



# The representation of cave lions in Paleolithic art: Temporal differences and anatomical accuracy

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## ABSTRACT

This study investigates the representation of cave lions (*Panthera [leo] spelaea*) in Upper Paleolithic art in France, dated between 40,000 and 12,000 years ago. Using an interdisciplinary approach, we aimed to identify depictions of cave lions among feline figures and assess the level of anatomical accuracy and familiarity prehistoric humans had with this extinct species. Our methodology combined a comprehensive survey of Paleolithic images (including cave art and portable objects), the reconstruction of a life-sized cave lion model, analyses of body proportions, and multivariate analyses of variance (MANOVA). The results reveal that most feline representations correspond closely to the proportions of the cave lion, particularly in terms of head dimensions, which remain consistent across pre-Magdalenian and Magdalenian periods. In contrast, body proportions show temporal variation, suggesting potential evolutionary changes in the species, shifts in artistic representations, cultural transformations in iconography, or stylistic preferences. Our findings highlight both the detailed anatomical knowledge and the complex symbolic and aesthetic choices of Paleolithic artists in their representations of large carnivores.

## 1. Introduction

In the context of the Upper Paleolithic (ca. 40,000–12,000 years BP), animals constituted a major source of artistic inspiration for hunter-gatherer societies. Numerous mammals are represented in decorated caves and on portable art objects. These material remains reflect an immaterial dimension of the cognitive systems of prehistoric societies. Beyond the needs of daily subsistence, a profound spiritual sphere is conveyed to us through Paleolithic art. What connections, then, could we establish between these ancient expressions and the long-lost worlds from which they emerged? (Leroi-Gourhan, 1995) These representations are most often dominated by herbivores, including horses, bison, deer, and ibex (Sauvet, 2019). However, sites such as the Chauvet Cave (Ardèche; Clottes, 2001; Fritz, 2024) and the La Marche Cave (Vienne; Pales, 1969) contain many paintings and engravings of felines, with the

majority of those in Chauvet attributed to the cave lion (*Panthera [leo] spelaea*; Clottes and Azéma, 2005). The felines at Chauvet are similar in style to a feline from Altzerri B Cave from the north of Spain that was created using fingertips (González-Sainz et al., 2013). They also bear resemblance to the well-known feline figurines from the Swabian Jura (Conard, 2007; Kind et al., 2014; Floss, 2015), as well as to an engraved feline with a pronounced dorsal line on quartzite from El Castillo Cave (Rivero, 2022). Despite representing only 2.6% of all cave art figures (Sauvet, 2019), feline depictions suggest that the cave lion played a distinct symbolic and cultural role in Upper Paleolithic societies.

However, the nature of the relationships between humans and cave lions remains poorly understood, partly due to the limited number of known depictions, and partly because those representations reflect the individuality and stylistic choices of the artist. Several hypotheses may be proposed to explain these interactions. Firstly, ecological competition

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probably existed between humans and large felines for access to prey and territories. This rivalry may have resulted in exclusion, confrontation, or cautious cohabitation. Secondly, interactions such as predation or scavenging are conceivable: humans may have been both victims and competitors of these large predators, but may also have benefited from the remains of their kills. The representations found in caves and on portable objects reflect the symbolic perceptions of different Paleolithic societies. In this study, our aim was to identify the cave lion among prehistoric feline figures by combining a quantitative analysis of Paleolithic art with a detailed understanding of anatomy and morphology. We further aimed to assess the degree of precision with which these representations were created. This raises several key questions: What do the traces left by prehistoric humans reveal about their understanding of the cave lion? Did the representations of cave lions change over the 25,000 years span of the Upper Paleolithic? And how faithful were the cave lions painted or engraved by Upper Paleolithic artists?

Felines known to have inhabited Europe during the Upper Paleolithic include the cave lion (*Panthera [leo] spelaea*), the panther (sometimes identified with the leopard, *Panthera pardus spelaeus*), the wildcat (*Felis silvestris*), the Eurasian lynx (*Lynx lynx*), and the Iberian lynx (*Lynx pardinus*) (Delpech, 2003; Sommer and Benecke, 2006; Gillard, 2018). These species were not frequently illustrated (Sauvet, 2019), and their representations often appear deep within caves or delicately rendered on valuable materials—for example, the large lion engraving at Trois-Frères Cave (Bégouen et al., 2014), or the iconic lion-man statue from the Hohlenstein-Stadel Cave (Hahn, 1986; Floss, 2007; Kind et al., 2014; Conard et al., 2015; Hussain and Floss, 2015; Wolf et al., 2020). Previous studies of feline representations in Upper Paleolithic art have highlighted their cultural importance and raised questions about the level of familiarity that hunter-gatherers had with these animals (Rousseau, 1967; Fritz et al., 2011; Gillard, 2018). Most of the representations for which the species has been identified consistently display morphological traits characteristic of cave lions, as evidenced by the examples cited above.

To better understand the nature of human–cave lion interactions as expressed through art, we developed an original, integrative approach. A 3D model of a cave lion was constructed based on scans of osteological remains. We then conducted a comprehensive survey of archaeological feline representations, followed by statistical analyses of their proportions using multivariate methods. A morphometric approach (García Bustos et al., 2024) was employed to objectively assess the proportions of Paleolithic depictions, in combination with an anatomically accurate life-size reconstruction of a cave lion. This approach provides new insights into how Paleolithic artists perceived and depicted this emblematic predator over time.

## 2. Materials and methods

### 2.1. Artistic corpus

This study focuses on representations of felines spanning the entire Upper Paleolithic, incorporating both cave art and portable art. Our research centers on French sites renowned for their richness and quality of representations of animals. We compiled a corpus of 69 feline representations on portable art (49 identified and 20 possible; Table 3) and 142 feline depictions for cave art (127 certain and 15 possible; Table 4). When a feline representation lacks one diagnostic feature, either in the body or the head, it is classified as a possible feline. By contrast, when the conventional “trefoil muzzle” motif characteristic of felines is present (Leroi-Gourhan, 1965; Gaussen, 1984, 1988; Lorblanchet, 1990; Clottes, 2003; Petrognani and Sauvet, 2012), the figure is identified as a definite feline. Of these (certain and possible), only 38 portable art pieces and 69 cave art images were sufficiently complete to be included in the statistical analyses. Our corpus consists of Paleolithic representations, the chronological framework of which is established based on

the radiocarbon dates. The oldest are those from charcoal drawings in Chauvet Cave, dated between 37,000 and 33,000 calibrated years BP (Quilès et al., 2016), as well as engravings from the Aldène Cave shutdown, dated between 35,200 and 34,370 cal. BP (Ambert et al., 2005). The most recent examples derive from La Vache, dated between 15,700 and 13,300 cal. BP (Delporte, 1993). The latter affirmed a human presence that was associated with the Aurignacians in Chauvet or Aldène. The portable arts from La Vache correspond to the Magdalenian or Azilian periods. Overall, the corpus comprises feline representations spanning more than 20,000 years. Felines were distinguished from other taxa (Table 1) by morphological criteria including a square or rectangular head with a squared muzzle and the presence of vibrissae, prominent canines, and a convex, prow-shaped chin followed by reduced mandibular height. The cervical region, from the top of the head to the shoulders, is short and robust with prominent scapulae. The spine is flexible; the body is cylindrical and elongated. The lumbar region is distinctly convex, and the calcaneus is protruding and angular. The claws are retractable (GRAPP, 1993; Gillard, 2018) (Fig. 1). In studying the diagnostic features of felines represented on Paleolithic figures (Table 2), the cave lion (*Panthera leo spelaea*) stands out through its formal similarity to most of feline depictions, notably the presence of a tail tuft (Gillard, 2018). The leopard (*Panthera pardus spelaeus*) is represented only once in Chauvet Cave, identified by its ocelli (Clottes and Azéma, 2005). In contrast, the identification of the wildcat (*Felis silvestris*) in the Upper Paleolithic record remains less certain, although the engraved plaquette from Labouiche was interpreted by Pales and Tassin de Saint-Péreuse (Pales and Tassin de Sainte-Péreuse, 1969) as possibly depicting this species. This representation appears questionable: the wildcat typically exhibits a short muzzle, whereas the figure depicts a prominent nose and rounded ears, inconsistent with the expected morphological traits. Lynx (*Lynx lynx* and *Lynx pardinus*) have been identified on the La Madeleine plaquette based on their characteristic ear tufts (Tosello, 2003).

### 2.2. Feline surveys

We conducted investigations into several feline representations by revisiting and resurveying portable art from the sites of La Marche, La Vache, and Gourdan-Polignan, as well as cave art at Les Combarelles, due to the significance of these representations and their accessibility. Our methodological approach involved a sequence of carefully structured steps: (1) initial direct observations and detailed sketching of the representations; (2) photographic documentation from multiple angles of incidence; (3) the creation of analytical drawings based on the photographs; and (4) distinguish engravings or paintings from natural features or later anthropogenic modifications. The final stage consisted of producing a comprehensive feline survey that integrated multiple layers of information superimposed on the photographs, which were digitally enhanced to improve the visibility of human-made traces. These layers included geological features of the wall surface, evidence of anthropogenic engravings or paintings, and any recent damage or alterations (Aujoulat, 1987; Fritz and Tosello, 2007; Paillet and Robert, 2022). This step is essential, as interpretations and results can vary significantly depending on the observer and their methodological framework (Petrognani et al., 2014).

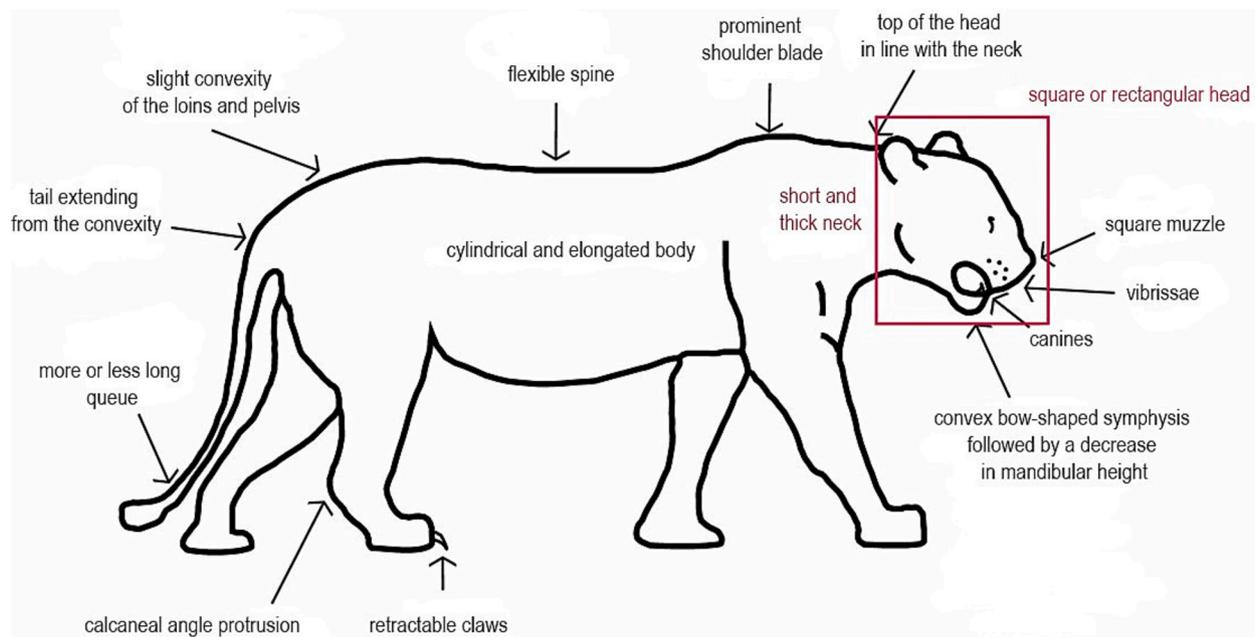
### 2.3. Reconstruction of a life-size model

To compare artistic representations and distinguish the cave lion from other potential felid taxa, we constructed a life-size anatomical model of a cave lion. This model was developed using 3D-printed bones obtained from scans of *Panthera [leo] spelaea* fossils, supplemented with bones from an extant lion (*Panthera leo*) to fill in missing elements. The skull was based on a cave lion specimen from Mars Cave (Alpes-Maritimes), housed in the Gallery of Palaeontology and Comparative Anatomy at the Muséum national d’Histoire naturelle (MNHN), while the

**Table 1**

Table of carnivore characteristic. Summary comes from R. Mittermeier and D. Wilson (2009).

	Size	Characters of head	Characters of body	Tail	Prehistoric Mammals
Felidae	Small to large 48.6 – 399 cm	rounded and rather flat head, facial whiskers, large eyes and ears	streamlined body with muscular legs	Variable Long tails as the Leopard Short tail as the lynx	Cave lion ( <i>Panthera leo spelaea</i> ), Panther or leopard ( <i>Panthera pardus spelaeus</i> ), Wildcat ( <i>Felis silvestris</i> ), Eurasian lynx ( <i>Lynx lynx</i> ), Iberian lynx ( <i>Lynx pardinus</i> )
Hyaenidae	Medium to large 85–185 cm	round or pointed ears relatively large in comparison to body size, exceptionally powerful jaw muscles	hindquarters long and sloping; very muscular	Bushy tail	Cave hyenas ( <i>Crocota crocuta spelaea</i> )
Canidae	Small to quite large 45.8–182 cm	triangular heads long, pointed muzzles well-developed jaws, and prominent, roughly triangular pointed ears	muscular, deep chested body, long and slender limbs	bushy tail	Grey Wolf ( <i>Canis lupus</i> ) Red fox ( <i>Vulpes vulpes</i> ) Arctic fox ( <i>Alopex lagopus</i> )
Ursidae	Large 100–280 cm	big head and thick neck, small eyes, rounded ears, no facial vibrissae	muscular bodies with stout legs, large paws	short tail	Cave bear ( <i>Ursus spelaeus</i> ) Brown bear ( <i>Ursus arctos</i> )
Mustelidae	Small to medium 13–195 cm	Small, flattish head, the muzzle is fairly long in terrestrial species, but is shorter in the otters.	Long slender bodies and short limbs	long tail	Wolverine ( <i>Gulo gulo</i> )

**Fig. 1.** Feline anatomical features: in black: according to L. Pales and M. Tassin de Saint-Péreuse (1969), in red: after M. Gillard. Diagram modified after Gillard 2018.

limb bones were sourced from a large modern lion specimen. Both specimens are male and adult. Due to budgetary constraints, the limb bones were not 3D-printed. Nevertheless, we selected bones from a single extant lion individual that closely matched the cave lion specimen, with a maximum length difference of less than 4 cm: scapula (28.5 cm vs. 27.2 cm), humerus (35.5 cm vs. 32.6 cm), radius (39.5 cm vs. 36.6 cm), ulna (31.5 cm vs. 28.3 cm), femur (41.5 cm vs. 37.1 cm), and tibia (32.5 cm vs. 30.7 cm). The bones of the extant lion are slightly larger than those of the cave lion, which may have influenced the dimensions of the reconstructed model. However, this offset was considered minor and not significant enough to impact the validity of our comparative analyses with archaeological representations.

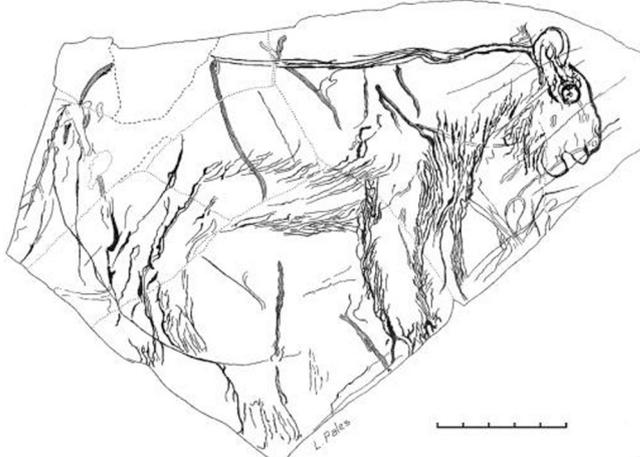
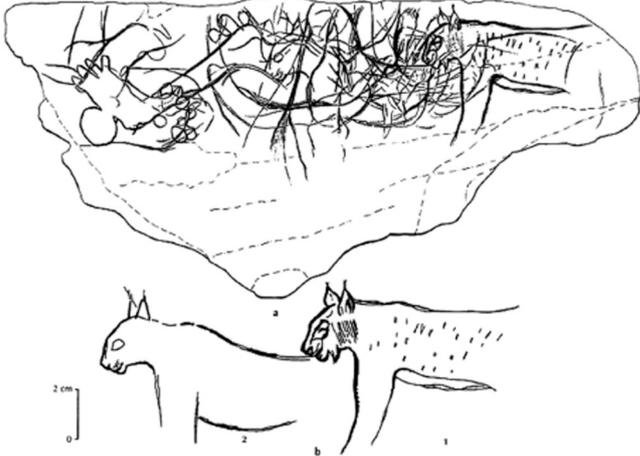
The posture adopted for the reconstructed cave lion is based on prehistoric depictions, prioritizing the most complete and anatomically precise figures (Fig. 2), particularly those whose morphological traits allow confident attribution to cave lions. These traits include a massive head with a short, rectangular muzzle; a long, muscular body with low

legs; a long tail ending in a tuft; and small, rounded ears. Such anatomical details, evident in sites like Chauvet Cave, strongly support their identification as cave lions (Clottes, 2001). The reconstruction integrated anatomical data from cave lion studies (*Panthera [leo] spelaea*; Pales, 1969; Clottes and Azéma, 2005; Pinçon, 2009) alongside muscular anatomy research from modern lions (*P. leo*; Ellenberger et al., 1956; Böhmer et al., 2020; Tsai, 2021). The full-scale model was assembled at the osteology and taxidermy preparation service of the MNHN. It serves as a reliable anatomical reference for assessing the proportions and musculature of the cave lion.

#### 2.4. Quantification of proportions

To assess the anatomical accuracy and fidelity of Paleolithic feline representations, we applied methods from morphometrics and comparative anatomy. Several identifiable anatomical segments were defined based on both the reconstructed cave lion model and the

**Table 2**  
 Characteristics of felines in Paleolithic art. Diagram

Species	Characteristics in Paleolithic art	Example
Cave lion ( <i>Panthera leo spelaea</i> )	the tail tuft or formal similarity	 <p data-bbox="986 508 1332 532">La Vache Cave. Photo © Marie Gillard, Cedarc</p>
Panther ( <i>Panthera pardus spelaeus</i> )	Presence of ocelli	 <p data-bbox="995 885 1323 908">Chauvet Cave. Photo © Jean Clottes – MC</p>
Wildcat ( <i>Felis silvestris</i> )	Presence of abundant fur (suggested by Pales and Tassin de Saint-Péreuse in 1969)	 <p data-bbox="970 1393 1348 1417">Labouiche Cave. ©Pales, Tassin de Saint- Péreuse</p>
Lynx ( <i>Lynx lynx</i> ) ( <i>Lynx pardinus</i> )	Tuft of hair above the ears	 <p data-bbox="1018 1885 1300 1908">La Madeleine shelter. © Gille Tosello</p>

adapted from M. Gillard (2018).

**Table 3**

List of felines figures on portable art from French sites (? : the question marks represent the possible felines).

Site	Number of felid representations	Period
Roc-la-Tour	1	Magdalenian
La Colombière	4	Magdalenian
Enval, Abris Durif	3	Magdalenian
La Marche	16 + 1?	Magdalenian
Roc-aux-Sorciers	3 + 2?	Magdalenian
Bois Ragot	1	Magdalenian
Badegoule	3 + 1?	Solutrean
Blanchard	1	Aurignacian
Laurgerie-Basse	3 + 2?	Magdalenian
Laurgerie-Haute	1	Solutrean
La Madeleine	3	Magdalenian
Morin	8?	Magdalenian
Isturitz	3	Magdalenian
Bruniquel	1?	Magdalenian
Gourdan-Polignan	2 + 1?	Magdalenian
Enlène	1?	Magdalenian
Labouiche	1	Magdalenian
La Vache	4 + 1?	Magdalenian
Mas d'Azil	1?	Magdalenian
Tuc d'Audoubert	1?	Magdalenian

**Table 4**

List of felines figures in cave art from French sites (? : the question marks represent the possible felines).

Site	Number of felid representations	Period
Arcy-sur-Cure	1	Aurignacian or Gravettian
Grotte des Gorges	3	Aurignacian or Gravettian
Roc-aux-Sorciers	2	Magdalenian
Les Bernoux	1	Aurignacian
Les Combarelles I	3 + 3?	Magdalenian
Font-de-Gaume	2	Magdalenian
Gabillou	3 + 1?	Magdalenian
Lascaux	5 + 1?	Begin of Magdalenian
Pech-Merle	1	Gravettian
Les Merveilles	1	Gravettian
Roucadour	16	Gravettian
Labastide	2	Magdalenian
Marsoulas	3?	Magdalenian
Les Trois-Frères	5 + 3?	Magdalenian
Le Tuc d'Audoubert	1	Magdalenian
L' Aldène	2 + 1?	Aurignacian
Baume-Latrone	1	Aurignacian
Bayol	1	Solutrean
Chauvet	76 + 2?	Aurignacian and Gravettian
Les Deux-Ouvertures	1	Gravettian- Solutrean
Cosquer	1?	Gravettian and Solutrean

archaeological figures. These segments allowed for the quantification of body proportions and facilitated species-level distinctions (Baron, 1976; Zelditch et al., 2012). Thanks to the morphological precision with which many figures were rendered by Paleolithic artists, landmarks were identifiable on the traced surveys. However, fully detailed representations of felines remain rare. Most Paleolithic depictions lack finer anatomical features, particularly the distal portions of the limbs. To address this, we established criteria for what constitutes a “complete body” or a “complete head” in the context of these representations.

A “complete body” representation includes a visible head, trunk, and at least one forelimb and one hind limb. For these cases, we recorded six key measurements (see Fig. 3): A: Distance from the back of the skull to the most prominent point of the scapula. B: Length of the thoracolumbar segment, from the top of the scapula to the base of the croup. C: Pelvic length, measured from the coxal tubercle to the ischial tuberosity. D: Length of the humerus. E: Length of the radius. F: Distance from the pelvis to the knee.

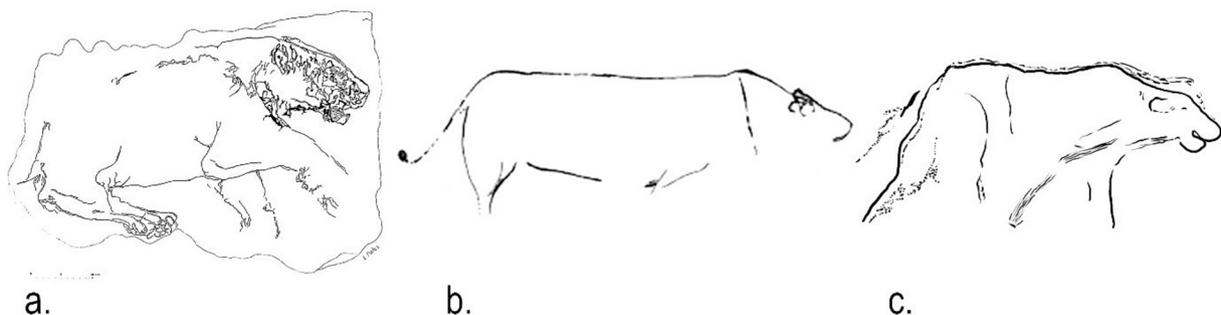
A “complete head” representation is defined by the clear presence of an eye, ear, nose, and mouth. For these, we extracted four craniofacial measurements:  $\alpha$  (alpha): Distance from the nose to the upper lip.  $\beta$  (beta): Distance from the frontal point (forehead) to the nose.  $\gamma$  (gamma): Distance from the frontal point to the upper lip.  $\delta$  (delta): Distance from the eye to the nose.

These selected measurements reflect relatively stable anatomical distances that are minimally affected by movement or minor postural changes, except in specific poses such as reclining or curled figures. Given that the majority of Paleolithic felines are depicted in profile our morphometric approach focused exclusively on figures rendered from this angle to maintain consistency in measurement and ensure comparability across the dataset.

The body and cranial measurements described above are illustrated and superimposed on selected Paleolithic representations in Fig. 4.

## 2.5. Statistical analyses

We performed statistical analyses to compare the supports of representations—cave art versus portable art—as well as two chronological periods: pre-Magdalenian and Magdalenian. Figures from pre-Magdalenian cultures reflect artistic conventions that distinguish them from those of the Magdalenian, such as the use of twisted perspective in animal depictions (Breuil, 1952; Leroi-Gourhan, 1965). Pre-Magdalenian representations are often more schematic and display a lower degree of standardization. For example, three characteristic features are commonly observed during this period: the concave stomach line of mammoths, the frontal view of bison horns, and horse muzzles shaped like a duck's bill (Petrognani, 2009; Petrognani, 2013; Petrognani and Robert, 2019). In contrast, Magdalenian art shows stylistic evolution. Anatomical details become much more prominent, formal and graphic refinements are multiplied, and proportions are carefully observed. This period is also marked by increased production and



**Fig. 2.** Prehistoric feline models used to establish the life-size model. a) La Marche (©Pales Léon) n° 9; b) Chauvet n°33 (©Azéma Marc); c) Roc-aux-Sorciers n°2 (sketch based on the photo by Geneviève Pinçon).

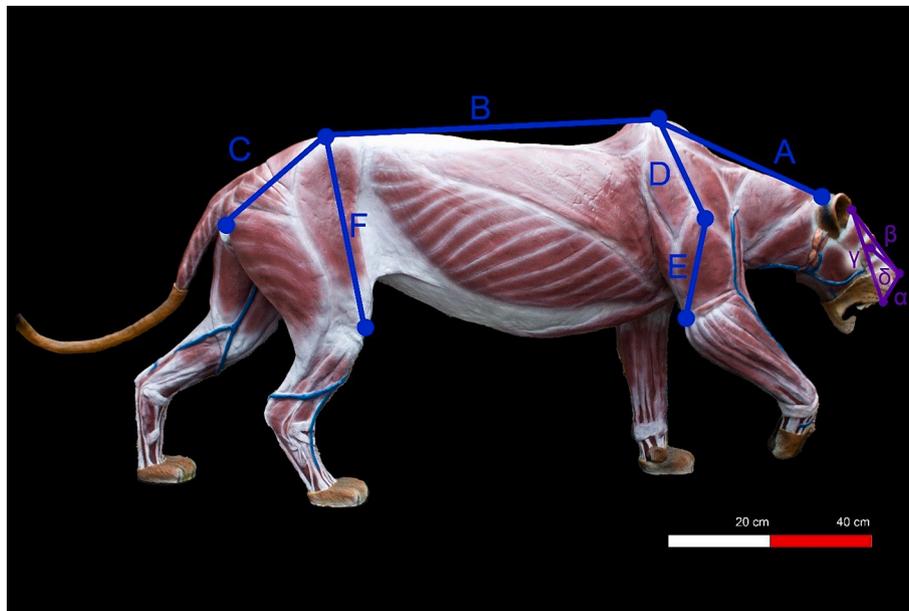


Fig. 3. Measurements on the life-size model for the analyses of proportions (head and body segments measured).

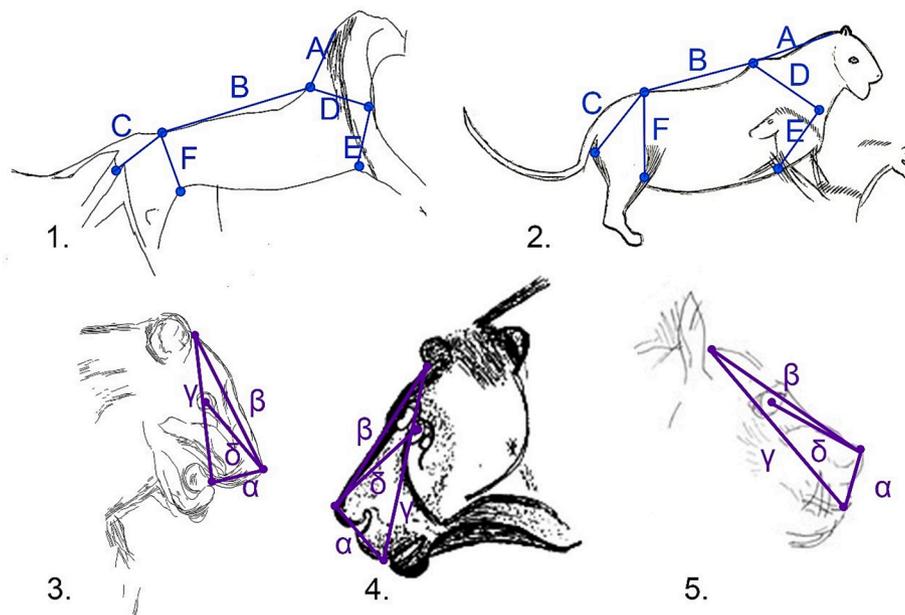


Fig. 4. Measurements taken on representations for body proportion analyses: 1) Deux-Ouvertures (©Gély Bernard and Porte Jean-Louis.) and 2) Font-de-Gaume (©Breuil Henri); for the head: 3) La Marche (©Pales Léon), 4) Chauvet (©Azéma Marc), and 5) Roc-la-Tour (©Colette Rozoy).

standardization of tools and a flourishing of portable art that reflects regional stylistic trends (Rivero and Sauvet, 2014; Ruiz-Redondo, 2016; Fuentes et al., 2019; Intxaurbe et al., 2024).

Because the objects used for measurements differ in size, we used log-shape ratios to normalize the data (Mosimann, 1970; Mosimann and James, 1979). A factor analysis with varimax rotation was conducted on the log-shape ratios of both the prehistoric representations and a life-size model of a cave lion, to visually explore their morphological proximity. Subsequently, a multivariate analysis of variance (MANOVA) was performed on the log-shape ratios to test for differences between periods (Magdalenian vs. pre-Magdalenian) and supports (portable vs. cave art). Separate analyses were conducted for the body and head datasets.

## 2.6. Methodological limitations

The combination of methods employed in this study facilitates a more objective interpretation of Paleolithic feline representations. Nonetheless, certain limitations persist, particularly regarding the availability and accuracy of measurements. The exact dimensions of feline depictions—whether found in caves or on portable artifacts—are not always accessible. In many instances, figures are initially interpreted by researchers, and our measurements are derived indirectly from their published drawings. This reliance introduces potential sources of subjectivity, as the placement of anatomical landmarks may vary depending on the observer's perspective. This issue is particularly evident in features such as the humeral length (section D), where inconsistencies are more likely to occur. Consequently, the reproducibility

and accuracy of certain measurements may be affected. Moreover, the reconstruction model was of a hybrid nature and represented only a single Paleolithic specimen. Its scope is therefore too limited to support a comprehensive comparative analysis of representations extending over approximately 28,000 years. Finally, distinguishing between feline species in Paleolithic art—such as the lynx, leopard, or wildcat—requires more extensive reference datasets concerning their respective body proportions. In the absence of such data, the present study can only highlight the morphological similarities between the proportions observed in the analyzed representations and those of the cave lion reconstruction model.

### 3. Results

Out of the 211 feline figures examined, 38 met our criteria for a “complete body.” Of these, 15 figures belong to the pre-Magdalenian periods, while 23 are from the Magdalenian. These include pre-Magdalenian parietal representations from the caves of Les Bernoux (1), Lascaux (4), Les Merveilles (1), L’Aldène (1), Roucadour (1), Baume Latrone (1), Chauvet (5), Les Deux-Ouvertures (1), and Le Roc-aux-Sorciers (1). The Magdalenian parietal examples come from Les Combarelles (3), Font-de-Gaume (2), Gabillou (1), Labastide (1), and Les Trois Frères (3). In addition, the corpus includes portable artworks from La Colombière (1), La Marche (3), Laugerie-Basse (1), La Madeleine (1), Isturitz (2), Bruniquel (1), Gourdan-Polignan (1), Labouiche (1), and La Vache (1) (Fig. A.1–A.7).

A factor analysis conducted on the data collected from these 38 prehistoric representations (Table A.1) extracted three principal axes, which together explain 73.4% of the total variance (Table 5). The first axis contrasts thoracolumbar distance with humerus length, while the second axis opposes radius length to femur length. The third axis differentiates between neck length and pelvis length.

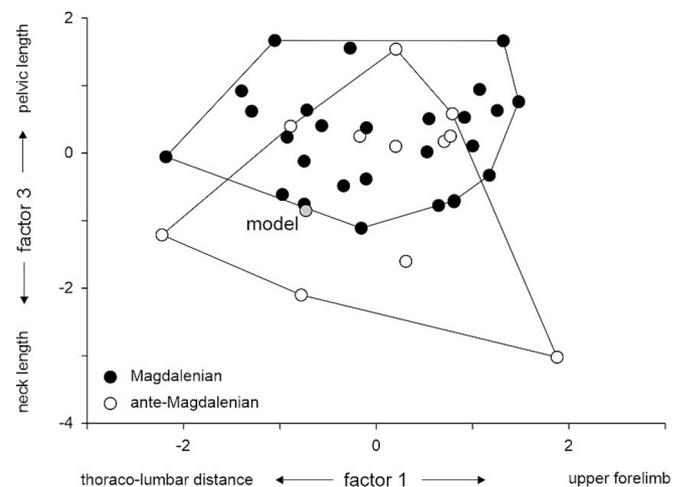
The scatter plot of Axes 1 and 3 reveals that the Magdalenian feline representations tend to cluster together, predominantly in the upper region of the graph. However, there is noticeable overlap between the two chronological groups, indicating that the distinction is not absolute. Interestingly, the cave lion model is positioned near the center of the distribution, situated at the intersection of Magdalenian and pre-Magdalenian representations (Fig. 5).

The MANOVA performed on the log-shape ratios revealed a significant effect of period on the representations (Wilks’ lambda = 0.68;  $F_{5,31} = 2.90$ ;  $P = 0.029$ ). In contrast, no significant effect was found for support type (portable art vs. cave art: Wilks’ lambda = 0.85;  $F_{5,31} = 1.07$ ;  $P = 0.39$ ). These results indicate that the stylistic variation in the figures is influenced by the period but not by the medium of representation. Subsequent univariate F-tests identified segments B ( $F_{1,35} = 4.15$ ;  $P = 0.049$ ) and C ( $F_{1,35} = 5.58$ ;  $P = 0.024$ ) as significantly contributing to the discrimination between Magdalenian and pre-Magdalenian figures. Specifically, pre-Magdalenian felines tend to have a relatively longer thoracolumbar distance (segment B) and a shorter pelvic segment (segment C) compared to their Magdalenian counterparts (Fig. 6). The other body proportions do not show significant variation between the two periods.

**Table 5**

Loadings of the variables on the factors extracted. Bold values represent high loadings.

segment	Factor 1	Factor 2	Factor 3
% variation explained	28.09	24.19	21.07
A: neck length	0.49	−0.10	<b>−0.75</b>
B: thoracolumbar distance	<b>−0.94</b>	0.22	−0.07
C: pelvic length	0.27	−0.03	<b>0.75</b>
D: upper forelimb length	<b>0.69</b>	0.29	0.00
E: lower forelimb length	0.03	<b>−0.87</b>	0.21
F: upper hind limb length	0.06	<b>0.75</b>	0.30



**Fig. 5.** Scatter plot of the factor analysis for the body proportions including pre-Magdalenian et Magdalenian feline figures with complete body) and the reconstructed model of a cave lion (grey dot).

#### 3.1. Variation in head proportions

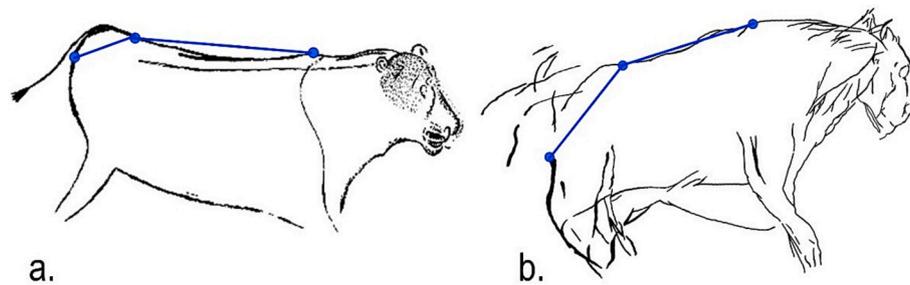
A total of 89 feline representations met the criteria for a “complete head” (Fig. A.4–A.17). Of these, 47 figures belong to the pre-Magdalenian period, while 43 are from the Magdalenian. The parietal figures derive from the pre-Magdalenian sites of Arcy-sur-Cure (1), Lascaux (5), Roucadour (4), and Chauvet (33), as well as from the Magdalenian sites of Roc-aux-Sorciers (2), Les Combarelles (2), Font-de-Gaume (1), Gabillou (4), Labastide (1), and Marsoulas (2). The portable arts originate from Magdalenian contexts, including Roc-la-Tour (1), La Colombière (2), Durif (2), La Marche (12), Laugerie-Basse (2), La Madeleine (3), Isturitz (2), Bruniquel (1), Gourdan-Polignan (2), Labouiche (1), and La Vache (3). Notably, only three pre-Magdalenian figures preserving a complete head are known, all from Badegoule (3). Finally, it should be emphasized that the figures from Chauvet Cave alone account for nearly 37 percent of the complete head corpus.

A factor analysis conducted on the head measurements (Table A.2) extracted two principal components that together explained over 82% of the total variance. Segments C (loading = 0.82) and D (loading = −0.96) loaded strongly on the first axis, while measurements A (loading = 0.92) and B (loading = −0.86) loaded strongly on the second axis. Visual inspection of the corresponding scatter plot showed that the cave lion model is located just outside the minimum convex polygon encompassing the Magdalenian representations. However, no clear differences between supports (cave vs. portable art) or periods (Magdalenian vs. pre-Magdalenian) were evident in the distribution (Fig. 7).

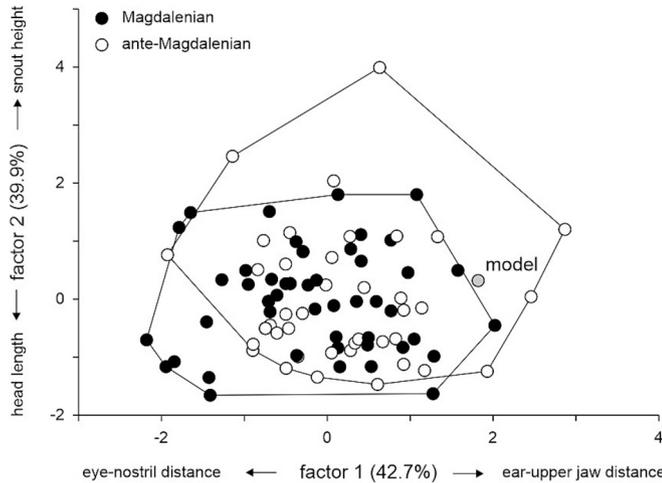
The MANOVA performed on the log-shape ratios of the head revealed no significant differences between periods (Wilks’ lambda = 0.98;  $F_{3,86} = 0.66$ ;  $P = 0.58$ ) or between supports (portable art vs. cave art: Wilks’ lambda = 0.98;  $F_{3,86} = 0.52$ ;  $P = 0.67$ ).

## 4. Discussion

Our data indicate that most of the studied representations closely align with the reconstruction model of the cave lion (*Panthera [leo] spelaea*). Notably, the head proportions of this model—constructed from fossil material—appear more consistent with pre-Magdalenian figures than with Magdalenian ones (Fig. 3). This may be attributable to the anatomical source of the reconstruction, as the skull was derived from a fossil specimen discovered in Mars Cave (Alpes-Maritimes). Unfortunately, no absolute dating has yet been conducted at this site. Nevertheless, the overall proportions of the life-size model fall within the range of variation observed in the prehistoric depictions, suggesting that the artists possessed a strong understanding of the species’ anatomy.



**Fig. 6.** Examples of lion figures with the complete body illustrating the differences in body proportions between periods. a: Chauvet n°72 (Aurignacian and Gravettian) (©Azéma Marc); b: Combarelles I n°2 (Magdalenian) (©Tsai Chi-Shan).



**Fig. 7.** Scatter plot for the head proportions including pre-Magdalenian et Magdalenian feline figures and the reconstructed model of a cave lion (grey dot).

#### 4.1. The evolution of the shape of cave lions as perceived by prehistoric artists

The statistical analyses conducted in this study reveal notable differences in the proportions of cave lion representations throughout the Upper Paleolithic. Interestingly, while body proportions vary significantly across periods, head proportions remain relatively stable. In particular, the relative length of the back changes over time: pre-Magdalenian representations tend to depict felines with more elongated bodies and shorter pelvic regions, whereas Magdalenian depictions are generally more compact. This shift suggests a transformation in the formal conventions employed by prehistoric artists to represent felines. Three hypotheses may explain this evolution: 1) biological changes in cave lion morphology over time, potentially captured by observant artists; 2) changes in the observational or drawing expertise of prehistoric artists; 3) stylistic or symbolic conventions that evolved independently of biological reality, despite the technical skill of the artists.

#### 4.2. The convention codes in Paleolithic societies

From a paleontological perspective, the size of cave lions decreased over time during the Middle and Late Pleistocene. Between 790 ka and 191 ka (MIS 19–17 to MIS 7–6), individuals were particularly large, with skulls exceeding 400 mm in length. Between 191 ka and 123 ka (MIS 6–5), this size remained considerable. However, from 123 ka to 60 ka (MIS 5–3), cave lions became more medium-sized, with male skulls generally measuring less than 400 mm—aside from the holotype from Zoolithen Cave, whose stratigraphic context is uncertain (Marciszak

et al., 2014; Diedrich, 2008). Between 57 ka and 29 ka (MIS 3–2), cave lions experienced a population decline and loss of genetic variability (Barnett et al., 2009), and the species eventually disappeared during MIS 1. This extinction may be linked to factors such as prey scarcity, habitat reduction, and human impacts (Stuart and Lister, 2011). The Paleolithic representations analyzed in this study may, in part, reflect what prehistoric humans observed. Thus, the reduction in body size could be captured in the changes in body proportions over time. However, this explanation seems unlikely given the lack of change in head proportions, suggesting that the evolution in body shape may instead reflect artistic choices rather than biological differences. It is possible that prehistoric artists intentionally altered body proportions while keeping the head size constant, either for stylistic reasons or due to symbolic conventions.

A notable discovery of a cave lion individual dated to 12,598–12,003 cal. BP, from the Azilian level of the Le Closeau site in the Paris Basin (Bodu and Mevel, 2008), confirms the species' persistence until the very end of the Pleistocene. The final fossil occurrences in North America are dated to 11,000–12,000 BP, from Fairbanks Creek (Alaska, United States) and Edmonton (Alberta, Canada) (Barnett et al., 2009; Stuart and Lister, 2011; Fosse et al., 2017). During MIS 2 to MIS 1—corresponding to the Upper Paleolithic and the Holocene—fossil evidence in France indicates that the species was mostly distributed in southern and western regions. As cave lions became rarer, direct familiarity with the species may have declined, potentially influencing how they were depicted in art.

Stylistically, pre-Magdalenian representations tend to be more schematic. Examples include sites such as Blanchard (Bourrillon and White, 2013), Les Bernoux (Petrognani et al., 2014), Pech-Merle, Les Merveilles, Roucadour (Lorblanchet, 2010), and Baume-Latrone (Azéma et al., 2012). A recurring motif is the so-called “clover snout”, a stylistic trait particularly associated with the Aurignacian period (Leroi-Gourhan, 1965; Gausson, 1984, 1988; Lorblanchet, 1990; Clottes, 2003; Petrognani and Sauvet, 2012). Despite differences in realism, the graphic skills of Paleolithic artists are evident across periods. Even the more schematic works—such as those from Roucadour—demonstrate accurate anatomical proportions, comparable to the life-size reconstruction. The more naturalistic style of Magdalenian figures, such as those from La Vache, does not necessarily indicate greater technical ability but rather a shift in artistic convention. The relatively longer backs and thighs observed in pre-Magdalenian figures likely reflect aesthetic or cultural choices, rather than limitations in observation or skill.

## 5. Conclusions

The cave lion, as a top predator, occupied the apex of the food chain. Humans not only observed but also hunted and utilized cave lions, as evidenced by finds at the Garma site in Spain (Cueto et al., 2016). This close interaction suggests that prehistoric people had an excellent understanding of the cave lion's anatomy. Our results support this, showing that artists consistently maintained accurate proportions across different media and varying scales of representation. The observed

graphic modifications in the lengths of the girdle and femur may reflect multiple factors: an effective evolution in cave lion size toward the end of the Pleistocene, decreasing familiarity with the species, or shifts in artistic conventions. Taken together, these elements demonstrate a deep and nuanced knowledge of the animal by Paleolithic humans. The high fidelity of the representations indicates a significant degree of familiarity with felines. Therefore, the relatively scarce archaeological remains of cave lions in faunal deposits may not reliably reflect the closeness of their relationship with humans. This constitutes the first step toward developing an understanding of the multiple forms of relationships between humans and felines. The complexity of these interactions indicates that the bonds that once connected them were far more diverse than previously assumed. As a perspective for future work, we intend to incorporate direct measurements of prehistoric representations—such as outlines and 3D models of portable pieces—to allow for more objective comparisons. These will be analyzed alongside the body proportions of modern felines (e.g., panthers, wildcats, lynxes) and other large carnivores such as hyenas and bears, with the aim of refining the identification criteria for cave lions within feline imagery.

### CRedit authorship contribution statement

**Chi-Shan Tsai:** Writing – original draft, Visualization, Conceptualization. **Christophe Voisin:** Visualization, Investigation. **Anthony Herrel:** Writing – review & editing, Supervision, Methodology, Investigation, Formal analysis, Conceptualization. **Eric Robert:** Writing – review & editing, Supervision, Conceptualization.

### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jasrep.2026.105683>.

### Data availability

I've shared the data in the supplementary material

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