SPANISH JOURNAL OF PALAEONTOLOGY

Spanish Journal of Palaeontology 40 (2), 2025
https://doi.org/10.7203/sjp.29840
Sociedad Española de Paleontología ISSN 2255-0550 / eISSN 2660-9568

OPEN ACCESS RESEARCH PAPER

Taphonomy of small mammals and palaeoenvironment of the QS-2/3 unit from the Quibas site (Early Pleistocene, southern Iberian Peninsula)

Tafonomía de los pequeños mamíferos y paleoambiente de la unidad QS-2/3 del yacimiento de Quibas (Pleistoceno Inferior, sur de la península ibérica)

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Abstract: The site of Quibas (Early Pleistocene, Murcia, Spain) represents the only European continuous succession preserving a record of continental vertebrates from pre-Jaramillo to post-Jaramillo age. The Quibas sequence immediately postdates the oldest known hominin records in the Early Pleistocene of Europe, represented at Barranco León and Fuente Nueva 3 (southern Spain), and Sima del Elefante (northern Spain). This study presents new evidence on the taphonomic processes that facilitated the accumulation of small vertebrates at the unit QS-2/3 of the Quibas-Sima section. We analysed alterations caused by predators (digestion and chewing), root marks, mineral precipitation, bone breakage, abrasion, corrosion, and the count of long bones. The results indicate that the accumulation of small mammals occurred *in situ*, primarily due to the activity of nocturnal birds of prey such as *Strix aluco*. The hydrodynamic influence is minimal. The palaeoecological analysis supports the development of a forest-mosaic environment with a significant presence of open spaces in the surroundings of the Quibas site at the onset of the Jaramillo subchron.

Resumen: El yacimiento de Quibas (Pleistoceno Inferior, Murcia, España) representa la única secuencia en Europa de edad pre-Jaramillo a Jaramillo con registro de vertebrados continentales. La secuencia de Quibas es ligeramente posterior al registro más antiguo de homininos del Pleistoceno Inferior de Europa, representado en los yacimientos de Barranco León y Fuente Nueva 3 (sur de España) y Sima del Elefante (norte de España). Este estudio presenta nuevas evidencias sobre los procesos tafonómicos que posibilitaron la acumulación de pequeños vertebrados en el nivel QS-2/3 de la sección de Quibas-Sima. Se han analizado las alteraciones producidas por depredadores (digestión y masticación), marcas de raíces, precipitación de minerales, fracturación ósea, abrasión, corrosión y recuento de huesos largos. Los resultados indican que la acumulación de pequeños mamíferos se produjo *in situ*, debido principalmente a la actividad de aves rapaces nocturnas como *Strix aluco*. La influencia hidrodinámica es mínima. El análisis paleoecológico sugiere el desarrollo de un entorno forestal en mosaico con una presencia significativa de espacios abiertos en los alrededores del yacimiento de Quibas al inicio del subcrón Jaramillo.

Received: 10 December 2024
Accepted: 15 May 2025
Published: 28 August 2025

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Keywords:
Jaramillo subchron
Small mammal accumulation
Birds of prey
Hydrodynamics
Bone alteration

Palabras-clave:
Subcrón Jaramillo
Acumulación de pequeños vertebrados
Aves de presa
Hidrodinámica
Alteración de huesos

INTRODUCTION

The Quibas karstic complex (southern Iberian Peninsula) is a significant palaeontological locality from the late Early Pleistocene, notable for its chronology, record of climate changes, and extensive vertebrate fossil record. The age of the site has been estimated to range between 1.1 and 0.9 Ma, encompassing a continuous sequence of terrestrial vertebrates from the pre-Jaramillo to Jaramillo subchron, a unique record in Europe (Piñero *et al.*, 2020, 2022). Quibas slightly postdates the earliest hominin presence in the Early Pleistocene of Europe, as documented at Barranco León and Fuente Nueva 3 (both in the Guadix-Baza Basin, southern Spain) (Toro-Moyano *et al.*, 2013), as well as at Sima del Elefante within the Atapuerca karstic complex (northern Spain) (Carbonell *et al.*, 2008). Additionally, sedimentological analyses at the site revealed a record of several alternating humid and arid phases resulting from the Early Pleistocene glacial-interglacial cycles. Thus, the different units of Quibas were correlated with the marine isotopic stages MIS-33 to MIS-27 (Laborda-López *et al.*, 2024).

The Quibas site was discovered in 1994 by excursionists and was first systematically excavated between 2000 and 2009. Following a period of inactivity, excavations resumed in 2014 and have continued to the present day. The first publication on this locality by Montoya *et al.* (1999) presented an extensive faunal list. Subsequent studies provided further insight, expanding the faunal list to include up to 80 species of vertebrates and invertebrates, encompassing large and small mammals, reptiles, amphibians, birds, and terrestrial molluscs and arthropods (see Montoya *et al.*, 1999, 2001; Carlos-Calero *et al.*, 2006; Made *et al.*, 2008; Alba *et al.*, 2011; Blain *et al.*, 2014; Sevilla *et al.*, 2014, 2024; Pérez-García *et al.*, 2015; Piñero & Alberdi, 2015; Piñero *et al.*, 2015, 2020, 2022; Blain & Bailon, 2019; Agustí *et al.*, 2022; Rosas *et al.*, 2022, 2023; among others). Nevertheless, several aspects of this palaeontological site remain to be elucidated.

The Quibas karstic complex consists of two main structures, Quibas-Cueva (**QC**) and Quibas-Sima (**QS**), along with a small cavity known as Quibas-Gruta-1 (**QG**). Quibas-Cueva and Quibas-Sima are connected internally (Laborda-López *et al.*, 2024). Preliminary taphonomic analyses of small mammals from Quibas-Gruta 1 were conducted in previous studies by Cuadros (2010) and Piñero *et al.* (2016). These studies suggested that the accumulation of skeletal remains in Quibas-Gruta 1 likely resulted from pellets deposited by nocturnal birds of prey. The taphonomy of the large-sized vertebrates from Quibas is currently under investigation.

To date, no taphonomic studies have been conducted on Quibas-Sima, a section that records significant environmental changes across its various detrital units (QS-1 to QS-7), including the transition from the interglacial MIS-31 to the glacial MIS-30 (Del Castillo *et al.*, 2023; Laborda-López *et al.*, 2024). A comprehensive study of the origin of the small vertebrate accumulation is essential to minimise biases in subsequent palaeoecological interpretations of the site.

Small mammal taphonomy is a relatively recent discipline, developed and published by Andrews (1990). This author analysed the various modifications inflicted by different present-day predators on their small mammal prey, focusing on the relative abundance of skeletal elements, patterns of breakage, and degrees of digestion. These taphonomic aspects not only provide valuable information for identifying the predator responsible for the accumulation in fossil assemblages, but also offer insights into the post-depositional processes that affected them. In Spain, its application has traditionally been limited in most small mammal taxonomic and palaeoecological studies to the identification of digestion patterns (*e.g.*, Álvarez-Vena *et al.*, 2023; Bañuls-Cardona *et al.*, 2017; Cuenca-Bescós *et al.*, 2008; Domínguez-García *et al.*, 2023; Rofes *et al.*, 2014). One of the first studies dedicated exclusively to the taphonomic analysis of small mammal assemblages was conducted by Fernández-Jalvo and Andrews (1992), who also refined the methodology proposed earlier by Andrews (1990).

Since then, although interest in small mammal taphonomy has grown, the number of studies explicitly addressing the processes involved in the accumulation of small mammal assemblages remains limited (see Domínguez-García, 2021; Fernández-García *et al.*, 2018; García-Morato *et al.*, 2019, 2023; Guillem-Calatayud, 2006, 2010, 2011; Marín-Monfort *et al.*, 2021). This is despite the critical role of such analyses in identifying potential prey-predator biases and post-depositional modifications that can significantly influence paleoenvironmental interpretations (García-Morato *et al.*, 2023; Marín-Monfort *et al.*, 2021).

In this context, the present study undertakes the first detailed taphonomic analysis of the small mammal assemblage from the unit QS-2/3 of Quibas-Sima, a stratigraphic level correlated with the Jaramillo subchron and glacial MIS-30. By examining skeletal preservation, fragmentation, and digestion patterns, we aim to reconstruct the taphonomic history of the assemblage, identify the primary accumulating agents, and assess the modifications introduced by predation and post-depositional processes. Establishing this taphonomic framework will not only refine the palaeoecological interpretations of the Quibas site but will also contribute to a broader understanding of the environmental dynamics that shaped the southern Iberian Peninsula during the late Early Pleistocene.

GEOGRAPHICAL AND GEOLOGICAL SETTING

The Quibas palaeontological site is located at the southeastern slope of Sierra de Quibas (Abanilla, Murcia, southern Spain) (Fig. 1A), in an abandoned quarry of false agate (Fig. 1B), at an altitude of 669 m masl. Quibas is situated within the Betic Cordillera System, a geological structure extending from the Gibraltar Strait to the Nao Cape (Alicante), with a WSW-ENE orientation. This mountain range comprises two main structural zones: the External Zones to the north and the Internal Zones at the south. The Sierra the Quibas (Fig. 1A) is part of the Middle Subbetic domain within the External Zones, characterised predominantly by Lower Jurassic limestone and dolomite formations (Rodríguez Estrella *et al.*, 2004). These elevations are interspersed with depressions subsequently infilled by Mesozoic and Cenozoic sedimentary deposits, consisting of Prebetic autochthonous and parautochthonous materials (Rodríguez Estrella, 1979). The Sierra de Quibas, with a maximum height of 968 m masl, is affected by compressive faults. However, during the Late Miocene, a phase of extensional tectonics led to the formation of cavities filled with false agate. Today, the region exhibits a Plio-Pleistocene karstic system, comprising both endo-karstic and exo-karstic structures, which facilitated the development of caves, galleries, and various formations within the deposit. The quarry was exploited in the 1970s in

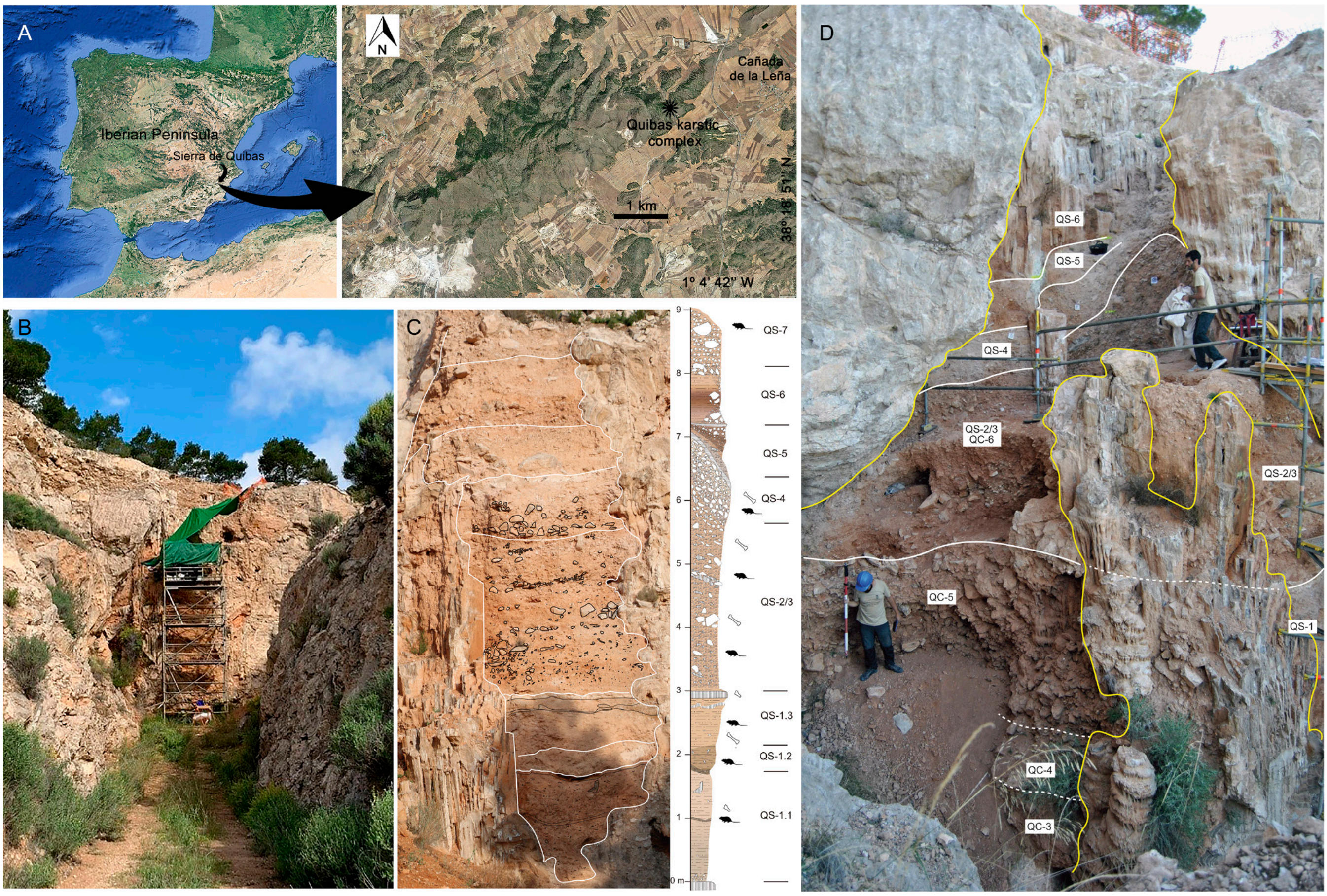

Figure 1. Geographic and geological context of the Quibas site. **A,** Geographic location of the Quibas karstic complex (source Google Earth Pro); **B,** field image of the Quibas site during the 2022 excavation campaign; **C,** stratigraphic profile of Quibas-Sima in 2014. The complete bone and the fractured bone indicate the presence of large vertebrates, while the rodent symbol indicates the presence of small vertebrates; **D,** stratigraphic correlation between the Quibas-Cueva and Quibas-Sima units.

search of false agate, but it was quickly abandoned, leaving exposed fossiliferous outcrop rich in vertebrate remains.

Within the Quibas karstic complex, Quibas-Cueva is a gallery reaching a height of 8 m, a width of 5 m, and an undetermined depth. Geophysical prospections suggested a minimum depth of 30 m. In contrast, Quibas-Sima is a pit with a depth of 9 m and a width of 2 m (Laborda-López *et al.*, 2024).

The pavement and walls of Quibas-Sima are covered by speleothems, indicating that stagnant water remained in the sealed cave for an extended period. The sedimentary column is divided into six distinct units (namely QS-1, QS-2/3, QS-4, QS-5, QS-6 and QS-7) (Fig. 1C) (Laborda-López *et al.*, 2024). Based on magnetobiostratigraphic correlations, the age of QS-1 is between 1.1 and 1.07 Ma, while QS-2/3 to QS-5 date from 1.07 to 0.99 Ma (Jaramillo subchron). The age of QS-6 and QS-7 ranges from 0.99 to 0.9 Ma (Piñero *et al.*, 2020, 2022).

The taphonomic and palaeoecological study conducted in this work is focused on the QS-2/3 unit, which consists of microbreccia gravels and breccias with normal and inverse grading with a polymodal brown to reddish light-yellow muddy sand matrix that hosts some large boulders (Laborda-López *et al.*, 2024). This unit is rich in both small and large vertebrate remains (Piñero *et al.*, 2020, 2022). When the QS-2/3 unit was deposited, the cave had ceased to form new speleothems. Instead, the sedimentation was primarily the result of the influx of allochthonous material through the cave entrance at the top of the cavity, which still retained some degree of humidity, although not as much as would be expected in a fully active cave system (Laborda-López *et al.*, 2024).

MATERIAL AND METHODS

The fossil material studied in this work was obtained by processing 40 kg of sediment excavated during the 2021 field season. Sediment was sourced equally from two contiguous excavation squares located toward the center of the detrital unit, O-23 and P-23, each contributing 20 kg. It was initially screened in the field using a 6 mm mesh sieve, retaining the fraction smaller than 6 mm, followed by a washing process with a 0.5 mm mesh sieve. The remaining sediment was then spread out on plastic sheeting and left to air dry. Sediment larger than 0.5 mm was bagged according to its reference and stored at the Departament de

Botànica i Geologia, Universitat de València (Valencia, Spain).

The sediment was further screened to separate the coarse fraction (> 2 mm) from the fine fraction (< 2 mm). The recovered remains were then sorted into taxonomic groups (mammals, herpetofauna, and birds), with a distinction made between cranial and postcranial elements. Micrographs of some specimens were taken with Environmental Scanning Electron Microscopy (**ESEM**) at the Servei de Recursos Científics i Tècnics de la Universitat Rovira i Virgili (Tarragona), whereas other images were taken with the Digital Microscope AM4115TL Dino-Lite Edge. The fossils are currently housed at the Departament de Botànica i Geologia, Universitat de València (Valencia, Spain), and the final deposit will be at the Museo Arqueológico de Murcia (**MAM**; Murcia, Spain).

The studied collection consists of 647 small mammal remains (excluding chiropterans and lagomorphs), including 259 isolated teeth (incisors included), 54 teeth inserted in mandibles and maxillae, 39 mandibles, 25 maxillae, and 270 disarticulated postcranial bones (Tab. 1). The remains of lagomorphs and chiropterans (two molars and a single isolated canine) have been excluded from this analysis because the taphonomic study of these groups follows a methodology different from that used for rodents and insectivores. The nomenclature used for the taxonomic identification of the dental remains of arvicolines follows Meulen (1973), for murids Van de Weerd (1976), for glirids Daams (1981), and for soricids Reumer (1984). With the corresponding taxonomical identification, the Minimum Number of Individuals (**MNI**) was determined. The MNI was calculated according to the most repeated identifiable dental element, considering laterality.

To reconstruct the ecological conditions that prevailed in the Quibas area during the deposition of the QS-2/3 unit, we applied the Habitat Weightings method on small mammals (Evans *et al.*, 1981; Andrews, 2006). This method is based on the distribution of each small mammal taxon in the habitats where they are found today (for extant species) or where they are assumed to have lived in the past (for extinct species). Habitats are classified into five categories: open dry meadows, open humid meadows, rocky areas, woodland and woodland-margin areas, and areas surrounding water (Cuenca-Bescós *et al.*, 2005, 2009; Blain *et al.*, 2008; López-García *et al.*, 2010, 2014; Piñero *et al.*, 2016, 2024). Each taxon was assigned a maximum score of 1.00, which was proportionally distributed according to its habitat preferences if the species occupied more than one habitat type. The application of the Habitat Weightings method required calculating the proportions of each taxon in the assemblage using the minimum number of individuals (MNI).

The taphonomic analysis of this material follows the methodologies outlined by Andrews (1990), Fernández-Jalvo and Andrews (1992), Fernández-Jalvo and Andrews (2016), and Fernández-Jalvo *et al.* (2016). This approach enables both the description and quantification of the alterations affecting the fossil remains, and in some cases, facilitates the identification of a potential predator. The following steps were undertaken to conduct the taphonomic analysis:

Table 1. Number of identified molars and premolars (**NISP**) and minimum number of individuals (**MNI**) for small mammal species recovered from QS-2/3.

Species	NISP	MNI	MNI%
Manchenomys orcensis	11	3	6.6%
Apodemus sylvaticus	53	16	35.5%
Castillomys rivas	30	11	24.4%
Eliomys quercinus	23	5	11.1%
Crocidura kornfeldi	65	10	22.2%
Total	182	45	100%

(1) Calculation of taphonomic indices for cranial and postcranial proportions. The indices for cranial and postcranial elements were applied following Andrews (1990). This includes:

- Postcranial-to-cranial ratio (**Pc/C**). Calculate the ratio of postcranial (**Pc**) to cranial (**C**) elements, using a correction factor where Pc values are multiplied by 8 an C values by 5.
- Femora and humeri index (**F + H/Mx + Md**). Assess the percentage of femora and humeri (**F + H**) in comparison with the Minimum Number of Elements (MNE) of mandibles and maxillae (**Mx + Md**).
- Tibiae and radii vs. femora and humeri ratio (**T + R/F + H**). Calculate the proportion of tibiae and radii (**T + R**) relative to femora and humeri (**F + H**).

(2) Calculation of the proportion of isolated teeth and tooth loss. Isolated teeth index compares the number of molars and incisors isolated in the sample with the number of total empty alveoli. Tooth loss compares the number of total empty alveoli with the number of total alveoli calculated for the sample analysed.

(3) Breakage patterns were identified for cranial and post-cranial remains following the scheme proposed by Andrews (1990):

- Maxillae: complete, preserving the zygomatic arch and without the zygomatic arch.
- Mandibles: complete, with ascending ramus broken, and without ascending ramus plus inferior border broken.
- Post-cranial elements: complete, proximal fragments, distal fragments, and shafts.

(4) Digestion evidences and predator marks. Damage caused by digestion follows the methodology outlined by Andrews (1990), Fernández-Jalvo and Andrews (1992), and Fernández-Jalvo *et al.* (2016) for murids, soricids, and arvicolids. For glirids, we followed the descriptions provided by Marín-Monfort *et al.* (2019). Bite marks were also recorded when present, and classified as punctures, pits, and perforations, following Fernández-Jalvo and Andrews (2016) descriptions.

(5) Post-depositional alterations in cranial and post-cranial elements. Post-depositional alterations refer

to processes that affect the remains after deposition and provide insights into the taphonomic history of the assemblage. These alterations include mineralization, the effects of plant roots, contact with water, abrasion, sediment compression, trampling, staining, corrosion, and other diagenetic changes. Identifying these factors is essential for reconstructing the sequence of events that affected the post-deposition of remains. The methodologies and criteria for recognizing these alterations are detailed in Andrews (1990), Fernández-Jalvo and Andrews (2016), Marín-Monfort (2018), and García-Morato *et al.* (2019).

RESULTS

Palaeobiodiversity

The small mammal assemblage from QS-2/3, according to cranial remains, comprises the arvicoline *Manchenomys orcensis*, the murids *Apodemus sylvaticus* and *Castillomys rivas*, the glirid *Eliomys quercinus*, and the soricid *Crocidura kornfeldi*. *Apodemus sylvaticus* and *Castillomys rivas* are the most abundant species in terms of MNI, together accounting for 59.9% of the sample (Tab. 1). *Crocidura kornfeldi* ranks second in terms of number of identified molars and premolars (NISP) but third in MNI, representing 22.2% of the total sample. *Eliomys quercinus* and *Manchenomys orcensis* are the least represented taxa, with 11.1% and 6.6% of the total assemblage, respectively.

Conservation of anatomical elements

The studied sample exhibits bilaterally, with approximately the same number of right and left postcranial elements. The sample includes 33 left and 29 right humeri, 22 left and 19 right ulnae, and 18 left and 15 right femora, suggesting that the postcranial elements retain a nearly natural proportion.

PC/C value is 130.8%, indicating that in this sample there is a significant loss of isolated molars and poor preservation of maxillaries and mandibles compared to the postcranial elements (Tab. 2) (Andrews, 1990).

The T+R/F+H ratio, with an index of 98.5%, suggests that the sample preserves a near-natural proportion between forelimbs and hindlimbs (Tab. 2).

Table 2. Conservation ratio of the anatomical elements, indicating ratio of postcranial *vs.* cranial elements, forelimbs *vs.* hindlimbs, and humeri plus femora *vs.* maxillaries plus mandibles.

Index	Percentage
Postcranial / cranial	130.8%
Tibiae + radii / femora + humeri	98.5%
Humeri + femora / maxillaries + mandibles	77.9%

The F+H/Mx+Md value is 77.9%, indicating that the postcranial elements are more abundant than the cranial ones (Tab. 2) and supports the previous value obtained by the PC/C index. It should be noted that the cranial elements are less resistant than the humeri and femora, which could reflect a subsequent loss or breakage after deposition.

Breakage of the remains

The results exhibit a high fracturing degree in the postcranial elements (Fig. 2). However, most of the fractured elements correspond to bones where only one of the epiphyses has been lost.

Cranial breakage is 98.4%, with no complete skulls and only 32% of the fragments preserving part of the zygomatic process. Regarding mandibles, 97.4% are broken. Most of them show the lower border broken (64.1%), with only one complete mandible (belonging to a glirid) preserved (Fig. 2).

The indices for the isolated molar and incisor are 81% and 156%, respectively (Fig. 2), indicating a higher number of molars compared to the corresponding mandibles and maxillae in the sample, which supports the postcranial/cranial index value.

The breakage degree in the molars and incisors is low. For *in situ* molars (*i.e.*, those inserted in their respective mandibles and maxillae), the breakage rate is slightly lower than that of isolated molars. In contrast, the breakage rate for *in situ* incisors is 20%, whereas 48.5% of isolated incisors show breakage. 59% of the mandibles and 100% of maxillae have lost their incisor.

Predator marks

Digestive marks have been identified on teeth (Tab. 3) and postcranial material (Tab. 4). These marks range from light to heavy degrees with one exception of extreme degree in one incisor.

Table 3. Percentage of digestion marks in teeth from QS-2/3, distinguishing among different degrees of digestion. **N**, number of specimens.

Degree of digestion	Muridae		Gliridae		Arvicolinae		Soricidae		Total		Incisors	
	N	%	N	%	N	%	N	%	N	%	N	%
Extreme	0	0	0	0	0	0	0	0	0	0	1	0.9
Heavy	7	6.7	2	8.7	0	0	2	3.1	11	8.7	2	1.8
Moderate	7	6.7	1	4.3	0	0	19	29.2	27	4.3	5	4.5
Light	16	15.4	4	17.4	1	9.1	0	0	21	10.3	15	13.6
Absent	74	71	16	69.6	10	90.9	44	67.7	144	70.9	87	79.1

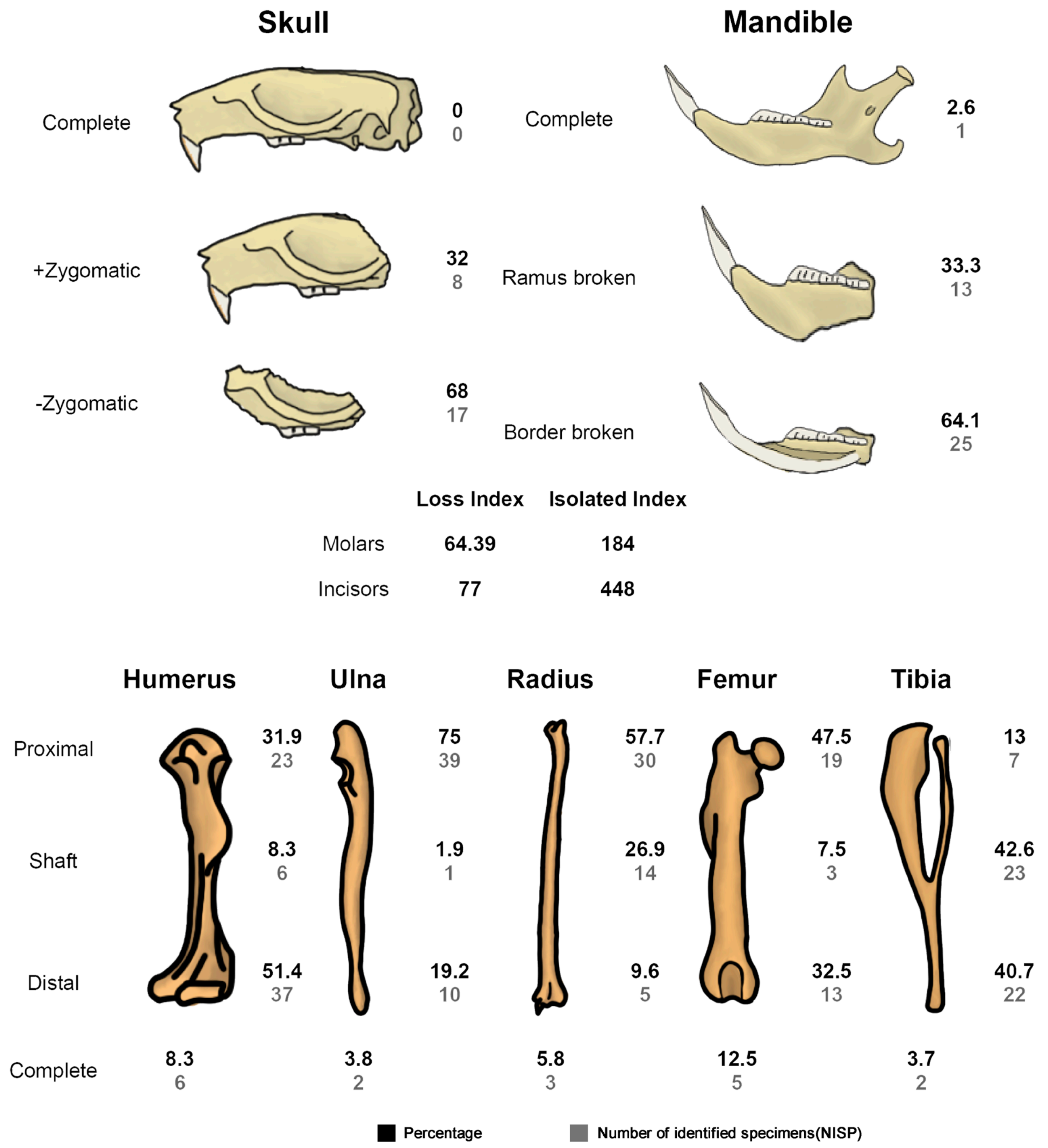

Figure 2. Breakage degree in the long bones and cranial elements from QS-2/3. Percentages are represented in black and the number of identified specimens (NISP) in grey.

In the molars, digestion was observed in 29.1% of the specimens. Of these, 10.3% showed a light degree of digestion, 13.3% a moderate degree, and 5.4% and 0% showed heavy and extreme degrees, respectively. The traces of digestion in each of the evaluated groups were as follows. In murids, light digestion marks are present in 15.4% of molars (16 specimens), in glirids in 17.4% (four specimens), in arvicolids in 9.1% (one specimen), and in soricids it is not possible to identify teeth with light digestion degree. Thus, murids and glirids were the most affected groups by this alteration among small mammals. Moderate degree digestion marks are present in 13.3% of the molar sample (27 molars). In murids, this alteration is present in 6.7% of the molars (seven specimens), in glirids in 4.3% (one specimen), in arvicolines there is no evidence of moderate digestion, and in soricids they are present in 29.2% (19 specimens). In this case, soricids are the most affected group by this alteration. Heavy digestion degree accounts for 5.4% of the molar sample: 6.7% in murids (seven specimens), 8.7% in glirids (two specimens), no evidence of heavy digestion in arvicolines, and 3.1% in soricids (two specimens). In incisors only 20.9% (23 specimens) present digestive marks, with 13.6% (15 specimens) showing light digestion degree, 4.5% (five specimens) showing moderate digestion degree, 1.8%

(two specimens) showing heavy digestion, and 0.9% (one specimen) showing extreme digestion degree (Tab. 3).

In the postcranial material (femora and humeri), 37.1% (33 remains) show signs of digestion, with 24.7% exhibiting light digestion (22 remains), 10.1% moderate digestion (9 remains), and 2.2% (2 remains) displaying heavy digestion (Tab. 4).

Another predator mark was identified, consisting of a small chew mark on a shrew mandible (Fig. 3A).

Post-depositional alterations

It is possible to observe different types of post-depositional alterations in molars and incisors, caused by chemicals and/or physical processes. Root marks affect 46.3% of the teeth sample (Tab. 5). Manganese mineralization is observed inside the fractures and the root marks in 72.7% of the teeth sample, indicating the presence of water (Tab. 5). The corrosion process affected 39.4% of the teeth sample, which is indicative of the presence of humic acids (Tab. 5). Abrasion was observed in two specimens (Fig. 3B, 3C).

Predator classification

When combining the data from this study with that compiled by Andrews (1990) to determine the predator category (see Tab. 6), based on the various taphonomic variables analysed, we find that the most frequent predator categories involved in the accumulation of the studied assemblage are categories 2 and 3. To a lesser extent, our results suggest influence of predators of category 1. Categories 4 and 5 are the least represented.

The percentage of digested molars suggests the influence of predators from categories 3 and 4. However, this value is much closer to a category 3 predator than to a category 4 predator. In contrast, the percentage of complete long bones and complete skulls aligns with a category 5 predator. Nonetheless, post-depositional processes may have influenced these values, increasing the fracture of bones and skulls. This is consistent with the result of the taphonomic variable of digestion in these same postcranial remains (Tab. 6), whose value points towards category 2 predators.

Table 4. Number of digested postcranial remains of small mammals from QS-2/3, categorised by light, moderate, and heavy degree of digestion. **N,** number of specimens.

	N	% total digested	Degree of digestion		
			light	moderate	heavy
Humerus	61	32.1	17	6	1
Femur	28	39.3	5	3	1
Total	89	37.1	22	9	2

Table 5. Post-depositional alterations in teeth, indicating number (**N**) and percentage (%) of specimens affected by root marks, manganese mineralization, and corrosion.

Post-depositional alterations in teeth	N	%
Root marks	158	46.3
Manganese mineralization	247	72.7
Corrosion	135	39.4

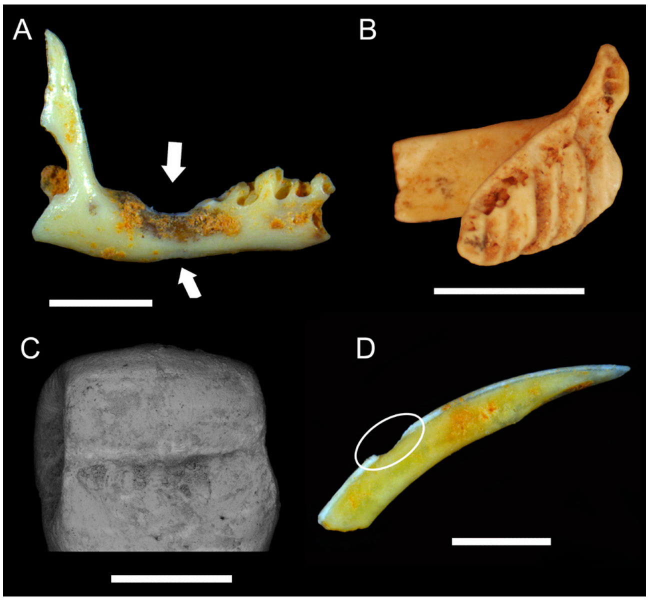

Figure 3. Optical and ESEM images of small mammal remains from QS-2/3 with alterations. **A,** Mandible of the shrew *Crocidura kornfeldi* with a possible bite mark, where two pressure points (indicated by the arrows) are observed, according to Fernández-Jalvo and Andrews (2016). However, the subsequent digestion of the mandible has softened and rounded this modification, making it difficult to classify clearly. IPHES-QS 2/3-TAF/96; **B,** fragment of maxillae of arvicoline showing abrasion, IPHES-QS 2/3-TAF/97; **C,** distal epiphysis of metapod with abrasion marks, IPHES-QS 2/3-TAF/98; **D,** rodent incisor with root marks (white circle), IPHES-QS 2/3-TAF/99; scale bar = 2 mm for A, C, D; 5 mm for B.

DISCUSSION

Taxonomic identification

Teeth are the most diagnostic elements in most fossil rodents and insectivores, enabling taxonomic identification at species level. Based on the morphology of the dental remains, the studied sample includes the species *Manchenomys orcensis*, *Apodemus sylvaticus*, *Castillomys rivas*, *Eliomys quercinus*, and *Crocidura kornfeldi*, all of which were previously identified at QS-2/3 by Piñero *et al.* (2020, 2022).

The lower first molars of arvicolines in the studied material exhibit a short, rounded anteroconid, lacking BSA4 or LSA5. the enamel is wider on the posterior face than on the anterior side. None of the molars possess roots, and the anteroconid complex is relatively short. The amount of cement in the re-entrant angles is always abundant. These characteristics are consistent with the microtine genus *Manchenomys*. Additionally, the size of the molars corresponds to that of the species *Manchenomys orcensis*, which has thus

Table 6. Predator category classification according to Andrews (1990) with the data from this study (modified from Marín-Monfort *et al.*, 2022).

Taphonomic variables	QS-2/3	Category	Category 1	Category 2	Category 3	Category 4	Category 5
PC/c	**130.8%**	**2**	>200%	100%–150%	50%–70%	<30%	-
F+H/Mx + Md	**77.9%**	**2**	100%–150%	90%–70%	50%–30%	<60%	-
			Barn owl, long eared owl, short eared owl, Verreaux owl and great grey owl owl, bat-eared fox, and pine marten	Tawny owl, Verreaux owl, spotted eagle owl, kestrel and genet	Hen harrier and artic fox	Snowy owl, little owl, mongoose, coyote, and red fox	-
T+R/F+H	**98.5%**	**1**	≈100%	85%–70%	70%–60%	60%–40%	40%–20%
			Barn owl, long eared owl, Verreaux owl, and tawny owl	Short eared owl, European eagle owl, great grey owl, artic fox, and coyote	Little owl and kestrel	Spotted eagle owl, hen harrier and red fox	Pine marten, mongoose, genet, bateared fox
Complete long bones	**6.7%**	**5**	90%–100%	90%–80%	70%–40%	40%	<30%
			Barn owl, long eared owl, great grey owl, and Verreaux owl	Snowy owl and European eagle owl	Tawny owl and spotted eagle owl	Little owl, kestrel, hen harrier, mongoose, genet, and bat-eared fox	Coyote, red fox, artic fox, and pine marten
Complete skulls	**0%**	**5**	70%–100%	50%–70%	30%–50%	-	0
			Barn owl, long eared owl, and great grey owl	Short eared owl, spotted eagle owl, tawny owl, and European eagle owl	Little owl, kestrel, and hen harrier	-	Mammalian carnivores
Complete mandibles	**2.6%**	**3**	70%–90%	15%–40%	2%–10%	0%	-
			Barn owl, long eared owl, Verreaux owl, and great grey owl	Snowy owl, short eared owl, European eagle owl, and tawny owl	Spotted eagle owl, kestrel, and hen harrier	Little owl and mammalian carnivores	-
Incisor loss	**87.2%**	**3**	20%–40%	50%–60%	80%–90%	90%–100%	100%
Molar loss	**89.9%**	**3**	20%–40%	50%–60%	80%–90%	90%–100%	100%
			Barn owl, snowy owl, long eared owl, short eared owl, Verreaux owl, spotted eagle owl, and European eagle owl	Great grey owl, mongoose, and coyote	Tawny owl, little owl, and bateared fox	Kestrel, genet, red fox, and pine marten	Hen harrier and artic fox
Molars digested	**29.1%**	**3-4**	<3%	4%–6%	11%–22%	50%–70%	50%–100%
			Barn owl, long eared owl, short eared owl, and Verreaux owl	Snowy owl, spotted eagle owl, and great grey owl	European eagle owl, tawny owl, bat-eared fox, mongoose, and genet	Little owl, kestrel, and pine marten	Hen harrier, coyote, red fox, and artic fox
Incisor digested	**20.9%**	**2**	5%–13%	10%–30%	50%–70%	60%–80%	100%
			Barn owl, short eared owl, and snowy owl	Long eared owl, Verreaux owl, great grey owl, and bat-eared fox	European eagle owl, spotted eagle owl, tawny owl, little owl, pine marten, and mongoose	Kestrel	Hen harrier, coyote, red fox, and artic fox
Postcranial digested	**31%**	**2**	6%–20%	25%–50%	60%–100%	-	100%
			Barn owl, short eared owl, long eared owl, Verreaux owl, and great grey owl	European eagle owl, spotted eagle owl, and tawny owl	Little owl, kestrel, and hen harrier	-	Mammalian carnivores

far only been identified at the sites of Quibas, Fuente Nueva 3, and Barranco León (see Agustí *et al.*, 2022). Two morphologically distinct murid samples have been identified in the sample from QS-2/3. One sample consists of 53 molars exhibiting common characteristics of the genus *Apodemus*, such as the presence of t7 and the t6-t9 connection in the M1 and M2, a well-developed labial cingulum, and the absence of a longitudinal crest in the m1 and m2. These teeth are similar in both size and morphology to those of *Apodemus sylvaticus* previously reported at the Quibas-Sima section (Piñero *et al.*, 2022). The second sample includes 30 molars with distinctive features of the genus *Castillomys*, such as the absence of t7, the development of a posterior crest on t1 in the M2, and the presence of a well-developed longitudinal crest on the m1. All specimens display well-developed longitudinal crests, completing the connection among the tubercles of the crown. The m1 and m2 feature a broad labial cingulum, separated from the protoconid by a valley. These morphological traits are consistent with the species *Castillomys rivas*. Moreover, these molars match in size with *Castillomys rivas* previously recovered from the Quibas site (Piñero *et al.*, 2015, 2022).

Glirids are represented by 23 teeth that are consistent with the genus *Eliomys*. The tooth morphology is relatively simple, with most of the lower molars lacking a posterotropid. The absence of a posterotropid is a distinguishing feature between the extant species *Eliomys quercinus* and the Pliocene and Early Pleistocene species *Eliomys intermedius*, which retains a posterotropid in most of its lower molars.

The soricid elements consist of 65 teeth attributed to the genus *Crocidura*. All of these elements are smaller than those of extant *Crocidura russula* and *Crocidura suaveolens* (see Furió *et al.*, 2015). The most notable morphological difference between the fossil species and the extant European ones is the position of the protocone in P4, which is not situated directly at the anterolingual corner, but is slightly displaced more labially. The material from QS-2/3 closely fits with *Crocidura kornfeldi*.

Palaeonvironmental reconstruction

Small mammals have been widely used as palaeoecological indicators, providing valuable insights into past environmental conditions (*e.g.*, López-García *et al.*, 2010, 2014; Piñero *et al.*, 2016, 2024). In this study, we aim to analyze the environment of the Quibas area during the deposition of the QS-2/3 unit.

Regarding the ecological preferences of the taxa identified in the analysed sample, *Apodemus sylvaticus* is currently found primarily along forest edges, within thickets, hedges, and ditch banks, provided these areas have arboreal or shrub cover (woodland and woodland-margin areas, 1) (Spagnesi & De Marinis, 2002).

Castillomys rivas is an extinct murid exhibiting dental morphological traits associated with stephanodonty, characterised by longitudinal ridges between molar cusps. This feature suggests a grass-based diet (Van Dam & Weltje, 1999; Renaud *et al.*, 2005), implying a preference for open meadow habitats (0.5 open dry; 0.5 open humid).

Manchenomys is an extinct vole distinguished by rootless lower teeth and the presence of cementum in the re-entrant angles (Agustí *et al.*, 2022). During the Plio-Pleistocene, various arvicoline lineages increased their molar hypsodonty and developed cementum, an evolutionary trend generally interpreted as an adaptation to an abrasive, grass-rich diet, thus indicating an expansion of open meadow environments (*e.g.*, Fejfar & Repenning, 1992). Based on this evidence, we infer that *Manchenomys orcensis* inhabited open dry meadows (0.5) and open humid meadows (0.5).

Eliomys quercinus underwent a significant expansion across Europe throughout the Pleistocene. Today, it is typically found in low-density deciduous and coniferous woodlands (0.5) as well as in rocky or stony environments (0.5) with some vegetation at forest margins, ranging from Spain to the Ural Mountains.

Lastly, the genus *Crocidura* currently occupies a wide range of habitats, predominantly across the African continent and southeastern Asia. As noted by Reumer (1984), considering only the species present in Europe (*i.e.*, *C. russula*, *C. suaveolens*, and *C. leucodon*), *Crocidura* exhibits a marked preference for relatively arid and open environments (0.5) as well as rocky areas (0.5).

The application of the Habitat Weightings method to the small mammal assemblage of the QS-2/3 unit indicates an environment characterised by woodland habitats (41.05%), along with open dry areas or shrublands (26.6%). Rocky areas (16.65%) and open humid meadows (15.5%) were also notably present (Tab. 7). The presence of forested environments at QS-2/3 is supported by the scarce occurrence of the flying squirrel *Hylopetes* sp., as well as the presence of browsing herbivores, such as the fallow deer *Dama* cf. *vallonnetensis* (see Piñero *et al.*, 2022; Rosas *et al.*, 2022). Additionally, the preferred habitats of the wild boar (*Sus* sp.), which is present at QS-2/3, include mixed forests. The existence of open environments and open woodlands around QS-2/3 is corroborated by the occurrence of large bovids, such as *Bison* cf. *voigtstedtensis* and *Capra alba*, the rhinoceros *Stephanorhinus* cf. *etruscus*, and the Iberian lynx (*Lynx pardinus*). The presence of open dry areas is also supported by the occurrence of the tortoise *Testudo* sp. and the snakes *Vipera latastei* and *Malpolon monspessulanus* in the same unit (Piñero *et al.*, 2020, 2022).

These results suggest a landscape dominated by a combination of forest patches or open woodlands, shrublands, and rocky habitats, alongside significant areas of open herbaceous meadows. This pattern is consistent with the development of a forest-mosaic environment near Quibas at the onset of the Jaramillo subchron. The extent of open areas, including rocky terrains, accounted for nearly 60% of the landscape. This aligns with the findings of Del Castillo *et al.* (2023) and Laborda-López *et al.* (2024), who associated the QS-2/3 unit with a period of aridity during glacial MIS-30.

Taphonomy

The taphonomic analysis suggests that predation was the primary agent responsible for the accumulation of the small mammal assemblage analysed in this study. Processes such as wind or water transport have been ruled out, although the influence of weak water currents cannot be entirely dismissed due to the presence of some abrasion (Fig. 3B, 3C). However, given that small mammal remains are easily displaced by low-velocity water currents (< 0.35 m/s; Dodson, 1973), the presence of skeletal elements from different hydrodynamic groups suggests that transport was not the dominant taphonomic agent (Korth, 1979; Andrews, 1990; Fernández-Jalvo & Andrews, 2016; García-Morato *et al.*, 2019). Other potential accumulation processes, such as natural death or catastrophic events (Denys, 1985; Andrews, 1990; Laudet *et al.*, 1997), are also unlikely, as there is no evidence of relatively complete or articulated skeletons, which are typically associated with such events (Andrews, 1990; Stahl, 1996).

Evidence of digestion in both cranial and post-cranial remains further supports predation as the primary accumulation process. Predation is a major factor in the formation of microvertebrate assemblages in both modern and fossil sites (*e.g.*, Andrews, 1990; Fernández-Jalvo & Andrews, 1992; Marín-Monfort *et al.*, 2018, 2021; Bisbal-Chinesta *et al.*, 2020; García-

Table 7. Relative abundances of each small mammal taxon from QS-2/3, with the distribution of their potential habitats. Abbreviations: **W**, woodland and woodland-margin areas; **R,** rocky areas; **OD,** open dry meadows or shrublands; **OH,** open humid meadows; **WE,** water-edges.

Species	**%MNI**	**Habitat**				
		W	**R**	**OD**	**OH**	**WE**
Manchenomys orcensis	6.6	-	-	0.5	0.5	-
Apodemus sylvaticus	35.5	1	-	-	-	-
Castillomys rivas	24.4	-	-	0.5	0.5	-
Eliomys quercinus	11.1	0.5	0.5	-	-	-
Crocidura kornfeldi	22.2	-	0.5	0.5	-	-
%Total		41.05	16.65	26.60	15.50	-

Morato *et al.*, 2022), with digestive corrosion being the most distinctive indicator of this process (Mellett, 1974; Raczynski & Ruprecht, 1974; Mayhew, 1977; Andrews & Evans, 1983; Andrews, 1990; Fernández-Jalvo & Andrews, 1992; Fernández-Jalvo *et al.*, 2016).

The results indicate that 29.1% of molars and 20.9% of incisors exhibit acid corrosion, while 37.1% of post-cranial elements show digestion damage. These percentages align with a category 2–3 predator, following Andrews (1990) (see Tab. 6), which is most characteristic of nocturnal birds of prey. Potential candidates with a Eurasian distribution include the snowy owl (*Bubo scandiacus*), great grey owl (*Strix nebulosa*), long-eared owl (*Asio otus*), European eagle owl (*Bubo bubo*), tawny owl (*Strix aluco*), and little owl (*Athene noctua*). While some Eurasian mammalian carnivores, such as the common genet (*Genetta genetta*) and the European pine marten (*Martes martes*), also fall within these categories, they typically generate assemblages with more than 50% of elements showing heavy to extreme digestion (Fernández-Jalvo *et al.*, 2016), a pattern that differs from the predominantly light to moderate digestion observed in this study.

The snowy owl and little owl can be ruled out based on the percentage of digested molars. Snowy owl assemblages typically exhibit total digestion percentages of only 4–6% (Andrews, 1990; Fernández-Jalvo *et al.*, 2016), whereas little owl assemblages display much higher digestion rates (50–70%; Andrews, 1990; Fernández-Jalvo *et al.*, 2016), significantly exceeding the 29.1% observed here. Instead, the digestion values align more closely with those characteristic of European eagle owls and tawny owls.

Similarly, post-cranial digestion percentages further support these predators. While incisor digestion values are relatively low for European eagle owls and tawny owls, they are more consistent with those produced by great grey owls. However, like the snowy owl, great grey owls typically generate assemblages in which no more than 6% of molars and 20% of post-cranial elements show digestion marks (Andrews, 1990; Fernández-Jalvo *et al.*, 2016), further suggesting they are not the primary accumulating agent.

Discrepancies between the observed and expected digestion percentages for incisors have been noted in previous studies (Fernández-Jalvo & Andrews, 1992; Demirel *et al.*, 2011; García-Morato *et al.*, 2019; Marín-Monfort *et al.*, 2021) and have been attributed to small sample sizes or post-depositional taphonomic processes (Andrews, 1990; Marín-Monfort *et al.*, 2021; Fried *et al.*, 2024). Preferential destruction of digested incisors compared to digested molars in fossil sites, may potentially explain this difference. Therefore, based on the digestion patterns observed, the most probable predators responsible for the accumulation of the assemblage are the European eagle owl (*Bubo bubo*) and the tawny owl (*Strix aluco*).

Anatomical representation indices and breakage variables presented in Table 6 seem to support the presence of one of these predators, although certain values may have been influenced by post-depositional processes. Depositional agents acting on the remains after initial accumulation by the predator may cause additional breakage and modifications, making it difficult to distinguish between a relatively intact predator assemblage and one that has undergone significant post-depositional alteration (Andrews, 1990; García-Morato *et al.*, 2023). A high degree of skeletal completeness in a fossil site typically indicates minimal post-depositional disturbance and supports the involvement of a nocturnal bird of prey. Conversely, extensive breakage could result from intense post-depositional processes, such as trampling, rather than necessarily indicating the involvement of a diurnal bird of prey or a mammalian carnivore (García-Morato *et al.*, 2023).

The breakage values observed for post-cranial elements and maxillae in this assemblage correspond to a category 5 predator (Tab. 6), which is not typically expected for species such as *Bubo bubo* or *Strix aluco*. Factors such as pre-burial breakage, trampling (Andrews, 1990; Fernández-Jalvo & Andrews, 2016), sedimentary pressure, and excavation or recovery damage (Marín-Monfort *et al.*, 2018) may have contributed to these results. However, most of the taphonomic variables related to anatomical representation and breakage align with categories 2 and 3 of predation, reinforcing the involvement of a nocturnal bird of prey (Andrews, 1990; Fernández-Jalvo *et al.*, 2016). In particular, indices such as PC/C, Distal/Proximal, and tooth loss appear to correspond more closely to the tawny owl (*Strix aluco*) rather than the European eagle owl (*Bubo bubo*) (Tab. 6).

The tawny owl (*Strix aluco*) was an abundant bird of prey in the Iberian Peninsula during the Early Pleistocene, with its oldest regional records documented at the site of Quibas and at the chronologically and geographically close site of Cueva Victoria (Montoya *et al.*, 2001; Sánchez-Marco, 2007, 2012; Gibert *et al.*, 2016). Today, *Strix aluco* predominantly inhabits natural forests and wooded areas, thriving in medium-sized and fragmented forests (Redpath, 1995; Sánchez-Zapata & Calvo, 1999; Fröhlich & Ciach, 2018; López-Peinado *et al.*, 2020). The palaeoecological results obtained in this study align with the habitat preferences of the tawny owl rather than those of the European eagle owl (*Bubo bubo*), which is more commonly associated with open areas such as bushlands or landscapes near watercourses (Mikkola, 1983; Andrews, 1990; Martínez *et al.*, 2003; Ortego & Díaz, 2004; Penteriani & Delgado, 2019).

Additionally, the present-day diet of *Strix aluco* in the Iberian Peninsula closely matches the small mammal assemblage recovered from QS/2-3, which is dominated by murids and soricids, along with occasional glirids and arvicolines (Adánez, 2000). The specimens of these groups identified in the studied sample (Tab. 3) exhibit heavy (Figs. 4C–4I, 5G) and moderate

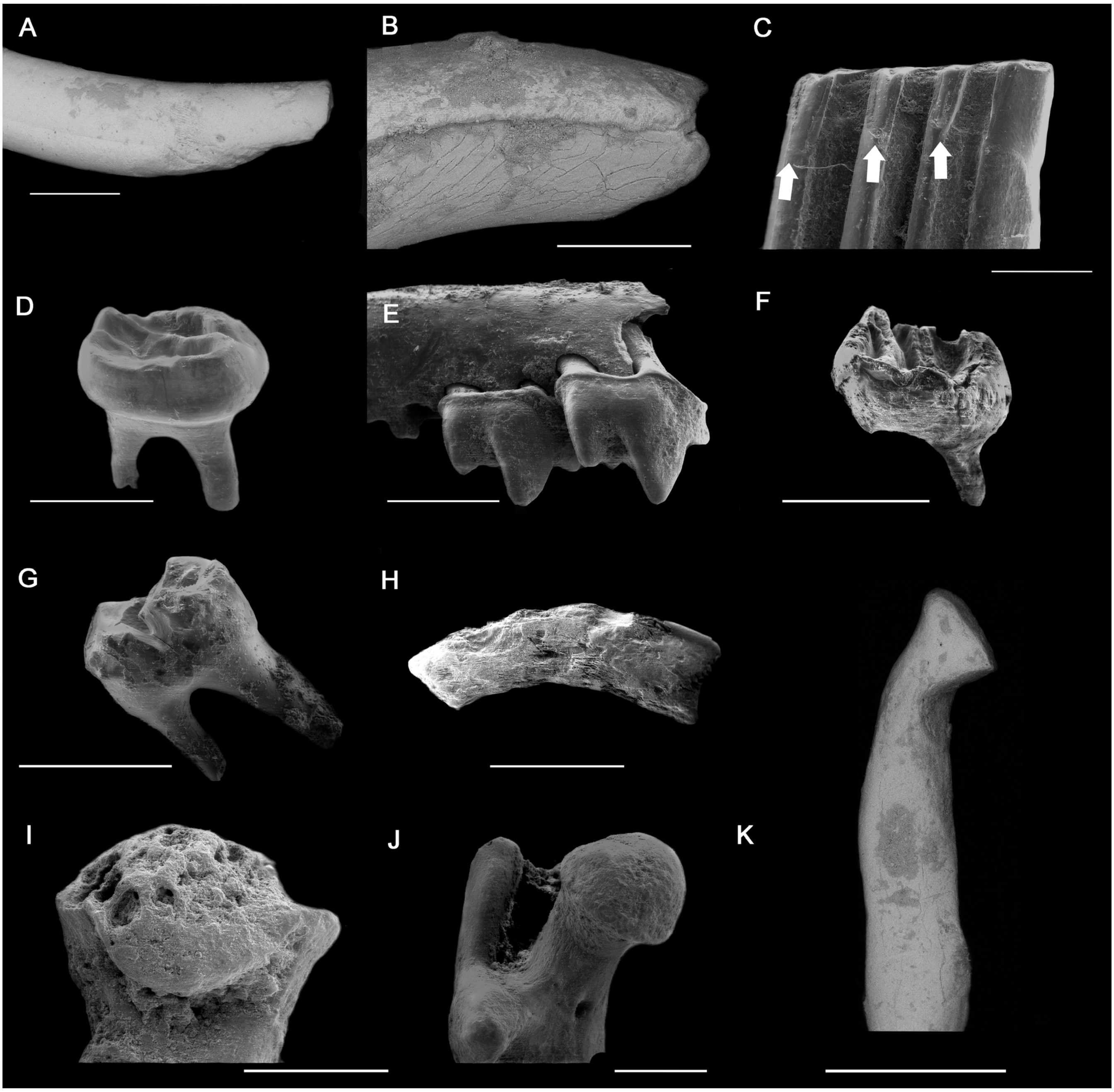

Figure 4. ESEM images of small mammal remains from QS-2/3 with alterations. **A,** Rodent incisor lightly digested, IPHES-QS 2/3-TAF/90; **B,** rodent incisor lightly digested, IPHES-QS 2/3-TAF/91; **C,** m1 of the arvicoline *Manchenomys orcensis* lightly digested (white arrows), IPHES-QS 2/3-TAF/11; **D,** m1-2 of the glirid *Eliomys quercinus* lightly digested, IPHES-QS 2/3-TAF/55; **E,** fragment of mandible with m1 and m2 of the shrew *Crocidura kornfeldi* moderately digested, IPHES-QS 2/3-TAF/65; **F,** m1-2 of the glirid *Eliomys quercinus* heavily digested and affected by corrosion, IPHES-QS 2/3-TAF/54; **G,** m2 of the murid *Apodemus sylvaticus* heavily digested, IPHES-QS 2/3-TAF/28; **H,** rodent incisor heavily digested, affected by corrosion and roots, IPHES-QS 2/3-TAF/92; **I,** proximal epiphysis of humerus moderately digested, IPHES-QS 2/3-TAF/93; **J,** proximal epiphysis of femora lightly digested, IPHES-QS 2/3-TAF/94; **K,** ulna moderately digested, IPHES-QS 2/3-TAF/95; scale bar = 0.5 mm for B; 1 mm for A, C–G, I, J; 3 mm for H; 2 mm for K.

(Fig. 4E, 4I, 4K) degrees of digestion, consistent with those produced by *Strix aluco* (see Fernández-Jalvo *et al.*, 2016). In contrast, the European eagle owl is considered a rabbit specialist in central and southern Iberia (Fernández-de-Simon *et al.*, 2014; Tobajas *et al.*, 2016), preying more frequently on microtines only in the absence of more profitable prey (Mikkola, 1983). While further analysis of rabbit remains could help determine whether multiple predators contributed to the Quibas small mammal assemblage, the available evidence suggests that tawny owls were the primary accumulator of small mammal remains in QS-2/3.

Regarding post-depositional taphonomic alterations in the studied sample, corrosion marks (Figs. 4F, 4H, 5A, 5D) indicate the presence of acidic conditions in QS-2/3. Three possible factors may have contributed to the corrosion observed in the skeletal remains. The first is the karstic environment, which exhibits

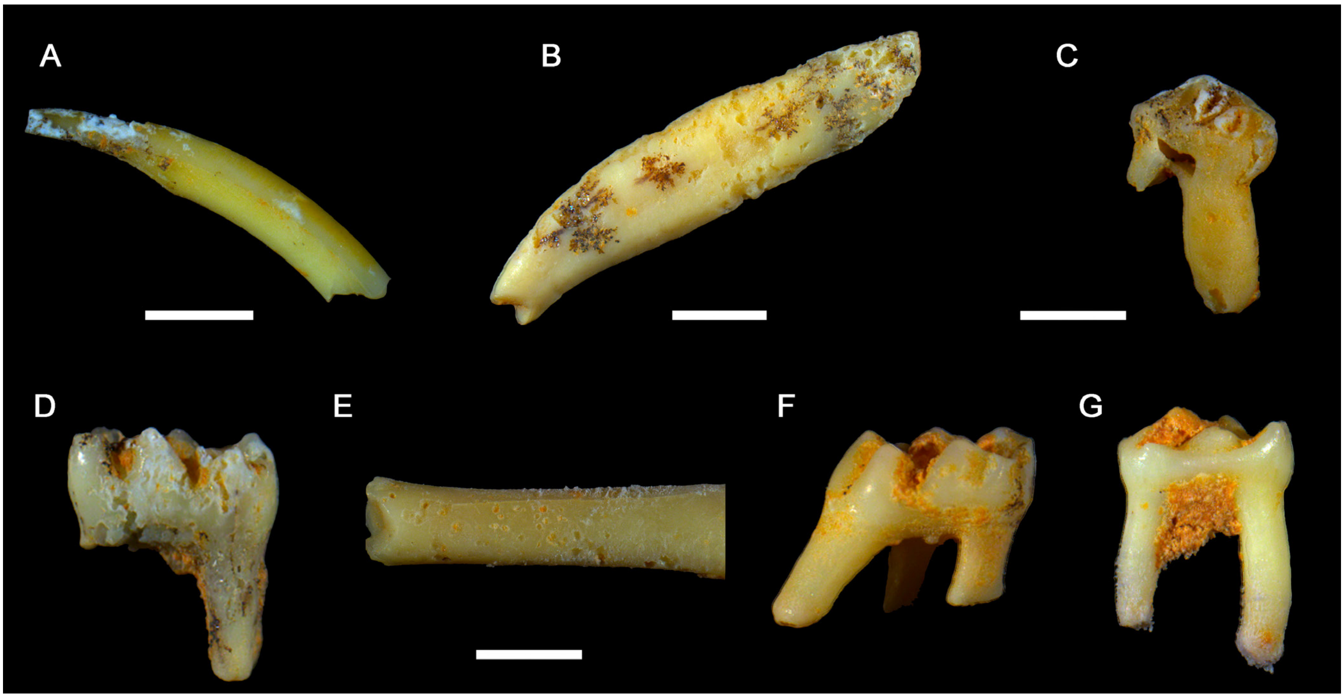

Figure 5. Digital images of small mammal remains from QS-2/3 with alterations. **A,** Rodent incisor affected in the point by roots and corrosion, IPHES-QS 2/3-TAF/100; **B,** teeth affected by roots and mineralization of pyrolusite inside the root marks, IPHES-QS 2/3-TAF/101; **C,** molar of the glirid *Eliomys quercinus* heavily digested, IPHES-QS 2/3-TAF/102; **D,** m1 of the murid *Apodemus sylvaticus* in lateral view affected by corrosion and roots, IPHES-QS 2/3-TAF/103; **E,** bone shaft with root marks, IPHES-QS 2/3-TAF/105; **F,** M1 of *Apodemus sylvaticus* lightly digested; **G,** m1 of *Apodemus sylvaticus* moderately digested, IPHES-QS 2/3-TAF/106; scale bar = 2 mm for A, B; 1 mm for C–G.

basic conditions due to the alkalinity of the cave, in contrast with the acidic water percolating through the karstic system. This interaction creates an optimal environment for the corrosion of skeletal elements. The second factor is the presence of a humus-rich stratum. Considering that at the time of fossil deposition, certain organisms such as chiropterans, reptiles, amphibians, and birds inhabited the site, along with significant plant growth, it is likely that a humus-rich stratum was formed. These humic acids could have contributed to some of the observed corrosion marks (Andrews, 1990; Fernández-Jalvo & Andrews, 2016). Additionally, there are root marks in the assemblage (Figs. 3D, 4H, 5A, 5B, 5D, 5E) that show characteristic spotted perforations rather than branching patterns. The root marks, present on 72.7% of the specimens, indicate that plants were able to grow. Plant growth may be associated with substrate acidifications (Macho-Callejo *et al.*, 2023), which may have contributed to some of the corrosion observed in this study. Furthermore, the presence of plants implies that there was sufficient light for their development, suggesting that the main opening to the cave was located near the fossil deposition site. Additionally, plant growth implies a prolonged period without high sedimentation rates or flooding events, as such occurrences would have hindered their growth.

Finally, the presence of manganese (Figs. 3A, 5A–5D) within fractures (Fig. 5C), on the surface of bones (Figs. 3A, 5A–5D), and within root marks (Fig. 5A, 5B, 5D) indicates a humid fossilization environment (Fernández-Jalvo & Andrews, 2016). Manganese precipitates in the presence of water, and its occurrence in specimens from the QS-2/3 unit suggests elevated humidity and water retention within the sediment following the previous alterations. This implies that water was retained within the cave, likely maintaining stable humidity levels.

CONCLUSIONS

According to the taxonomic analysis of small mammal remains from the Quibas-Sima 2/3 level, we have identified five species: *Manchenomys orcensis, Apodemus sylvaticus, Castillomys rivas, Eliomys quercinus,* and *Crocidura kornfeldi*.

The palaeoenvironmental reconstruction indicates that the QS-2/3 landscape was characterised by a combination of forest patches or open woodlands, shrublands, and rocky habitats, alongside areas of open meadows. The presence of taxa associated with open environments, together with faunal evidence of browsing herbivores and large bovids, supports the development of a heterogeneous landscape at Quibas around 1 Ma, during the glacial MIS-30 (Fig. 6).

Taphonomic analyses suggest that predation was the primary agent responsible for the accumulation of small mammal remains, with minimal influence from water transport or other depositional processes. The digestion patterns observed in the assemblage align most closely with predation by nocturnal birds of prey, particularly the tawny owl (*Strix aluco*), which was likely the main accumulating agent. Tawny owls preferentially hunt in forested environments, suggesting a potential bias towards a higher representation of such habitats in the assemblage. Nevertheless, independent palaeoenvironmental proxies confirm the presence of nearby forested areas, which would also have provided suitable habitats for tawny owls, increasing their probabilities for being the primary accumulation agent of the small mammal assemblage. The presence of post-depositional modifications, including corrosion marks, root etching, and manganese precipitation, further indicates that the fossilization process occurred under relatively stable, humid, and acid/basic conditions. The interesting results obtained in this study motivate and justify future research on the taphonomy of the rich microvertebrate small vertebrate assemblages from the Quibas karstic site. The ongoing objective is to expand the sample from QS-2/3, both in terms of the number of remains and taxonomic groups, to include chiropterans, lagomorphs, and herpetofauna. Additionally, a comparison will be made between the taphonomic processes involved in the accumulation of small vertebrates at QS-2/3 and those observed in QS-1 and in the units of the Quibas-Cueva section.

Supplementary information. This article has no additional data.

Authors’ contribution. ANG, sampling, analysis, data acquisition, research, writing of the original text; SGM, editing, writing of the original text, text review; MF, conceptualization, editing, research, text review, supervisor of the present Master’s Thesis; SP, sampling, text review; CI, sampling, text review; JA, conceptualization, research, project manager; PP, conceptualization, editing, research, writing of the original text, project manager, supervisor of the present Master’s Thesis.

Conflict of interest. The authors have no conflict of interest.

Funding. This work was supported by the Abanilla Town Council, the Comunidad Autónoma de la Región de Murcia (Dirección General de Patrimonio Cultural), the Spanish Ministry of Science and Innovation (grant number PID 2021-123092NB-C21), the Palarq Foundation, AGAUR-Generalitat de Catalunya (grant number 2021SGR-1238), and the University Rovira i Virgili (grant number 2023PFR-URV-01238). PP is supported by a “Ramón y Cajal” contract (grant RYC2023-044218-I) funded by MICIU/AEI/10.13039/501100011033 and “ESF+”. MF is a Serra Húnter Fellow.

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Figure 6. Recreation of the environment of the Quibas site during the deposition of QS-2/3 (1.07–0.99 Ma). The illustration depicts a tawny owl (*Strix aluco*), the main accumulator of small mammal remains in QS-2/3, feeding on a rodent (upper left) in an open landscape with forest patches, above what would have been the entrance hole to the cave that served as the fossil deposit. The owl is shown sharing its habitat with some of the taxa identified in QS-2/3. From top to bottom and left to right: tawny owl (*Strix aluco*), horse (*Equus altidens*), fox (*Vulpes alopecoides*), Etruscan rhinoceros (*Stephanorhinus etruscus*), Hermann’s tortoise (*Testudo hermanni*), vole (*Manchenomys orcensis*), golden eagle (*Aquila chrysaetos*), porcupine (*Hystrix refossa*), Iberian lynx (*Lynx pardinus*), mouse (*Castillomys rivas*), Barbary macaque (*Macaca sylvanus*), fallow deer (*Dama vallonnetensis*), European badger (*Meles meles*), Lataste’s viper (*Vipera latastei*), land snail (*Palaeoglandina montenati*), green toad (*Bufotes viridis*), Mediterranean pika (*Prolagus calpensis*), and garden dormouse (*Eliomys quercinus*). Artwork: Núria Malo.

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Acknowledgments. We would like to sincerely thank the Abanilla Town Council for their kind financial and logistical support, which has been a great help to the Quibas site team during the various field campaigns. We also gratefully acknowledge the support of this work by Gregorio Romero and the Servicio de Patrimonio Histórico de la Dirección General de Patrimonio Cultural of the Murcia Region. Last but not least, we would like to express our sincere gratitude to Yolanda Fernández Jalvo for her generous support and assistance throughout this work. We sincerely appreciate the valuable comments of the anonymous reviewers and the editor Humberto Ferrón.

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