European evidence for the representation of the woolly rhinoceros in art

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Abstract

In this work, we focus on art featuring woolly rhinoceroses from the Eurasian continent. We will provide an overview of cave paintings, engravings, and other evidence of art in terms of (i) geographic scope, (ii) chronology, (iii) representation, (iv) associated fauna, (v) material and technique used, and (vi) creator.

Since rhinoceros and birds presently constitute a shared landscape, we examined the links between fossil rhinos and birds and other animals in the evidence of Paleolithic art. We found that rhinoceroses make a minor contribution (2.6 %) to Paleolithic art. Evidence comes from France, Belgium, Czech Republic, Germany, Slovakia, Spain, Romania, and Russia and is attributed to the Aurignacian, Gravettian, Solutrean, and Magdalenian cultures. The animal is usually shown alone or co-occurring with woolly mammoths and other fauna. The depictions are not juxtaposed with birds, contrary to the present state of affairs. This is due to the presence of fur on the rhinoceros and the climatic demands of birds. The rhinoceroses are shown superficially as an outline and in detail with a hump, with a black stripe, bleeding, or fighting one. These paintings woolly rhinoceroses can be linked to modern humans who used charcoal, ochre and manganese oxides to represent them in the artworks. Engravings of woolly rhinoceroses also occur on mobile objects such as reindeer antlers and rock slabs.

Key words: woolly rhinoceros, art, paintings, Pleistocene, Paleolithic, Europe

1. Introduction

Art is a way of knowing, of obtaining spiritual fulfillment through creativity, and of inquiry, and also has a role in science. Prehistoric art, however, presents difficulties in terms of understanding prehistoric behavior and intentions, and it is also difficult to interpret objects that relate to pareidolia—the psychological phenomenon of seeing meaningful forms in random patterns, such as faces in clouds, and which is a universal feature of our visual system (Wisher et al., 2024). Paleolithic visual art (such as cave paintings, rock engravings, small sculptures, and personal ornaments) is unlikely to be the only creative expression of that era, but it is the only one to have survived to our time. Observations of various communities today show that the transmission of content can also conveyed through dance, song, and rhetoric (Gąssowski, 2008).

Creating art, today and in the past, requires skills and aptitude. The skills needed to create visual arts include an enhanced capacity to attend to, manipulate, or process specific aspects of visual information more efficiently, visual memory, the ability to integrate local details into global representations of objects, flexibility in shifting between global and local attention, and the ability to generate and transform mental images (Rivero et al., 2024).

Various animals are depicted in Paleolithic art and even give an idea of how likely it was that hominids might capture them. One animal represented in Paleolithic art is the woolly rhinoceros (*Coelodonta antiquitatis* Blumenbach, 1799), an extinct rhinoceros species most closely related to the extant Sumatran rhinoceros, as DNA studies have shown (Orlando et al., 2003). The ancestors of the woolly rhino, which include *C. tologoijensis* and *C. thibetan*, came from areas of Asia and Tibet. Woolly rhinoceroses spread westward and entered Central Europe and, in several cases, Western Europe, during all of the subsequent Middle to Late Pleistocene cold stages, as a result of preferable environmental conditions—namely, extended phases of low temperature and aridity (Kahlke & Lacombat, 2008; Puzachenko et al., 2022). By the end of the Pleistocene (until ca. 40 ka, Stuart & Lister, 2012), the woolly rhinoceros was already widely distributed geographically in Eurasia as syntheses show (including Spain: Álvarez-Lao and García, 2011; UK: Stuart & Lister, 2012; France: Guérin, 1980; Poland: Pawłowska et al., 2024). It can be assumed that the low grass density and lack of suitable habitat prevented it from crossing the Bering Strait to the American continent (Prothero et. al., 1989).

Woolly rhinos and mammoths are the major representatives of Pleistocene megafauna. Megafauna are usually defined as a subset of the largest terrestrial species in a community or an ecosystem. Perhaps surprisingly, mammoths have received much more attention in studies of Paleolithic art than the woolly rhinoceros (Braun and Palombo, 2012; Lioubine, 1996; Paterson et al., 2025). The depiction of the rhinoceros in art in synthetic terms was dealt with more than four decades ago (Millan Cascallo, 1982; Nougier & Robert 1957) but, as the results show, new evidence has come to light. It would thus be extremely valuable to compare aspects of the woolly rhinoceros' natural history in Eurasia by showing its representation in art and, for the first time, its co-occurrence with other mammals, fish and

birds. To this end, we here examine Paleolithic art that feature extinct rhinoceroses from the Eurasian continent, which were a means for humans to express their experiences and events.

2. Material and Methods

We examined rock paintings, engravings and other evidence of art from Europe that depicts the woolly rhinoceros (*Coelodonta antiquitatis*). In total, our collection includes 63 pieces of evidence of the presence of the rhinoceros in European art. All these cases were considered from the points of view of (i) geographic scope, (ii) chronology, (iii) representation, (iv) associated fauna, (v) material and technique used, and (vi) creator.

This research is a part of a recently launched project entitled "Unraveling the chronological, geographical, and taphonomic complexities of the occurrence of the woolly rhinoceros in the Pleistocene contexts of Poland (WOOLRHINOPOLI) and Europe", carried out in cooperation with eleven researchers from Beringia, Czechia, France, Germany, Italy, Moldova, the Netherlands, Poland, Romania, Spain, and the United Kingdom.

3. Results

A review of 250 sites from Eurasia at which Paleolithic art was found made it possible to identify at least 44 sites at which there are 63 cases of depictions of rhinoceroses (Table 1; S1).

Most of these sites with evidence of Paleolithic activity are located in France (n = 29), especially its southern part, with some pieces of evidence from Belgium (n = 1), Czech Republic (n = 2), Germany (n = 4), Slovakia (n = 1), Spain (n = 5), Romania (n = 1), and Russia (n = 1) (Figure 1). These sites represent only 17% of all sites with Paleolithic art. Even in France, the number of rhinoceros representations accounts for less than 3% of all animal depictions, with horses (about 33%), bison (20%), and mammoths (11%) dominating (Table 2).

In total at least 143 individuals are shown in Paleolithic art at these sites. In certain cases, attention can be drawn to the gender of the animals which, being depicted with more delicate structure (especially regarding the horns), can be identified as females (Rouffignac, n = 2; La Mouthe Cave: Space 4, n = 1; Chauvet, n = 5). One male is also reported from the Rouffignac panel.

As a general rule, the entire body of the rhinoceros is shown, highlighting details of its body in the form of the snout, eyes, ears and tail. Not all instances of the art are well preserved, as shown by the example of Siega Verde (Gravettian and Magdalenian; S1) and Chauvet (Aurignacian and Gravettian). When shown partially, this is with more emphasis on the head and horns than the forelimbs or hindlimbs. The body is generally naked, but in many cases with the presence of fur is marked (Los Casares: Aurignacian (questioned by Serangeli (2006) who considers him to be a wild boar); Les Combarelles, Font-de-Gaume, Trois Frères, Rouffignac: Magdalenian; S1). Certain notable paintings show a black band in the middle of the body (Chauvet: Aurignacian and Gravettian) or a stripe on the back of the body (Trois Frères, Magdalenian). The rhinoceroses of Les Combarelles, attributed to the Magdalenian

period, appear to be fat (S1). In turn, from La Colombière, from the same period, are shown with three or 4 arrows lodged in the underside of their bellies (S1).

Rhinoceros bodies are generally massive, with two horns on the head and the prominent dorsal line bent to show a bump at the front end. Exceptions to this are the examples from Kapova Cave (Russia; Solutrean and Magdalenian period), where rhinoceroses display a unique set of features in form of one horn with a second short one barely outlined, a short head in low position, and massive body with a quite straight-backed outline (S1).

Representation of other animals in the art at these sites is significant, and includes various animals from major groups such as mammoths (woolly mammoth), bovids (aurochs, bison, muskox, ibex, caprids, and antelope), cervids (giant deer, moose, and reindeer), horses, camels, carnivores (cave lions, panthers, bears, wolves, and felids), birds (owls, swans, and ravens), fish, snakes, and hominids (human males, human females, and anthropomorphic forms) (Table 3). Representations of art that have a mosaic of features of different animals can be called 'enigmatic animals'.

Rhinoceroses often appear together with mammoths in the same paleolithic sites, but rhinos do not co-occur with birds except in rare cases, where birds are shown in the same site or same panel. Art involving birds is found at the Arcy-sur-Cure (Aurignacian), Chauvet (Aurignacian and Gravettian), Cussac (Gravettian), Margot (Gravettian and Magdalenian), Lascaux, and Trois Frères (Magdalenian) sites, dating to approximately 30–15 ka BP. The Chauvet Cave contains the oldest image of an owl in paleolithic art, at ca. 30 ka BP. A bird of unknown taxonomy is also shown in this site cave paintings next to a giant deer. The birds in the Margot Cave are thought to be cygnets, corvids, and an owl. Even rarer are the juxtapositions of rhinoceros with fish, which are only known from Marche-les-Dames (Aurignacian; S1).

Paleolithic art involving rhinoceroses is associated with the Aurignacian, Gravettian, Solutrean, and Magdalenian cultures and some details of these cases are discussed next.

3.1. Aurignacian–Magdalenian

At least 15 pieces of evidence from ten sites depicting a rhinoceros are associated with the Aurignacian culture (Table 1; S1). One representation of a rhinoceros in a cave rite comes from the Bernoux site, where it forms part of a triptych with a mammoth and a bear; however the features are not entirely consistent with a rhino (S1). Generally, rhinoceroses are depicted with numerous details, such as eyes, ears, and fur. However, in the case of Arcy-sur-Cure, the woolly rhinoceros has only one leg at the front and one leg at the back, which appear to be painted incompletely.

The oldest rock art depiction of a rhinoceros found to date, dating to 33–30 ka BP, comes from Chauvet Cave. In total, the Chauvet Cave contains as many as 65 rhinoceros paintings and many other species of fauna within several panels. Rhinoceroses are variously depicted there, as just a head in the Bear Hollow Chamber and as a half-length body in the Red Panel Gallery. Red pigment was used in both cases. In the Megaloceros Gallery of this cave, two entire rhinos with black bands around their stomachs are shown. One of these

combines painting and rock engraving techniques; this was created after a previous depiction was removed, and the remnants of the previous layer can still be seen as a horn and ears. One unique feature of this cave is the depiction of a procession of four rhinos and fighting rhinos along with one running.

Animals are also shown in motion in the End Chamber, where the depictions of rhino are found among images of lions, horses, bison, and aurochs. The rhinoceroses, like other animals, are presented with anatomical details on the head and muzzle, and the use of techniques, such as the strengthening of certain edges and smearing pigment, gives the paintings a three-dimensional impression. The rhinoceros in the upper part of the panel has been repeated many times, which may have been intended to simulate either movement or an infinite number of these animals.

The second scene in this chamber uses a combination of black and red pigment to represent a bleeding rhinoceros. This panel also includes representations of lions, a bison, and an aurochs. The red lines, symbolizing blood and wounds on the body, are less terrifying than the frightened look of the animal, which is more accurately depicted than in the other images.

The image of a rhinoceros or bison made of hand prints in the Brunel Chamber is unique. It was determined that depiction was made by one person, about 180 centimeters in height, using his or her right hand to apply the pigment. The artist had a slightly crooked little finger, which allowed it to be determined that he or she was also the creator of other handprints deeper in the cave (Herzog, 2011). A computer reconstruction confirmed this hypothesis.

3.2. Gravettian and Magdalenian

The rhinoceros is shown on several sites dating to the Gravettian period using engraving and painting (Table 1; S1). It is usually depicted alone. In the case of La Mouthe Cave, the rhinoceros is superimposed with a mammoth in one case and with an ibex in another.

3.3. Solutrean and Magdalenian

The only known Paleolithic site with cave painting as far east as the Urals is Kapova Cave (Figure 1). Paintings involving rhinoceroses come from Kapova Cave (Shulgan–Tash) where their visual appearance varies by number of horns but not body exposure, as all rhinos are shown from the left side. Heads are in a low position and horns are projected forward, with their legs giving an impression of movement (Ruiz-Redondo et al., 2020).

3.4. Magdalenian

During the Magdalenian period, rhinoceroses are shown in art at twenty sites, mostly in France but with examples in Spain and Germany (Table 1; S1). The left and right body parts are shown in paintings and engravings made mainly using black pigment, or red in the case of Font-de-Gaume.

At Lascaux, the rhinoceros is apparently unrelated to the figure of the man (clearly a shaman, as he is equipped with a bird-headed staff) (Bataille, 1955; Aujoulat, 2003; S1). Both arms end

in hands, each with four fingers, which therefore seem to be from a bird rather than human hands (Braun, 2018). This painting is one of the few where dots occur in close proximity to the rhinoceros, which was done in a more realistic style, with thicker outlines than the shaman. In Les Combarelles, the rhinoceros is depicted as a rather fat animal. At the Bad Kösen-Lengefeld site there is a painting of a rite with an unusual rhinoceros, with the head being omitted from the depiction on the limestone slab (Richter et al., 2024).

4. Discussion

Pleistocene fauna can be studied through their remains (bones, skins, fluids, etc.) and their depictions in art. The former approach is dominant, and especially uses bones and teeth, on account of the great potential for taxonomic and morphometric investigations, chronological issues (Davoli et al., 2024; Pawłowska, 2015a, 2015b; Svenning et al., 2024), symbolic significance (Pawłowska, 2020a,b; Wolfhagen et al., 2020). It offers opportunities to determine the age of death, to differentiate genders, to reconstruct diseases, and to examine tools made from them (Demay et al., 2021; Gaudzinski-Windheuser et al., 2023; Pawłowska et al., 2014, 2025). Such an approach also makes it possible to investigate the demographic history of the population through studies of ancient DNA (Rossi et al., 2024; Van Der Valk et al., 2021). Faunal remains can also be subjected to isotope studies aimed at reconstructing diets, determining faunal assemblage redeposition issues, and more (Ballatore, 2016; Hrynowiecka et al., 2018, 2022; Ma et al., 2024; Pawłowska, 2023; Pushkina et al., 2020; Tiunov and Kirillova, 2010).

Depictions of animals on rock walls, mainly in caves, as well as on mobile objects, convey well their characteristics and features and even give an idea of how likely it was that hominids might have captured them. Here we focus on representations of the woolly rhinoceros, a member of the megafauna—the largest terrestrial species in a community or an ecosystem (Moleón et al., 2020).

4.1. Rhinoceros contributions to art over space and time

Our dataset revealed that there are 44 sites in Europe with 63 cases with rhinoceros depictions in Paleolithic art. The difference in numbers is due to the presence of several, often different, depictions of rhinoceros at a given site. This has to do with the size and spatial arrangement of the site: for example, in Chauvet Cave, sequences of corridors form channels that vary in the quality of cave art.

Evidence for the presence of art involving rhinoceros is concentrated mainly in France, however even there they are uncommon (less than 3%). The same observation applies to Spain, where out of 155 sites with figurative parietal decoration (García-Bustos and Rivero, 2023), only five contain rhinoceros (WOOLRHINOPOLI data). This result corresponds to the overall distribution pattern of Paleolithic art, estimated to be spread over approximately four hundred sites in Europe (Table 1). Most of these are located in southern France and northern Spain. A smaller number of caves with animals paintings and rock engravings have been found in Portugal, England, Italy, Sicily, Romania, Slovakia and the western Urals. However, we do

not find rhino images in each of these locations, and in fact such images occur only in some location in each ofBelgium, Czech Republic, Germany, Slovakia, Spain, Romania, and Russia. There is only a few rock art representations in central Europe, as shown exampe in Czech Republic, Slovakia and Romania, which is quite strange considering the abundance of caves and shelters in the Carpathians. This is all the more striking considering the strong movement of amateur speleologists between the 1970s and around the 1990s, who enriched the speleological inventory. One would expect a scientific aspect of karst in the field of art. The finding is striking since, as is well known, the woolly rhinoceros was geographically widely distributed in Eurasia. Thus, its absence is not a function of its poor representation in the environment but rather of hominid choices. One justification for this is the animal's limited contact with hominids, the lack of a positive relationship, the cultural approach, or the circulation of artistic knowledge. However, the last hypothesis is weakened by the breadth of the places with depictions of a woolly rhinoceros (La Pileta–Kapova Cave transect; Figure 1) which demonstrate the wide scope of these artistic activities, which occurred for over 20 ka BP. From the painterly reflection of nature, it is also real that people at that time did not have enough time to calmly observe a rhinoceros and analyze its anatomical structure, which is why few people were able and willing to create its images.

Generally, art involving rhinoceros appears at the sites from the early Upper Paleolithic. The oldest cave paintings discovered to date in Europe are in the Chauvet Cave, while the youngest are in Combarelles Cave, both in France, where the rock art is dated to 36.5 ka BP and 11 ka BP, respectively. Given the extinction date of the rhinoceros, now recognized as 15–16 ka BP (Stuart and Lister, 2012; Rey-Iglesia et al., 2021), we can conclude that its image survived for several thousand years in the consciousness of hominids, or that they duplicated depictions known to them. Whatever the case may be, rhinoceros size, posture, and arguably defensiveness must have played a role. There is also the possibility of explaining the late representation of the woolly rhino by an imprecise dating of the representation.

4.2. The representation of rhinoceroses in art

Woolly rhinoceroses had a strong, stocky body covered in long, thick hair that allowed them to survive in the extremely cold and harsh mammoth steppe. Its two horns were useful for fighting, defense, and clearing snow to gain access to food (Boeskorov et al., 2011). It seems that there is a consensus in identifying European Paleolithic rhinoceros images that have such features as woolly rhinoceroses. However, a rhinoceros painting at Dordogne Caves and Villars is believed to be a different species, *Stephanorhinus hemitoechus*, a contemporary of the woolly rhino (Guérin and Faure, 1983). In turn, the painted rhinoceroses with one horn in Rouffignac and in Kapova Cave could, according to Schaurte (1964) and Gromov (Bader, 1965), be an *Elasmotherium*. However, the differences in the depictions of rhinos with one or two horns from this site may also be due to stylistic variants, as suggested by Ruiz-Redondo et al. (2020). This approach is supported by the art in the caves of Arcy-sur-Cure, where animals, including rhinoceroses, are painted with one leg at the front and one leg at the rear; the

animals' legs are often drawn with dotted, rather than solid, lines. The single leg on each limb of the rhinoceros shown there, which appears to be incompletely painted, is a feature unrelated to the species and can be attributed to specific features of the art in these caves. In one case, the representation of a rhinoceros in a cave rite in the Bernoux site might not be a rhinoceros, given its features, but rather a wild boar. If this is so, then the triptych of animals depicted would be a mammoth, a wild boar, and a bear.

Our data show that at least 143 individuals were captured in Paleolithic art, regardless of the period. This is not a significant amount if compared to depictions of horses and bovids, which appear in much greater numbers, even considering only data from France (about 700 and 1,200, respectively, Table 2). In the iconography of Paleolithic art, horse appears to be the main image in what can be interpreted as a hierarchy of animal images chosen for depiction by the paleolithic image-makers and in what may be seen as a conceptual dominance and a key image in the organizing principles for image making (Sauvet, 2019). It means, that the animals represented in Paleolithic art seem to have been structured, with dominance of the horse over others, from the Aurignacian until the end of the Magdalenian, and with the ninth position of the rhinoceros in the hierarchy of animals in Paleolithic cave art (Sauvet, 2019).

There are attempts to distinguish females among the rhinoceros specimens, as they are supposed to be characterized by thinner and smaller horns. This could be a criteria except that it also points to the age of the individual, which may overlap with the degree of horn development. Additionally, the nasal horns of woolly rhinoceroses from Russia have been estimated to grow by 13–95 mm per year, reducing with age (Kirillova and Shidlovskiy, 2010).

An analysis of the body parts of the rhinoceros in Paleolithic art revealed that, as a rule, its entire body is shown, with attention to details such as the snout, eyes, ears, and tail. When, however, it is shown fragmentarily, attention is focused on the head and horns. An exception is the rhinoceros of Bad Kösen-Lengefeld, which is shown headless. Richter et al. (2024) suggested that the headlessness of the animal may indicate some relation to the headless women of Magdalenian art. This result is consistent with the results for the mammoth, which is mostly shown from the front end and uppermost parts (Lioubine, 1996), indicating a similar approach to depicting these large mammals by the artists. For mammoth, Lioubine (1996) pointed out the significance of the thick hair cover, which hid the contours of the body, as a factor in rendering the animals. There is a consensus that anatomical details of rhinoceroses have been reproduced in Western Europe in the form of the hump, the bending of the back line, and the massive limbs. This image differs in Eastern Europe where Kapova's rhinoceroses display different features, such as a short head with one large horn and a second short horn barely outlined; the body has a rather straight-backed outline.

Various paintings and engravings display distinctive marks on the body of the rhinoceros. Ours analysis of the features of Rouffignac's rhinoceros paintings led to conclusion that a stripe of the back of the body may suggest a sable coat. In the case of Chauvet rhinoceros, the black belt across the belly may represent a localized color change of the fur related to pigmentation. The woolly rhinoceros' overhair, guard hair, and underhair varied in color, from colorless, through dingy yellow, to red/orange and brown (which itself ranged

from pale brown to dark brown, almost black) (Tridico et al., 2014). This color diversity is related to pigments such as eumelanin (predominant in dark brown/black hair) and phaeomelanin (predominant in red and blonde hair).

That both the left and right sides of the body are shown suggests that this feature did not matter to the artists. However, considering all the data, we found that the left side was depicted twice as often. In chronological terms, we did not notice any regularity in the distribution of symmetry across European sites over time.

The static nature of the rhinoceros, usually shown standing, is contrasted with examples of rhinoceros in motion (examples from Chauvet: End Chamber; Hilaire Chamber: Panel of Horses; Megaloceros Gallery) and Trois Frères; S1), giving in some cases the impression that the animals are running. A scene of rhinoceroses confronting and fighting each other with their horns was depicted in the Chauvet Cave in France (32–30 ka BP). Both rhinoceros from Kapova Cave, on the same panel, seem to be charging, due to the movement of their legs and the low position of their heads, with the horn projected forward (Ruiz-Redondo et al., 2020; S1).

4.3. Association of rhinoceroses with other mammals

The representation of animals in art at sites which also depict a rhinoceros is significant, as indicated by the diversity of the fauna and the groups they represent. These include woolly mammoths, bovids (aurochs, bison, muskox, ibexes, caprids, and antelopes), cervids (giant deer, moose, and reindeer), horses, camels, carnivores (cave lions, panthers, bears, wolves, and felids), birds (owls, swans, and ravens), fish, snakes, and hominids (male humans, female humans, and anthropomorphic forms).

Despite the taxonomic abundance of these fauna, the rhinoceros is usually depicted alone, which can be explained by both its behavior and nature. The males of modern rhinos migrate alone as they are highly territorial animals. This is seen by their spatial and temporal separation which is achieved through olfactory communication using dung piles and urine spraying, while scrapes and broken vegetation may offer visual evidence of the presence of other individuals (Hutchins and Kreger, 2006). This means that adults tend to be solitary and aggressive (Owen-Smith, 2004), and there is no reason to think that things were different in the past. This implies a perception of the rhino as a solitary individual by Paleolithic people, who translated this image into art. The paintings from Chauvet (Red Panels Gallery_1; S1) are outstanding in this regard, because they show the march of three individuals in one direction. These are probably females given that contemporary female rhinoceroses move in groups, especially with their young.

The fighting rhinoceroses from Chauvet mentioned earlier illustrate the animal's aggressive nature, although this must have been a rarity, as rhinos generally avoid confrontation and physical contact which could cause them subcutaneous wounds or arterial bleeding. However, another painting from Chauvet depicting a bleeding rhino, which indicates that this type of border-crossing did take place. The lack of an arrow or human in the depiction rather rules out the possibility that a hunting scene or human input into this injury is being

depicted. The aggressive nature of rhinos is corroborated by the contemporary reactions of very young rhinos that humans attempt to approach. Fighting rhinos can also be understood in a sexual manner. Jerry Haigh, a wildlife veterinarian from Kenya with experience treating the African white rhino, suggests that this scene may represent females and males engaging in sexual foreplay; this can last for several hours, and the female is often injured.

Such aspects of the rhino may have influenced the superimposition onto depictions of rhinos of other animal images, such as mammoths and ibexes, as in the La Mouthe Cave (S1). It is also possible to suppose that the commonest animal encountered was shown in art by imprinting it over an already existing image.

The perception of the rhino as dangerous is later corroborated by images from the Grande Grotte d'Arcy, which juxtapose the rhino with other dangerous species, such as mammoths, bears, and lions; this is in contrast to the iconography seen in Franco-Cantabrian art, where horses, bison, and deer predominate.

The association of woolly rhinoceros with mammoths in the art of the same Paleolithic sites, or even on the same panel, is not particularly striking given their occurrence in the similar ecological niches. It would seem that these species, which make up the *Mammuthus–Coelodonta* Faunal Complex, should be fairly equally represented in art. However, the woolly rhinoceros is less frequently depicted in cave art than the mammoth, as indicated by its rareness (2.6% of artworks from France). The exceptions are the caves of Chauve (n = 65; Aurignacian and Gravettian), Rouffignac (n = 11; Magdalenian), and Margot Cave (n = 9; Gravettian-Magdalenian) where we note more depictions of this animal (S1).

Evidence from Chauvet (End Chamber 1; Aurignacian and Gravettian), Trois Frères, and Rouffignac (Magdalenian) further indicate that the rhino was also perceived in art as part of a large herd of animals or faunal community (S1).

The rhinoceros is not shown in Paleolithic art in direct relation with humans, with the exception of a painting at Lascaux, where it is seemingly unrelated to the figure of a man (seemingly a shaman with a bird-headed staff) (Bataille, 1955; Aujoulat, 2003). The lack of relationship with the human suggests that humans had a certain mental distance from this animal or took little interest in the rhino at the subsistence level. We are indirectly informed of potential rhino hunting by depictions of rhinos from La Colombière, where three or four arrows are piercing the animal's belly (S1). However, it is difficult to assess whether these are fatal blows. All this suggests a cultural taboo in relation to woolly rhinoceros.

4.4. Associations of rhinoceroses with fish and birds

The juxtaposition of rhinoceros and fish on an ivory plate (Marche-les-Dames; Aurignacian culture) is striking due to the association of animals from two different environments and the rarity of depictions of fish in prehistoric art (S1). Fish are known from a few cases, such as a pike at Pech Merle Cave, a halibut at La Pileta Cave, a salmon in the Abri du Poisson, a trout at Niaux Cave, and a salmon at the Ekain Cave in Spain, among others.

Although birds are represented in cave and mobile art in the Pleistocene and Holocene across continents, the combination of a rhinoceros image with a bird image on the same site

is also rare and does not exceed 1% of cases. The low representation of birds in art is partly a function of an environment that, particularly in the Late Glacial, was not suitable for them. Some of the bioclimatic variables, such as temperature extremes, the intensity of wet and dry seasons, can have direct effects upon birds, leading to limits upon their distributions (Huntley et al., 2006. Remains of birds are found much more rarely in paleozoological materials than in archeozoological materials, which also shows (taphonomic issues aside: Pawłowska, 2010), that birds did not play a significant role in the subsistence strategy of hominids. However, in order not to generalize, attention is drawn to the owl, which is the most common motif in the cave paintings we examine here. Evaluating avian taxonomy based on ancient art is difficult, but the anatomical characteristics of the animal indicate that it may be a long-eared owl (*Asio otus*)—although it could also be the case that the bird is facing forward and that the species might actually be an eagle owl (*Bubo bubo*).

In no case is the rhinoceros in a symbiotic relationship with birds, as can be seen with the extant oxpecker. This bird feeds on insects and ticks, cleaning the skin of African white and black rhinos. The bird's Swahili name means "rhino guard", and alludes to its role of alerting as danger approaches, which is valuable given that rhinos do not have acute vision. The lack of depiction of the woolly rhino with birds in Paleolithic art suggests the absence of such a relationship. This can be explained by the climate which, being periglacial (Pawłowska et al., 2022), was hard for birds, and may also be explained by the fur-covered woolly rhinoceros' lack of exposed skin.

4.5. The artists and their techniques

Archaeological evidence associate modern humans are the producers of the cave art which developed in Europe around 40 ka BP (White et al., 2020). Most examples of Paleolithic art involving rhinoceros are associated with Aurignacian, Gravettian, Solutrean, and Magdalenian cultures, with the first and last of these predominating.

Only fragmentary aspects of hominid material culture have survived to the present, as organic materials such as wood and leather would have degraded much more rapidly than stone and mineral pigments. The cave paintings and all their details are thus a source of environmental, artistic, behavioral, and other information.

Research into the processes involved in Upper Paleolithic artistic activity has revealed that Paleolithic techniques required specialized training in contemporary experts, as was recently shown by Rivero et al. (2024). This suggests that hominids shared knowledge which resulted in many engravings across Europe. This is also confirmed by the art in Chauvet, where the paintings, made of dots with sequence of handprints, were done by people of different ages and genders. This suggests either a shared experience or masters passing on their secrets to their apprentices (Fritz et al., 2016).

Interpreting certain paintings is often difficult on account of their incompleteness or their poor state of preservation. This is compounded by our perception constructing a complete picture despite lacking visual information, often causing us to 'see' things that are

not there as a result of the attempt to resolve ambiguous visual cues (Frith, 2007; Hong et al., 2013).

The presence of paintings and engravings—including those which occur in the same place, such as in Chauvet (Megaloceros Gallery 3; Aurignacian and Gravettian), Margot Cave (Gravettian–Magdalenian), and Les Combarelles (Magdalenian)—shows that different techniques were used to depict the organic world, including the rhinoceros (S1). The depictions of animal were created as independent works or else were created after previous depictions were removed, as indicated by the remnants of previous layers, which can still be seen. The strengthening of certain edges and the smearing of pigment in some art indicates the skill of the artists in showing animals in a three-dimensional impression.

The cave wall was used as a canvas to create art, using black, red, brown, and white pigments, consisting of charcoal, ochre, and manganese oxides. There are different types of manganese oxide identified in cave paintings such as Lascaux, Font-de-Gaume, Rouffignac caves that allowed painters to obtain subtle colour hues (Aujoulat et al., 2002; Chalmin et al., 2004; Vignaud et al., 2006). Further analysis from the Lascaux cave painting, including depiction of rhinos, has shown that artists likely used natural manganese oxides, rather than heat-treated ones, for these pigments. Variable mixtures of manganese oxides are likely to have been employed to make the Rhinoceros frieze at Rouffignac Cave (Lahlil et al., 2012). Engravings accompany wall painting or were made on stone (limestone or shale) or on reindeer antlers. Evidence from Lascaux, where the rhinoceros is drawn in a more realistic style with thicker outlines than the shaman, show that it is not always possible to discern whether different techniques were used on the same panel or whether the panels are separated by time and creator.

5. Conclusions

Paleolithic art is animalistic art. Both the herbivores (horses, bison, mammoths, rhinoceros, aurochs, and deer) and the predators (felids and lions) that formed a natural element of the landscape are represented on the walls of the caves of paleolithic world. Other smaller animals, including birds, are rare (0.5% of all cases). In one case, a bird is shown next to a rhinoceros, while in other cases, they merely appear at the same site.

The woolly rhinoceros (*Coelodonta antiquitatis* Blumenbach 1799), as one of the main representatives of the Pleistocene megafauna (Pawłowska, 2022; Stefaniak et al., 2014, 2021), is not often shown in Paleolithic art, despite its demonstrable population on Eurasia. Depictions of rhinoceroses with other animals are rare, and rhinos are mainly represented alone. However, the study of the representation of woolly rhinoceroses in Paleolithic art has important implications for our understanding of the role of the rhino in the ecosystem and how Paleolithic art, with its representations, was created. Our research found 63 paintings and rock engravings of rhinoceroses on cave walls in Paleolithic Europe. Some works combine both techniques. The paintings were executed in red and black pigment. The vast majority of these rhinoceros depictions are in France, with only a few examples in other European

countries, such as Belgium, Czech Republic, Germany, Slovakia, Spain, Romania, and Russia. All visual art of woolly rhinoceroses in caves was created by early *Homo sapiens.*

The oldest depictions are found in the Chauvet Cave and date back to 33 ka BP, while the youngest come from the Combarelles Cave and date to 11 ka BP. This means that these representations of rhinoceros, including birds, were created over a period of 20 ka BP and are associated with the Aurignacian, Gravettian, Solutrean, and Magdalenian cultures, with the vast majority being Aurignacian and Magdalenian. It is striking that the youngest painting goes well beyond the 15–16 ka BP cut-off date for the occurrence of rhinoceroses in Europe, at least according to current knowledge. This would imply the survival of the rhinoceros's image in human consciousness. The evidence we have collected is not always sufficient to allow us to draw conclusions about the message which the Paleolithic artists were trying to communicate. However, given the paucity of research into visual arts expertise and the inconsistency of the findings (Rivero et al., 2024), our study has filled a gap using evidence of Paleolithic art depicting ancient species.

What ties Paleolithic, Holocene, and present art together is that it is constantly marked by the visualization of animals, from exhibitions featuring live animals to taxidermy, paintings, installations and other innovative visual representations that show the role of animals in our cultural development.

Acknowledgments

This research was funded in whole or in part by the National Science Center, Poland (grant no. 2021/43/B/ST10/00362; WOOLRHINOPOLI). For the purpose of Open Access, the author has applied a CC-BY public copyright license to any Author Accepted Manuscript (AAM) version arising from this submission.

Authorship contribution statement

Kamilla Pawłowska: Conceptualization, Methodology, Investigation, Data curation, Writing – original draft, Writing – review & editing, Funding acquisition, Supervision, Resources, Project administration, Visualization. **Zofia Pogoda**: Investigation, Data curation. **Kajetan Dedła**: Investigation, Data curation, Figure 1. All authors have read the article and made corrections, along with data input.

Conflicts of Interest

The authors declare no conflicts of interest.

Funding

This work was supported by the National Science Center, Poland, 2021/43/B/ST10/00362.

Data Availability Statement

The data that supports the findings of this study are available in the Supporting Information of this article.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. Data S1: Catalog of all depiction of woolly rhinoceros in Paleolithic Europe and Asia (as of 2025). Sources: Data S2. Data S2: Supplementary references for European evidence for the representation of the rhinoceros in art.

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719

Table captions

Table 1. List of main Paleolithic depictions of rhinoceroses in Europe. Sources: S2.

Table 2. Main and collateral representatives of the fauna in Paleolithic art in France.

Table 3. Representations of other (at least) animals in Paleolithic art at sites depicting rhinoceroses. Sources: S2.

Figure captions

Figure 1. Map of the distribution of European sites with Paleolithic art of rhinoceroses.

Supplementary data

S1. Catalog of all depiction of woolly rhinoceros in Paleolithic Europe and Asia (as of 2025). Sources: S2.

S2. Supplementary references for European evidence for the representation of the rhinoceros in art.

734 **Table 1.**

No.	Country	Region	Site	Site dating (14C) and the source of dating	Paleolithic culture
44	France	Nouvelle-Aquitaine	**Limeuil**	12 ka BP (stylistic comparison)	Magdalenian
43	Germany	Sachsen-Anhalt	**Bad Kösen-Lengefeld**	15.3 cal ka BP	Magdalenian
42	France	Nouvelle-Aquitaine	**Placard Cave**	ca 21 cal ka BP	Magdalenian
41	France	Dordogne	**Rouffignac**	13 ka BP	Magdalenian
40	France	Dordogne	**Commarque Cave**	13370 BP ± 340, 12760 BP ± 200 with a mean of 12880 BP ± 170 (reindeer bones)	Magdalenian III/ IV
39	France	Occitania	**Lourdes**	ca 15 ka BP	Magdalenian
38	Germany	Vulkaneifel	**Gönnersdorf**	16.5–15.5 cal ka BP	Magdalenian
37	Germany	Thuringia	**Teufelsbrücke**	17–14.5 cal ka BP	Magdalenian
36	Germany	Thuringia	**Kniegrotte**	17 cal ka BP	Magdalenian
35	France	Ariège	**Trois Frères**	15 ka BP	Magdalenian
34	France	Ain	**La Colombière**	16 ka BP; 17.9–16 cal ka BP	Magdalenian
33	France	Dordogne	**Font-de-Gaume**	17–14 ka BP	Magdalenian
32	France	Dordogne	**Les Combarelles**	18 ka–13ka BP (rock engravings); 13.6, 11.3 ka BP (animal bones)	Magdalenian
31	France		**Gourdan Cave/Cougnac Cave**	21–14.5 ca ka BP	Magdalenian
30	France	Dordogne	**Villars**	18.7–18.4 ka BP (worked bones)	Magdalenian
29	France	Dordogne	**Lascaux: the Well or the Shaft**	22–17 ka BP (estimation); 15.5 ka BP, 16 ka BP, 17.1 ka BP (charcoal)	Magdalenian
28	France	Lourdes	**Espélugues Cave**	21–14.5 cal ka BP	Magdalenian

27	Spain	Basque Country	**Ekain Cave**	21–14.5 cal ka BP	Magdalenian
26	Russia	Bashkortostan	**Kapova Cave (Shulgan-Tash)**	19.6–16 cal ka BP; 14.6 ka BP (charcoal)	Magdalenian
25	France	Dordogne	**Bara Bahau Cave**	15 ka BP	Magdalenian IV
24	Spain	Asturias	**Las Caldas Cave**	23–14.5 cal ka BP	Solutrean and Magdalenian
23	Spain	Salamanca	**Siega Verde**	22–10 ka BC	Gravettian; Magdalenian
22	France	Dordogne	**La Mouthe Cave**	22–12 ka BP	Gravettian–Magdalenian
21	France	Dordogne	**Cussac**	25 ka BP (U–Th and 14C for speleothems, 14C for bone and charcoal)	Gravettian
20	Czech Republic	South Moravian	**Pavlov**	30 cal ka BP	Gravettian
19	Czech Republic	Moravian	**Dolni Vestonice**	31 cal ka BP	Gravettian
18	France	Lot	**Pech Merle: The Chapel of Antelopes**	29 ka BP, 25 ka BP (charcoal), 16 ka BP or 24.6 ka–11.2 ka BP	Gravettian and Magdalenian
17	France	Mayenne	**Margot Cave**		Gravettian and Magdalenian
16	France	Pyrenees	**Gargas Cave**		Gravettian
15	France	Yonne	**Trilobite Cave (Arcy-sur-Cure Cave)**	23.1 ka BP	Gravettian
14	France	Loire	**Saut-du-Perron**		Magdalenian ?
13	Slovakia		**Deravá skala**	approximately 50–40 ka BP; 17–14.5 cal ka BP	Aurignacian; Magdalenian
12	France	Dordogne	**La Ferrassie**		
11	France	Gard	**La Baume-Latrone**		Aurignacian
10	France	Cesseras, Hérault	**Aldene Cave**		Aurignacian

9	Spain	Málaga or Andalucía	**La Pileta**		Solutrean, earlier and later
8	Belgium	Wallonia	**Marche-les-Dames**		Aurignacian
7	France	Yonne	**Arcy-sur-Cure Cave**	stylistic comparison and 28 ka years ago (charcoal)	late Aurignacian and early Gravettian
6	Spain	Guadalajara	**Los Casares**	48 ka BP (U-Th); 44.9–42.2 ka cal BP; 30 ka–25 ka BP	Aurignacian
5	France		**Chanlat**		Aurignacian
4	France	Agonac	**Les Rebières**	42–23 cal ka BP	Aurignacian (Upper) and Gravettian
3	France	Dordogne	**Bernoux**	33 ka–30 ka BP (charcoal and stalagmites)	Aurignacian (engraved frieze)
2	Romania	Bihor	**Coliboaia Cave**	35–23 ka BP or 42-23 cal ka BP	Aurignacian and Gravettian
1	France	Ardèche	**Chauvet**	36.5 ka BP; 32 ka–29 ka BP (charcoal) and 27 ka–24.5 ka BP (flambeau marks)	Aurignacian and Gravettian

735

736 **Table 2.**

Main fauna representative	Number of cases	% of total	Collateral fauna representative	Number of cases	% of total
Horse	1258	33.3%	Giant deer	22	0.05%
Bison	779	20.6%	Birds	20	
Mammoth	440	11.7%	Fish	13	
Ibex	318	8.4%	Ibex	10	
Aurochs	220		Seal	8	
Cervid	122		Snake	6	
Red deer	146		Musk ox	3	
Reindeer	129		Penguin	3	
Lion	120		Hare	2	
Rhinoceros	**97**	**2.6%**	Saiga antelope	2	
Bear	52	1.4%	Canidae	2	
			Weasel	1	
Total				**3773**	

737

738 **Table 3.**

Country	Site	Representation of animals in art (number)
France	**Placard Cave**	caprid, cervid
France	**Rouffignac: plafond**	mammoth (n = 158), bison (n = 29), horse (n = 16), ibex (n = 12), snake (n = 6), human (n = 4), bear (n = 1), unidentified (n = 4)
France	**Trois Frères**	horses, bears, bison, mammoths, ibex, reindeer, lion, bird (owl), anthropomorphic figures
France	**La Colombière**	horse, reindeer, cervid, bear, felids, caprid, rupicapra, Capra, Alces, Ovibos, bovids, mammoth, human?
France	**Font-de-Gaume**	bison, aurochs, mammoth, horses, reindeer, cervids, felids, wolves, human (?)
France	**Les Combarelles**	horses, reindeer, ibex, mammoths, bears, lions and a few bison and aurochs, anthropomorphic figures
France	**Villars**	horses, bison, ibex, anthropomorphic figures and humans
France	**Lascaux: the Well or the Shaft**	about 900 animal pictures, including horses (n = 364), cervids (n = 90), bovids, bison, felids (n = 7), bear, bird (n = 1), and human
Russia	**Kapova Cave (Shulgan-Tash)**	mammoths, horses (n = 2), bison, bears, camels, a few anthropoid figures
Spain	**Siega Verde**	bison, reindeer, giant deer, Felidae
France	**La Mouthe Cave: Space 3 (Hut room, left panel)**	bison, aurochs, horses, reindeer, cervids, felids, wolves
France	**La Mouthe Cave: Space 4 (Spotted Reindeer Hall or Large Reindeer and Rhinoceros Hall) (Rhinoceros panel)**	mammoth, bison, horse, reindeer, cervid, Felidae, ibex, and wolve
France	**Cussac**	caprids, bison, mammoths, horses, birds, human (woman ?)
France	**Pech Merle: Chapel of Antelopes**	mammoth (n = 21), horses (n = 12), bison (n = 7), aurochs (n = 6), reindeers (n = 6), ibex (n = 2), lion (n = 1), bear (n = 1), antelope, human (n = 12), and illegible (n = 3)
France	**Margot Cave**	horses (n = 7), birds (n = 2) (swan and craven), bovids (n = 2) (including bison), cervids (n = 2) (including reindeer), anthropomorphic figures (n = 2), women (n = 1)
France	**Trilobite cave (Arcy-sur-Cure Cave)**	ibex?
Spain	**La Pileta**	mountain goats or ibex (n = 54), horses (n = 36) and deer (n = 36) and bovine species (n = 24;

		aurochs: n = 1, bison: n = 4), fish (n = 15), anthropomorphs (n = 9)
Belgium	**Marche-les-Dames**	fish
France	**Arcy-sur-Cure Cave**	mammoth, giant deer, cervid, bear, ibex, felids, horses, bovids, birds and fish, woman?
Spain	**Los Casares**	Felidae, Cervidae, bison?
France	**Bernoux**	mammoth (n = 3), horse (n = 1), felids (n = 1), unidentified figures (n = 6)
Romania	**Coliboaia Cave**	bison, felids or horse, bear (n = 2), rhinoceros or mammoth
France	**Chauvet**	mammoths, felids, horses, bison, ibex, reindeer, bears, aurochs, giant deer, cave lion, panther, birds (owl)
France	**Chauvet: Brunel Chamber**	"dotted animal" – rhino or bison
France	**Chauvet: End Chamber 1**	mammoths, cave lions, felines, horses, bison, aurochs, women
France	**Chauvet: End Chamber 2**	lions, bison or aurochs
France	**Chauvet: Hilaire Chamber, Panel of Horses 1**	horses, bison or aurochs, reindeer or deer
France	**Chauvet: Megaloceros Gallery 1**	mammoth (n = 2), feline (n = 1)?
France	**Chauvet: Megaloceros Gallery 2**	horse, giant deer, bird
France	**Chauvet: Red Panels Gallery 1**	mammoth, bears, and "enigmatic animal"

739

740 **Fig. 1**


N
Kapova Cave (Shulgan-Tash)
La Pileta
0
400
800 km
N
Bad Kösen-Lengefeld
Marche-Les-Dames
Teufelsbrücke
Kniegrotte
Gönnersdorf
Dolní Vestonice
Pavlov
Margot Cave
Arcy-sur-Cure Cave
Deravá skala
Trilobite Cave
Coliboaia Cave
Saut-du-Perron
La Colombière
Placard Cave
Chauvet
Villars
La Baume-Latrone
Las Caldas Cave
Ekain Cave
Gargas
Aldene Cave
Bernoux
Les Rebières
Lourdes
Trois Frères
Gourdan Cave/Cougnac Cave
Chanlat
Siega Verde
Los Casares
Espélugues Cave
Rouffignac
La Ferrassie
Commarque Cave
Bara Bahau Cave
Limeuil
Les Combarelles
Font-de-Gaume
Cussac
La Mouthe Cave
La Pileta
0
200
400 km
Pech Merle

741