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RESEARCH PAPER

Stephanorhinus hemitoechus (Mammalia, Rhinocerotidae) from the cave site of Mas des Caves (Lunel-Viel, SE France, MIS7): demography and ecology of a paleontological cohort

Antigone Uzunidis[1,2,3,4] · **Luca Pandolfi**[5] · **Jean-Philip Brugal**[4]

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Abstract
The Mas des Caves site at Lunel-Viel (Hérault, Southeast France) has yielded abundant and diversified Late Middle Pleistocene faunal remains, among which *Stephanorhinus hemitoechus*. The recent discovery of a well-preserved skull in 2021 has led to new investigation on this taxon and all the material collected since the beginning of scientific investigations in those cavities. Here, we present the first integrated analysis of the demographic structure and ecological adaptations of this cohort. A minimum of nine individuals was identified on the basis of postcranial and dental remains with at least two very young (below 2 months), three young (between 6 months and 1.5 years), two older juveniles (between 1.5 and 4 years) and two adults (above 5.5 years). The imbalance between juvenile cranial remains and adult postcranial elements suggests differential accumulator agents and, among them, the crucial role of hyenas. Dental microwear analysis of deciduous and permanent teeth reveals a mixed-feeding regime with grazing tendencies, consistent across age classes, suggesting similar plant selection between the various age classes. The dietary niche of *S. hemitoechus* compared with other sympatric herbivores indicates that it was among the herbivore species that selected the most abrasive plants.

Keywords Rhinocerotidae · Hyena den · Middle Pleistocene · Taxonomy · Morphometry · Age estimation · Dental microwear

Introduction

The site of the Mas des Caves at Lunel-Viel is a major western European site due to its rich and diversified faunal collection but also due to its historical dimension for Pleistocene archaeological and paleontological studies since the XIXth century (Brugal et al., 2021, 2022). The rhinoceros were among the species discovered in the first excavations, between 1824 and 1827. Since then, the rhinoceros remains from Lunel-Viel have undergone numerous taxonomic reassignments, reflecting the evolving understanding of Pleistocene rhinoceros taxonomy.

In 1838, de Serres, along with Dubreuil and Jeanjean, initially attributed the Lunel-Viel rhinoceros to *Rhinoceros minutus* Cuvier, 1822, based on misidentified dental remains (de Serres, 1838). *Rhinoceros minutus* [*Protaceratherium minutum*] is a small Oligocene rhinoceros to which many diminutive specimens were attributed during the XIXth and early XXth centuries (Viret, 1961). Subsequent analysis revealed that these teeth belonged to a juvenile individual, leading the same authors to reassign the specimens

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✉ Antigone Uzunidis
antigone.uzunidis@univ-amu.fr

1 ASM-Archéologie des Sociétés Méditerranéennes, UMR 5140, CNRS, MCC, Univ Paul-Valéry, 34000 Montpellier, France

2 Université de Paris 1 Panthéon-Sorbonne, Paris, France

3 UMR 7041 ArScAn-Archéologies Environnementales, Nanterre, France

4 CNRS, UMR7269 LAMPEA, Univ.Aix-Marseille, Minist. Culture, 13097 Aix-en-Provence, France

5 Dipartimento di Scienze della Terra, Università di Pisa, Via S. Maria 53, 56126 Pisa, Italy

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to *Rhinoceros africanus* Blumenbach 1797 (Gervais & de Serres, 1846), a species now considered synonymous with *Diceros bicornis* Linnaeus, 1758. They argued that the Lunel-Viel specimens were indistinguishable from the extant black rhinoceros from the African Cape. Gervais (1848–1852) proposed a new species, *Rhinoceros lunellensis*, which he later considered synonymous with *R. etruscus* Falconer 1860 (de la Rive et al., 1849; Gervais, 1867). In 1853, Duvernoy associated the Lunel-Viel rhinoceros with *R. protichorhinus* Duvernoy, 1853, a species later regarded as synonymous with *Rhinoceros mercki* Kaup, 1841 (= *Stephanorhinus kirchbergensis* Jäeger, 1839) (Depéret, 1923). This classification was not widely accepted, prompting further studies. In 1867, Dawkins attributed the specimens to *R. leptorhinus* (Dawkins, 1867), a designation previously mentioned by Blainville in Gervais (1867). However, this taxon encompassed two distinct species described by Cuvier (1822) and Owen (1846), leading to taxonomic confusion. That same year, Lartet (1867) associated the Lunel-Viel rhinoceros with *R. merckii*. In 1868, Falconer, after establishing the new taxon *Rhinoceros hemitoechus* Falconer in Gaudin (1859), noted significant similarities between the Gower Caves rhinoceros, associated with *R. hemitoechus* (= *Stephanorhinus hemitoechus*), and the Lunel-Viel specimens (Falconer & Murchison, 1868). Following renewed excavations in the 1960s by E. Bonifay, further studies were conducted. In 1973, M.-F. Bonifay attributed the Lunel-Viel rhinoceros to *Dicerorhinus etruscus* (Bonifay, 1973). Subsequently, Guérin (1973, 1980) reclassified the specimens as *Dicerorhinus hemitoechus*, likely based on illustrations published by de Serres (1838) and Falconer and Murchison (1868), though without explicit justification (Guérin, 1973, 1980). Finally, in 2003, Lacombat (2003) adopted Guérin's classification, that is also accepted in following works (Uzunidis-Boutillier, 2017; Brugal et al., 2021).

Since 2019, renewed excavations at the Mas des Caves site in Lunel-Viel by one of us (J.-P.B.) have led to the discovery of new fossil remains attributable to *Stephanorhinus hemitoechus*. Among these, a notably well-preserved skull stands out, offering a rare opportunity to enhance the fragmentary juvenile cranial record of this species in Europe. *Stephanorhinus hemitoechus* in Europe is indeed documented mainly by adult or subadult crania (Pandolfi et al., 2025), which makes it difficult to accurately reconstruct ontogenetic patterns and in particular the variation of cranial features at early ontogenetic stage. Historically, the Lunel-Viel rhinoceros has been the subject of extensive taxonomic debate throughout the XIXth and XXth centuries. However, prior research has predominantly focused on its classification, leaving the palaeobiological context, such as age composition and ecological features of the associated cohort, largely unexplored. This study aims to address this gap by providing a detailed and comprehensive analysis of the demographic structure and ecological adaptations of *S. hemitoechus* at Lunel-Viel.

Lunel-Viel site

The cave-sites named Lunel-Viel or Mas des Caves are located near the small city of Lunel-Viel (Hérault, Southeast of France) (Fig. 1). Lunel-Viel is a complex of several caves, Lunel-Viel I, II, III and IV, that are developed in a calcareous marine-detritical formation from the Miocene (Burdigalian). The two main cavities, Lunel-Viel I (LV I) and Lunel-Viel IV (LV IV), were a single tunnel-shape gallery now separated by a sinkhole. The latter was the Pleistocene natural entrance of the caves but it is now completely sealed, and only LV I is accessible and excavated. Lunel-Viel II and III are small longitudinal cavities, subparallel to Lunel-Viel I without any connection between them.

All the rhinoceros remains come from Lunel-Viel I and IV; the former is a straight oriented NNE-SSW gallery of 150 m long, about 10 m wide, with an infilling of about 6 m where about 250 m^2 were excavated. The accumulation was dated using a combination of ESR/U-series and pIR-IR290 dating methods applied on fossil tooth enamel and on K-feldspars, respectively and is suggested to date between 300 and 200 ka, contemporaneous with the Marine Isotopic Stage (MIS) 7 (Falguères et al., 2024), in agreement with the temperate and evolutive nature of the faunal association (Brugal et al., 2021).

The site was discovered in the XIXth century during the exploitation of a quarry that opened a small entrance into Lunel-Viel I cave. In 1824, some visitors discovered a bone they sent to the science faculty of Montpellier where it was identified by Professor de Serres as an aurochs and what prompted him to conduct excavations between 1824 and 1827. They dug a trench of about 60 m long in Lunel-Viel I (along east wall) which led to the discovery of 1200 bones, including rhinoceros ones, that were published in monographs (de Serres et al., 1828, 1839). At that time, the role of the humans in the accumulation was put aside since de Serres did not believe in the "great antiquity of humankind" and in human presence prior to the *diluvium*. The first written mention to lithic artefacts from Lunel-Viel are indeed more recent (Garrigou, 1865). One hundred and fifty years later, new excavations were conducted by E. Bonifay between 1962 and 1982. Those excavations led to the discovery of the sinkhole and of Lunel-Viel IV (Bonifay & Bonifay, 1965; Bonifay, 1968). The vast majority of the material from Lunel-Viel was discovered during the Bonifay's excavations. Since 2019, new research projects and excavations are conducted in order to date the sequence and precise the taphonomy and sedimentary dynamic, as well as

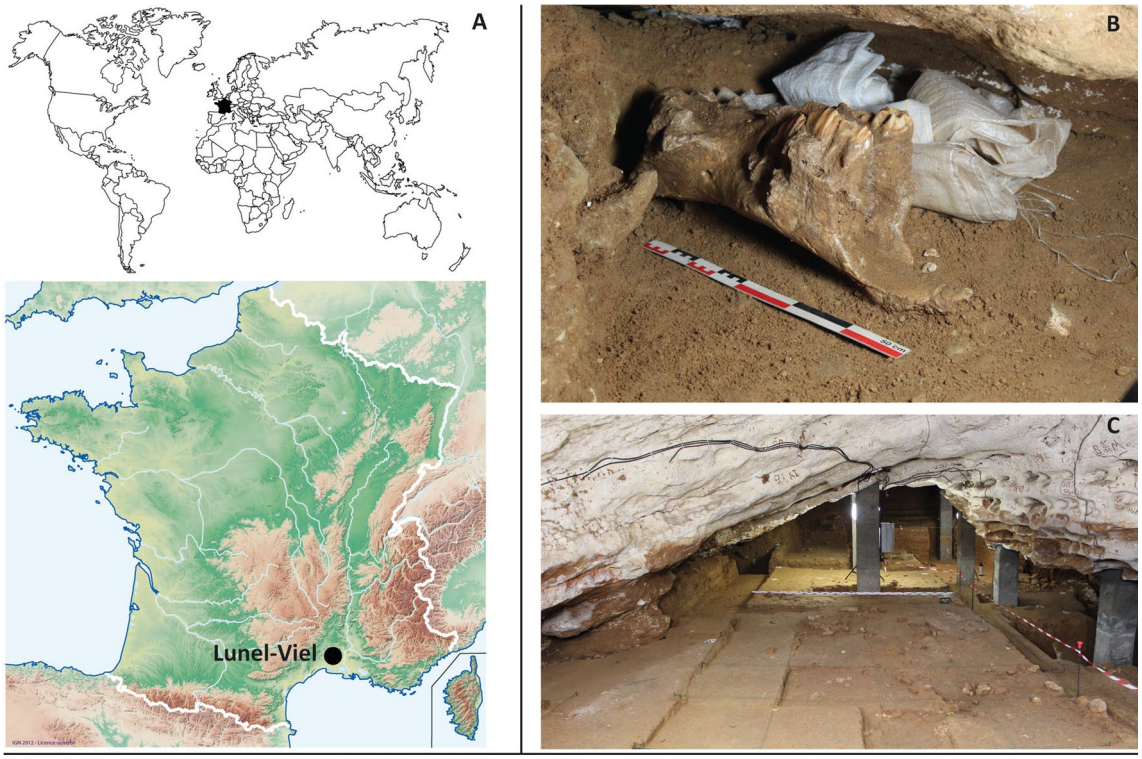

Fig. 1 Overview of Mas des Caves site (Lunel-Viel, Hérault, France): **A** location of the site, **B** skull of the rhinoceros during its excavation, **C** general view of the site

the role played by humans and other agents in the accumulation (Brugal et al., 2021).

Lunel-Viel has yielded a very abundant and diversified herbivore and carnivore assemblage (Bonifay, 1973, 1980, 1991; Mourer-Chauvire, 1975; Jeannet, 1976; Donard, 1982; Brugal, 1985; Argant & Mallye, 2005; Croitor et al., 2008; Boudadi-Maligne, 2010; Fourvel, 2012; Uzunidis-Boutillier, 2017; Pelletier, 2018; Fosse et al., 2021; Brugal et al., 2021, 2022) with 14 species of carnivores: *Cuon priscus, Canis lupus lunellensis, Vulpes vulpes, Lynx pardinus spelaeus, Felis monspessulana, Panthera* (*Leo*) *spelaea, Panthera pardus, Crocuta spelaea intermedia, Hyaena prisca, Ursus* cf. *deningeri, Mustela* sp., *Lutra* sp., *Meles thorali spelaeus*, pinnipeds (*Monachus* sp.). Eleven species of herbivores are also present: *Bos primigenius trochoceros, Megaloceros* sp., *Cervus elaphus, Haploidoceros mediterraneus, Capreolus* sp., *Sus scrofa, Stephanorhinus hemitoechus, Stephanorhinus kirchbergensis, Equus mosbachensis palustris, Equus hydruntinus minor,* Proboscidean indet. Meso- and microtaxa are also abundant: insectivores (*Talpa, Sorex*), lagomorphs (*Oryctolagus cuniculus lunellensis*), chiropterans, rodents (*Microtus brecciensis, Apodemus sylvaticus, Eliomys quercinus, Pliomys lenki, Pitymys duodecimcostatus, Microtus agrestis*) (Jeannet, 1976), birds (nearly 32 species) (Mourer-Chauvire, 1975), reptiles (*Testudo* sp.), amphibians (*Rana*), fish, gastropods.

Numerous evidence of hyenas' activities are observed in Lunel-Viel I which are thought to be the main accumulators of the herbivore remains in the cavity (Fosse, 1996). However, about 780 lithic artefacts (flint, quartzite and quartz) also attest of the human presence with chopping cores and Levallois blanks which define cultural technique by early Neandertals (Mathias et al., pers. com.; Falguères et al., 2024).

Material and methods

This study focuses on bones and teeth of rhinoceros ascribed to *S. hemitoechus* from LV I and IV with a total of 91 fossil elements (NISP) mostly from LV I (91.2%). The material comes from the excavations of de Serres (11%), Bonifay (70.3%) and Brugal (18.7%). The fossils from the excavations of de Serres are housed at the *Université de Montpellier* (Montpellier, France), the ones from E. Bonifay's excavations are located at the *Musée National de Préhistoire* (Les-Eyzies-de-Tayac, France) and the ones from Brugal's field work are currently in the *Maison Méditerranéenne des Sciences Humaines* (UMR 7269, Aix-en-Provence, France).

A quantitative approach was performed, primarily utilizing the R programming environment (R Core Team, 2014). Graphs were generated using the ggplot2 package

(Wickham, 2016), enabling the exploration of relationships between various cranial dimensions, including occipitonasal length (OL), zygomatic breadth (ZB), occipital breadth (OB), occipital height (OH), toothrow length (TL), basal length (BL), and mastoid breadth (MB) (measurements described and illustrated in Groves, 1965; Guérin, 1980). The investigation of ontogenetic growth patterns involved fitting linear regression models to the data via the geom_smooth function with method = "lm" (Wickham, 2016). This allowed for the assessment of correlations between key measurements, such as OL and OB or OH, across various ontogenetic stages. The comparative data are reported as Supplementary File 1 that can be downloaded at https://doi.org/10.5281/zenodo.17563365.

Institutional abbreviations – **CNHM**, Croatian Natural History Museum, Department of Geology and Paleontology, Zagreb, Croatia; **GRQ-SERP**, La Guixera laboratory, Castelldefels, Spain; **IfG**, Institut für Geowissenschaften, Heidelberg, Germany; **IGF**: Museo di Storia Naturale dell'Università di Firenze, sezione di Geologia e Paleontologia, Florence, Italy; **IQW**, Senckenberg Research Station for Quaternary Palaeontology, Weimar, Germany; **LHV**, Landesmuseum für Vorgeschichte, Halle, Germany; **MKP**, Kosmos, Museo di Storia Naturale dell'Università di Pavia, Pavia, Italy; **MMSHS**, Maison Méditerranéenne des Sciences Humaines et Sociales, Aix-en-Provence, France; **MNHN**, Naturhistorisches Museum, Mainz, Germany; **MNP**, Les Eyzies-de-Tayac-Sireuil, France; **MPAC-SCL**, Museo Civico "Virginio Caccia", San Colombano al Lambro, Italy; **MPI**, Museo Paleontologico di Isernia, Isernia, Italy; **MPAP**, Museo Paleoantropologico di San Daniele Po, Cremona, Italy; **MPP**, Museo Paleontologico Parmense, Parma, Italy; **MPUR**, Museo di Paleontologia, Sapienza Università di Roma, Rome, Italy; **MSNUP**, Museo di Storia Naturale di Calci, Pisa, Italy; **MZ**, Museum of the Earth of the Polish Academy of Sciences, Warsaw, Poland; **NAS**, National Alliance of Shidlovskiy "Ice Age," Ice Age Museum, Moscow, Russia; **NHMUK**, The Natural History Museum, London, UK; **NHMW**, Naturhistorisches Museum, Wien, Austria; **RGM**: Rijksmuseum van Geologie en Mineralogie, Leiden, Netherlands; **SMNK**, Staatliches Museum für Naturkunde, Karlsruhe, Germany; **ZIN**, Zoological Institute of the Russian Academy of Science, St. Petersburg, Russia.

Paleontological identification

The paleontological identification of bones and teeth of *S. hemitoechus* was based on morphological criteria identified in previous works (Guérin, 1980; Lacombat, 2006; van der Made, 2010; Pandolfi & Tagliacozzo, 2015; Pandolfi et al., 2015, 2017, 2025).

The identification of the skull was based on the morphology of associated upper teeth and a comprehensive morphometric and morphological comparison with a selection of Pleistocene *Stephanorhinus* crania representing various ontogenetic stages (Pandolfi et al., 2025).

Age estimation

To estimate the age of the individuals based on teeth wear and eruption patterns, we followed a several steps protocol. Firstly, since most of the teeth were isolated, we matched mesial and distal wear patterns of isolated teeth to reconstruct the D1–D4 series of adjacent teeth from single individuals.

Secondly, "reconstructed teeth rows" dental eruption and wear patterns were compared to age estimation studies. The "reconstructed teeth rows" were labeled as individual 1 to 5 (number 5 being the skull). In some case, it was not possible to associate isolated teeth with others. Accordingly, we compared their wear and height with their counterpart that were associated to a dental row. In that aspect, it was possible to associate those teeth with a wear stage as well. Several studies investigate ageing for several rhinoceros species such as *Diceros bicornis* (Goddard, 1970; Hitchins, 1978), *Ceratotherium simum* (Hillman-Smith et al., 1986). Hillman-Smith et al. (1986) found very similar patterns between the two extant African rhinoceroses with the exception of the first lower and upper premolars, which persist longer in *D. bicornis*. The eruptive-wear patterns are similar between the two extant species, even though they do not share the same ecology given that the eruption sequence in rhinos is quite conserved throughout their evolutionary history (Böhmer et al., 2016). Therefore, for the purposes of our study, we considered the sequence and timing of dental eruption and wear of *S. hemitoechus* to be analogous to the ones of *C. simum* and *D. bicornis*. Based on that principle, several studies have adapted age estimation to fossils species such as *Coelodonta antiquitatis* (Garutt, 1992, 1994) and *Stephanorhinus hemitoechus* (Louguet, 2006). More recently, a study (Hullot & Antoine, 2020) proposed a new method that investigates dental eruption and tooth wear patterns based on a definition by Hillman-Smith et al. (1986), calibrated on three current species (*Diceros bicornis*, *Rhinoceros sondaicus*, *and R. unicornis*). We employed this last method as it includes the most species and integrates therefore potential diet biases.

Unfortunately, similar studies about the timing of epiphyseal fusion on bones are not available. Investigations on fossil rhino that attempt to correlate age estimation based on teeth with long bone epiphyses fusion have been done

for *S. kirchbergensis* (Bratlund, 1999) and *C. antiquitatis* (Shpansky, 2014). Shpansky (2014) estimated that the proximal epiphysis in the woolly rhinoceros fused to the diaphysis between 7 and 14 years old and that both epiphyses are totally fused after 14 years old, while Bratlund (1999) estimated that the fusion of the epiphyses in *S. kirchbergensis* is complete after 7 years old. In this study, we will consider the fused bones to belong to adult individuals above 7 years old out of cautious and because *S. hemitoechus* is possibly closely related with *S. kirchbergensis* (Pandolfi, 2023).

Weight estimation

The weight was estimated using the equations published by Fortelius and Kappelman (1993). We used the measurements of the maximum proximal transverse and anteroposterior diameters of the radius, femur and tibia since rhinoceros limb bone size strongly correlate with body mass (Mallet et al., 2022a, 2022b). Only the bones that were without a doubt attributed to adults (totally fused epiphyses) were selected to estimate the weight of Lunel-Viel rhinoceroses.

Dental microwear

All the *S. hemitoechus'* teeth are either not worn or at the beginning of the wear process. The first ones were obviously discarded from dietary reconstruction analysis while the others were suitable only for dental microwear analysis. Indeed, dental microwear require only use wear facet on the enamel while dental mesowear investigate the shape of the cuspid of teeth with an entire occlusal surface worn (Walker et al., 1978; Fortelius & Solounias, 2000). Thus, since only dental microwear analysis was applicable, only the individuals' last meals could be reconstructed (last few days to about a month) (Teaford, 1988; Hoffman et al., 2015; Winkler et al., 2020, 2022). These results are strongly impacted by seasonality (Rivals et al., 2015a, 2020) and are not related with the general trend of the diet over years detectable using dental mesowear.

Dental microwear is a technique that examines the micro traces left on the enamel during the chewing process that are primarily influenced by the presence of phytoliths (Walker et al., 1978; Rivals et al., 2015a) and thus indicative of the diet of the animal. However, external particles such as grit and dust participate in the trace formation at a microscale level (Rivals & Semprebon, 2017; Gallego-Valle et al., 2020; Schulz-Kornas et al., 2020). Microwear analysis was conducted following the protocols and classification criteria established by Solounias and Semprebon (2002) and Semprebon et al. (2004). The occlusal surface of each tooth was cleaned with 96% ethanol, after which high-resolution molds were produced using vinylpolysiloxane silicone (Rivals, 2015). Transparent casts were then created using clear epoxy resin. Observations were carried out under a stereomicroscope at 35 × magnification, restricted to a standardized area of 0.16 mm^2 delineated by an ocular reticle. Microwear features were categorized into pits (small and large), scratches (fine, coarse, hypercoarse), and gouges. Pits were defined as rounded or sub-rounded features, whereas scratches were elongate, linear features with parallel margins. Small pits were shallow and exhibited high reflectivity, while large pits and gouges were deeper, darker, and less regular in shape due to reduced light refraction. Large pits were approximately twice the size of small pits, and gouges—about three times larger—had highly irregular edges. Scratch textures were classified based on width and refractivity: fine scratches were narrow and shallow with low reflectivity; coarse scratches were wider, deeper, and more reflective. Depending on surface characteristics, teeth were assigned a univariate Scratch Width Score (SWS): '0' for predominantly fine scratches, '1' for a mix of fine and coarse scratches, and '2' for predominantly coarse scratches.

Most of dental microwear studies are focusing on adult permanent tooth (Rivals et al., 2015b; Xafis et al., 2017). Decidual teeth are often avoid due to them being less mineralized and with a thinner enamel compare to permanent ones making them more prone to non-dietary alterations (Estalrrich & Krueger, 2022). Following other successful studies that investigated juvenile dietary parameters (Smith & DeSantis, 2018; Estalrrich & Marín-Arroyo, 2021; Estalrrich & Krueger, 2022; Rivals et al., 2022) we include both juvenile and adult teeth in our sample in order to investigate ontogenic differences between age groups. Thus, teeth with enamel modified by taphonomical processes were discarded from the analysis following the descriptions from (King et al., 1999; Uzunidis et al., 2021; Micó et al., 2024a, 2024b). The selection of the teeth was conducted after the dental row reconstruction allowing to select only one tooth per individual (mainly the fourth upper decidual) and avoiding the artificial over-representation of one individual through multiple teeth. Only three isolated teeth were selected after verifying that they did not correspond to any dental row or that they did not fit together.

Results

Description of the skull and representation of the skeleton elements

In total, 91 dental and skeletal elements ascribed to *S. hemitoechus* have been recognized in Lunel-Viel I and IV. The upper and lower teeth show a rough enamel, contrary to *S. kirchbergensis* that is instead characterized by smooth enamel (Fortelius et al., 1993). In addition, the upper premolars bears a well-developed paracone folds, while the

Table 1 Inventory of the *S. hemitoechus* remains from Lunel-Viel I with side, degree of epiphysis fusion for the bones and associated age group for the teeth

Element	Proximal epiphysis fused		Fused		Unknown		Agegroup:0–I		Age group: III–IV		Age group: V–VII			Age group: VIII–XII		Age group: VIII–XIII		Total
	Left	Right	Left	Right	Left	Right	Left	Right	Left	Right	Left	Right	No lat.	Left	Right	Left	Right	
Skull													1					**1**
Upper D1						1			1									**2**
Upper D2					1		1	2		3		1						**8**
Upper D3					1	1	2	1	1	2	1	1						**10**
Upper D4							2	1	2	2								**7**
Upper P1					1													**1**
Lower D3					1													**1**
Lower P3																	1	**1**
LowerP4															1			**1**
Scapula			1															**1**
Humerus					1	1												**2**
Radius	1	1	1	1														**4**
Ulna					2	4												**6**
Hamatum						1												**1**
Pisiform						1												**1**
Meta carpal II			1	1		1												**3**
Meta carpal III	1					1												**2**
Meta carpa lIV			1															**1**
Coxal					3													**3**
Femur				1	3	1												**5**
Tibia	1	1	1															**3**
Calcaneus					5	4												**9**
Talus					3	4												**7**
Cuboid						1												**1**
Metatarsal II			2	1														**3**
Metatarsal III			1	1														**2**
Metatarsal IV				1	1	2												**4**
																		91

The age groups refer to the ones described by Hillman-Smith et al. (1986): group 0–I (0–0.5 year old), group III–VI (0.5–1.5 years old), group V–VII (1.5–4 years old), group VIII–XII (4–20 years old) and group VIII–XIII (4–28 years old)

lower teeth have V-shaped lingual valleys (cfr. Fortelius et al., 1993; Lacombat, 2005). Despite some postcranial bones do not preserve useful morphological features, carpals, tarsals and metapods are instead consistent with the description reported by Pandolfi and Tagliacozzo (2015) for *S. hemitoechus* from Valle Radice. They correspond to a Minimum Number of Individuals (MNI) of 6 with the right upper second decidual (Table 1). It is worth mentioning that one bone of *S. kirchbergensis*, a talus, is also documented (Guérin, 1980) and described in Brugal et al., (2021). The cranial elements represent 36.3% of the NISP and all teeth and the skull have been found from LV I. Almost all the long bones of the appendicular skeleton are represented, when smaller elements as phalanges, and small carpal/tarsal bones are missing as well as the axial vertebras and ribs (only one fragment of atlas). Among post-cranial bones, the ones from rear leg are dominant (63.8%, with several calcaneus, talus, then femur) on the ones from the front leg (36.2% with many radius and ulna). There are as many right elements as there are left elements. Most of these elements are complete or sub-complete but almost 41% show strong evidence of gnawing made by large carnivores, most probably hyenas (Fig. 2). At this point, we notice also that the skull displays groove marks on the nasal bone and along the nuchal crest (Fig. 3). When modified by hyenas, the long bones are strongly attacked on their proximal and distal ends, and some of them are reduced as shaft cylinder. The recognition and identification of carnivore activities and marks on bones have been the subject of abundant literature for nearly two centuries, notably developed in Quaternary paleontology since the mid-twentieth century (e.g., Buckland, 1822; Breuil, 1938; Pei, 1938; Sutcliffe, 1970; Richardson, 1980; Brain, 1981; Bunn, 1983, to name only the oldest works). At the macroscopic scale, the carnivore damage is expressed mainly as rounded-to-oval tooth pits and deeper punctures showing cortical crushing (often with inset flaking), together with elongated, shallow scores that have a broad U-shaped cross-section; more intensive gnawing produces epiphyseal furrowing and scalloped/crenulated margins as cancellous bone is scooped out. This combination of internal crushing, U-section grooves and crenulated edges is characteristic of carnivore chewing, and contrasts with stone-tool cut marks which more typically form sharper V-section grooves and may preserve internal microstriations/shoulder effects under magnification. In the case of marks left on the rhinoceros elements from Lunel-Viel, they are typical of predators such as hyenas (Zonneveld et al., 2022) although not reaching the degree of exploitation observed notably on the skulls of megafauna (Mielgo et al., 2026).. Finally, the rhino fossils are distributed in all the deposit even if most of them (73.9%, excluding the ones from LV IV) comes from the lower levels.

The skull belongs to a juvenile individual, corresponding to Stage II as defined by Groves (1965) and further elaborated by Pandolfi et al. (2025) and the stage VI–VII (3–4 years old) according to its tooth wear and eruption patterns. In ventral view, the postglenoidal apophyses are massive and subtrapezoidal. The hypoglossal foramina are relatively large and positioned anteriorly within the condylar fossa, while the occipital condyles are triangular with a sinuous anterior border. The sagittal crest on the basilar process is absent. Most of these characteristics are consistent with the young age of the individual (e.g., absence of sagittal crest, sinuous anterior border of the condyles, large hypoglossal foramina), as observed in extant rhinoceroses (Pandolfi et al., 2025). The shape of the postglenoidal apophysis and the position of the hypoglossal foramina resemble those observed in *S. hemitoechus*. In lateral view, the nuchal crest protrudes slightly posteriorly, the auditory pseudomeatus is ventrally closed, and the area between the temporal and nuchal crests is flattened, consistent with observations in *S. hemitoechus* crania. In the occipital face view, the occipital face is subtrapezoidal with sinuous lateral borders, a common feature in young individuals.

The occipitonasal length and occipital breadth of the Lunel-Viel skull align closely with small-sized individuals of *S. hemitoechus* and with the *S. kirchbergensis* skull from Daxlander (city district of Karlsruhe, Germany, latest Middle-early Late Pleistocene) (individual n°17 in Fig. 4), as consistently plotted at the lower range of the comparative graphs (Fig. 4A). Both the occipital height and occipital breadth also fall within the established variability of *S. hemitoechus* (Fig. 4B), suggesting these characters can be effectively used for taxonomic identification even in juvenile specimens.

Age repartition, ontogenetic growth of the skull and weight estimation of Lunel-Viel rhinoceros

Over the main limb bones of *S. hemitoechus* the observation of their epiphysis fusions was impossible for 17 of them due to breakage and action of hyena activities and only five proximal portions were present. Fourteen bones were instead complete, allowing to determine if they belong to adult or juvenile individuals (Table 1). The epiphyses of the 14 complete and of the five proximal portions of limb bones were completely fused, suggesting they belong to adult individuals (Bratlund, 1999; Shpansky, 2014). The two left second metatarsal bones indicates that at there were at least two adults in Lunel-Viel I according to limb bones.

The weight of the adults was estimated using six totally fused limb bones (2 radius, 1 femur and 3 tibia), completed by eleven morphometric traits (Supplementary Data 1), with a mean of 1325.5 ± 192 kg.

Fig. 2 Long bones from Lunel-Viel I and IV with marks attributed to carnivores' actions. **A** Right femur (LV IV n°MNP-14398); **B** Left femur (LV I n°MMSHS-460); **B'** Same bone already figured by de Serres et al., 1828 (planche XII); **C** Right femur (LVI n°MNP-2307); **D** Left humerus (LV IV n°MNP-15628); **E** Right ulna (LV I n°MMSHS-455); **F** Right ulna (LV I MNP-3446). The black arrows indicate the main marks attributed to large carnivores, typical of hyena activities: serrated edges, notches (punctures), tooth gouges and dental pits (femur, ulna), reduction to diaphysal cylinders (humerus, femur)

Thirty-two isolated teeth, almost all decidual, were found only in Lunel-Viel I. We were able to reconstruct the dental row of four individuals using 16 teeth associated with age group as defined by Hillman-Smith et al. (1986) (Fig. 5). We also associated ten isolated teeth to an age group by comparing them with their counterpart in the reconstructed-row.

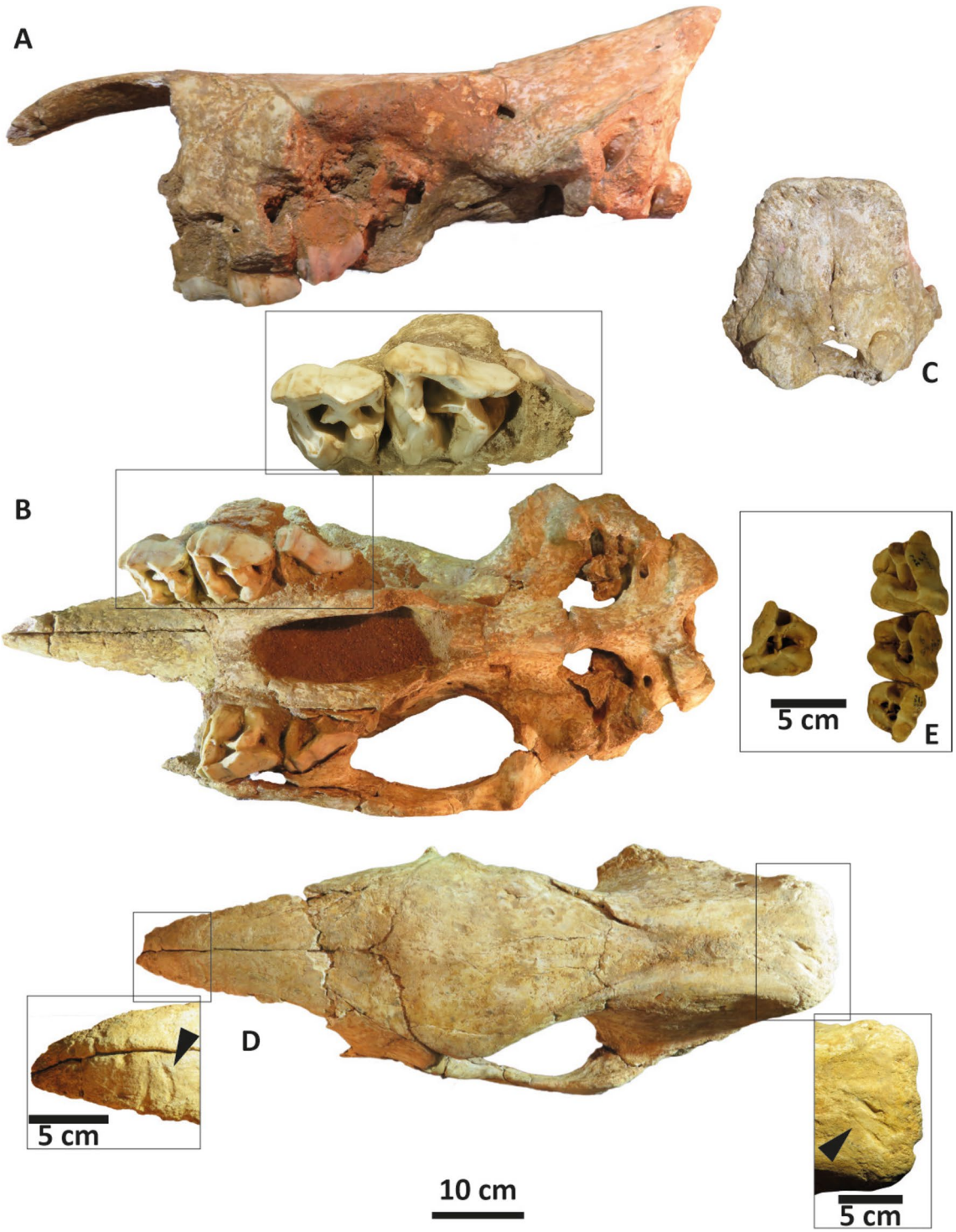

Fig. 3 Cranial remains from Lunel-Viel. **A**–**C** The skull of *S. hemitoechus* (n° MMSHS-LVI-1830): **A** lateral view, **B** palatal view, **C** occipital view; **D** Upper view with a zoom on the carnivore marks (tooth scorings on nasal and parietal edge, highlighted with a black arrow); **E** "Reconstructed dental row" in occlusal view of the individual I (age group = I, age estimation = 0–0.5 year) with left upper D4 (n°MNP-9570), left upper D3 (n° MNP-2590), left upper D2 (n° MNP-3614) and right upper D3 (n° MNP-2589)

Lastly, five teeth (one fourth decidual, two first molars, and two second molar still inside the alveoli) can be observed on the skull still embedded in the maxillary. Eight teeth are associated with the age category 0–I, the 0 to 2 months' age group, belonging to at least two individuals (2 right upper second decidual) (Fig. 5). Eleven belong the categories III

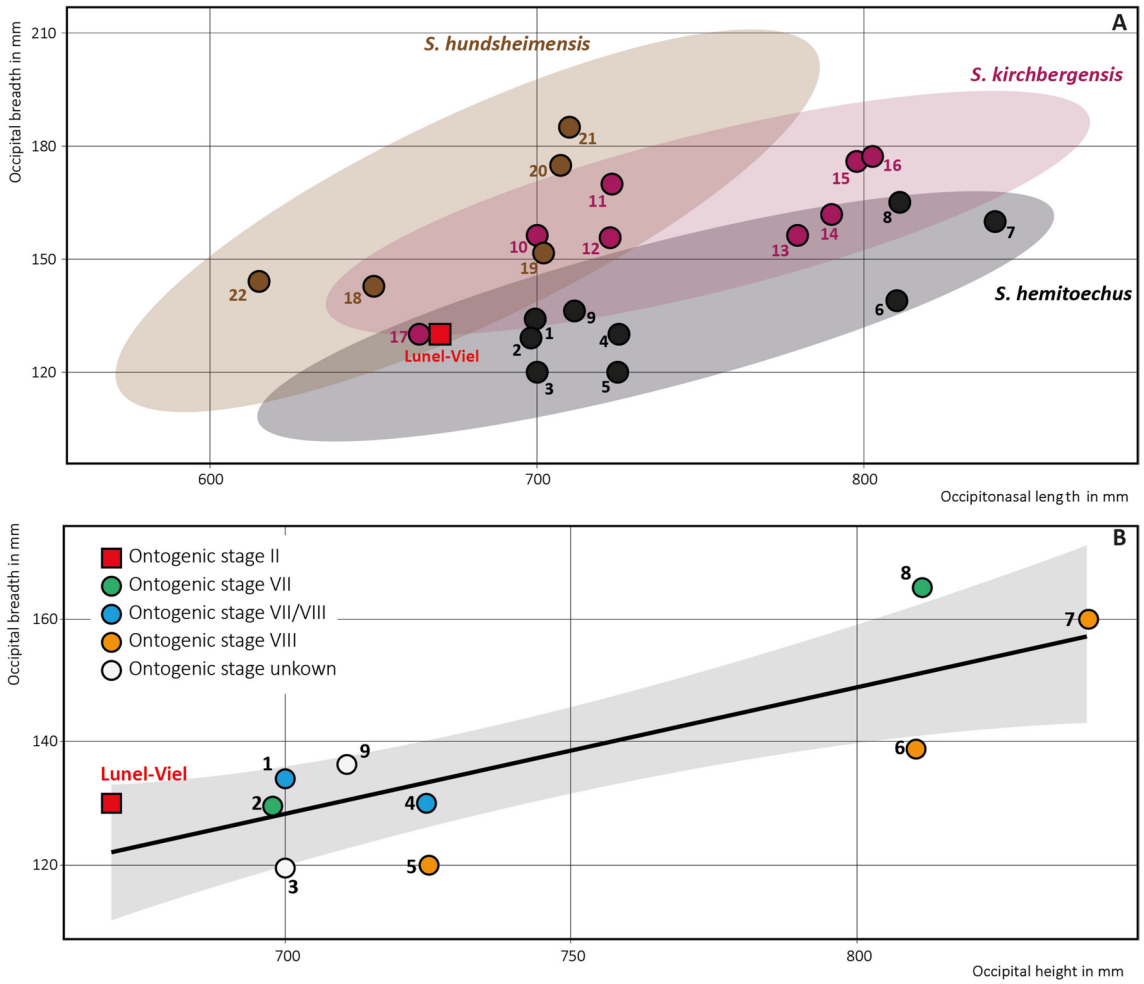

Fig. 4 Biplot comparing the measurements of various skulls attributed to *Stephanorhinus* spp. **A** Distribution of *S. hundsheimensis, S. kirchbergensis* and *S. hemitoechus* according to their occcipitonasal length compared to their occipital breadth with confidence ellipse at 95%. **B** Distribution of *S. hemitoechus* occipital height and breadth according to the ontogenic stage as defined by Groves, 1967. 1: IGF 10792, Pogi (Italy, MIS 6), 2: MPACSCL, San Colombano (Italy, Late Pleistocene), 3: MSNUP I17769, Maspino (Italy, MIS6-4), 4: IGF 1105, Ponte alla Nave (Italy, MIS 6), 5: IGF 1109, Maspino (Italy, MIS 6-4), 6: NHMUK 45205, Ilford (Great Britain, MIS 7), 7: LHV 189 – HK 88, Neumark-Nord (Germany, MIS 7), 8: RGM 93302, Westerveld (Netherlands, late Pleistocene), 9: NHMUK 27836, Clacton (Great Britain, MIS 11), 10: LVH 198, Neumark-Nord (Germany, MIS 7), 11: MZ VIII Vm-450, Warsaw (Poland, middle or late Pleistocene), 12: CNHM, Krapina (Crotia, MIS 5e), 13: LVH 193 and 14, LVH 200-E 24, 241-243, Neumark-Nord (Germany, MIS 7), 15, NAS F4160, Chondon (Russia, MIS 5e), 16: ZIN 10718, Irkutsk (Russia, late Pleistocene), 17: SMNK PAL4254, Daxlanden (Germany, MIS9?), 18: ifG, Mauer (Germany, MIS 15), 19: MNHN PW 1958-764, Mosbach (Germany, MIS 15), 20: MPI 33085, Isernia (Italy, MIS 15), 21: MPP sn, Torrente Stirone (Italy, MIS 25-23), 22: MNHN PW 1977-13, Mosbach (Germany, MIS 15). More detail about comparative sample in Supplementary data, sheet 1

to VI, the 4 months to 1.5 years' age group, belonging to, at least, three individuals (3 right upper second decidual). Two belong to the categories V to VII – between 1.5 and 4 years, and one to the categories VI to VII – between 3 and 4 years. The skull can be as well estimated to have an age encompass between 3 and 4 years. Given the overlap between the wear stages and dental eruption, we can estimate that at least two individuals are represented within the V–VII categories. At last, the two definitive teeth, a lower third premolar and a lower fourth premolar belong respectively to the categories VIII–XII – between 4 and 20 years and to the categories VIII–XIII – between 4 and 28 years old, that do not match together (Fig. 5). Thus, using age estimation, the Minimum Number of Individuals by combination (MNIc) can be estimated to be 9 with at least seven juveniles (less than 4 years) and 2 possible subadults/adults (above 4 years old).

The juvenile age of the Lunel Viel skull allows for the investigation of ontogenetic growth in *S. hemitoechus*

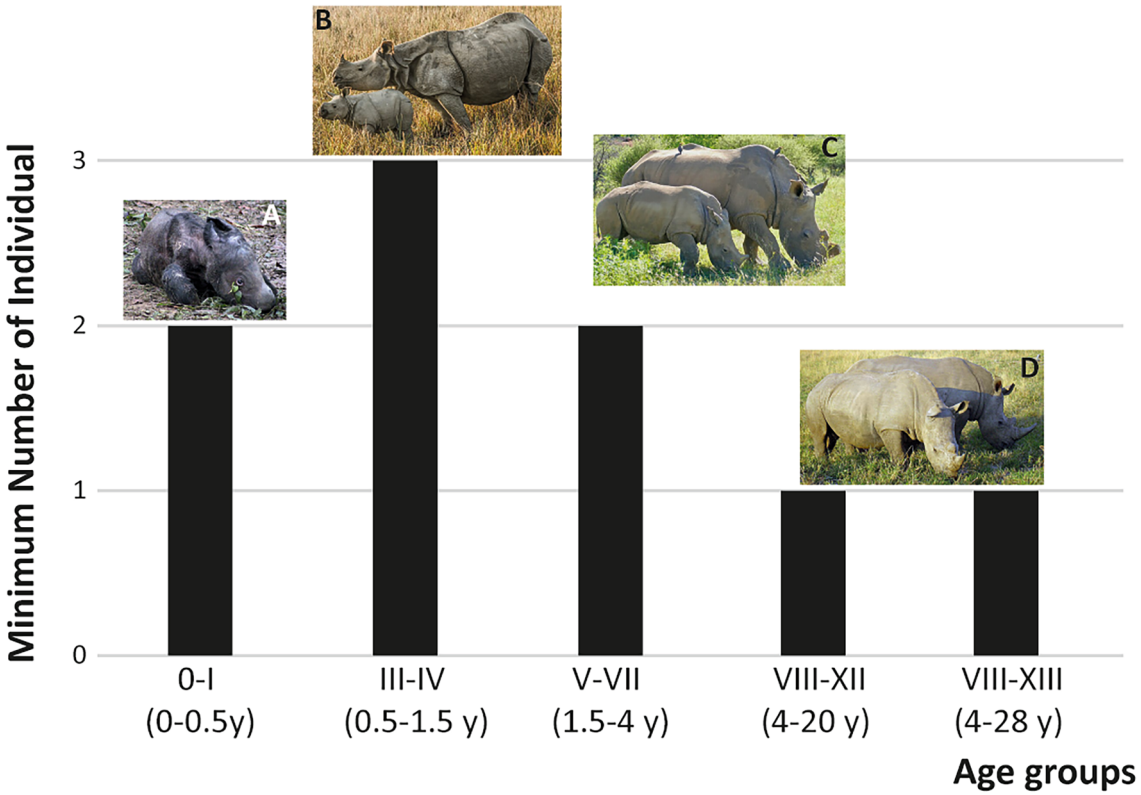

Fig. 5 Distribution of *S. hemitoechus* according to their age groups by their Minimum Number of Individual by combination (MNIc). Each age group is illustrated by representation of current rhinoceros: **A** *Dicerorhinus sumatrensis*, **B** *Rhinoceros unicornis*, **C** & **D** *Ceratotherium simum*. Photos from https://commons.wikimedia.org, Creative Commons Attribution-Share Alike 2.0 Generic license

individuals. Analysis of the comparative plots reveals a linear correlation between occipitonasal length and occipital breadth (Fig. 4B), and similarly for occipitonasal length and occipital height (Fig. 4A). Interestingly, these correlations appear to be less strictly tied to the estimated age at death of the individuals, and more plausibly influenced by sexual dimorphism, with (probable) male individuals tending to cluster towards the upper-right portion of the corresponding graphs, indicating larger overall cranial dimensions. This hypothesis needs to be supported by further cranial remains.

Diet of the *S. hemitoechus* from Lunel-Viel

Few days prior their death, *S. hemitoechus* from Lunel-Viel is characterized by both a moderate number of pits and scratches, and they fall within the variability of the mixed-feeders (Fig. 6A). They have very few large pits, a mostly mixed scratch texture, no gouges or hyper-coarse scratches and almost no puncture pits (Table 2). Age group 0-I was excluded from the dental microwear analysis due to the lack of wear on the teeth and no differences can be spotted between the age groups III-IV, V-VII, VI-VII and VIII-XIII. Only the individual 5 (the skull) and the teeth #83 (from the VI-VIII) display a slightly higher number of scratches that indicates they may have been more grazers than the other individuals.

Discussion

Demographical composition of the Lunel-Viel S. hemitoechus *cohort*

Lunel-Viel I *S. hemitoechus* cohort corresponds to at least nine individuals (MNIc). Seven of the individuals are juveniles with ages encompass between 0 and 4 years old and two are adults (or subadults) with an age at least above 4 years old. Among the juveniles, several age groups are represented: two very young (below 2 months), three young (between 6 months and 1.5 years) and two older

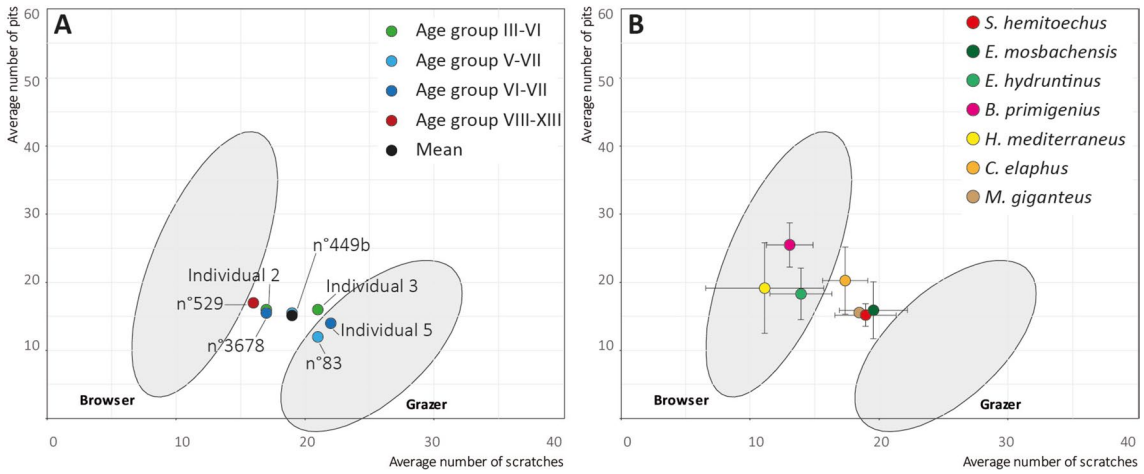

Fig. 6 Bivariate plot of the number of pits and scratches of ungulates from Lunel-Viel. **A** Comparing the age groups of *S. hemitoechus* and **B** comparing the diet of the contemporaneous herbivores from the same location (data from Uzunidis-Boutillier, 2017; Uzunidis, 2020; Brugal et al., 2021; Uzunidis et al., 2021, 2024. *Equus hyduntinus* data are unpublished). The mean is also indicated in black and the error bars correspond to the standard deviation (±1 SD). The ellipses correspond to the Gaussian confidence ellipse (p. = 0.95) on the centroids of current grazers and browsers published by Solounias and Semprebon (2002)

Table 2 Microwear row data for the *S. hemitoechus* from Lunel-Viel I according to the age group of the teeth as described by Hillman-Smith et al. (1986)

Age group	Reference for the individual	Microwear						
		NP	NS	LP	G	SWS	HC	XS
III-IV (0.5–1.5 y)	2	16	17	0	0	1	0	1
	3	16	21	0	0	1	0	1
V-VII (1.5–4 y)	N°MMSHS-LVI-449b	15.5	19	0	0	0.5	0	1
	N° MMSHS-LVI-83	12	21	0	0	1	0	1
VI-VII (3–4 y)	N°MNP-LVI-3678	15.5	17	0	0	1	0	1
	5	14	22	0	0	1	0	1
VIII-XIII (4–28 y)	N° MMSHS-LVI-529	17	16	0	0	1	0	1
		NP	NS	%LP	%G	SWS	%HC	%XS
Mean		15.1	19	0	0	0.9	0	100
Standard deviation		1.6	2.4					

Abbreviations: NP = Mean number of pits; NS = Mean number of scratches; LP: Presence (1)/Absence (0) of large pits; %LP = Percentage of specimens with large pits; G: Presence (1)/Absence (0) of gouges; %G = Percentage of specimens with gouges; SWS = scratches width score; HC: Presence (1)/Absence (0) of hypercoarse scratches; %HC = Percentage of specimens with hypercoarse scratches; XS: Presence (1)/Absence (0) of cross scratches %XS = Percentage of specimens with cross scratches

juveniles (between 1.5 and 4 years). Among extant rhinoceros (black, white and Indian rhinos), the mortality differ according to the age groups with the majority of the death occurring at birth time or below 6 months followed by the adult category, while the young and sub-adult individuals are the less prone to die (Laurie, 1982; Owen-Smith, 1988). Setting poaching aside, at Chitwan in Nepal, most of the Indian rhinoceros calves' deaths were due to tiger predation (Laurie, 1982) and under 4 month black rhinos from Hluhluwe (South Africa) were documented being preyed upon by lions and hyenas (Hitchins & Anderson, 1983; Owen-Smith, 1988). At sub-adult and adult age stages, rhinoceros mortality is more related to accident, illness and fights between males, especially for the sub-adults (Laurie, 1982; Owen-Smith, 1988). Although, successful attacks of lions toward sub-adult and adults rhinos are also documented (Owen-Smith, 1988; Brain et al., 1999) and Goddard (1970) estimate that 16% of the black rhino from Tsavo Park (Kenya) under two years died after hyena and lion attacks. Both for the African and the Indian rhino, an imbalance in the sex ratio at death is observed with more male dying in predatory encounters and during fights (Owen-Smith, 1988; Berger & Cunningham, 1995). Similar sex-related mortality patterns were described for Miocene rhinoceros (Mihlbachler, 2003) and the sex attributed to the Lunel-Viel skull is male. In Pleistocene

human accumulated sites, the rhinoceros (*S. hemitoechus* and *S. kirchbergensis*) mortality profiles also display a lot of young individuals, like at Taubach (Bratlund, 1999), Arago l. F (Chen & Moigne, 2018), Biache-Saint-Vaast (Louguet-Lefebvre, 2005) or Payre l.G/F (Daujeard et al., 2018). However, adult individuals, above 5 years old, are usually better represented in those sites: about 32% at Taubach and 38% at Arago l.F, and reaching even 60% at Biache-Saint-Vaast. At hyena-accumulated sites (e.g., Fouvent–Saint-Andoche, dominated by *Coelodonta antiquitatis*), individuals older than 5 years account for only 22% of the cohort (Fourvel et al., 2015), which is close to the proportion observed at Lunel-Viel (25%). This pattern suggests that direct predation by large carnivores on the six Lunel-Viel individuals older than 6 months is unlikely, although it cannot be ruled out; by contrast, predation is more likely for the two youngest individuals. It is more plausible that most of them could have died of other causes and then, being scavenged by hyenas.

The mean weight the *S. hemitoechus* from Lunel-Viel was estimated to be of 1325.5 ± 192 kg which made it close in size to *Rhinoceros sondaicus* (Mallet et al., 2019). We did not find any precise data on wild rhinoceros nor on this species in particular describe their growth through age groups nor the weight of their body parts. Current captive *R. unicornis*, which are in average heavier than *S. hemitoechus*, weight around 71.3 kg at birth, their weight double in one month and at one year they are 10 times heavier than at birth (Laurie et al., 1983). While their growth is noticeably slower in the wild (Laurie et al., 1983), weight estimation on *C. simum* also support the idea of a rapid growth in this taxon with a yearling already reaching half a ton after weighing around 40–110 kg at birth (Hillman-Smith et al., 1986). For *C. simum*, their head weighed around 400 kg (Daujeard et al., 2018) which corresponds to about 15% of their total mass. Thus, accompanying the rapid growth of the body, especially during the first year of its life, the head alone might reach several dozens of kilograms quickly during the rhinoceros growth. Current *Hyaena* spp. carry carcasses up to 6.4 km with a record of 15 km for a calf of 7.5 kg (Mills, 1990). Prey carrying is somewhat similar for current *Crocuta* sp. with an example of goat transportation of about 20 kg up to 10 km. Heavier body parts can be also carried: for example, the back leg of a giraffe over 1.4 km (Brain, 1981). While it is difficult to extrapolate the weight of the prey or portion of prey that Pleistocene hyenas were able to carry, the possibility that they transported an adult rhinoceros head to their den can be reasonably ruled out.

Megaherbivore preys (proboscideans, rhinoceroses) are uncommon in anthropogenic accumulations while they are relatively frequent in hyena dens context, especially rhinoceros (Discamps, 2011). Remains of wooly rhinoceros *Coelodonta antiquitatis* are regularly found in Upper Pleistocene sites across Western and Central Europe (Diedrich, 2012; Fourvel et al., 2015) where they can account in some cases for more than 40% of the total mammal remains showing the actions of hyenas. The common features of all these sites are: many individuals often dominated by juveniles with many isolated teeth, overrepresentation of large leg bones and very low frequency of axial elements and distal part of the limbs, highly damaged bones gnawed by hyenas and reduced to shaft cylinders (Diedrich & Zák, 2006; Lansing et al., 2009; Diedrich, 2012; Jimenez et al., 2022). The same pattern is observed for the rhinoceros from Lunel-Viel cave site (Figs. 2 and 3). In the same way, a difference is often noted in the representation between juveniles and adults in terms of skeletal representation, with more often dental remains found in young individuals. It seems that long bones of this cohort are either heavily destroyed or not transported back in the den, while adult rich-meat long bones are more frequently brought into the den.

The pattern observed at Lunel-Viel could be explained in term of predation selection and bone damage. If it is possible to admit the active hunting of young rhinoceroses by a clan of hyenas (sometimes up to 50 individuals), it is more likely that these were adult animals that were scavenged and whose bones were selectively transported in the cave. Furthermore, in the case of Lunel-Viel, there is a relatively vertical access to the cavity, known as a karst sinkhole or *doline*, which could function as a natural trap. This topography implies the possibility to trap both young and adult animals, secondarily scavenged with selectively brought pieces into the deeper part of the karst. The example of the LV I skull could also correspond to this explanatory hypothesis.

Ecological position of S. hemitoechus *among the herbivores from Lunel-Viel*

Lunel-Viel *S. hemitoechus* average dental microwear parameters are characterized by moderate quantity of pits, a lot of scratches, very few large pits, a mostly mixed scratch texture, no gouges or hyper-coarse scratches and almost no puncture pits. It can reflect the diet of a mixed-feeder with no bark or fruit consumption. It could correspond to feeding on a mix of grass and leaves of medium to small size. Its dietary patterns are similar for this species in Great Britain (Rivals & Lister, 2016; Saarinen et al., 2016) or Germany (Hernesniemi et al., 2011; van Asperen & Kahlke, 2015) and this species was described as a generalist mixed-feeder that incorporates more grass than *S. kirchbergensis* into its diet.

In Lunel-Viel, we didn't find major differences between age groups with weaning juveniles, post-weaning juveniles and adults showing the same dietary patterns. Only, two individuals (individual 5 - the skull and n°MMSHS-83), have a slightly higher value of scratches indicating that

they selected a bit more grass than the others, putting them in the range of the grazers. Several hypotheses can explain this slight shift such as the sex of the animal or the season of death that can induce dietary changes in relation with seasonal plant availability (Rivals et al., 2015a; Uzunidis & Rivals, 2023). Several dental microwear studies have already highlighted no dietary partitioning among juveniles and adults in hyenas (Rivals et al., 2022), elephants (Smith & DeSantis, 2018) and humans (Estalrrich & Marín-Arroyo, 2021; Estalrrich & Krueger, 2022). In current rhinoceros, dietary partitioning according to age is limited since juveniles are precocial. *C. simum* and *R. unicornis* tend to incorporate vegetation into their diet at about the same age, around 3 months, and stop suckling over of their first year (Laurie et al., 1983; Owen-Smith, 1988). Weaning decreases progressively between 6 months and 1 year after birth (White et al., 2007). In contrast, even in non-social species, such as *Rhinoceros unicornis*, mother-juvenile relationship last for a long period: around 3 years when the young copy the mother behavior (Laurie, 1982; Medhi & Saikia, 2019). Thus, the vegetation spectra that the young come into contact and select is expected to be the same as the adult one.

In comparison with the other herbivores from Lunel-Viel, the dietary features of the rhinoceros from Lunel-Viel are quite similar to those of the *Megaloceros giganteus* (Fig. 6B). When comparing the number of pits to the number of scratches, they fall also in the variability of the horses' diet (*Equus mosbachensis palustris*). However, horses are also characterized by a larger proportion of large pits indicating a highest ingestion of sandy particles (Uzunidis, 2020) reflecting probably a feeding closer to the ground (Semprebon et al., 2011) which is not the case for the giant deer (Uzunidis et al., 2024). Rhinoceros, horses and giant deer are the taxa displaying the largest number of scratches in the site indicating that they were the species that included the largest amount of grasses into their diet. The dietary niche of the rhinoceros from Lunel-Viel is similar to the ones described in MIS11 Germany sites (Steinheim and Heppenloch) where *S. hemitoechus* is also a mixed-feeder with grazing tendencies that share similar traits with horses or even outcompete them for the access to the more abrasive plants (Rivals & Ziegler, 2018).

Conclusion

The rhinoceroses of Lunel-Viel are among the earliest studied paleontological assemblages, especially for this taxon. For over a century, research has focused on the taxonomic attribution of this collection. Two rhinoceros' species have been described from the site: *Stephanorhinus kirchbergensis* and *S. hemitoechus*. The former is represented by only a single bone whereas an abundant collection of skeletal and dental remains has been attributed to the latter, including a well-preserved skull recently discovered. Our study aims, for the first time, to describe the ecological and demographic characteristics of *S. hemitoechus* cohort from Lunel-Viel I and IV.

We have been able to show that a minimum of nine individuals were present at Lunel-Viel. The majority of them are juveniles. The age distribution within the cohort, with a notable underrepresentation of adults, is similar to that observed at other Pleistocene hyena dens, and differs in this respect from anthropogenic accumulations.

The identification of the Lunel-Viel skull as a juvenile *Stephanorhinus hemitoechus* specimen is based on a combination of (1) observed morphological characters (such as the postglenoidal apophyses, hypoglossal foramina, and the absence of a sagittal crest), and (2) its position in comparative plots (e.g., those showing the relationship between occipitonasal length, occipital breadth, and occipital height), where it clusters with smaller-sized individuals and other *S. hemitoechus* specimens. The juvenile age of the Lunel-Viel skull offers a rare opportunity to investigate the ontogenetic growth of *S. hemitoechus* individuals. Analyses reveal a linear correlation between occipitonasal length and occipital breadth which appears not to be strictly correlated with the estimated age at death, but rather potentially with the sex of the animal (as visible in the comparative plots). A similar result is observed for the relationship between occipitonasal length and occipital height, with supposed male individuals tending to cluster towards the upper-right portion of the corresponding graph (Fig. 4), suggesting sexual dimorphism in cranial dimensions as the individual grows. These data enrich the fragmentary cranial record of this species in Europe, especially concerning juvenile stages, contributing to a clearer reconstruction of ontogenetic patterns and the variation of cranial features at early developmental stages.

While young individuals are mostly represented by their teeth, the postcranial skeleton is overwhelmingly composed of adult remains. This disparity in age between cranial and postcranial elements may reflect differential acquisition and transport by hyenas, depending on the weight of the skeletal parts. For instance, the heads of juveniles may have been carried by predators to their den and their bones to neglected and abandoned in the kill-site, while skulls of adults may have been too heavy to transport and only their long-bones richest in meat and marrow selected and introduced in the den. The age groups represented at Lunel-Viel, along with the differential selection of anatomical parts, could indicate that hyenas were at least partly responsible for the formation and modification of the rhinoceros' assemblage, in a mixed acquisition

strategy, by active hunting on juveniles and subadults and a more scavenging way for adults.

Similarly, as described for other *S. hemitoechus* cohorts, the individuals from Lunel-Viel had a mixed-feeding diet with a grazing tendency and occupied an ecological niche relatively similar to that of horses and giant deer. The study of dietary changes with age shows a high degree of homogeneity across age classes. This would suggest that even the youngest individuals at Lunel-Viel (between 6 months and 4 years old) either were weaned or closely imitated the feeding habits of older individuals.

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Author contributions AU: conceptualization, investigation, palaeoecological analysis (age and weight estimation and dental wear), writing—original draft preparation, writing—review and editing. LP: investigation, paleontological analysis of the skull, writing—original draft preparation, writing—review and editing. JPB: investigation, taphonomical analysis, excavation of the fossils, writing—original draft preparation, writing—review and editing.

Data availability All data supporting the findings of this study are available within the paper and its Supplementary Information that can be download at https://doi.org/10.5281/zenodo.17563365.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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