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Research article

First record of well-preserved canid coprolites from Eurasia: New insights into the unique ecological niche of Yuanmou Basin

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ABSTRACT

This study reconstructs the Early Pleistocene paleoenvironment of the Yuanmou Basin through coproecology of the third member of the Yuanmou Formation. We examined 38 exceptionally well-preserved coprolites from a new fossil locality, and attributed the putative defecating agent to the hypercarnivorous diet canid, *Sinocuon yuanmouensis* through geochemical and quantitative analyses. A new ichnogenus and ichnospecies, *Cuocopros yuanmouensis* igen. et. isp. nov., was established based on distinctive characteristics. Multi-disciplinary analysis, including sediment palynology and lithostratigraphy, helped primarily reconstruct a significant climatic event during the early Pleistocene, coinciding with the emergence of Yuanmou Man during the fourth member of the Yuanmou Formation's deposition. The findings provide insights into coexistence between canids, hyaenas, hominoids, and other fauna, revealing a rich paleoecosystem and food chain in the region's history. This study contributes to understanding the complex ecological dynamics during this period in the Yuanmou Basin.

1. Introduction

Coprolites, fossilized feces, offer invaluable direct evidence of ancient animal behavior in the fossil record. Their study dates back to the early 19th century when William Buckland [1] coined the term "coprolite." Coprolites have been recorded from throughout the Phanerozoic in terrestrial and marine sequences, coprolites play a crucial role in various deposits, notably cave sediments [2,3]. Multi-proxy research on coprolites has provided significant insights into the past, becoming indispensable tools in paleobiological studies [2,4–6]. They reveal a wealth of information, including ecological interactions between predators and prey, feeding habits,

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Abbreviations

CAS	Chinese Academy of Sciences, P.R. China
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, P.R. China
MCYNAP	Museum of Chuxiong Yi Nationality Autonomous Prefecture, Chuxiong, P.R. China
NMH	Natural History Museum of Los Angeles, USA.
PKU	Peking University, Beijing, P.R. China
UCAS	University of Chinese Academy of Sciences, Beijing, P.R. China
YNU	Yunnan University, Kunming, P.R. China

trophic relations, coprophagy, digestive tract structure, and dietary analysis. Importantly, coprolites shed light on aspects that body fossils alone cannot provide, such as animal behavior [7–21]. Additionally, when containing plant material, coprolites aid in paleoenvironmental reconstructions [21,22]. Advancements in methodologies have even enabled the retrieval of bacteria, fungal, parasitic, and organic geochemical data, including DNA and lipids content, from coprolites [23–28].

Pleistocene vertebrate coprolites, particularly those of carnivores, have been extensively documented in the literature, with a focus on hyaenas and canids. Hyaena coprolites are most abundant across Africa, Europe, and Asia, while felid and canid coprolites are widespread but understudied (see compilation by Hunt & Lucas [29] for a detailed list; e.g. Refs. [30–36]). Certain members of the Canidae and Hyaenidae families have independently evolved powerful masticatory muscles for bone-crushing adaptations [34,37], likely related to social hunting behavior [38,39]. This is supported by the morphology of their dentition and skull [38,40,41] and their highly durable gastrointestinal systems, which break down consumed bones into high-carbonate content [42–45].

The latest records of carnivorous coprolites in China date back to the Nihewan series [46]. Du & Yu [47] conducted a palynology analysis on hyaena coprolites from the Beijing Zhoukoudian Peking man site, marking the first paleoecological reconstruction using coprolites in China. Pollen analysis of hyaena coprolites was again seen in the Tuozi Cave fauna reconstruction [48]. One of the most significant discoveries of carnivorous coprolites was made in Yuanmou, Xiaohe, where Zhang et al. [49] believed to have found a hyaena latrine. From 1998 to 1999, a total of 547 well-preserved and exquisitely intact coprolites were obtained. While the locality was filled with fragmented animal bone fossils, the hyaena coprolites were perfectly preserved and found throughout, suggesting *in situ* burial. Most carnivore coprolites in Eurasia have been ascribed to hyaenas, with no records of canid origins. It is important to note that large canids are among the most iconic components of the Chinese Pleistocene faunas and play a pivotal role in paleoecological reconstructions [50].

The Yuanmou Basin, situated in southwestern China's Yunnan province, lies 120 km northwest of Kunming City, along the Jinsha River's south bank and the Yangtze River's upper contacts (Fig. 1). During the Asiatic Expedition in 1926–1927, for the first time, American vertebrate paleontologist Walter W. Granger acknowledged the fossil record of this area [51–53]. Since then, numerous subsequent excavations led to the discovery of many new fossil sites and the establishment of the Yuanmou Formation [54–58]. The formation's significance soared with the groundbreaking unearthing of the Yuanmou Man (*Homo erectus yuanmouensis*) (1.54 ± 0.06 Ma) during the fourth member of the Yuanmou Formation's deposition in 1965 [59–62].

The Yuanmou Formation comprises thick sedimentary rock depositions of the Plio-Pleistocene epoch (5.3–2.6 Ma). Renowned for

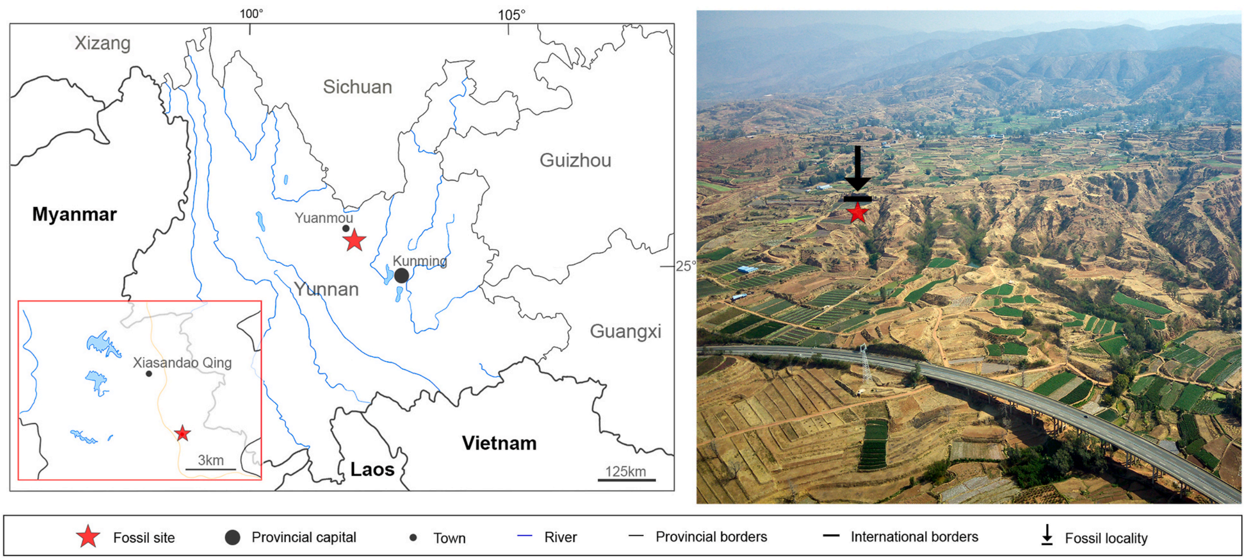


Fig. 1. The early Pleistocene fossil localities in the Yuanmou Basin that coprolite materials utilized in this study had been recovered.

its abundant fossil record, the formation has yielded numerous significant findings, encompassing early humans, mammals, reptiles, fish, and plants. Notably, it has provided crucial evidence of early humans in China, making it a pivotal site for exploring human evolution and paleobiology.

In this study, we present a descriptive and analytical analysis of 38 rare coprolites, which are potentially attributed to the ancient dhole, *Sinocuon yuanmouensis*, from the Early Pleistocene Yuanmou Formation (Member 3) in Yuanmou County, Yunnan, China. The discovery of a new ichnogenus and ichnospecies, *Cuocopros yuanmouensis* igen. et. isp. nov. enhances the diversity of Pleistocene ichnotaxonomy for canid coprolites. The only known Pleistocene dhole, *Sinocuon yuanmouensis* [50,55], is represented by a single body fossil, a skull material collected near Madahai in Yuanmou, initially referred to as *Canis yuanmouensis* [55]. Additionally, we employed a multi-disciplinary approach, incorporating palynological and lithostratigraphic analyses, to reconstruct a brief but significant climatic event during the Early Pleistocene. These climatic events played a pivotal role in the emergence of Yuanmou Man during the deposition of the fourth member of the Yuanmou Formation. Our findings shed light on the coexistence of once canids with hominoids and other fauna, offering a unique snapshot of a diverse paleoecosystem and intricate food chain within the region. This comprehensive study contributes significantly to our understanding of the ancient ecological dynamics and provides valuable insights into the complex interplay of life forms during this fascinating period in Yuanmou Basin's history.

1.1. Geological settings

The materials utilized in this study have been found approximately 16 km south of Yuanmou City, on the outskirts of Juna village (Fig. 2). The site lies about 520 m east of the highway on a hillside. These coprolites and other specimens were found serendipitously during agricultural activities. The 2.4 m spanned outcrop comprised continental deposits, including brownish clay, silt, a thick layer of gravel with sandy lenses, and yellowish cross-bedded sand. The coprolites were principally unearthed inside the sandy lenses, together with invertebrate fossils and a newly identified species of *Eirictis zhangi* [63] (Fig. 2). By comparing the lithological characteristics, and a brief stratigraphic correlation, we associate this locality with the third member of the Yuanmou Formation, which also resembles the deposits near the Shangnabang Village. The third member of the Yuanmou Formation comprises reddish-brown sandstones, siltstones, and claystone composition. This geological unit dates back to the early Pleistocene epoch (2 Ma) and houses numerous remains of fossil mammals (e.g., rhinoceroses, deer, and other ungulates) (see Discussion of Yuanmou (Member 3) Paleoecology), offering invaluable insights into the evolution and diversity of mammalian fauna during the Pleistocene.

1.2. Systematic ichnotaxonomy

Cuocopros igen. nov. Rummy and Halaçlar, 2024.
(in Farjand et al., 2024)
Type ichnospecies. *Cuocopros yuanmouensis* isp. nov.
Included ichnospecies. Known only from the type ichnospecies.
Etymology. The ichnogenus name "*Cuon*" from the Greek for dog and the Greek "*kopros*" for dung.
Distribution. Early Pleistocene (2.6–1.7 Ma).
Diagnosis. *Cuoncopros yuanmouensis* igen. et. isp. nov. displays a length range of 15 mm–55 mm and a maximum width range of 17 mm–35 mm. Their overall shape is rounded, with one end appearing more tapered than the other, in addition, disk shape morphology

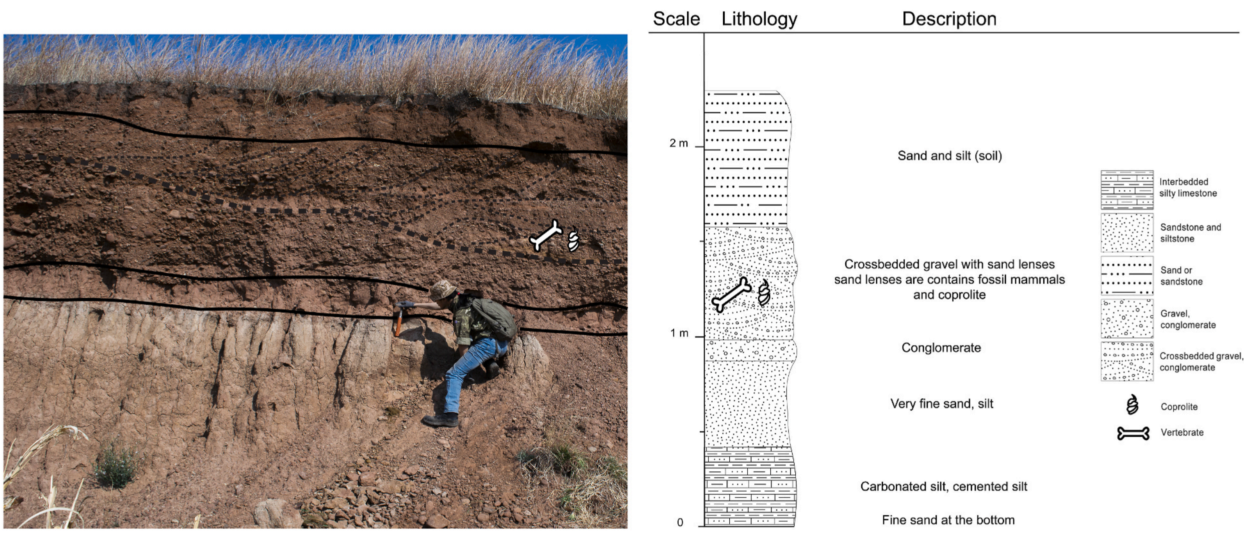


Fig. 2. The stratigraphy profile of the newly discovered fossil locality with the coprolite material that also contains the newly discovered *Eirictis zhangi* [63]. This plot only consists of the fossil locality while a detailed stratigraphy profile of the third member is undergoing.

is absent in the ichnogenus. The coprolites exhibit a color variation from white to yellowish-brown (HUE 10 YR 8/1 to 5/4) and contain fewer bone fragments alongside possible pollen.

Discussion. This ichnogenus is directly referring to a bone-cracking carnivorous diet. Notably, they differ in both color, morphology, and size when compared to other ichnogenus, *Hyaenacopros* [64], and also possess fewer bone inclusions than *Borocopros* [35].

Cuocopros yuanmouensis isp. nov. Rummy and Halaçlar, 2024.

(in Farjand et al., 2024; Fig. 3; urn:lsid:zoobank.org:pub:52814EF7-6E38-4484-93AC-957683264DE1)

Holotype. 2015-LCZN-T1-135.1, a complete coprolite pellet with constriction mark (Fig. 3).

Etymology: The ichnospecies name "*yuanmouensis*" from the Yuanmou Formation, where the holotype originates.

Type locality: Member 3 of the Yuanmou Formation, Juna village, Yuanmou County, Yunnan, Southwest China.

Distribution: Early Pleistocene (2.6–1.7 Ma).

Referred specimens: 2015-LCZN-T1-135.2 to 2015-LCZN-T1-135.38 (Fig. 3).

Fig. 3. All 38 coprolite specimens of *Cuocopros yuanmouensis* igen. et. isp. nov. Asterisk (*) indicates holotype specimen. Housed at MCYNAP. Scale as indicated in the photo.

Diagnosis. As for ichnogenus.

Description. The holotype (2015-LCZN-T1-135.1) comprises two integrated droppings, measuring 41.17 mm in length, with a maximum width of 24.33 mm and a second width of 24.93 mm. It exhibits a concave end and a tapered end, displaying a circular cross-section (Fig. 3). Constriction lines are present on the holotype and some referred specimens, resulting from pressure in the producer's rectum, which fused two droppings into one [46,65]. Middle droppings exhibit an oval shape with circular cross-sections. Most Yuanmou coprolites consist of isolated pellets, displaying variations in preservation, from perfectly intact to fragmented with some desiccated cracks, with visible borings on the surfaces. The coprolite surfaces are rugose, showing diagenetic traces. Internally, the coprolites' predominant color is white (HUE 10 YR 8/1), differing from the surface and surrounding matrix. Some parts of the coprolites may exhibit darker hues. It is evident from the broken surface that the internal texture is porous. The specimens exhibit diverse morphology and sizes, aligning with the terms defined by Diedrich [66], and the disk morphology is not present in our coprolite samples. The smallest complete specimen, 2015-LCZN-T1-135.2.4, measures 16.51 mm in length, while the largest complete specimen, 2015-LCZN-T1-135.5.1, measures 56.58 mm in length. For detailed measurements of the main morphotypes, please refer to supplementary data (see also Table S1).

Comparison and Discussion. The observed color differences between the interior and surface of the coprolites may be attributed to sediment mineralization during the diagenetic process, suggesting that the original color of the coprolites is white. In comparison to the type species of the genus, *Hyaenacopros*, *H. bucklandi* [64] from Late Pleistocene England, the Yuanmou coprolites are notably smaller and display distinct morphologies, while Diedrich [66]'s study on Late Pleistocene spotted hyaena *Crocuta crocuta spelaea* coprolites, shows a lower morphological variability ([66], Fig. 6; see also Fig. S3); in addition, a study on coprolites from Pleistocene Argentina suggests they were produced by a saber-toothed cat, *Smilodon*, and the small hyaenid, *Protictitherium*, containing fragmentary bones indicative of a bone-cracking diet [67]. Those of *Protictitherium* are smaller than *C. yuanmouensis* igen. et. isp. nov., while those of *Smilodon*'s tend to be larger than *C. yuanmouensis* igen. et. isp. nov.; such longer morphotype was also found for the 'false' saber-tooth cat, *Albanosmilus*, from the late Middle Miocene of south eastern Austria [36]; similarly, Late Miocene coprolites from California, USA, studied by Wang et al. [34] and later ichno-systematically examined by Hunt and Lucas [35] led to the erection of a new ichnogenus and ichnospecies, *Borocopros wangi*, which shares size and morphology similarities with *Cuocopros yuanmouensis* igen. et. isp. nov. but with more bone inclusions. Fig. 4 shows quantitative analysis of *Cuocopros yuanmouensis* igen. et. isp. nov. using maximum width (Wmax) distribution of some extant carnivorous mammals' feces, Carnivora coprolite, and *Cuocopros yuanmouensis* igen. et. isp. nov [34,45,68].

In our analysis, we prioritize the evaluation of ichnotaxa based on fundamental criteria such as content, morphology, and size. Notably, the distinguishing factor for the newly proposed ichnogenus lies in its content, setting it apart from *Borocopros*. Specifically, certain instances of *Crococopros naduongensis* [21] exhibit morphological similarities with *Cuocopros yuanmouensis* igen. et isp. nov., yet they display significant differences in content. The content of *Crococopros naduongensis* tends to be nearly sterilized due to the highly acidic nature of crocodilian digestive systems. This stands in contrast to *Borocopros*, which is characterized by the presence of large and abundant bone fragments, while *Cuocopros* displays smaller and fewer bone fragments. The primary distinction between *Cuocopros* ichogen. nov. and *Borocopros* lies in content, with minor variations in color, size, and morphology further reinforcing this differentiation. Lucas and Hunt [35] emphasized that complete canid feces and coprolites exhibit less elongation compared to *Hyaenacopros*, and rounded segments are more commonly observed. *Cuocopros* ichogen. nov. is differentiated from *Hyaenacopros* by its distinctively rounded and small-sized morphology. Furthermore, there are no records of disk-shaped coprolites in the current collection used in this

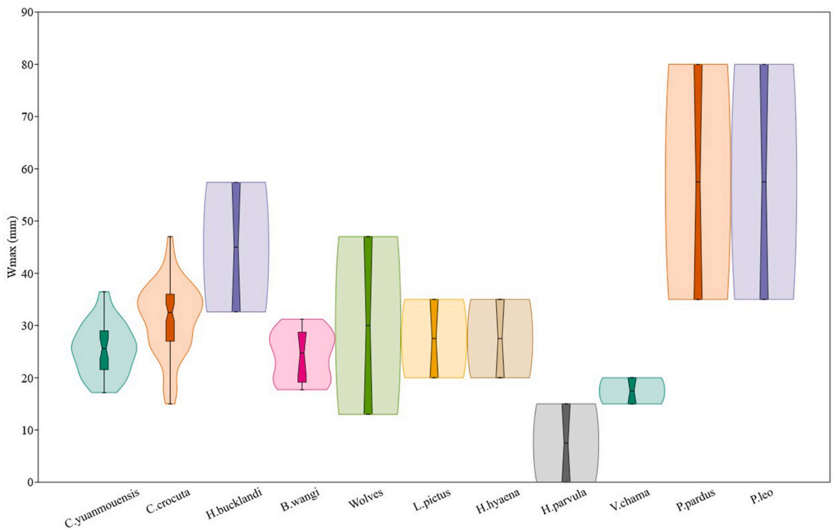


Fig. 4. Quantitative analysis of *Cuocopros yuanmouensis* igen. et. isp. nov. Violin graph shows maximum width (Wmax) distribution of some extant carnivorous mammals' feces, Carnivora coprolite, and *Cuocopros yuanmouensis* igen. et. isp. nov. Data collected from Larkin et al. [45]; Harrison [67]; Wang et al. [34]; Hunt and Lucas [35].

study.

2. Results

Surface adhesion and borings. All specimens contained some degree of bone fragments and hair inclusions. Most specimens have rugose surfaces with little abrasion. Borings and tiny holes are visible on the surface of most of the specimens (Fig. 5a–c).

Inclusions. Through CT scans and surface observation, we noticed that all specimens contained bone fragments of varying degrees. It is difficult to identify them individually. CT scan reconstruction was conducted on referred specimen 2015-LCZN-T1-135.5.6, a conical pellet, (Fig. 6a–i), whereby CT slice images showed prey bones of an unknown part, and also two bone fragments, which might be part of a scapula of a small mammal. The matrix is porous, and microglobular structures are visible through SEM (Fig. 7).

SEM-EDS analyses. All of the coprolite samples exhibited significant peaks of calcium (Ca) and phosphorus (P). In addition, the samples also displayed peaks of carbon (C), oxygen (O) and iron (Fe). Silicon (Si) content are very low. Gold (Au) appeared because of the coated element. (Fig. 8a–d).

Taphonomy inferences. The coprolites show no signs of abrasion, suggesting minimal transport. The well-preserved state of the specimens suggests an *in situ* deposition. Furthermore, the presence of multiple coprolites in close proximity indicates gregarious behaviour among the producers.

Palynology. A total of 37 pollen and spores belonging to 13 types were obtained after conducting four batches of extraction experiments (Fig. 9.1–23; Table S2). 48.6 % of the pollen grains were the arboreal type, the herbaceous and scrubby types accounted for the same 48.6 %, and the remaining 2.8 % were fern spores. Among the pollen of tree types, only *Pinus* occurs in coniferous trees, broad-leaved trees include Juglandaceae, *Castanea* and Symplocaceae, and shrub types mainly include Elaeagnus. Herbaceous types consist of *Artemisia*, Chenopodiaceae, Asteraceae, Poaceae, Rosaceae, Gentianaceae and Labiatae. Only the Trilete spore type is present.

3. Discussion and interpretation

It is widely recognized that specific coprolites serve as exceptional preservation sites, qualifying as Konservat-Lagerstätten. Coprolites often contain valuable dietary residues, resembling Lagerstätte within its own [21,69–75], which are often underrepresented in the fossil record. Determining the potential producer of coprolites presents considerable challenges due to their diverse morphological variations and varying preservation conditions. The methods employed to deduce their origin are intricate and encompass a range of approaches, including stratigraphy, geographical relationships, chemical analysis, fauna lists, and etc.

Primarily, the coprolites discovered in Yuanmou can confidently be attributed to a carnivorous origin based on several compelling lines of evidence. Firstly, they exhibit characteristics and morphology commonly found in both hyaenid and canid coprolites. The significant proportions of CaO and P_2O_5 content, along with the presence of bone fragments within the coprolites, are key indicators that align with previous studies [27,45,76–78]. Moreover, the coprolites' consistent morphological shapes, which individual pellets displaying distinct configurations, further support their identification as carnivorous in origin [34,45]. Furthermore, the prominent whitish color and gritty texture observed in the coprolites provide additional compelling evidence of their hypercarnivorous and bone-rich content [79]. These features can be attributed to the gastrointestinal characteristics of these animals. For instance, the lower part of the intestine contains the album graecum, a green paste, that, upon contact with calcium hydroxyapatite, results in the typical whitish color of the coprolites when exposed to the atmosphere [80–84]. Additionally, coprolite colors may appear darker when the animals' diet consists of large quantities of flesh and grease, serving as direct evidence of an abundance of organic matter inclusions [82].

The size of coprolites can offer valuable insights into potential producers and even provide rough estimates of the defecating agent's body mass [85,86]. However, it is crucial to interpret size-related data cautiously. Although the total volume of feces generally corresponds to body size, direct correlations can be misleading due to potential incompleteness of fossilized fecal deposits. For

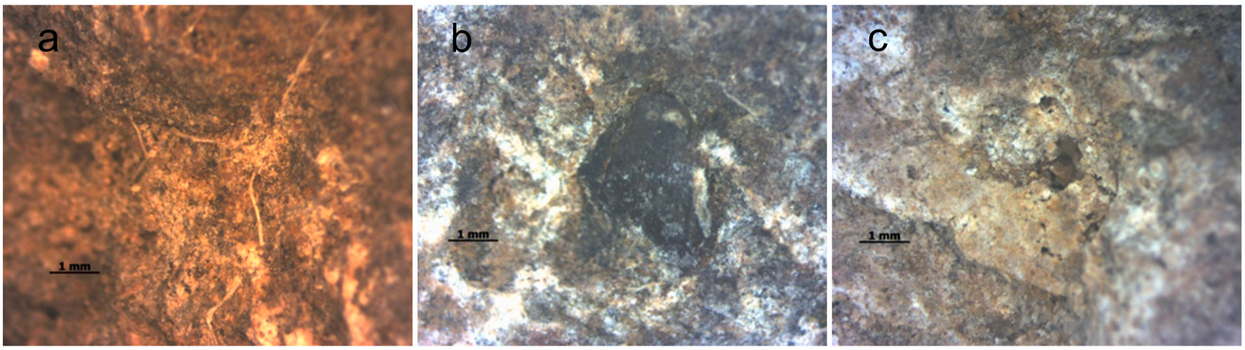


Fig. 5. Light microscopy photos of various surface adhesion on the coprolites. **a,** hair inclusion; **b,** bone fragment; **c,** possible boring. (scales are indicated in the diagrams).

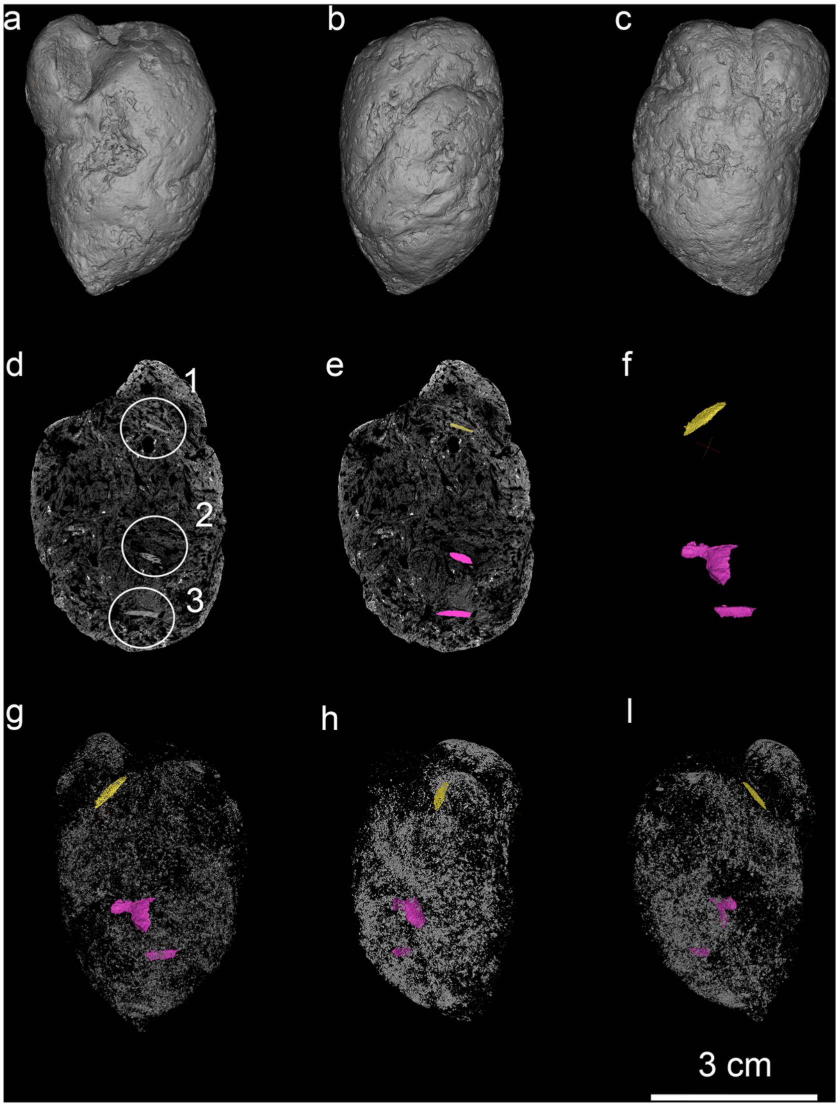


Fig. 6. Diagrams showing CT scan images of *Cuocopros yuanmouensis* igen. et. isp. nov. coprolite, referred specimen 2015-LCZN-T1-135.5.6, a conical pellet. **a, b, c,** 3D models of the specimen in different view; **d, e, f,** CT slice images showing prey bones, where yellow (1) represent a piece of an unknown bone part, while purple (2 & 3) might indicate scapula bone fragments of a small mammal; **g, h, i,** CT volume metric images showing the composition of the bone particles. MIMICS (v 21.0) was used for producing the above images. Colors are altered for better effects and visualization. Scale as indicated in the diagram.

instance, a small coprolite might have broken off from a larger fecal mass. Similarly, some large extant animals produce quantities of small pelletoid feces, leading to the possibility of an isolated pelletoid coprolite being produced by a relatively large animal. Conversely, small animals cannot produce large fecal masses. Thus, it is more appropriate to use total fecal volume to infer minimum sizes of possible producers. The diameter of a fusiform scat serves as a useful diagnostic criterion as it correlates with the morphology of the anus and the size of the animal [87]. However, other factors, such as the season of the year, the health and age of the individual, and the type and amount of food ingested, can also influence the final morphology, size, and composition of the coprolite. Considering these complexities, it is reasonable to conclude that carnivore species of different sizes can produce scats that overlap metrically [68, 88–91]. Nonetheless, bone-cracking hyaenas, with their relatively low dietary variability, are likely to exhibit less variation in fecal morphology than other carnivores with more varied diets [66,85,86,92]. On the other hand, coprolites of non-bone-cracking carnivores tend to contain more organic content than bone fragments.

Given the likely carnivorous origins of the majority of these coprolites, we opted not to subject the specimens to destructive analysis for palynology. This cautious decision aimed to prevent potential false error results or insufficient pollen numbers arising from the coprolites' possibly low silicon content, as suggested by the EDS analysis. Past studies [93–95] have highlighted considerable variability in pollen concentration within carnivorous coprolites, including hyaenas, ranging from absence to abundance. To preserve the

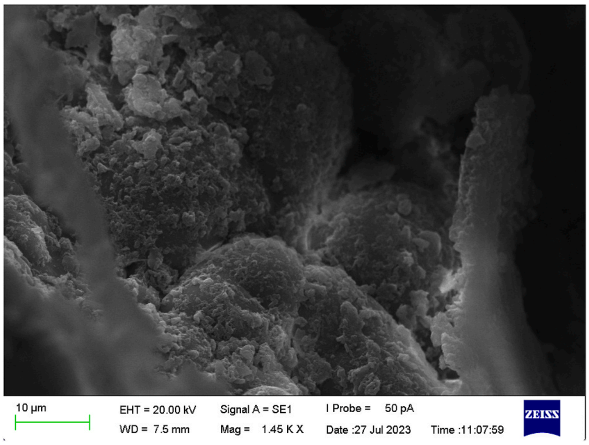


Fig. 7. SEM image of microglobules from specimen 2015-LCZN-T1-135.5.27. Scale as indicated in the diagram.

coprolites and minimize any risk of damage, we conducted pollen analysis directly on the surrounding sediment layers (see the paleoenvironment section for further details). Throughout various previous studies, pollen analysis has proven to be a valuable tool in understanding paleoenvironmental vegetation. However, it is essential to acknowledge that hypercarnivorous animals often consume the intestines of their herbivorous prey, potentially influencing the pollen assemblages found in the coprolites.

Based on our thorough observations, we propose that the entire assemblage of bones and coprolites was rapidly deposited, likely produced by at least two individuals or more. This conclusion is bolstered by the clear identification of two distinct similar sizes of conical pellets. By analyzing the ratio of these conical sizes, we deduce that the producers could have been adults canids. However, to verify this hypothesis, further analysis using extant dogs as comparative models is indispensable. The preservation condition of the coprolites provides invaluable insights, indicating that the majority of them are *in situ* and not transported from elsewhere. Furthermore, we noticed that all 38 coprolites exhibited no signs of deformation, suggesting that the fresh feces were remarkably hard and rigid, withstanding trembling and breakage effectively. This robustness likely stems from the coprolites' high calcareous content. Much like the preservation process observed in hyaenid coprolites, *Cuocopros yuanmouensis* igen. et. isp. nov. likely started as a sticky substance that rapidly hardened upon subaerial exposure, and was quickly buried, preserving its original morphology while sealing its high calcite and phosphate matrix [96]. The exceptional preservation of these coprolites has provided vital clues about the nature of the feces and the potential implications for the ecological dynamics of the Yuanmou Basin during that period. Such well-preserved specimens offer a unique opportunity to gain deeper insights into the ancient environment and the behaviors of the organisms that inhabited the region.

Fossil latrines, also referred to as latrinite [84], present a promising source of paleoecological information when studied comprehensively [96]. Several carnivores, including hyaenas, canids, and wolves, are known to utilize designated "latrine" grounds for social defecation and scent-marking, primarily to establish territorial boundaries, although other hypotheses have been proposed in recent years (e.g. Refs. [34,79,96,97]). However, the term "latrine" and its usage can be broad and potentially misunderstood. Buesching and Jordan [97] define it as the repetitive use of the same place for defecation, resulting in the accumulation of feces ranging from two to several hundred specimens. In the context of the Yuanmou coprolites, we prefer to use the term "temporary latrines" rather than "long-term latrines" (*sensu* [98]) since we believe that the 38 coprolites were defecated in a short-term period around sites of interest, such as areas near ancient riverbanks during the dry season. We base this assumption on the presence of bone fragments from rhinos and proboscideans found nearby. These "temporary latrines" likely served as specific spots where carnivores gathered to defecate while possibly feeding on the carcasses of these larger animals in the vicinity.

Macroscopic and microscopic observations of the Yuanmou coprolites reveal an internal granular-like structure with porosity, indicative of shrinking patterns resulting from early desiccation, which can also include cavities originating from decomposed inclusions during dehydration [17,26,66,99]. Additionally, scanning electron microscopy (SEM) images (Fig. 7) confirmed the presence of calcium phosphatic microglobule structures. Several researchers [26,27,36] have discussed the occurrence of these microglobules in their studies of carnivorous coprolites, proposing that they represent pseudomorphs formed after cocciform bacteria originating from the gastrointestinal microbiome of the defecating agent or the surrounding environment. These bacterial agents are considered crucial factors contributing to the enhanced preservation potential of the feces. However, it is important to note that the presence of calcium phosphatic microglobules in coprolites should not be solely relied upon as a diagnostic criterion for determining the potential dietary utility of the producer [36]. Hair inclusions are found in the Yuanmou coprolites and this may be of the defecating agent itself or from its prey.

Borings are usually evident of coprophagy organism by invertebrates (e.g. marine bivalve or arthropods) [100,101]. Traces of micro-borings are visible in many of the Yuanmou coprolites, suggesting that the temporarily open latrine site was close to a water source. Not all borings are considered burrows, some of them might be "pseudo-burrow" abandoned in early stages [19]. Micro CT show a variety forms of micro-borings, which is hard to be interpreted in our coprolitic context. Numerous tiny holes known as microvoids or "degassing holes" were visible on most of the Yuanmou coprolites surface, as well as within it, and these were most

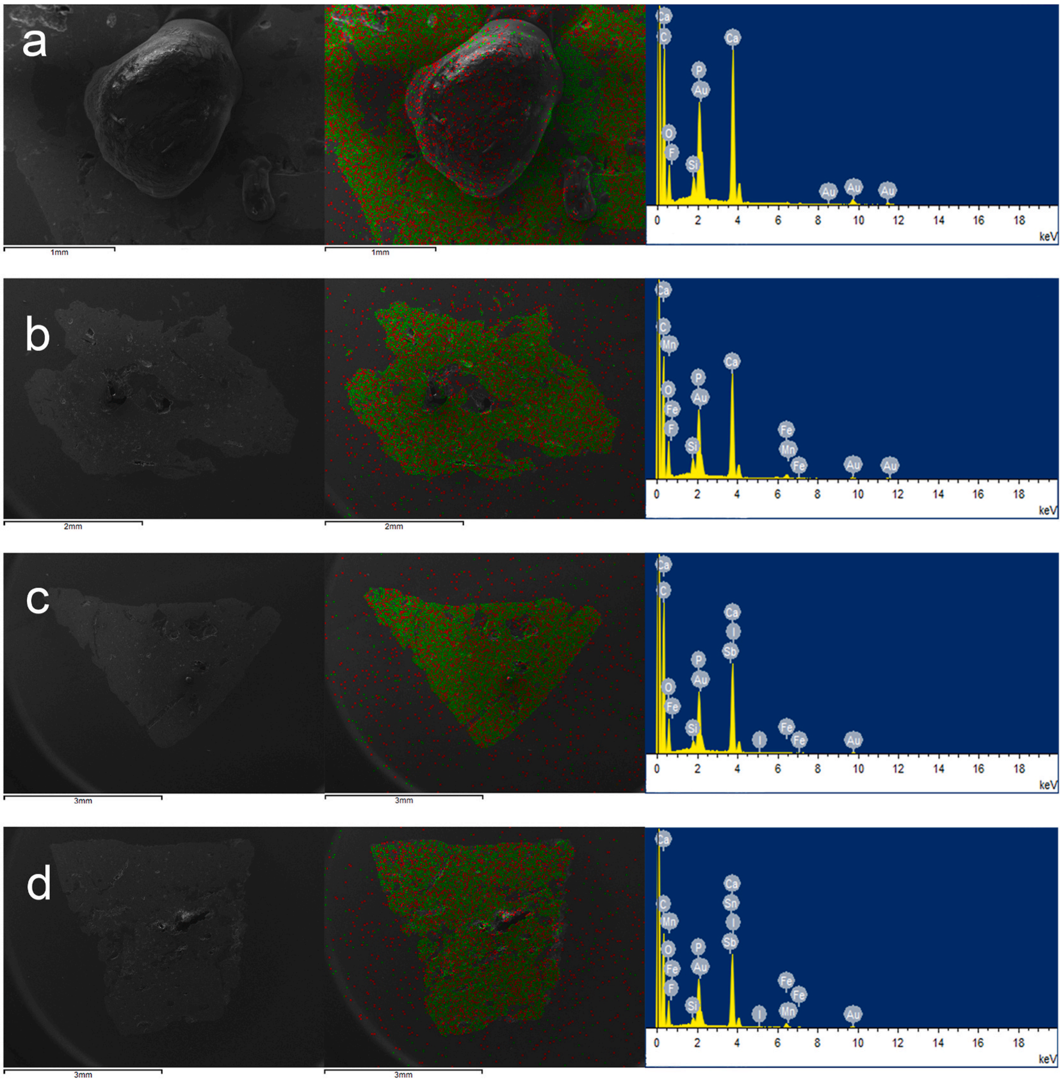
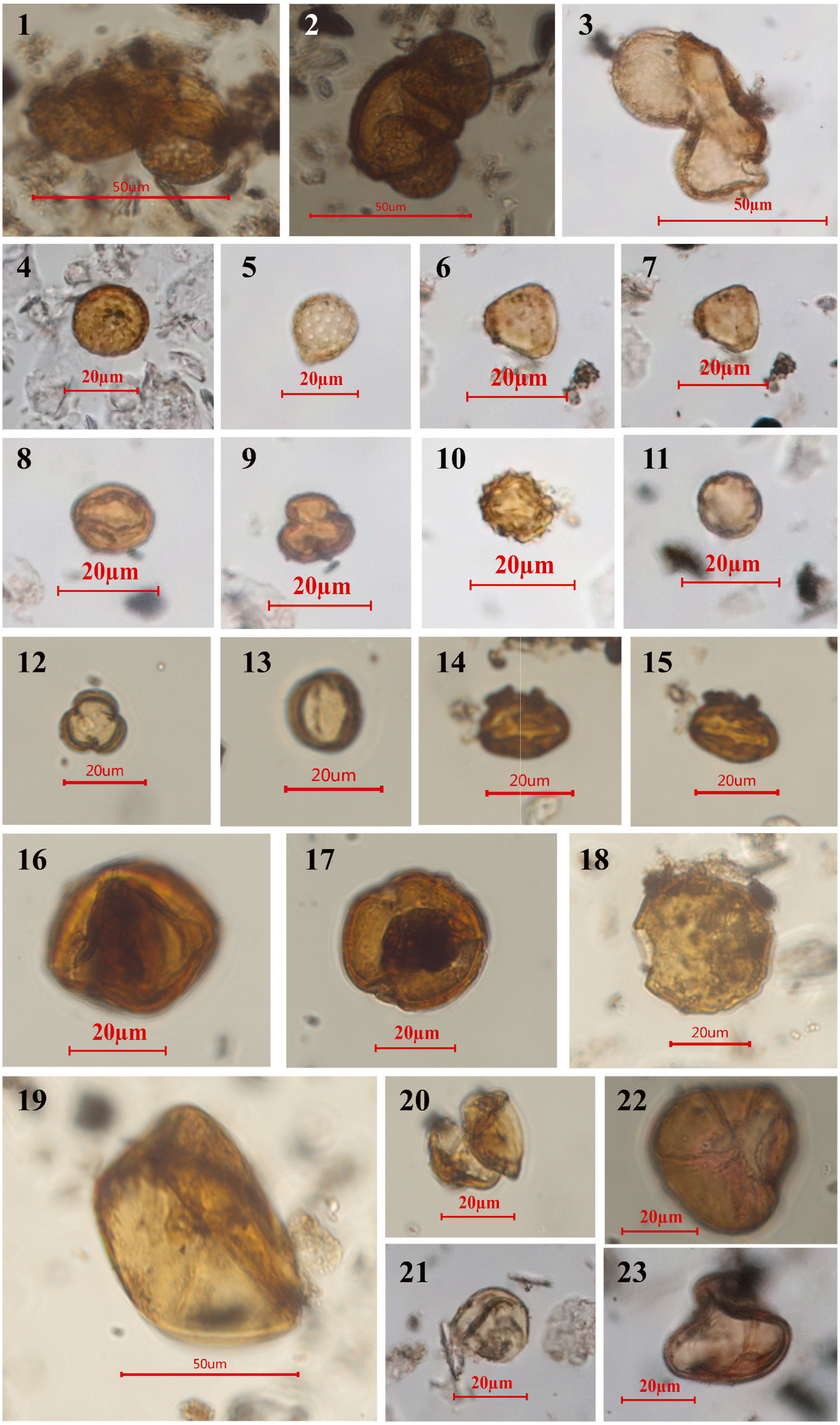


Fig. 8. SEM images and EDS analyses of *Cuocopros yuanmouensis* igen. et. isp. nov. In each of the coprolites sample. **a,** 2015-LCZN-T1-135.5; **b,** 2015-LCZN-T1-135.5.27; **c,** 2015-LCZN-T1-135.5.37; **d,** 2015-LCZN-T1-135.38, the first image is an overall photo of the sample, the green color in the second image shows Calcium element, and the third image shows the element peaks. Major abbreviations of elements as indicated in the text.

probably caused by gases within the fecal matters [45,102,103]. Microvoids are quickly filled with water when fecal matter is excreted from the animal body in the shallow water environment, thus making the fecal becoming heavy and sinking to the lake floor [86].

Within the Canidae family, species such as the grey wolf, wild dog, dhole, and bush dog are known for their remarkable ability to take down prey much larger than themselves, often hunting in coordinated packs [38]. Considering the importance of coprolite size relative to the body mass of the producer, we deduce that the coprolites do not belong to the giant, short-faced hyaena *Pachycrocuta brevirostris licenti*, previously recorded in the Yuanmou fauna. Espigares et al. [79] and Palmqvist et al. [104] have described *P. brevirostris* as a massive animal capable of efficiently cracking and consuming bones, with a body mass of roughly 100 kg and producing coprolites approximately 7–8 cm in diameter. These characteristics align more closely with the coprolites of the extant *Crocuta crocuta*, commonly known as the spotted hyaena, which exhibits small bone fragments in its droppings. In contrast, the feces of the striped hyaena (*Hyaena hyaena*) tend to contain a higher proportion of organic matter [103]. Our biometrical analysis further supports this conclusion, as the size of the Yuanmou coprolites is smaller than those of extant *Crocuta crocuta* and comparable in size to those of the striped hyaena. Some Yuanmou coprolites exhibit a tube-shaped morphology, similar to the feces of non-hyaena scats, such as those of felids and other canids like domestic dogs [85,92,99,105–107] (Fig. 10a–d). Further, the Yuanmou coprolites lacks the disk morphology, which strengthens its support for a non-hyaena producer. Given their flesh-eating habits, felids can be excluded from the potential producers of the Yuanmou coprolites. Felids generally produce sausage-shaped feces, and their dentition is not suited for bone-cracking, further supporting their exclusion from consideration [85]. The available information rules out *Panthera pardus* and *Panthera tigris* as potential producers, as they cannot create coprolites of the size observed in Yuanmou. Chinese *Vulpes* cf.



(caption on next page)

Fig. 9. Results yielded from palynology studies. Common palynomorphs from surrounding matrix. Yuanmou basic pollen plate: **1–3,** *Pinus*; **4–5,** Chenopodiaceae; **6–7,** Symplocos; **8–9,** Rosaceae; **10,** Asteraceae; **11,** Labiatae; **12–13,** Artemisia; **14–15,** Castanea; **16–17,** Gentianaceae; **18,** Juglandaceae; **19–21,** Poaceae; **22,** Trilete spores; **23,** Unknown type spores. (Scales as indicated in each diagram).

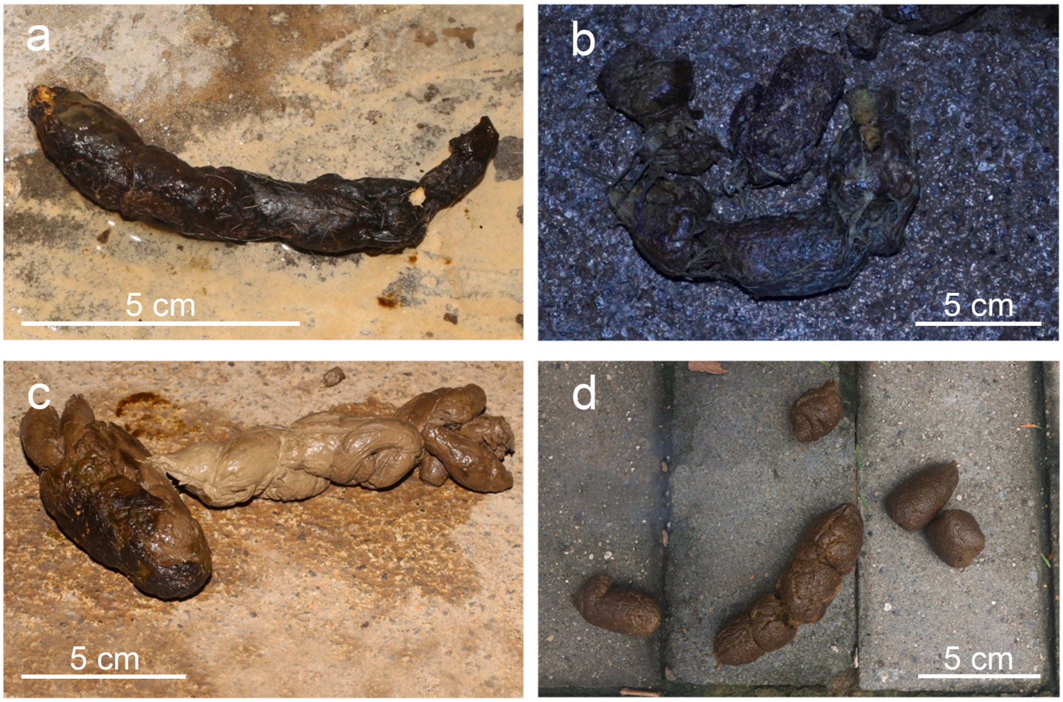


Fig. 10. Feces of extant felid and canid species. **a,** *Lynx lynx*; **b,** *Panthera leo*; **c,** *Puma concolor*; **d,** domestic dog (Border Collie). **a-c,** were taken in Izmir Sasali Zoo, Turkey; **d,** was taken in Beijing, produced by a pure breed dog named Sina-Marley. Credits by K.H. and P.R. (Scales as indicated in each diagram).

chikushanensis [55], a middle-sized fox with an omnivorous diet, generally consumes small mammals, fish, and birds, making it unlikely to produce coprolites of such diameter. According to Harrison [68], extant African *Vulpes chama* (cape fox) creates feces with a diameter of 15–20 mm. *E. zhangi*, a small-sized mustelid, and its diet and body mass are not conducive to producing coprolites of the observed size in Yuanmou. According to Harrison [68] (2011), the African species dwarf mongoose (*Helogale parvula*) does not create feces larger than 15 mm in diameter. Several studies has indicated that mustelid scats are usually oblong in shape [85], with less corroded and sharp-edged undigested bone remains, often including articulated bones [45,108,109].

Considering all these factors, the most likely producer of the Yuanmou coprolites is the ancient dhole, *Sinocuon yuanmouensis*, which was a native species of the Yuanmou fauna. To further support this hypothesis, we conducted a comparison of the molars of *Sinocuon*, *Boraphagus*, and *Pachycrocuta* (Fig. 11a–c). We observed that both *Borophagus* and *Pachycrocuta* possess robust molars that are well adapted to bone cracking, while *S. yuanmouensis* exhibits a more hypercarnivorous dentition [50]. This distinction explains why the Yuanmou coprolites contain fewer bone fragments compared to those of *B. wangi*. Further, according to Fig. 4, the size of *C. yuanmouensis* igen. et. isp. nov. coprolites is comparable to those of *B. wangi*, extant wolf feces, *Lycaon pictus* feces (African hunting dog), and *H. hyaena* feces. Notably, the Yuanmou faunal list does not include a hyaena species of the size implied by *H. hyaena* feces. This size implication strongly suggests that the possible producer of the coprolites should be a canid rather than a hyaenid.

3.1. Taphonomy, paleoclimatic and paleoenvironment inferences: reconstruction of past vegetation

The paleo-vegetation data distribution reveals that a significant proportion (>81 %) of the pollen is concentrated in the lower fraction. Consequently, our interpretation of the vegetation landscape in the lower layers remains preliminary, given the available pollen data. Within this layer, *Pinus* dominates, accounting for 33 % and standing out as the most abundant taxon. Moreover, the presence of subtropical broadleaf evergreen forest components, including Juglandaceae, *Castanea*, and Symplocaceae, further adds to the diversity of the vegetation in this stratum. In addition to the dominant *Pinus*, the herbaceous pollen taxa exhibit notable diversity, with the appearance of drought-tolerant steppe types such as *Artemisia*, Asteraceae, and Rosaceae in this layer. A few other taxa, like Poaceae, Gentianaceae, and Labiatae, are also observed. The coexistence of subtropical evergreen forests and drought-tolerant herbs and shrubs suggests a relatively warm climate and high water vapor evaporation during this period.

The modern Yuanmou Basin, located in northern Yunnan, falls within a typical dry and hot river valley. While regional

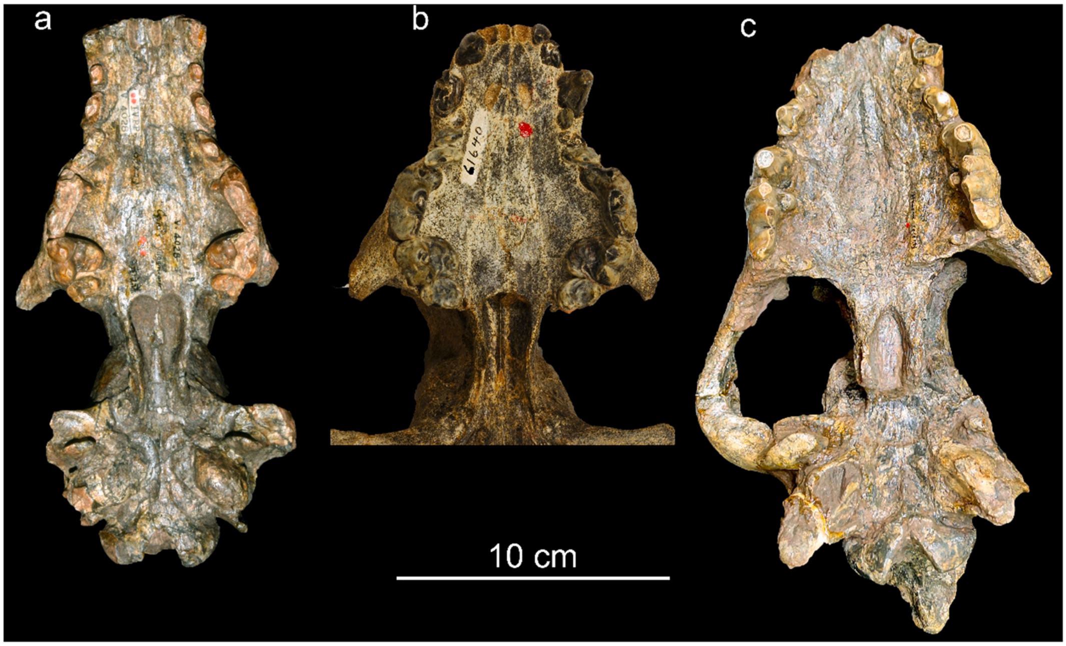


Fig. 11. Skull comparison of big Carnivora. **a,** *Sinocuon yuanmouensis,* V 4028 (photo credit to Jiangzuo, Q.G, IVPP); **b,** *Borophagus secundus*, F:AM 61640 (photo credit to X. Wang, NMH); **c,** *Pachycrocuta brevirostris licenti* (photo credit to Liu, J., IVPP). (Scale as indicated in the diagram).

precipitation is influenced by the Indian monsoon, the topographic relief factors in the region significantly moderate its impact, leading to a higher evaporation rate than precipitation. Studies have identified the rain shadow and valley-foehn wind effects resulting from the deep topographic closure as the contributors to the local dry and hot climate [110]. This distinct climate has shaped the unique appearance and zonal composition of the regional vegetation, termed as the "Savanna of valley type" by some scholars [111, 112]. Dominant herb and shrub taxa in the area include *Bombax ceiba*, *Cymbopogon goeringii*, *Eulalia phaeothrix*, *Andropogon chinensis*, *Bauhinia faberi*, *Wikstroemia dolichantha*, *Pentaneura indicum* var. *hypoleucum*, and *Barleria cristata*. *Pinus yunnanensis*, *Castanopsis delavayi*, and other tree species dominate the tree community [113]. Comparing the Early Pleistocene vegetation landscape of the Yuanmou Basin to modern times, some similarities can be observed. Gradually, it exhibits characteristics of a dry-hot valley landscape. However, during this period, the overall humidity appears to be slightly higher than that of the present era.

In addition, some information on vegetation fluctuations can be glimpsed in combination with other layers of the section although their number is limited. For example, two grains of *Pinus* and one grain of Chenopodiaceae appeared in the upper layer; two grains of Chenopodiaceae, one grain of *Artemisia* and Trilete spore respectively were present in the middle layer. Due to the insufficient number of statistics, the evolutionary history of the regional vegetation could not be effectively reconstructed, and only preliminary inferences could be made. The disappearance of subtropical evergreen components and the occurrence of only *Pinus* in the above two layers implied that the regional woodlands were small-scale coniferous forests. The only remaining herbaceous plants are the drought-tolerant Chenopodiaceae and *Artemisia*, both of which are the main representative plants of the modern northern steppe. The disappearance of thermophilic woodland components and other herbaceous plants in the upper-middle layer may be related to regional cooling or vegetation scarcity. This suggests some oscillations in regional vegetation changes. Nevertheless, it is acknowledged that there is some uncertainty in the above inferences, and more accurate regional vegetation-climate change requires more detailed pollen-based reconstruction work.

Our paleovegetation data are supported by other research work. Previous studies have pointed out that a similar vegetation landscape of dry-hot valleys type occurred in the Pleistocene. Yao et al. [114] carried out pollen reconstruction analysis in the Yuanmou Basin, and the results indicate a warm and humid subtropical climate with a mean annual temperature of ca. 16–17 °C and a mean annual precipitation of 1500–1600 mm in the Late Pliocene rather than a dry, hot climate today. Previous pollen data show that since the early Pleistocene, the vegetation composition of the dry-hot valley in Yuanmou has decreased in the tropical subtropical broadleaf forest component and increased in the grassland component; at the same time, the differentiation of habitat conditions has intensified, with the coexistence of forest, grassland, swamp and other intermediate types, showing vegetation similar to that of the savanna type [115–117]. Similarly, pollen records from the Eryuan area in the western part of the Yuanmou Basin show a high level of Early Pleistocene conifer pollen (~80 %) and a decrease in broadleaf pollen, signaling an important shift in the regional environment [118]. There is a lack of information on the Middle Pleistocene paleovegetation in Yuanmou area. Some studies point out that the closed Yuanmou Basin began to form at ~0.1Ma, and forest species mainly *Picea*, *Tsuga*, *Quercus*, *Juglans*, etc. The dominant herbaceous species was *Artemisia*, and there were also a few *Apiaceae* and Poaceae taxa [60,119]. The above results indicate that the vegetation climate in Yuanmou Basin during Early Pleistocene may be in an important stage of transition to the dry hot valley type.

From the aforementioned factors, we deduce that the coprolites were accumulated during the dry season by the shallow silt and sandy river bank, with low energy fluvial flow, where the open-site latrines were quickly buried under rapid conditions. Concentric cracks evident from the coprolites also support the moisture from the fresh feces was vastly evaporated due to hot weather and left for subaerial exposure before embedment. This spatial use of latrines and seasonal patterns align with the findings of Vitale et al. [120], who documented that *C. crocuta* latrines were mainly accumulated during the dry season and disappeared during the rainy season.

3.2. *The paleoecology of Yuanmou Formation (member 3)*

An initial assessment of the fossil horizon indicates that during the Early Pleistocene, this region experienced a semi-arid climate accompanied by the presence of flowing fresh water. This climatic context may offer an explanation for the coexistence of both large and small mammals within this stratum, as well as the notable diversity of carnivores observed. The Early Pleistocene epoch is widely recognized as a period marked by swift climate fluctuations across both eastern and western Asia [121–123]. which in turn influenced the decline or reduced biodiversity of several large carnivore species in the North China region [63].

A significant portion of the fauna list and paleoenvironmental studies pertaining to the Yuanmou Formation have been meticulously documented in Qian et al. [124]. This comprehensive dataset underscores the intriguing cohabitation of various carnivore species (Table S3) sharing similar ecological habitats, such as *Sinocuon yuanmouensis*, *Panthera pardus*, *Panthera tigris*, *Pachycrocuta brevirostris licenti*, and *Vulpes* cf. *chikushanensis*, alongside herbivores like *Stegodon* sp., *Cervus* sp., *Rhinoceros sinensis*, *Equus yunnanensis*, and Bovidae. Recent discoveries of Mustelids have further enriched this roster, painting a vivid picture of a unique prey-predator paleoenvironment. Each species occupied distinct roles or niches within the ecosystem, minimizing competition for resources and contributing to the intricate balance of a trophic cascade inherent to a functioning ecosystem.

Building upon the preceding context, the renowned Yuanmou Formation, renowned for preserving some of the earliest hominoid records in South China, has now yielded a wealth of ichnofossil evidence showcasing coexisting predators of the same era (see reconstruction drawing, Fig. 12). These contemporaneous predators likely shared the landscape and potentially interacted with the hominids present at the time. The insights gleaned from pollen analysis have unveiled a brief period of climate instability during the Early Pleistocene within this stratum. The pollen data vividly illustrates a rapid and pronounced climatic shift, during which a significant portion of the prevailing vegetation experienced rapid decline or disappearance. This climatic upheaval may have played a role in compelling larger predators to vacate the area. This phenomenon elucidates the unique abundance of carnivorous coprolites found exclusively within this specific layer of the Yuanmou Formation. Thus, our deduction leads us to infer that the subtropical conditions prevailing during this epoch exerted a pivotal influence on mammalian evolution and potential migration patterns.

4. Limitation of studies

The majority of trace fossil research is subject to some limitation related to the objects of study. Firstly, since this is the first record of *Cuon* coprolites in Eurasia, there is a lack of existing materials or data for comparison. Without comparative data from other sources, it can be challenging to draw robust conclusions or fully understand the significance of the findings. Secondly, to solidify the findings and gain a comprehensive understanding of *Cuon* coprolites, it is essential to conduct further comparison studies. Specifically, comparing *Cuon* coprolites with coprolites of other animals, such as hyenas and canids, could provide valuable insights into their differences and similarities. And finally, the producers of canid coprolites from the Early Pleistocene are relatively limited in number and diversity. This scarcity of specimens may hinder the ability to make broader generalizations or interpretations about canid behavior during that time period.

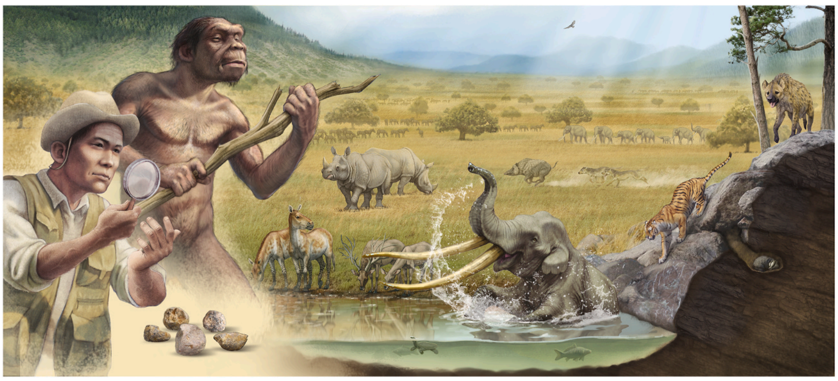


Fig. 12. Paleoenvironment reconstruction titled `Who Ate Who?' A vivid portrayal of the illustrious Yuanmou Formation. This geological formation in South China has gained renown for its exceptional preservation of some of the earliest hominoid records. In a remarkable discovery, the Yuanmou Formation has unveiled a plethora of ichnofossil evidence, providing insight into coexisting predators from the same era. (Flora and fauna constituent in the drawing were an actual reconstruction based on palynology analyses, and of body fossil findings from various workers; illustration by Wenyu Ren).

5. STAR methods

5.1. Resource availability

5.1.1. Lead contact

Further information and requests for resources and materials should be directed to and will be fulfilled by the lead contact, Paul Rummy (paulrummy@ivpp.ac.cn).

6. Materials availability

All 38 coprolite specimens are accessioned and accessible Museum of Chuxiong Yi Nationality Autonomous Prefecture (MCYNAP) ventured into the Yuanmou Basin, Yunnan, China. Palynology samples are stored in the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences in Beijing, China.

7. Data and code availability

Data.

- Data have been deposited at text and supplementary material

Code.

- This paper does not report original code.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request

8. Experimental model and subject details

We do not have experimental model and subject.

9. Method details

9.1. Fossil material

In the summer of 2015, an expedition led by the Museum of Chuxiong Yi Nationality Autonomous Prefecture (MCYNAP) ventured into the Yuanmou Basin, Yunnan, China (Fig. 1) to gather significant specimens for our study. Excavations on a hillside slope yielded a collection of 38 coprolites, accompanied by several mammalian tooth fragments. While most of these coprolites were carefully extracted *in situ*, a few were found on the surface. To facilitate further analysis, the gathered materials were subsequently transported to Yunnan University (YNU) for detailed examination. Each specimen was assigned a unique identifier in the form of the acronym “2015-LCZN-T1-135,” followed by a sequential number from 1 to 38 (Fig. 2). To ensure precise data acquisition, we adhered to standardized measurement procedures (reference and Table S1). Each coprolite’s dimensions were meticulously recorded using a Vernier caliper, with measurements taken to the nearest millimeter by visual observation. This method allowed us to capture vital characteristics and variations within the coprolite specimens.

In this study, specific terminologies have been adopted to precisely describe the characteristics and morphology of coprolites. The term “maximum width” pertains to the widest diameter of the coprolite, while the “second width” is measured at a 90-degree angle to the maximum width, following the conventions set by previous researchers [19–21,45]. To categorize the shapes of carnivore coprolites (see also Figs. S1 and S2), we have used the commonly employed terms in the existing literature. These include “conical,” “oval, ” “round,” “irregular”, and “drop” which have been extensively utilized by researchers such as Diedrich [66] and Wang et al. [34]. Criteria of descriptions are based on Chame [85], Jouy-Avantin et al. [14], and Hunt & Lucas [125], Furthermore, the presence of "constriction lines" on the surface of coprolites is noteworthy. These lines are formed due to the muscular pressure exerted during the extrusion of feces through the anal or cloacal sphincter, as described in the studies by Hunt and Lucas [125]. Additionally, the term "cross section" refers to a lateral cut or revealed surface of a coprolite, enabling a view of its internal structure, as observed by Milàn [126]. By adopting these standardized terminologies, we ensure clear and consistent communication of our findings, facilitating comparability with previous research in the field.

Imaging and Coloration. Coprolites were examined and described under normal light using a Zeiss PrimoTech microscope. Images were captured using an integrated microscope camera. Photographs and EDS graphs were compiled using Adobe Photoshop CC 2018 and Adobe Illustrator CC 2018. To accurately determine coloration, the Munsell soil color chart [127] was employed in the analysis. Pie chart was created with Grapher (Golden Software, LLC).

9.2. SEM-EDS analysis

Scanning electron microscopy (SEM) using a Zeiss EVO 25 instrument coupled with energy-dispersive X-ray spectroscopy (EDS)

(Oxford X-act) was employed to analyze the coprolite samples. Tiny pieces of the coprolite samples were broken off for analysis, samples were taken from the surface and inner portion of the coprolites. Four coprolites (2015-LCZN-T1-135.5, 2015-LCZN-T1-135.5.27, 2015-LCZN-T1-135.5.37, 2015-LCZN-T1-135.38) were selected for these studies. Prior to analysis, all samples were attached to a stub and coated with a thin layer of gold by high vacuum evaporation. The operating voltage of the EDS analysis was 15 KV.

9.3. Computed tomography

Non-destructive examination of the coprolite content and generation of 3D models (STL files) were accomplished using Computed Tomography (CT) scanning and a portable 3D scanning device. All 38 coprolite specimens were scanned using a 240 kV micro-computerized tomography (developed by the Institute of High Energy Physics, CAS) at the Key Laboratory of Vertebrate Evolution and Human Origins, IVPP, CAS. The scans were performed with a beam energy of 170 kV and a flux of 150 μA, at a resolution of 53.977 μm per pixel. A 360° rotation with a step size of 0.0° was used, resulting in total of 720 projections were reconstructed in a 3071*3458 matrix of 1317 slices using a two-dimensional reconstruction software (developed by the Institute of High Energy Physics, CAS[128]). While specimen 2015-LCZN-T1-135.6 was scanned using a 240 kV micro-computerized tomography (developed by GE, Model – phoenix v|tome|x m) at the Key Laboratory of Vertebrate Evolution and Human Origins, IVPP, CAS. The scans were performed with a beam energy of 170 kV and a flux of 110 μA, at a resolution of 14.164 μm per pixel. A 360° rotation with a step size of 0.0° was used, resulting in total of 720 projections were reconstructed in a 2738*3519 matrix of 2631 slices. The data were output in the TIFF file format and imported into MIMICS Research (V 21.0).

9.4. Palynology

Three pollen samples were collected from mammal fossil sites, representing the upper, middle, and lower stratigraphic layers. Considering the difficulty of pollen and spore extraction from Pleistocene sediments, we used the combination of HF treatment, sieving, and heavy liquid floatation [129–131] progressively increasing the sample weight and number of floatation for the same batch of samples. The complete experimental technique is as follows:

We mashed enough samples with a mortar to guarantee that the sediment were less than 1 mm on diameter and then weighed each sample of ~100 g, depending on the lithology. All samples were added with exotic *Lycopodium* spores (27560 grain/tablet) to estimate the pollen concentrations before proceeding with acid-alkali treatment. The subsamples were treated with 2 mol/L HCL to remove carbonates. After washing in water to neutralize, each sample was then treated with 70 % HF to remove impurities and siliceous matter. We conducted alkali treatment (5 % NaOH) for samples with high organic content. A heavy liquid ($ZnCl_2$ and KI/ZnI_2) with a density of 2.05–2.10 g/cm^3 was used to extract the pollen. All samples were treated with a 1: 9 solution of concentrated sulfuric acid and acetic anhydride. The extracted pollen was identified and counted with a Zeiss Axioplan Imaging 2 microscope at × 400 magnification. The analyses were conducted at the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences.

9.5. Life reconstruction

Reconstruction drawings were created with the assistant of Wenyu Ren under the direction of P.R & K.H. The paleoenvironment reconstruction was based on various literature sources published on Yuanmou fauna. The floral components in the image were actual reconstructions derived from palynology analyses. The figures were prepared using Adobe Photoshop CC 2018 and Adobe Illustrator CC 2018 software. Graphical abstract of the article was contributed by Novia Shin. Additionally, line drawings were made to scale by referring to the original specimens.

9.6. Ethics

Review and/or approval by an ethics committee was not needed for this study because no live vertebrates and higher invertebrates are involved. The study strictly adhered to all existing regulations, and no permits were required in this context. The collection material described in this study was conducted lawfully and in accordance with the guidelines of the Society of Vertebrate Paleontology. The authors are aware and against any unethical practices of parachute science in paleontology and comes from diverse ethnic and cultural backgrounds.

9.7. Nomenclatural acts

This published work and its associated nomenclatural acts have been registered in ZooBank, an online registration system for the International Code of Zoological Nomenclature (IZCN). The LSID (Life science identifiers) for this publication is urn:lsid:zoobank.org:pub:52814EF7-6E38-4484-93AC-957683264DE1. The associated information can be accessed through any standard web browser by appending the LSID to the prefix “http://zoobank.org/”.

10. Quantification and statistical analysis

For comprehensive quantitative paleontological investigations and the graphical representation of findings, we employed PAST version 4.0 [132].

CRediT authorship contribution statement

Arya Farjand: Writing – review & editing, Writing – original draft, Validation, Software, Funding acquisition, Conceptualization. **Liya Fu:** Validation, Resources. **Paul Rummy:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Kazim Halaçlar:** Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Jian Wang:** Writing – review & editing, Writing – original draft, Validation, Software, Resources, Methodology, Investigation, Formal analysis, Data curation. **Qiong You:** Validation, Resources. **Hui Su:** Validation, Resources. **Shundong Bi:** Writing – review & editing, Validation, Project administration, Funding acquisition.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.heliyon.2024.e30072.

References

[1] W. Buckland, On the discovery of coprolites, or fossil faeces, in the Lias at Lyme Regis, and in other formations, Trans. Geol. Soc. Lond. Ser. 2 (1829) 223–236.
[2] A.P. Hunt, K. Chin, M.G. Lockley, M.G, The palaeobiology of vertebrate coprolites, in: S.C. Donowan (Ed.), The Palaeobiology of Trace Fossils, John Wiley, London, 1994, pp. 221–229.
[3] A.C. Mancuso, C. Marsicano, R. Palma, Vertebrate coprolites from the triassic of Argentina (cuyana basin), Ameghiniana Rev. Asoc. Paleontol. Argent. 41 (2004) 347–354.
[4] W. Häntzschel, F. El-Baz, G.C. Amstutz, Coprolites, and annotated bibliography, Mem, Geol. Soc. 108 (1968) 1–132.
[5] M.E. Eriksson, J. Lindgren, K. Chin, U. Mansby, Coprolite morphotypes from the Upper Cretaceous of Sweden: novel views on an ancient ecosystem and implications for coprolite taphonomy, Lethaia 44 (2011) 455–468.
[6] J. Krause, C. Piña, C, Reptilian coprolites in the eocene of central patagonia, Argentina, J. Paleontol. 86 (2012) 527–538, https://doi.org/10.2307/41480215, 2012.
[7] M. Waldman, Jr.W.S. Hopkins, Coprolites from the upper cretaceous of alberta, Canada, with a description of their microflora, Can. J. Earth Sci. 7 (1970) 1295–1303.
[8] V.G. Ochev, Nekotoryye zamechaniya o koprolitakh triasovykh pozvonochnykh, Paleontol (Translated as: Some remarks on coprolites of Triassic vertebrates) Zh. 2 (1974) 146–148.
[9] W.A.S. Sarjeant, Fossil tracks and impressions of vertebrates, in: The Study of Trace Fossils, Frey, Springer-Verlag, New York, 1975.
[10] J.D. Stewart, J.D, Enterospirae (fossil intestines) from the upper cretaceous niobrara formation of western Kansas, university of Kansas, paleont, Contr. 89 (1978) 9–16.
[11] R.A. Rodriguez-de la Rosa, S.R.S. Cevallos-Ferriz, A. Silva-Pineda, Paleobiological implications of Campanian coprolites, Palaeogeogr. Palaeoclimatol. Palaeoecol. 142 (1998) 231–254.

[12] R.A. Thulborn, R.A, Morphology, preservation and palaeobiological significance of dinosaur coprolites, Palaeogeogr. Palaeoclimatol. Palaeoecol. 83 (1991) 341–366.
[13] H. Poinar, et al., Molecular coproscopy: dung and diet of the extinct ground sloth *Nothrotheriops shastensis*, Sci 281 (1998) 402–406, https://doi.org/10.1126/science.281.5375.402.
[14] F. Jouy-Avantin, A. Debenath, A.M. Moigne, H. Moné, H, A standardized method for the description and the study of coprolites, J. Archaeol. Sci. 30 (2003) 367–372, https://doi.org/10.1006/jasc.2002.0848.
[15] S. Hu, Q. Zhang, C. Zhou, Fossil coprolites from the middle triassic luoping biota and ecological implication, J. Earth Sci. 21 (2012) 191–193, https://doi.org/10.1007/s12583-010-0209-7.
[16] P. Dentzien-Dias, J.D. Carrillo-Briceño, H. Francischini, R. Sánchez, Paleoecological and taphonomical aspects of the late Miocene vertebrate coprolites (urumaco formation) of Venezuela, Palaeogeogr. Palaeoclimatol. Palaeoecol. 490 (2018) 590–603, https://doi.org/10.1016/j.palaeo.2017.11.048.
[17] M. Qvarnström, J.V. Wernström, R. Piechowski, M. Tałanda, P.E. Ahlberg, G. Niedwiedzki, Beetle-bearing coprolites possibly reveal the diet of a Late Triassic dinosauriform, R. Soc. Open Sci. 6 (2019) 181042, https://doi.org/10.1098/rsos.181042.
[18] M. Cueille, E. Green, C.J. Duffin, C. Hildebrandt, M.J. Benton, Fish and crab coprolites from the latest triassic of the UK: from Buckland to the mesozoic marine revolution, Proc. Geol. Assoc. (2020), https://doi.org/10.1016/j.pgeola.2020.07.011.
[19] P. Rummy, K. Halaçlar, H. Chen, The first record of exceptionally-preserved spiral coprolites from the Tsagan-Tsab formation (Lower Cretaceous), Tatal, western Mongolia, Sci. Rep. 11 (2021) 7891, https://doi.org/10.1038/s41598-021-87090-5.
[20] K. Halaçlar, P. Rummy, T. Deng, T.V. Do, Footprint on a coprolite: a rarity from the eocene of vietnam, Palaeoworld 31 (2022) 723–732, https://doi.org/10.1016/j.palwor.2022.01.010.
[21] K. Halaçlar, P. Rummy, J. Liu, A. Hunt, T.V. Do, N.T. Minh, T. Deng, Exceptionally well-preserved crocodilian coprolites from the late eocene of northern vietnam: ichnology and paleoecological significance, iSci (2023), https://doi.org/10.1016/j.isci.2023.107607.
[22] M. Barbacka, et al., Early Jurassic coprolites: insights into palaeobotany and the feeding behavior of dinosaurs, Pap. Palaeontol. (2022) e1425.
[23] M. Hofreiter, D. Sette, H.N. Poinar, M. Kuch, S. Paabo, Ancient DNA, Nat. Rev. Genet. 2 (2001) 353–359, https://doi.org/10.1038/35072071.
[24] T. Hollocher, K. Chin, K. Hollocher, M. KrugeM, Bacterial residues in coprolite of herbivorous dinosaurs: role of bacteria in mineralization of feces, Palaios 16 (2001) 547–565, https://doi.org/10.2307/3515628.
[25] N. Sharma, Fungi in dinosaurian (*Isisaurus*) coprolites from the Lameta Formation (Maastrichtian) and its reflection on food habit and environment, Micropaleontol. 51 (2005) 73–82.
[26] M.D. Pesquero, V. Souza-Egipsy, L. Alcalá, C. Ascaso, Y. Fernández-Jalvo, Calcium phosphate preservation of faecal bacterial negative moulds in hyaena coprolites, Acta Palaeontol. Pol. 59 (2014) 997–1005.
[27] M. Luo, et al., Fungal-induced fossil biomineralization, Curr. Biol. 33 (12) (2023) 2417–2424, https://doi.org/10.1016/j.cub.2023.04.067.
[28] W. Zhao, et al., Volatile organic compounds (VOCs) as rapid means for assessing the source of coprolites, iSci (2023), https://doi.org/10.1016/j.isci.2023.106806.
[29] P. Hunt, S.G. Lucas, Hyena hegemony: biogeography and taphonomy of Pleistocene vertebrate coprolites with description of a new mammoth coprolite ichnotaxon, Ichnos (2019), https://doi.org/10.1080/10420940.2019.1612393.
[30] M. Verde, M. Ubilla, Mammalian carnivore coprolites from the sopas formation (upper Pleistocene, lujanian stage), Uruguay, Ichnos 9 (2003) 77–80.
[31] L. Braillard, M. Guélat, P. Rentzel, Effects of bears on rockshelter sediments at tanay sur-les-creux, southwestern Switzerland, Geoarchaeol 19 (2004) 343–367.
[32] C. Diedrich, Extinctions of late ice age cave bears as a result of climate/habitat change and large carnivore lion/hyena/wolf predation stress in Europe, ISRN Zoology (2013), https://doi.org/10.1155/2013/138319.
[33] V.M. Bravo-Cuevas, N.M. Morales-Garcıa, C.R. Barron- Ortiz, J.M. Theodor, M.A. Cabral-Perdomo, Canid coprolites from the late Pleistocene of hidalgo, Central Mexico: importance for the carnivore record of North America, Ichnos 24 (2017) 239–249.
[34] X. Wang, S.C. White, M. Balisi, J. Biewer, J. Sankey, D. Garber, Z.J. Tseng, First bone-cracking dog coprolites provide new insight into bone consumption in *Borophagus* and their unique ecological niche, Elife 7 (2018) e34773, https://doi.org/10.7554/eLife.34773.
[35] A.P. Hunt, S.G. Lucas, Coprolites of *Borophagus* (Mammalia: Canidae) from western North America and the distribution of the coprolites of bone-cracking carnivores in the late Cenozoic, Bull. N. M.Mus. Nat. Hist. Sci. 82 (2021) 151–159.
[36] M. Gross, J. Prieto, F. Grímsson, H. Bojar, Hyena and 'false' sabre-toothed cat coprolites from the late Middle Miocene of south-eastern Austria, Hist. Biol. (2023), https://doi.org/10.1080/08912963.2023.2237979.
[37] Z.J. Tseng, Testing adaptive hypotheses of convergence with functional landscapes: a case study of bone-cracking hypercarnivores, PLoS One 8 (2013) e65305, https://doi.org/10.1371/journal.pone.0065305.
[38] B. Van Valkenburgh, K.P. Koepfli, Cranial and dental adaptations to predation in canids, in: N. Dunstone, M.L. Gorman (Eds.), Mammals as Predators, Oxford University Press, , Oxford, 1993, pp. 15–37.
[39] B. Van Valkenburgh, T. Sacco, X. Wang, Pack hunting in Miocene borophagine dogs: evidence from craniodental morphology and body size, in: L.J. Flynn (Ed.), Vertebrate Fossils and Their Context: Contributions in Honor of Richard H. Tedford. 279, Bull. Am. Mus. Nat. Hist., 2003, pp. 147–162, https://doi.org/10.1206/0003-0090.
[40] B. Van Valkenburgh, Carnivore dental adaptation and diet: a study of trophic diversity within guilds, in: J.L. Gittleman (Ed.), Carnivore Behaviour, Ecology and Evolution, Cornell University Press, Ithaca, 1989, pp. 410–436.
[41] J.A. Holliday, S.J. Steppan, Evolution of hypercarnivory: the effect of specialization on morphological and taxonomic diversity, Paleobiol 30 (2004) 108–128.
[42] D.W. Macdonald, Observations on the behaviour and ecology of the striped hyaena, *Hyaena hyaena*, in Israel, Isr, J. Zool. 27 (1978) 189–198.
[43] R.D. Estes, The Behavior Guide to African Mammals, Including Hoofed Mammals, Carnivores, Primates, University of California Press, Berkeley, 1991, p. 328.
[44] A. Hulsman, F. Dalerum, L. Swanepoel, A. Ganswindt, C. Sutherland, M. Paris, Patterns of scat deposition by brown hyaenas *Hyaena brunnea* in a mountain savannah region of South Africa, Wildl, Biol. 16 (2010) 445–451, https://doi.org/10.2981/09-110.
[45] N.R. Larkin, J. Alexander, M. Lewis, Using experimental studies of recent faecal material to examine hyaena coprolites from de West Runton Freshwater Bed, Norfolk, U.K, J. Archaeol. Sci. 27 (2000) 19–31, https://doi.org/10.1006/jasc.1999.0437.
[46] F.T. Kao, Notes on coprolites from the nihowan series, Vert, PalAs. 6 (1962) 390–403.
[47] N.Q. Du, Q.L. Yu, Zhoukoudian cave hyena coprolite's palynological analysis, Vert. PalAs. 18 (1980).
[48] R.R. Hao, J.Y. Xiao, Y.S. Fang, L.J. Liu, X.F. Tong, Pollen analysis of Hyaena coprolites from the Tuozi cave at tangshan, nanjing, Acta Palaeontol. Sin. 47 (2008) 123–128.
[49] Y.X. Zhang, L. Zheng, X.P. Ji, J.H. Zhang, Taphonomy of the hominoid fauna in the Yuanmou Basin yunnan, acta palaeontol, Sin. 76 (2002) 45–49.
[50] Q.G. Jiangzuo, Geographical and chronological distribution of Chinese Pleistocene large canids: current status and prospects (in Chinese), Chin. Sci. Bull. 66 (2021) 1, https://doi.org/10.1360/TB-2020-0690, 1.
[51] M.N. Bian, Geology of the Yuanmou Basin, yunnan, Bull. Geol. Surv. Can. 20 (1940) 23–32.
[52] E.H. Colbert, Pleistocene mammals from the Ma kai valley of northern yunnan, China, Am. Mus. Novit. 1099 (1940) 1–10.
[53] Z.Q. He, Yuanmou Hominoid Fauna, vol. 1, Yunnan Science Press), Kunming, 1997, p. 270 (in Chinese, with English summary).
[54] M.C. Chow, The discovery of *Enhydriodon* at Yuanmou and its application toward the correlation of Late Tertiary mammal bearing sediments in eastern Yunnan Province, Vert, PalAs. 5 (1961) 164–167 (in Chinese, with English abstract).
[55] Y. You, G. Qi, New Pleistocene mammalian fossils from Yuanmou, yunnan province, Vert, PalAs 11 (1973) 68–87 (in Chinese, with English abstract).
[56] Y. Tang, Y. You, H. Liu, Y. Pan, New materials of Pliocene mammals from Banguo basin of Yuanmou, Yunnan and their stratigraphical significance, Vert. PalAs. 12 (1974) 60–67 (in Chinese, with English abstract).
[57] Y. You, H. Liu, Y. Pan, Late Cenozoic Stratigraphy and Fossil Vertebrates from the Yuanmou and Banguo Basins, Beijing, Geological Publishing House, Yunnan, 1978, p. 69 (in Chinese, with English summary).

[58] J. Cheng, X.Q. Liu, J.W. Yue, H.Z. Wang, X.J. Zhang, A discussion on the "Yuanmou Formation" and "Yuanmou fauna" from the Yuanmou Basin of North yunnan, J. Stratigr. 26 (2002) 146–150 (in Chinese, with English abstract).
[59] P. Li, F. Chien, H.H. Ma, C.Y. Pu, L.S. Hsing, S.C. Chu, Preliminary study on the age of Yuanmou man by palaeomagnetic technique, Sci. Sin. 20 (1977) 645–664 (in Chinese, with English abstract).
[60] F. Qian, Q. Pu, D. Wang, The discovery of the teeth of Yuanmou Man, in: G. Zhou, X. Zhang (Eds.), Yuanmou People: A Collection of Pictures and Texts of Ancient Humans and Ancient Cultures in Yuanmou, Yunnan, Yunnan People's Publishing House, Kunming, 1984, pp. 3–7 (in Chinese, with English summary).
[61] C.K. Ho, A new Pliocene hominoid skull from Yuanmou southwest China, Hum. Evol. 5 (1990) 309–318.
[62] L. Luo, D.E. Granger, H. Tu, Z.P. Lai, G.J. Shen, C.J. Bae, X.P. Ji, J.H. Liu, The first radiometric age by isochron 26Al/10Be burial dating for the Early Pleistocene Yuanmou hominin site, southern China, Quat. Geochronol. 55 (2020) 101022.
[63] A. Farjand, L.Y. Fu, Q.G. Jiangzuo, et al., A new species of *Eirictis* (Mammalia, Carnivora, Mustelidae) from lower Pleistocene of Yuanmou Basin, yunnan, China, Palaeoworld (2023), https://doi.org/10.1016/j.palwor.2023.05.005.
[64] A.P. Hunt, S.G. Lucas, J.A. Spielmann, New coprolite ichnotaxa from the Buckland collection at the oxford university Museum of natural history, Bull. N. M. Mus. Nat. Hist. Sci. 57 (2012) 115–124.
[65] K. Halaçlar, Analysis of Middle Miocene Locality of Afyon-Gebeceler Coprolite Findings, Master Thesis, Ege University, 2015 (in Turkish with English abstract).
[66] C.G. Diedrich, Typology of ice age spotted hyena *Crocuta crocuta spelaea* (Goldfuss, 1823) coprolite aggregate pellets from the European Late Pleistocene and their significance at dens and scavenging sites, in: A.P. Hunt, J. Milan, S.G. Lucas, J.A. Spielmann (Eds.), Vertebrate Coprolites, Bull. N. M. Mus. Nat. Hist. Sci., vol. 57, 2012, pp. 369–377.
[67] A. Moreno-Rodriguez, N. Chimento, F. Agnolin, G. Jofré, A. Gentil, A possible *Smilodon* (Mammalia, Felidae) coprolite from the Pleistocene of Argentina, Palaios 37 (2022) 402–410, https://doi.org/10.2110/Palo.2021.056.
[68] T. Harrison, Coprolites: taphonomic and paleoecological implications, in: T. Harrison (Ed.), Paleontology and Geology of Laetoli: Human Evolution in Context, 1Geology, Geochronology, Paleoecology and Environment, Springer, Vertebrate paleobiology and paleoanthropology series, New York, 2011, pp. 279–292.
[69] A.P. Hunt, S.G. Lucas, The ichnology of vertebrate consumption: dentalites, gastroliths and bromalites, Bull. N. M.Mus. Nat. Hist. Sci. 87 (2021) 1–215.
[70] P.R. Wilby, D.M. Martill, Fossil fish stomachs: a microenvironment for exceptional preservation, Hist. Biol. 6 (1992) 25–36.
[71] A. Seilacher, C. Marshall, H.C.W. Skinner, T. Tsuihiji, A fresh look at sideritic "coprolites", Paleobiol 27 (2001) 7–13, https://doi.org/10.1666/0094-8373.
[72] I.D. Bull, J. Matthew, J. Lockheart, M.M. Elhmmali, D.J. Roberts, R.P. Evershed, The origin of faeces by means of biomarker detection, Environ. Int. 27 (2002) 647–654, https://doi.org/10.1016/s0160-4120(01)00124-6.
[73] K. Hollocher, T.C. Hollocher, Early process in the fossilization of terrestrial feces to coprolites, and microstructure preservation, in: Bull, N.M. Mus (Eds.), Vertebrate Coprolites, Hunt, Nat. Hist. Sci., vol. 57, 2012, pp. 79–92.
[74] M. Qvarnström, G. Niedzwiedzki, Ž. Žigaite, Vertebrate coprolites (fossil faeces): an underexplored Konservat-Lagerstätten, Earth Sci. Rev. 162 (2016) 44–57, https://doi.org/10.1016/j.earscirev.2016.08.014.
[75] C.M. Gordon, B.T. Roach, W.G. Parker, D.E. Briggs, Distinguishing regurgitalites and coprolites: a case study using a Triassic bromalite with soft tissue of the pseudosuchian archosaur *Revueltosaurus*, Palaios 35 (2020) 111–121.
[76] H. Kruuk, The Spotted Hyena a Study of Predation and Social Behaviour, in: Wildlife Behavior and Ecology Series, The University of Chicago Press, 1972, p. 335.
[77] K. Chin, D.A. Eberth, M.H. Schweitzer, T.A. Rando, W.J. Sloboda, J.R. Horner, Remarkable preservation of undigested muscle tissue within a Late Cretaceous tyrannosaurid coprolite from Alberta, Canada, Palaios 18 (2003) 286–294, https://doi.org/10.1669/0883-1351(2003)018%3c0286:RPOUMT%3e2.0.CO;2.
[78] K.T. Hollocher, T.C. Hollocher, J.K. Keith Rigby Jr., A phosphatic coprolite lacking diagenetic permineralization from the Upper Cretaceous Hell Creek Formation, Northeastern Montana: importance of dietary calcium phosphate in preservation, Palaios 25 (2010) 132–140, https://doi.org/10.2110/palo.2008.p08-132r.
[79] M.P. Espigares, et al., Sharing food with hyenas: a latrine of *Pachycrocruta brevirostris* in the early Pleistocene assemblage of fuente nueva-3 (orce, baza basin, SE Spain), Archaeol. Anthropol. Sci. 15 (81) (2023), https://doi.org/10.1007/s12520-023-01784-7.
[80] W. Buckland, Account of an assemblage of fossil teeth and bones of elephant, rhinoceros, hippopotamus, bear, tiger and hyaena, and sixteen other animals; discovered in a cave at Kirkdale, Yorkshire, in the year 1821; with a comparative view on five similar caverns in various parts of England, and others on the continent: philos, Trans. R. Soc. 112 (1822) 171–236.
[81] W. Buckland, Reliquiae Diluvianae; or, Observations on the Organic Remains Contained in Caves, Fissures, and Diluvial Gravel, and on Other Geological Phenomena, Attesting the Action of an Universal Deluge, John Murray, London, 1824, p. 303.
[82] L.H. Matthews, The bionomics of the spotted hyaena, *Crocuta crocuta* Erxl, Proc. Zool. Soc. Lond. Ser. A 109 (1939) 43–56, https://doi.org/10.1111/j.1096-3642.1939.tb00046.x.
[83] C.J. Duffin, Records of warfare...embalmed in the everlasting hills:" A history of early coprolite research, Mercian Geol 17 (2009) 101–111.
[84] A.P. Hunt, S.G. Lucas, Classification of vertebrate coprolites and related trace fossils, New Mex. Mus. Nat. Hist. Sci. Bull. 57 (2012) 137–146.
[85] M. Chame, Terrestrial mammal feces: a morphometric summary and description, Memórias do Inst. Oswaldo Cruz 98 (Suppl. 1) (2003) 71–94.
[86] K. Chin, Analyses of coprolites produced by carnivorous vertebrates, Paleontol. Soc. Pap. 8 (2002) 43–50, https://doi.org/10.1017/S1089332600001042.
[87] J. Halfpenny, E. Biesiot, A Field Guide to Mammal Tracking in North America, second ed., Johnson Publishing, New York, 1986, p. 161.
[88] L.E. Farrell, J. Roman, M.E. Sunquist, Dietary separation of sympatric carnivores identified by molecular analysis of scats, Mol. Ecol. 9 (2000) 1583–1590, https://doi.org/10.1046/j.1365-294x.2000.01037.x.
[89] V. Linseele, H. Reimer, J. Baeten, D. De Vos, E. Marinova, C. Ottoni, Species identification of archaeological dung remains: a critical review of potential methods, Environ. Archael. 18 (2013) 5–17, https://doi.org/10.1179/1461410313Z.00000000019.
[90] V. Taglioretti, N.H. Sardella, M.H. Fugassa, Morphometric analysis in modern faeces as a tool to identify artiodactyls' coprolites, Quat. Int. 352 (2014) 64–67, https://doi.org/10.1016/j.quaint.2013.12.055.
[91] L.M. Shillito, J.C. Blong, E.J. Green, E.N. van Asperen, The what, how and why of archaeological coprolite analysis, Earth Sci. Rev. 207 (2020) 103196, https://doi.org/10.1016/j.earscirev.2020.103196.
[92] C. Stuart, T. Stuart, A Field Guide to the Tracks and Signs of Southern and East African Wildlife, Southern Books Publishers, Cape Town, 1998, p. 310.
[93] J.S. Carrión, J.A. Riquelme, C. Navarro, M. Munuera, Pollen in hyena coprolites reflects late glacial landscape in southern Spain, Paleogeogr. Palaeoclimatol. Palaeoecol. 176 (2001) 193–205.
[94] J.S. Carrión, A taphonomic study of modern pollen assemblages from dung and surface sediments in arid environments of Spain, Rev. Palaeobot. Palynol. 120 (2002) 217–232, https://doi.org/10.1016/S0034-6667(02)00073-8.
[95] J.S. Carrión, et al., Quaternary pollen analysis in the Iberian Peninsula: the value of negative results, Internet Archaeol. 25 (2009) 1–53. http://intarch.ac.uk/journal/issue25/5/toc.html.
[96] A. Pineda, et al., Characterizing hyena coprolites from two latrines of the Iberian Peninsula during the Early Pleistocene: Gran Dolina (Sierra de Atapuerca, Burgos) and La Mina (Barranc de la Boella, Tarragona), Palaeogeogr. Palaeoclimatol. Palaeoecol. 480 (2017) 1–17, https://doi.org/10.1016/j.palaeo.2017.04.021, 2017.
[97] C.D. Buesching, N. Jordan, The social function of latrines: a hypothesis-driven research approach, in: C.D. Buesching (Ed.), Chemical Signals in Vertebrates, vol. 14, Springer, 2019, pp. 94–103, https://doi.org/10.1007/978-3-030-17616-7_8.
[98] S.K. Bearder, R.M. Randall, The use of fecal marking sites by spotted hyenas and civets, Carnivore 1 (1978) 32–48.
[99] M. Sanz, J. Daura, N. Éguez, J.P. Brugal, Not only hyenids: a multi-scale analysis of Upper Pleistocene carnivore coprolites in Cova del Coll Verdaguer (NE Iberian Peninsula), Palaeogeogr. Palaeoclimatol. Palaeocol. 443 (2016) 249–262, https://doi.org/10.1016/j.palaeo.2015.11.047.
[100] L. Tapinila, E.M. Roberts, M. Bouaré, F. Sissoko, M. O'Leary, Bivalve borings in phosphatic coprolites and bone, Cretaceous-Paleogene, Northeastern Mali, Palaios 19 (2004) 565–573.

[101] P. Dentzien-Dias, A.P. Hunt, S.G. Lucas, H. Francischini, M. Gulotta, Coprolites from shallow marine deposits of the nanjemoy formation, lower eocene of Virginia, USA, Lethaia 54 (2021) 26–39.
[102] A. Guatier, Animal life along the prehistoric nile: the evidence from saggai I and geili (Sudan), Origini 12 (1983) 50–115.
[103] L.K. Horwitz, P. Goldberg, A study of Pleistocene and Holocene hyaena coprolites, J. Archaeol. Sci. 16 (1989) 71–94.
[104] P. Palmqvist, B. Martínez-Navarro, J.A. Pérez-Claros, T. Torregrosa, B. Figueirido, J.M. Jiménez-Arenas, M.P. Espigares, S. Ros-Montoya, M. De Renzi, The giant hyena *Pachycrocuta brevirostris*: modelling the bone-cracking behavior of an extinct carnivore, Quat. Int. 243 (2011) 61–79, https://doi.org/10.1016/j.quaint.2010.12.035.
[105] K. Murray, Scatalog: quick ID guide to southern african animal droppings, Struik Nature, Cape Town, 2011.
[106] A. Sanchis, C. Real, V. Sauqué, C. Núnez-Lahuerta, N. Éguez, C. Tormo, M. Pérez Ripoll, Y. Carrión Marco, E. Duarte, M. Rasilla, Neanderthal and carnivore activities at llonin cave, asturias, northern iberian peninsula: faunal study of mousterian levels (MIS 3), C. R. Palevol. 18 (2019) 113–141, https://doi.org/10.1016/j.crpv.2018.06.001.
[107] A. Bellusci, J. Fernández Fernando, M.O. Beltrame, Carnivore coprolites from "Gruta del Indio" site as source of paleoparasitological and paleoecological evidences (late Pleistocene-Holocene, Mendoza, Argentina), Archaeol. Anthrop. Sci. 13 (29) (2021), https://doi.org/10.1007/s12520-021-01272-w.
[108] P. Andrews, E.M. Nesbit Evans, Small mammal bone accumulations produced by mammalian carnivores, Paleobiol 9 (1983) 289–307, https://doi.org/10.1017/S0094837300007703.
[109] D.L. Lofgren, C.Y. Shen, N.N. Buday, C.A.C. Ylagan, K.K. Lofgren, R. Lai, D.D. Santana-Grace, A.R. Tabrum, Coprolites and mammalian carnivores from Pipestone Springs, Montana, and their paleoecological significance, Ann. Carnegie Mus. 84 (2017) 265–285, https://doi.org/10.2992/007.084.0402.
[110] J. Zhang, Z. Yang, D. Wang, X. Zhang, Climate change and causes in the Yuanmou dry-hot valley of Yunnan, China, J. Arid Environ. (2022) 153–162.
[111] X. Li, D. Walker, The plant geography of yunnan province, southwest China, J. Biogeogr. 13 (1986) 367–397.
[112] L. Tao, L. Jianping, Z. Zhiwei, Z. Arbuscular mycorrhizas in a valley-type savanna in southwest China, Mycorrhiza 14 (2004) 323–327.
[113] Z. Wu, Y. Zhu, Vegitation of Yunnan, Science Press, Beijing, 1987.
[114] Y.F. Yao, A.A. Bruch, Y.M. Cheng, V. Mosbrugger, Y.F. Wang, C.S. Li, Monsoon versus uplift in southwestern China–late Pliocene climate in Yuanmou Basin, yunnan, PLoS One 7 (5) (2012) e37760.
[115] X. Ji, Yuanmou, in: C. Smith (Ed.), Encyclopedia of Global Archaeology, Springer New York, New York, 2004, pp. 7950–7952.
[116] Z. Jin, X. Ou, Y. Zhou, The general situation of natural vegetation in dry-hot river valley of Yuanmou, Yunnan Province, Chin, J. Plant Ecol. 11 (1987) 308.
[117] L. Zhou, Vegetation evolution in Yuanmou dry-hot valley since Quaternary period, Mt. Res. 14 (1996) 239–243.
[118] F. Wu, S. Gao, F. Tang, Q. Meng, C. An, A late Miocene-early Pleistocene palynological record and its climatic and tectonic implications for the Yunnan Plateau, China, Palaeogeogr. Palaeoclimatol. Palaeoecol. 530 (2019) 190–199.
[119] J. Yang, et al., Review of research on the vegetation and environment of dry-hot valleys in Yunnan, Biodivers, Sci. 24 (2016) 462, 447.
[120] J.D. Vitale, N.R. Jordan, G.D. Gilfillan, J.W. McNutt, T. Reader, Spatial and seasonal patterns of communal latrine use by spotted hyenas (*Crocuta crocuta*) reflect a seasonal resource defense strategy, Behav. Ecol. Sociobiol. 74 (2020) 120, https://doi.org/10.1007/s00265-020-02895-0.
[121] M. Raymo, K. Ganley, S. Carter, D.W. Oppo, J. McManus, Millennial-scale climate instability during the early Pleistocene epoch, Nat 392 (1998) 699–702.
[122] L. Lisiecki, M. Raymo, Plio-Pleistocene climate evolution: trends and transitions in glacial cycle dynamics, Quat. Sci. Rev. 26 (2007) 56–69.
[123] X. Wang, H. Wei, M. Taheri, F. Khormali, G. Danukalova, F.H. Chen, Early Pleistocene climate in western arid central Asia inferred from loess-palaeosol sequences, Sci. Rep. 6 (2016) 20560, https://doi.org/10.1038/srep20560.
[124] F. Qian, Quaternary geology and paleoanthropology of Yuanmou yunnan, China, in: Y. Pan, G. Zong (Eds.), Quaternary Geology and Paleoanthropology of YuanmouYunnan, China, Science Press, Beijing, 1991, pp. 191–215 (in Chinese, with English summary).
[125] A.P. Hunt, S.G. Lucas, Descriptive terminology of coprolites and Recent feces, Bull. N. M.Mus. Nat. Hist. Sci. 57 (2012) 153–160.
[126] J. Milàn, Crocodylian scatology - a look into morphology, internal architecture, inter- and intraspecific variation and prey remains in extant crocodylian feces, Bull. N. M.Mus. Nat. Hist. Sci. 57 (2012) 65–71.
[127] Munsell Color (Firm, Geological Rock-Color Chart: with Genuine Munsell Color Chips, Munsell Color, Grand Rapids, MI, 2011.
[128] B. Liu, Z. Wei, C. Wei, et al., An industrial computed laminography imaging system, in: Digital Industrial Radiology and Computed Tomography DIR, 2015.
[129] R. Clark, Point count estimation of charcoal in pollen preparations and thin sections of sediments, Pollen Spores 24 (1982) 523–535.
[130] X. Li, X. Shang, X. Zhou, H. Zhang, Integrative method of sieving and heavy liquid in pollen analysis of loess, Arid, Land Geography 295 (2006) 663–666.
[131] P. Moore, J. Webb, M. Collison, Pollen Analysis, Blackwell Scientific Publications, 1991.
[132] Ø. Hammer, D. Harper, Pryan, PAST: paleontological statistics software package for education and data analysis, Palaeontol. Electron. 4 (2001) 1–9.