.65	0.0	1	1	1	1	R
Rx90-G1 M-c.62-182	27.0	19.84	51.72	114.6	75.00	0.1	1	1	1	0	R
Rx86-D2-D3- M	23.56	16.69	–	100.0*	66.39	–	1	1	1	0	L
Rx89-G2 N-c.62-20	24.52	18.42	50.00	104.89	71.21	0.0	1	1	1	0	R
Rx89-F3 N-c.62-219	25.90	19.13	49.41	109.29	73.75	–	1	1	1	0	L
Rx89-G2 N-12	26.26	19.20	54.92	115.52	74.54	0.0	1	1	1	0	L
Rx89-F2 M-c.62 ♢	–	–	–	–	–	0.0	1	1	1	0	L
Rx90-G1 N-c.63 ♢	–	–	–	–	–	0.0	1	1	1	0	R
Rx89-G2 M-c.60	–	–	–	–	–	0.0	1	1	-	0	L
Rx90-G1 M-c.62-280	26.5*	19.6*	54.29	76.5*	–	0.0	1	1	1	0	L
Rx88-E8 N-c.60	28.62	20.45	52.44	118.7	81.58	0.0	1	1	1	1	R
Rx90-F4 N-c.62-166	26.70	20.33	49.35	109.72	79.50	0.0	1	1	1	0	R
Rx89-G30-c.62-45	28.91	22.48	55.97	–	–	0.0	1	1	1	0	R
Rx87-D2 N-c.54-124 ✚	–	–	43.7	–	–	0.0	1	1	1	0	L
Rx87-D2 N-c.54-124 ✚	–	–	–	–	–	0.0	1	1	1	0	R
Rx90-G2 N-c.63-179	33.95	25.02	64.2*	–	–	0.0	1	1	1	0	L

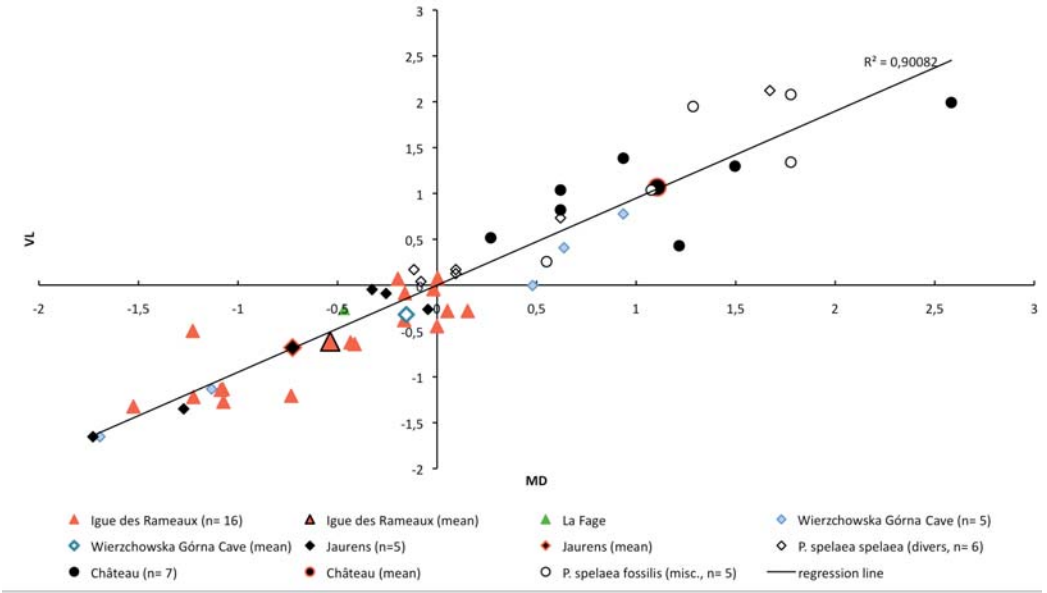


Fig. 10. *Panthera spelaea intermedia*, Igue des Rameaux, lower canines, scatter diagram (standardized values), comparison.

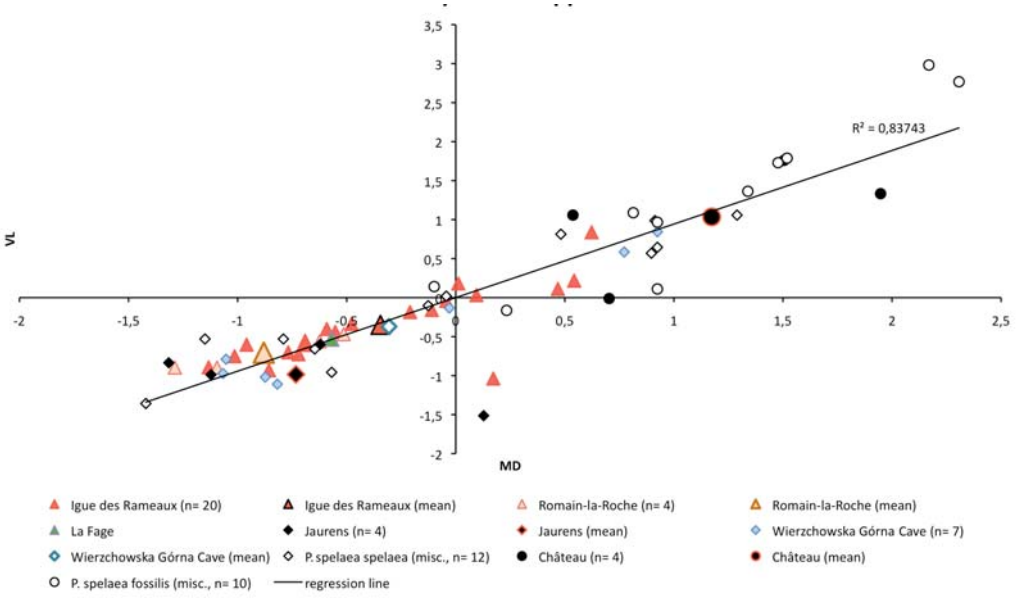


Fig. 11. *Panthera spelaea intermedia*, Igue des Rameaux, upper canines, scatter diagram (standardized values), comparison.

Table 10

Panthera spelaea intermedia, Igue-des-Rameaux, P4/, morphometric data.
★, ☆ – same individual. * – approximately

Igue des Rameaux	1	2	3	4	5	6	7	8	9	10	11		
P4/	Max. length	Length at the constriction	Length at the parastyle	Max. width	Length protocone	Length Paracone	Length Metacone	Width behind the protocone	Rear max. width	Max. height paracone	Degree of wear	C1	Lat.
Rx90-F5M-c.62-42	37.73	35.00	36.55	19.06	12.2	15.13	13.94	14.08	12.19	21.54	0.0	C.1-1	R
Rx88-F2N-c.621	38.13	36.10	37.01	18.34	12.48	14.0*	15.08	13.04	14.13	19.79	1.8	C.1-1	L
Rx90-G2N-c.63-175 ★	35.24	33.2	33.61	18.72	12.06	14.19	13.52	14.61	14.72	19.3*	2.2	C.1-1	L
Rx90-G2N-c.63-175 ★	36.32	33.41	34.13	19.21	11.75	13.84	13.61	13.94	13.89	19.59	2.0	C.1-1	R
Rx90-F4N-c.42-211	38.70	37.02	37.73	18.28	12.33	14.66	14.66	14.09	13.37	21.19	0.0	C.1-1	R
Rx89-G1N-c.62-54	36.84	34.58	35.78	18.07	12.36	14.30	14.74	13.03	13.45	20.86	0.0	C.1-1	L
Rx90-F4N-c.62-185	42.74	39.30	41.21	22.50	14.31	17.24	16.92	14.56	15.44	22.39	0.0	C.1-1	R
Rx90-G10 -c.62	38.94	35.93	37.19	21.0*	13.27	15.40	14.73	13.74	14.31	21.31	0.0	C.1-1	R
Rx90-F4N -c.62-130	36.40	34.94	34.18	18.83	11.5	14.65	13.42	14.09	14.35	20.62	0.0	C.1-1	L
Rx90-F1 - c.60	38.39	36.52	37.20	20.17	13.13	15.66	14.25	14.57	14.92	22.08	0.0	C.1-1	L
Rx90-G10 -c.62	38.45	36.03	37.73	20.35	13.36	14.83	14.66	13.77	12.81	21.08	–	C.1-1	L
Rx86-D2 M-"10-09"	36.60	35.02	35.75	18.52	11.30	14.30	13.79	12.08	13.06	19.97	0.5	C.1-1	L
Rx89-F2 M-c.62-66 "101-04"	–	–	–	–	–	16.24	15.16	14.12	14.23	20.41	0.0	–	R
Rx90-G1 M-c.62-280	39.14	37.85	38.36	18.48	12.45	15.70	15.22	14.50	13.13	23.1*	0.0	C.1-1	L
Rx90-F4N-c.62-145	37.81	36.69	36.82	18.97	12.20	15.04	13.91	13.84	13.97	20.15	0.5	C.1-1	R
Rx91-F5	38.28	35.98	38.06	18.39	12.10	15.14	13.70	13.31	13.69	21.31	0.2	C.1-1	L
Rx89-F4M -c.62-1	39.20	37.03	38.11	20.09	12.91	15.71	14.31	14.97	13.81	21.41	0.0	C.1-1	R
Rx89-G30 -c.62-45	–	–	–	–	–	–	15.80	–	–	–	0.0	–	R
Rx87-D2 N-c.54-124 ☆	38.10	36.60	37.03	19.07	12.43	15.34	14.44	14.2*	13.26	20.7*	0.0	C.1-1	L
Rx87-D2 N-c.54-124 ☆	37.79	35.58	35.90	18.77	12.20	15.61	15.05	13.32	12.62	20.30	0.0	C.1-1	R
Rx90-G2 N-c.63-179	42.84	40.72	43.02	22.46	14.50	17.70	16.63	15.11	15.32	22.30	0.0	C.1-1	L

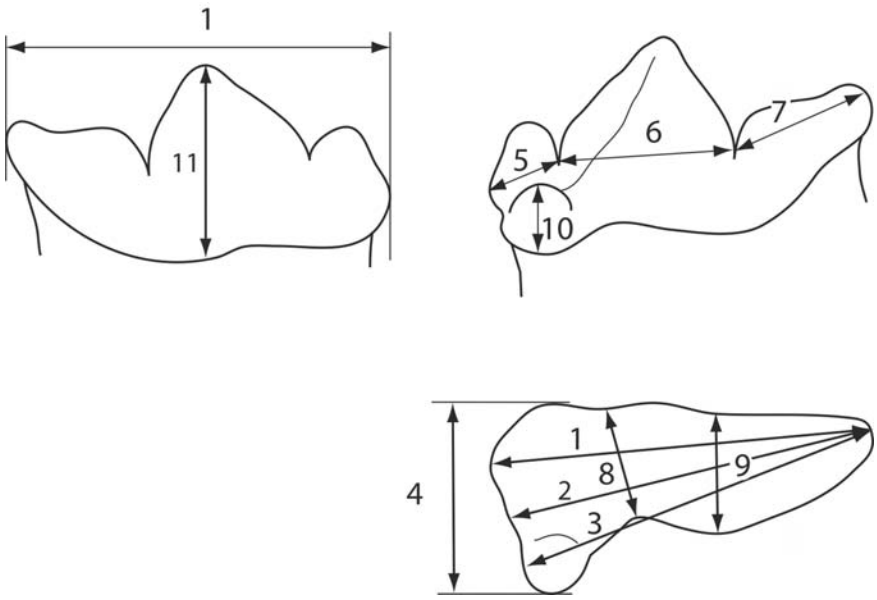


Fig. 12. *Panthera spelaea*, measurements of P4/ (PFEMA. 17).

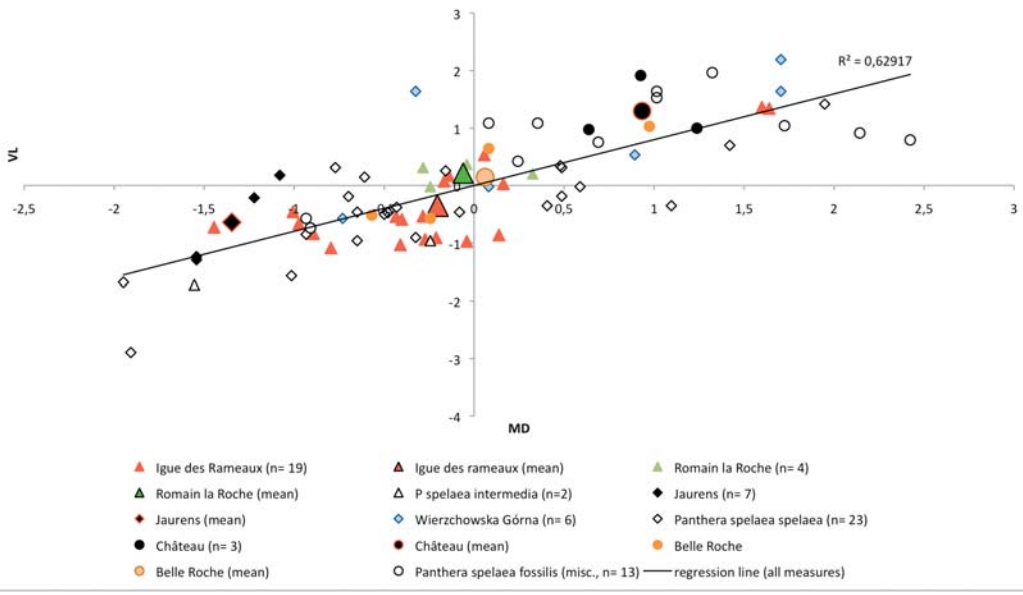


Fig. 13. *Panthera spelaea intermedia*, Igue des Rameaux, P4/, scatter diagram (standardized values), comparison.

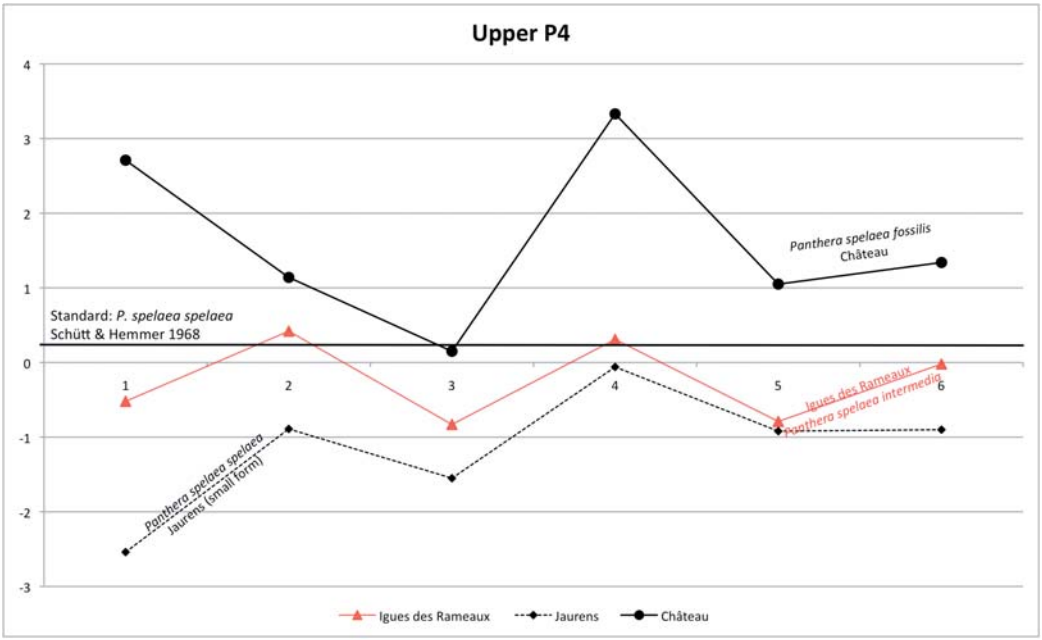


Fig. 14. Simpson's ratio diagram comparing 6 measurements of upper P4 of samples from Igue des Rameaux, Château and Jaurens. The standard is *Panthera spelaea spelaea* (SCHÜTT & HEMMER 1968, p. 246).
1 – Length; 2 – Length of paracone; 3 – Length of metacone; 4 – max. width; 5 – TD max. of the talon (rear max. width); 6 – width behind the protocone.

talonid of these four P4/, while one is noticeable at the Igue des Rameaux and one appears very pronounced in the case of *Panthera spelaea fossilis.*

The P4/ of *Panthera spelaea intermedia* of Igue des Rameaux (Fig. 14) is clearly different from *Panthera spelaea fossilis* from Château, in both size and proportions of the talon corresponding to the metacone. In this respect, the P4/ of Igue des Rameaux is in an intermediate position between the premolar of Château and Jaurens *Panthera spelaea spelaea*, typical for the small form of the end of the Upper Pleistocene, with the talon wider at Igue des Rameaux.

Mtc.5

Fig. 15, Table 11

The metacarpals 5 of the Igue des Rameaux are easily distinguished from those of the ancient forms, *Panthera spelaea fossilis,* because of their clearly smaller size, less massive epiphyses and the absence of a marked longitudinal crest on the lower third of the diaphysis (Plate 3, 8b). Their dimensions (Fig. 15) and proportions are not very different from the

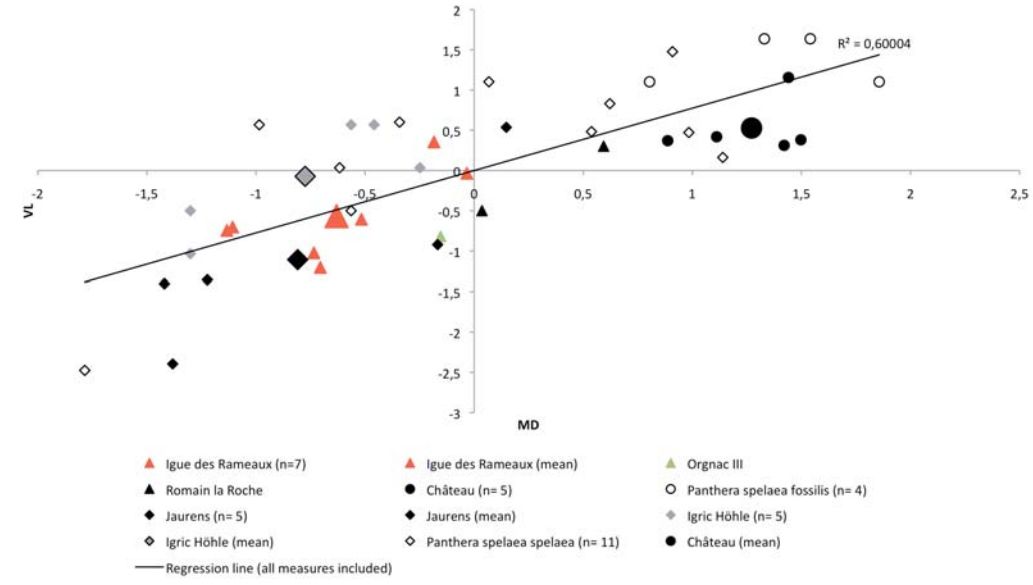


Fig. 15. *Panthera spelaea intermedia*, Igue des Rameaux, post cranial skeleton, scatter diagram of Mtc. 5 (standardized values), comparison.

Table 11

Panthera spelaea intermedia, Igue-des-Rameaux, Mtc.5, morphometric data

Igue des Rameaux	1	2	3	4	5	6	7	8	
Mtc.5	L	prox. TD	prox. APD	med. TD	med. APD	dist. TD	dist. APD	Dist.arti-cul. TD	Lat.
Rx90-F4M-c.62-259	96.38	23.72	25.17	14.02	15.8	22.27	21.54	19.30	L
Rx90-F2M-c.62-110	92.84	22.06	25.56	14.62	12.66	21.17	19.81	19.63	L
Rx89-G1M-c.62-90	103.04	24.89	27.01	15.87	13.12	23.42	22.28	21.15	L
Rx90-F4M-c.62-294	98.45	26.42	28.56	14.8	16.92	22.97	23.64	–	L
Rx90-F4N-c.62-206	96.66	23.91	25.28	13.68	14.86	22.12	20.95	19.66	R
Rx90-F4N-c.62-198	92.59	24.97	26.13	14.54	12.86	21.15	20.55	18.89	R
Rx89-G1M-c.62-107	101.61	25.66	27.48	16.60	13.05	23.76	22.79	20.49	R
Rx89-G1N-c.62-83	–	23.39	22.79	12.88	10.19	–	–	–	R

Mtc.5 of small forms of *Panthera spelaea spelaea* of the Upper Pleistocene. On the other hand, there is no morphological characteristic which enables us to distinguish these two subspecies.

Calcaneum

Fig. 16, Table 12, Table 13, Plate 3

The calcaneum is robust and usually the best preserved bone in fossil sites. The Table 12 gives all the dimensions available from the Igue des Rameaux site. We find the general morphology of the calcaneum of *P. spelaea* with a greater massiveness, a larger width at the articulations and a clearly more protruding *sustentaculum tali* than *P. leo*. Compared to the calcaneum of *P. spelaea fossilis*, the Igue des Rameaux is clearly smaller, less massive and its muscles attachments are less in relief and less powerful. Its size corresponds to the recent forms of *P. spelaea spelaea* from the Upper Pleistocene of Jaurens. However the morphological changes are small, and correspond to individual variations.

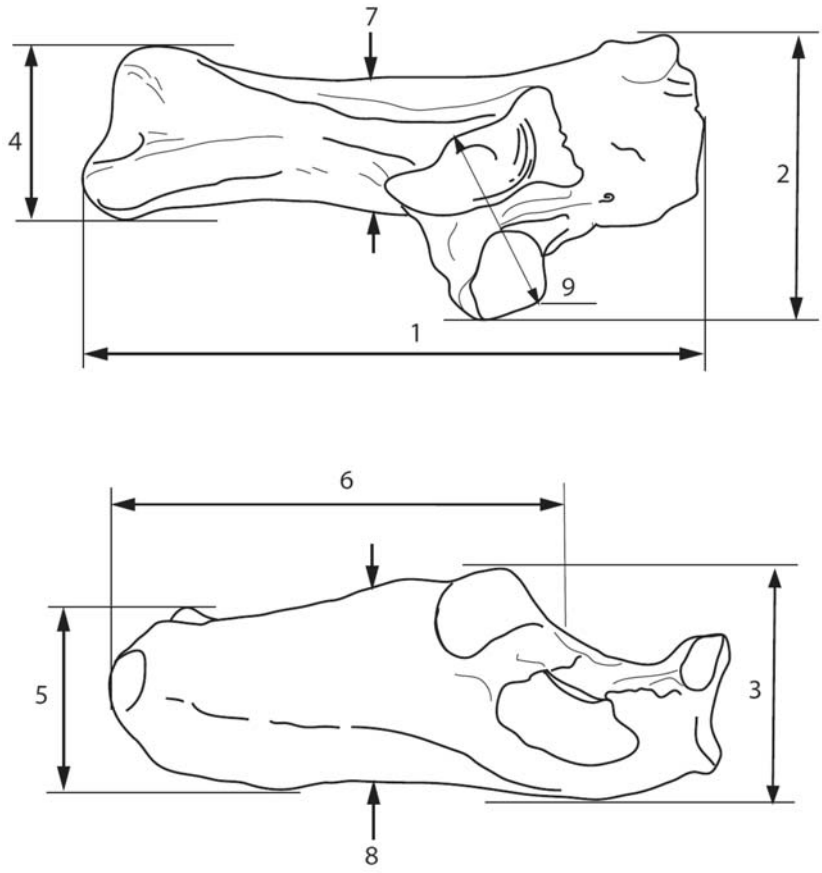


Fig. 16. *Panthera spelaea*, measurements of calcaneum (PFEMA. 641).

Table 12

Panthera spelaea intermedia, Igue-des-Rameaux, calcaneum, morphometric data.
✦, ★ – same individual. * – approximately

Igue des Rameaux	1	2	3	4	5	6	7	8	
Calcaneum	L	dist. TD	dist. APD	TD tuber calcanei	APD tuber calcanei	L manub-rium	min.TD diaphysis	APD middle diaphysis	Lat.
Rx89-F3M-c.62-148 ★	122.85	54.86	52.55	34.41	33.65	87.95	20.49	38.39	R
Rx89-F3M-c.62-155 ★	124.72	52.71	51.14	33.97	33.45	88.81	20.69	38.14	L
Rx90-F3M-c.62-396	118.14	49.84	48.45	31.46	32.56	84.21	21.30	36.34	L
Rx89-F2N-c.62-63	113.73	48.88	48.1	31.55	32.84	81.12	21.03	35.02	L
Rx89-G30-c.62	121.83	46.75	48.13	31.97	33.86	86.63	20.10	38.08	L
Rx90-F3M-c.62-335	115.29	54.12	47.26	31.04	33.03	83.76	20.94	37.10	R
Rx83-G4M-c.62-25	124.50	46.34	52.63	33.72	35.61	88.72	21.77	37.83	L
Rx89-F1N-c.62-21	–	46.18	50.02	–	–	–	19.75	36.11	L
Rx90-F4N-c.62-167 ✦	–	56.58	56.54	–	–	–	23.10	42.01	L
Rx90-F4M-c.62-132 ✦	–	59.46	58.01	–	–	–	23.67	41.15	R
Rx90-F4N	–	47.09	44.14	–	–	–	20.38	30.79	L
Rx89-G2M-c.62-39	–		46.94	–	–	–	20.79	33.50	L
Rx89-F4M-c.62-49 ?	–		46.64	–	–	–	18.64	32.52	L
Rx89-G1N-c.62 ?	–	52.14		–	–	–	18.75	32.65	R
Rx88-F2-4M-c.62-2	–	48.5*	49.11	–	–	–	20.54	37.45	R
Rx90-G1N-c.62-144	–		46.62	–	–	–	17.47	31.84	R
Rx90-G1N-c.62-52	–	48.26	48.36	–	–	–	19.45	32.84	R
Rx90-F4M-c.62-27	–	–	–	31.15	–	–	–	–	L
Rx90-F4N-c.62-26	–	–	–	30.70	–	–	–	–	R
Rx90-E14-c.60	115.6*	–	–	–	–	–	–	–	L
Rx89-F4M-c.62-25	–	–	45.61	–	–	–	18.80	28.09	R
Rx90-G1N-c.62-224	–	–	–	27.74	–	–	–	–	R

VI.3. DIAGNOSIS OF A NEW SUBSPECIES

Panthera (Leo) spelaea intermedia, *nov. subspecies*, has the morphometrical characteristics of the population of Igue-des-Rameaux represented by an abundant material. The hemimandible retained here is considered to be representative and is the holotype.

Holotype

Hemimandible: left, Rx.90-F4N-c.62-58, pictured Plate 1 (1a, 1b, 1c), dimensions Tab.4 and comparison Tab.5.

It belongs to a young individual with not very worn teeth (0.1 to 0.3), apart from the incisors which show increased wear (U = 1). It appears in good condition, although slightly broken at the angular apophysis end and on both ends of the condyle. All the teeth are present. The ramus, long but relatively narrow, has almost parallel edges. The upper edge forms a 40° angle with the axis of the horizontal part of the mandible (Fig. 6, C.7). The massseter fossa does not go under the M/1 (Fig. 6, C.1). The constriction of this fossa exists, but is slight (Fig. 6, C.6). There are three chin foramina corresponding to type D (Fig. 7, Tab.5).

Derivatio nominis

Intermedia, morphometrically intermediate between the more ancient forms of *Panthera spelaea fossilis* (VON REICHENAU, 1906) of the Mid Middle Pleistocene and the more recent ones of the type *Panthera spelaea spelaea* (GOLDFUSS 1810) of the Late Pleistocene.

Diagnosis

Cave lion from the recent Middle Pleistocene, of small size in comparison with the ancestral forms *Panthera (Leo) spelaea fossilis* (VON REICHENAU, 1906), characterised by ancestral features less pronounced, but still present, than the typical more recent forms *Panthera* (*Leo*) s*pelaea spelaea* (GOLDFUSS 1810).

Differential diagnosis

The hemimandible of *P. spelaea intermedia* from Igue des Rameaux has the following characters:

– small size, average massiveness and marked muscles attachments but without more,

– elongated ramus, relatively narrow, with two parallell edges. The vertical projection of the coronoid apophysis is behind the condyle,

– the masseteric fossa extends as far forward under the rear of the M/1 (Tab.4, C.1, in 9 out of 14 cases observable), and presents a small to average constriction (Tab. 4, C.6),

– foramina: character C.3, Tab.4 and Fig. 7: type A two holes in 5 out of 15 observations (Type A, n=5; Type B, n=2; Type C, n=4; Type D, n=4).

For *P. spelaea fossilis*:

– very big size, great massiveness and powerful muscles attachment,

– triangular and shorter ramus. The vertical projection of the coronoid apophysis is in front of the condyle, the angular process is clearly more developed,

– the deep masseteric fossa clearly extends as far forward under the M/1, with a marked constriction,

– two foramina, type A, 9 out of 9 observations.

For *P. spelaea spelaea*:

– very variable size, small for the most recent forms of the Upper Pleistocene like Jaurens, comparable to the dimensions of Igue des Rameaux. In that case, massiveness and muscle attachments are in relation with the size,

– ramus fairly elongated, relatively narrow, with two parallel edges,

– masseteric fossa which does not extend under the M/1 or rarely so, constriction weak or absent,

– foramina: type A common, type C sometimes occuring.

Locus typicus

Igue des Rameaux site, commune of Saint-Antonin-Noble-Val (Tarn-et-Garonne, Quercy, France), excavation François Rouzaud from 1985 to 1991.

Stratum typicum

Layer 62 (main layer for *P. spelaea intermedia*).

Place of deposit

This material is kept in the collections of the LAMPEA – Aix-Marseille University, Maison Méditerranéenne des Sciences Humaines, Aix-en-Provence (France).

Paratype

Right hemimandible, Rx.88-F3-4N-c.62-20-4 complete but extremity of the ramus without the coronoid apophysis.

Additional material

Beyond the holotype, some teeth and bones provide helpful complemental informations in order to characterize the population of *Panthera spelaea intermedia* of Igue des Rameaux:

M/1: right M/1, isolated and complete, Rx.89-G30-c.60, U = 0.3 on the external face, the small posterior root is broken at its end, pictured Pl.1 (2a, 2b, 2c), dimensions Tab. 6. At the rear, the tooth finishes with a talonid clearly visible (Tab.6, C.1-12) although not very large, a slight tip occurs in the middle of the internal face of the crown (Tab. 6, C.2-11) without any furrow at its top (Tab.6, C3-0). The metaconid is slightly longer than the protoconid.

The M/1 of the *P. spelaea intermedia* from the Igue des Rameaux has the following characters:

– small size, relatively elongated and of medium width,

– protoconid slightly more elongated than the paraconid, clear posterior talon but not much developed (Fig.8, C.1),

– internal edge of the crown slightly bulgy in its median part (C.2) with neither marked relief nor groove at the top (C.3),

– paraconid and protoconid separated by a relatively important furrow on the external face of the crown.

For *P. spelaea fossilis*:

– wide and massive,

– protoconid and paraconid almost of the same length, talonid very much developed (C.1)

– median bulge of the edge of the crown (C.2) very clear, sometimes with a groove at the top (C.3),

– paraconid and protoconid separated by a moderate furrow on the external face of the tooth.

For *P. spelaea spelaea*:

– medium to small size, varying in size and massiveness from case to case, consistent with Igue des Rameaux for the recent forms, like Jaurens.

– protoconid more elongated than the paraconid, reduced posterior talon,

– internal edge of the crown rather rectilinear, with no relief (C.2) and no groove (C.3),

– paraconid and protoconid separated by a less marked furrow on the external face.

Lower canine: left lower C, isolated and complete, Rx.89-F4N-c.62-04, U = 0, posterior edge and median crest of the crown clearly visible, as usual two parallel furrows on its external face, but none on the internal face, without any possibility of erasure by wear in this case.

The lower canine of *P. spelaea intermedia* from the Igue des Rameaux has the following characters:

– small canine with a short and compact crown.

For *P. spelaea fossilis*:

– massive and very big canine.

For *P. spelaea spelaea*:

– varying in size and massiveness from case to case, consistent with Igue des Rameaux for the recent forms, like Jaurens.

Upper canine: right upper C, Rx.89-G2N-c.62-20, young individual, U = 0, wide nutrient foramen at the base of the root, clear antero-internal crest, posterior crest with clear and sharp relief also, two parallel furrows on the internal and external face.

The upper canine of *P. spelaea intermedia* from the Igue des Rameaux has the following characters:

– small canine with a long and quite slender crown.

For *P. spelaea fossilis*:

– massive and very big canine.

For *P. spelaea spelaea*:

– varying in size and massiveness from case to case, consistent with Igue des Rameaux for the recent forms, like Jaurens.

P4/: left P4/, Rx.90-F4N-c.62-130, U = 0.5, isolated and complete, anterior protocone relatively small, reduced parastyle on the internal talon, with a not very marked relief only in the form of a slight protuberance on the slope of the paracone, tooth relatively narrow with the crown slightly enlarged at the front, dimensions Tab. 10.

The P4/ of *P. spelaea intermedia* from the Igue des Rameaux has the following characters:

– small size, reduced width because of the both weakness of the protocone at the front and of the antero-internal parastyle,

– the paracone is slightly longer than the metacone,

– the parastyle, small, has only a slight peak at the base of the slope which joins it to the top of the paracone,

– the lingual edge of the crown is almost rectilinear,

– the vestibular edge is constricted by the paracone, the constriction is prolonged by a slight curve which gives an undulating form to this edge, but without exaggeration.

For *P. spelaea fossilis*:

– big size, wide and massive,

– well developed protocone,

– antero-internal talon well developed, with a pronounced relief,

– internal edge of the crown in shape of a curve,

– external edge of the crown slightly curved, with a strong central bulge.

For *P. spelaea spelaea*:

– size and massiveness variable, till the low values of the most recent forms,

– paracone and metastyle slightly developed at the front of the tooth,

– slight antero-internal talon, with almost no relief,

– internal and external edges of the crown rather parallel, without large curves.

Mtc.5: right Mtc.5, Rx.90-F4N-c.62-198, complete, well preserved, small, dimensions Tab. 11.

The Mtc.5 of *P. spelaea intermedia* from the Igue des Rameaux has the following characters:

– small size, average massiveness and marked muscle attachments but without more,

– the articular facet with the Mtc.4 stops at the distal extremity of the relief which fits into this Mtc.4 and seems less large than *P. spelaea fossilis*, which could indicate less possible freedom of movement. It is in a more oblique position.

For *P. spelaea fossilis*:

– big size, strong massiveness of the epiphyses and powerful muscle attachments,

– morphology of the articulation with the Mtc.4 different: more developed and more longitudinal relief, articular facet elongated and clearly hollow.

For *P. spelaea spelaea*:

– very variable size, small for the more recent forms of the Upper Pleistocene like Jaurens which dimensions are close to Igue des Rameaux, although slightly shorter:

L Mtc.5: Igue des Rameaux, n = 7, mean = 97.37, range = 92.6 – 103.0, σ = 3.99 / Jaurens: n = 6, mean = 95.08, range = 89.5 – 105.5, σ = 6.85

Median TD Mtc.5: Igue des Rameaux, n = 8, mean = 14.62, range = 12.9 – 16.6, σ = 1.18 / Jaurens: n = 7, mean = 15.57, range = 14.0 – 18.0, σ = 1.36.

Calcaneum: left calcaneum, Rx.89-G30-c.62-63, complete, well-preserved, small, not very massive, without well-developed muscle attachments, dimensions Tab.12, comparisons Tab.13.

The calcaneum of *P. spelaea intermedia* from the Igue des Rameaux has the following characters:

– small size, not massive, muscles attachments not much accentuated, relatively elongated,

– anterior articular facet connecting with the cuboid higher than it is wide, in the shape of an off-centre rib.

Table 13

Panthera spelaea intermedia, Igue-des-Rameaux, calcaneum, comparison.

	PFEMA 641 Calcaneum	Lat.		1	2	3	4	5	6	7	8	9	Source
				L	prox. TD	prox. DPD	TD tuber calca nei	DPD tuber calca nei	L manu brium	TD min. diaph yse	median DPD	TD art. astrag.	
extant *P. leo*	Tchad. male lion			101.0	47.0	42.2	27.7	28.2	–	16.0	–	–	Coll. UCB Ly.1
	Lioness	R		98.6	43.1	44.4	26.6	29.2	72.9	14.0	33.3	38.0	ARGANT
	BALLESIO 1975		n	14									BALLESIO, 1975
			min-max	92.0-113.8									
			mean	101.3									
			sd	40.3									
P. s. fossilis	CHA 1-98 - D6-61	R		135.5	57.9	59.8	38.6	42.3	99.7	23.7	51.1	49.3	ARGANT
	CHA 1 - H5 -69	R		140.7	64.5	66.1	38.0*	41.2	106.2	26.1	54.0	52.0	
	Moggaster Höhle	L		150.0	65.0								GROISS, 1992
P. s. Intermedia	Rx. 90 - F3M - C 62 - 335	R		118.8	53.0	47.6	31.5	32.3	91.1	21	39.3	42.8	ARGANT
	Rx. 89 - G 112 - C 62 - 38	R		121.8	53.6	52.1	33.7	37.1	88.7	22.2	42.5	41.8	
	RO - FEL. 43	L		128.5	47.7	54.7	32.6	39.7	70.2*				
P. s. spelaea	Jaurens (Corrèze, F.)		n	4	4		4			4			BALLESIO, 1980
			min-max	115-130	42.0-51.0		35.0-43.5			18.2-23.2			
			mean	122.5	46.0		39.43			20.58			
			sd	8.10	4.45		4.45			2.41			
	FSL 301046	R		126.9	62.0	55.7	34.2	–	102.7	22.4	42.9	48.6	Coll. UCB Ly.1
	FSL 300867	R		114.2	51.2	50.2	32.4	31.5	86.2	18.9	37.1	42.8	
	Wierzchowska Górna (Poland)		n	25						25			Janossy, 1969
			min-max	108.0-150.0						17.0-30.0			
			mean	137.04						25.28			
			sd	10.16						3.20			

For *P. spelaea fossilis*:

– big size, pronounced general massiveness, powerful muscles attachments, massive sustentaculum tali giving a large width to the articular facet connecting with the astragalus,

– wide and massive manubrium, powerful tuber calcanei,

– strong protrude of the anterior lateral tuberosity having the groove of the lateral tendon,

– anterior facet connecting with the cuboid wider than it is high, with parallel edges and the upper part in shape of an arc of a circle,

For *P. spelaea spelaea*:

– variable size and slenderness. The calcanei of the most recent forms like Jaurens have a similar size to those of Igue des Rameaux and their slenderness is close to that of *Panthera leo*.

The distinction between *P. s. intermedia* and *P. s. fossilis* is not a problem because of the difference in size, massiveness and strength of the muscles attachments of the large ancient forms compared to those of the new subspecies from the Igue des Rameaux. These differences are found in all cases. The distinction between *P. s. intermedia* and *P. s. spelaea* is more difficult. The distinction is still quite easy in the case of the larger forms from MIS 5 and MIS 4, but the forms from MIS 3, at the end of the decrease in size, become comparable to the population at Igue des Rameaux. The morphological differences then play an essential role and the chronology provides a major indication.

VII. CONCLUSION

All the comparisons come to the same conclusion. The population of Igue des Rameaux is clearly different from the more ancient forms *Panthera spelaea fossilis* of the median Middle Pleistocene (MIS 19 to MIS 11) because of its smaller size. This appears clearly on the diagrams through the relative position of the points corresponding to the means when they can be calculated. It also highlights once more that the data collected on a single individual should be taken only as an indication. The distinction between the population of Igue des Rameaux and the more recent forms *Panthera spelaea spelaea* becomes more uncertain. As a result of the ranking of data on the scatter diagrams, all the small sized pieces fall together, those of the *Panthera spealae intermedia* from Igue des Rameaux, related upper Middle Pleistocene ones (MIS 10 à MIS 6) as well as the populations of *Panthera spelaea spelaea* of smaller size, especially those of late Upper Pleistocene (MIS 3). On the contrary, a lot of *Panthera spelaea spelaea* of the early Upper Pleistocene (MIS 5 and 4) reach large size, sometimes larger than in ancestral forms. For a best characterisation of *Panthera spelaea intermedia* the morphology should then be used and criteria of distinction established. The evolution of *Panthera spelaea* seems obviously heterogeneous in the course of the Middle and Upper Pleistocene. Its different forms indicate adaptations to the changes of climatic conditions, location of the refuges zones in difficult time and potential prey for animals as strictly carnivorous as lions. The ancient forms of *Panthera spelaea fossilis* are probably different from *Panthera spelaea intermedia* for these reasons, because the break within these two populations is large. A genetic renewal can be assumed, for reasons that are now unclear to us, at the end of the Holsteinian period (MIS 11) and from this time, a new population dynamics during the upper Middle Pleistocene (MIS 10 to 6).

Finally, the notion of species in the broad sense enables us to envisage evolutionary models, which take into account the taxonomic flexibility of the subspecies. These reflect the importance of the variability of the populations, as much genetic as geographic or climatic. However global evolutive processes remain complex with the likely existence of geographic centres of speciation with more or less advanced morphotypes. The dynamics of the populations enable these morphotypes to spread, and to succeed one another, or even to coexist, within the same geographical zone. In the case of *Panthera spelaea fossilis* and *Panthera spelaea*

spelaea for example, these dynamics explain more logically the replacement of the first subspecies by the second and the changes during the transition between MIS 6 and MIS 5. However, this by itself is not able to explain all of the evolutionary record that we know, which is the basis for biochronology. The reality is necessarily much more complicated, combining chance meetings between males and females, genetic evolution, climatic and environmental adaptations, prey resources, and the dynamics of the populations, which allow all possible exchanges in these contexts.

The idea of a linear evolution of chrono-species or subspecies on a Western European scale does not withstand analysis. One subspecies can only correspond to a well-defined geographical context (i.e. regional) especially when, as in the case of the cave lion, it is a species that has a very wide geographical and chronological distribution.

The subspecies *Panthera spelaea intermedia* clearly corresponds to the existence in the South West of France of a population (MNI adults = 21; MNI juveniles = 9), which is morphologically homogeneous, is relatively well-supported chronologically, and which has provided sufficient material for statistical reliability, which is not often the case with felids. It represents another reference point for comparisons between the fossil series of *Panthera spelaea* of Western Europe. Morphologically, the form from Igue des Rameaux sits between the large forms with powerful muscles corresponding to *Panthera spelaea fossilis* of the median Middle Pleistocene and the smaller forms from the Upper Pleistocene, *Panthera spelaea spelaea*. This fossil series is largely sufficient to enable the definition of a new subspecies of biochronological and geographical importance.

Other new subspecies will be welcome in order to complete an evolutive framework closer to reality which future research on *Panthera spelaea* will have to explore, by means which are becoming more clear. It will then be possible to validate the hypothesis of geographical centres with more or less advanced morphotypes by defining their locations.

Some authors recognise two different species, *Panthera fossilis* and *Panthera spelaea*, to distinguish the two forms of the cave lion (BARYSHNIKOV & BOESKOROV 2001; SOTNIKOVA & NIKOLSKIY 2006; SABOL 2014). Nethertheless it seems best to keep the name *Panthera spelaea* for all these forms. This allows its use when the material is sparse or fragmented, when complete skulls are not available to enable a reliable conclusion. It nevertheless remains possible to include the sub-species when there is enough material to make the determination certain.

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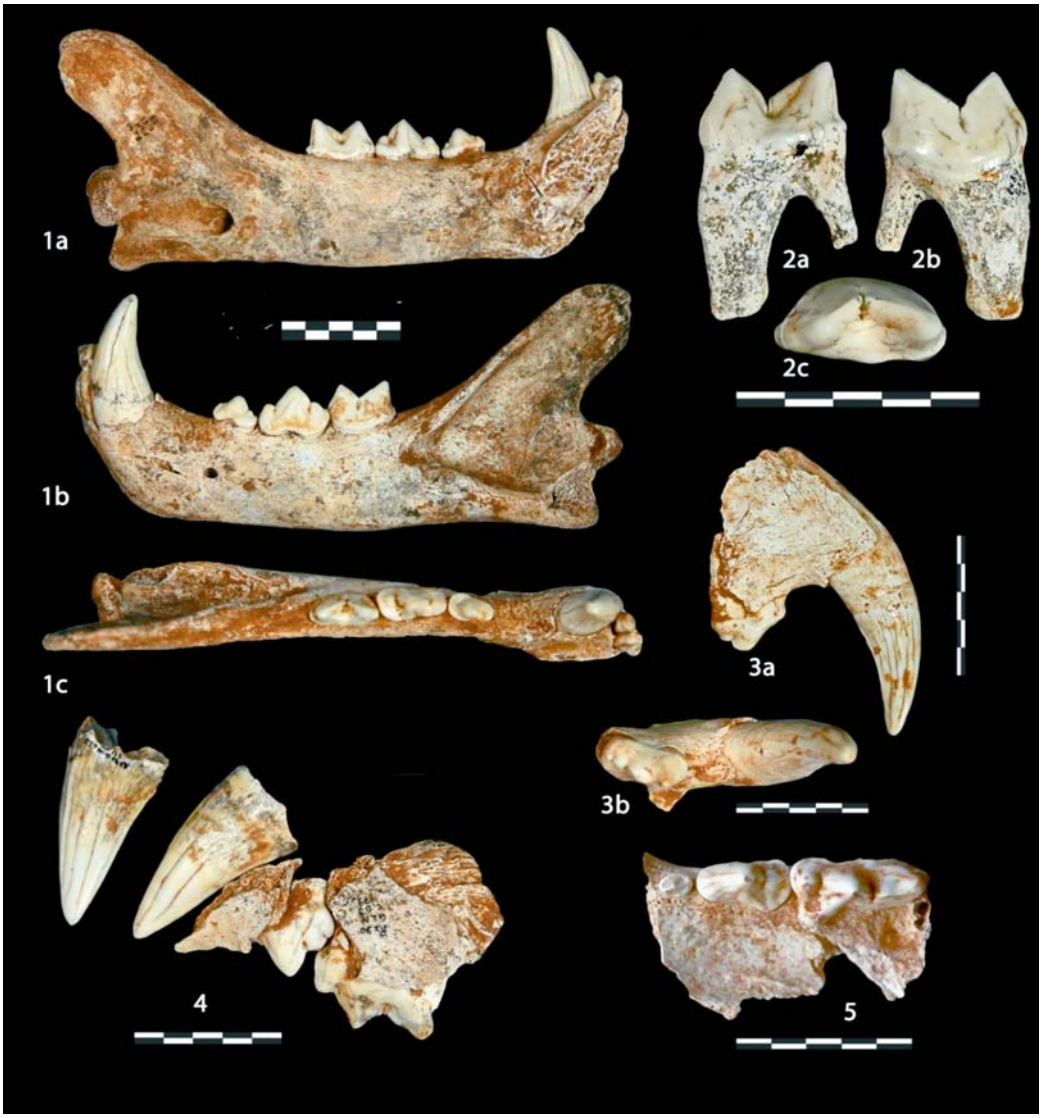

Plate 1. *Panthera spelaea intermedia*, Igue des Rameaux. Hemimandible and teeth.
1 – Left hemimandible Rx90-F4 N-c.62-58: a – lingual view, b – vestibular view, c – oclusal view. 2 – Right lower molar M1: a – lingual view, b – vestibular view, c – occlusal view. 3 – Right upper canine and P3 (note that P2 is lacking) Rx 89- F2 N-c. 62. 4 – Fragment of the left maxillar bone of a young individual (Rx 90-G2 N- c.63-179) with the empty canine and P3 still inside the bone, and P4. The right canine, Rx 90-G1N-c.63-213, is not in place. 5 – Left upper row of teeth (P2, P3 and P4 and alveolus of the M1).

Plate 2. *Panthera spelaea intermedia*, Igue des Rameaux. Hemimandible, comparison with Jaurens and Château. 1 – *Panthera spelaea spelaea*, Jaurens (FSL 301 035). Right hemimandible, large forme, BALLESIO 1980: a – vestibular view; b – lingual view of the M/1 (FSL 300 821). 2 – *Panthera spelaea intermedia*, Igue des Rameaux, left hemimandible (IgRx-F4N-c.62-58), vestibular view. 3 – *Panthera spelaea fossilis*, Château Breccia: a – right hemimandible (CHA.1-D4-99), vestibular view; b-c – fragment of mandible with P/4 and M/1 (CHA.1-D5-20), occlusal and lingual view.

Plate 3. *Panthera spelaea intermedia*, Igue des Rameaux. Long bones, calcaneum, comparison of the Mtc 5 with *Panthera spelaea fossilis* from Château. Long bones: 1 – Humerus; 2 – Radius; 3 – Cubitus; 4 – Femur; 5 – Tibia; 6 – Fibula (fragmented); Calcaneum: 7 – Right calcaneum: a – internal view; b – anterior view ; Mtc 5: 8 – Left Mtc 5 from Château CHA.1- 99-C5-200: a – anterior view; b – external view; 9 – Rigth Mtc 5 from Igue des Rameaux: a – anterior view; b – internal view.