

The first record of *Palaeoloxodon cf. antiquus* (Proboscidea, Middle Pleistocene) from the Eastern Guadalquivir Basin (SE Spain): taphonomy and relation with other outcrops

Primer registro de Palaeoloxodon cf. antiquus (Proboscidea, Pleistoceno Medio) del sector oriental de la Cuenca del Guadalquivir (SE España): tafonomía y relación con otros yacimientos.

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ABSTRACT

The first record of a proboscidean from the Eastern Guadalquivir Basin is located in the alluvial fans developed during an intense erosive phase of the reliefs of the outermost mountain front of the Betic Cordillera. The remain is a fragment of a fossil tusk (74 cm length) transported by water streams during the Middle Pleistocene and deposited with high energy detritic sediments (coarse sands to boulders). The fossil is coated by a laminated crust (< 2 cm) composed by carbonate. Detailed analysis of this crust evidences it was a cover of mosses around the bone that was cemented early and preserved as a thin phytoherm. The presence of this coating favoured the preservation of the bone in a high energy environment, and its fast burial also favoured preservation. Analysis of the Schreger lines in the internal structure of the tusk allow us to assign this remain to the straight-tusked elephant *Palaeoloxodon cf. antiquus*. The studied specimen from the Eastern Guadalquivir Basin is found between populations of *P. antiquus* from the Western Guadalquivir Basin and from the Guadix-Baza Basin. Seasonal migrations of *P. antiquus* between low lands of the Western Guadalquivir Basin (< 200 m above sea level) and high lands of the Guadix-Baza Basin (> 900 m above sea level) are not discarded.

Keywords: Elephantidae, alluvial fan, preservation, fossil bryophyte

RESUMEN

El primer registro de un proboscídeo en el sector oriental de la Cuenca del Guadalquivir se ha localizado en los abanicos aluviales desarrollados durante una etapa intensa de erosión de los nuevos relieves del frente montañoso

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más externo de la Cordillera Bética. El fósil estudiado es un fragmento de defensa de 74 cm de longitud que fue transportado por las corrientes que alimentaban el abanico deltaico durante el Pleistoceno medio. Este resto se encuentra dentro de unos depósitos detríticos de alta energía que varían entre tamaño arena gruesa y bloques. El fragmento de defensa se encuentra revestido por una costra carbonatada laminada de un espesor inferior a 2 cm. El análisis detallado de esta costra ha permitido identificar estructuras asignables a briofitas fósiles. Por lo tanto, se interpreta que la defensa fue recubierta casi completamente por musgo que experimentó una cementación temprana. Posiblemente la formación de esta costra favoreció que el fragmento de defensa se preservara. Un posterior enterramiento rápido también debió favorecer la preservación. El análisis de las líneas de Schreger en superficies de fractura de la defensa ha permitido asignar el resto a la especie de elefante *Palaeoloxodon cf. antiquus*. El ejemplar estudiado en el sector oriental de la Cuenca del Guadalquivir se encuentra entre las poblaciones del sector occidental de la Cuenca del Guadalquivir y las de la Cuenca de Guadix-Baza. No se descarta la posibilidad de que existieran migraciones estacionales de *P. antiquus* entre las tierras bajas de la Cuenca del Guadalquivir a menos de 200 m de altura sobre el nivel del mar, y el altiplano de la Cuenca de Guadix-Baza, por encima de 900 m de altura.

Palabras clave: Elephantidae, abanico aluvial, preservación, briofita fósil

Introduction

The fossil record of large continental vertebrates in Eastern Andalusia is abundant, mainly related to the sedimentary infilling of intramountain Neogene basins (e.g. Aguirre, 1957; Aguirre *et al.*, 1973; Martín-Penela, 1988; Arribas & Palmqvist, 1998; Álvarez-Lao *et al.*, 2009; Arribas *et al.*, 2009; Ros-Montoya, 2010; Madurell-Malapeira *et al.*, 2014; Martínez-Navarro *et al.*, 2018). These basins evolved from marine to lacustrine environments due to the elevation of the Betic Cordillera (e.g. Vera, 1970; Braga *et al.*, 1990, 2003; Viseras, 1991; Fernández *et al.*, 1993; Viseras & Fernández, 1994; Viseras *et al.*, 2003). The high erosion rate of the reliefs favoured the development of fan deltas and alluvial fans in these basins, as well as the development of endorheic basins (Braga *et al.*, 1990; Fernández *et al.*, 1993; Viseras & Fernández, 1994; Viseras *et al.*, 2003; Soria *et al.*, 2003; García-García *et al.*, 2006a, b; Stokes, 2008; Harvey *et al.*, 2018). Some records of large mammals have been traced to Miocene and Pliocene fan deltas (e.g. Reolid *et al.*, 2016; Sendra *et al.*, 2020). These intramountain Neogene basins are related with the Internal Zones of the Betic Cordillera, but the record of large land mammals in the Guadalquivir foreland basin is scarcer and exclusively linked to the Western Guadalquivir Basin (Van der Made & Mazo, 2001; Baena-Escudero *et al.*, 2011).

In this work we report the first record of a proboscidean from the Eastern Guadalquivir Basin related to alluvial fans coming from the outermost mountain front of the Betic Cordillera, and we describe the taphonomic history and conditions that favoured its preservation.

Geological setting

The studied Cuadros outcrop (37°48'19''N, 3°24'51''W) is located on the north side of the Sierra Mágina (Betic Cordillera) in Jaén province (Fig. 1). The outcrop is found 1.8 km from Bedmar, along road JV-3222 to Cuadros. From a geological point of view, the outcrop is located by the southern margin of the Guadalquivir Basin, the foreland basin of the Betic Orogen (Fig. 1), whose formation began in the Miocene (García-Castellanos *et al.*, 2002). A transpressive accretionary complex occupies this southern margin, with heterogeneous tectonic units that move over a thick evaporitic sole of Subbetic affinity (Pérez-Valera *et al.*, 2017). Miocene infill consists of marls, sandstones and bioclastic sandstones (García-García *et al.*, 2014). In the Eastern Guadalquivir, where the outcrop lies, marine sedimentation reaches the Early Messinian (Martín *et al.*, 2014).

The alternation of thrust and strike-slip faults together with the abundance of subsoil salt (Pérez-Valera *et al.*, 2017) forms a smooth but varied landscape in the Guadalquivir Valley, with low hills and endorheic and quasi endorheic mini-basins (Ortega *et al.*, 2006). Lakes, many of them saline, were a common feature (López-González *et al.*, 1998). Towards the south, thicker tectonic units of Mesozoic carbonates are structured as a fold-and-thrust belt (García-Rossel & Pezzi, 1975) that results in a mountain range (Sierra Mágina) with peaks above 2000 m high. An intricate mountain front separates the accretionary wedge from Sierra Mágina (García-Tortosa *et al.*, 2008). Frequent and mighty springs drain into the valley at the foot of the mountain front (Gollonet *et al.*,

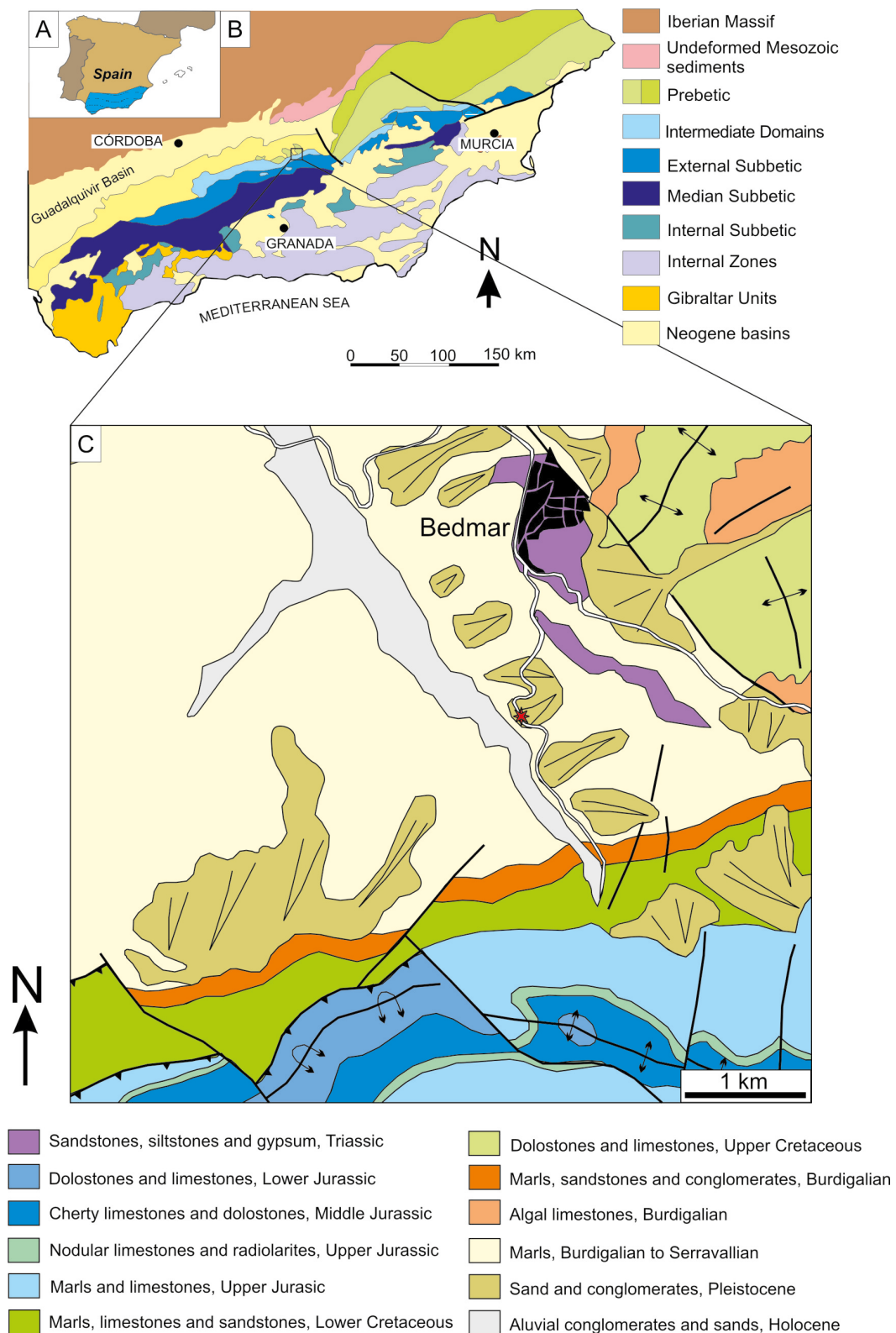


Fig. 1.— Location of the studied fossil bone. A. Studied area in South Spain. B. Geological map of the Betic Cordillera and Guadalquivir Basin. C. Detailed geological map of the studied area on the north side of Sierra Mágina, with location of Cuadros outcrop.

2002; González-Ramón *et al.*, 2013), where the tributaries of the Guadalquivir are born.

Tectonic activity remains until nowadays (Sanz de Galdeano *et al.*, 2012; Sánchez-Gómez *et al.*, 2014) through large-scale faults and folds that could have controlled the development of subsiding and uplifting areas, favouring either the preservation or the erosion of Quaternary deposits in the Guadalquivir Valley (Pérez-Valera *et al.*, 2012).

The tusk remain is located in a dissected conglomeratic body, part of a lateral alluvial fan developed over the Bedmar valley floor at that time. The approximate height of the top and bottom of this alluvial fan would be respectively 40 and 60 m above the current riverbed (Cuadros river). This height correlates with the two levels of terraces, of +30 and +50 m, attributed to the Middle Pleistocene (300–600 ka respectively; Calero *et al.*, 2008), situated in the Guadalquivir main valley, 50 km away from the Bedmar outcrop. Nevertheless, another tributary stream, 16 km away, has fluvial infilling indicating a humid climate; it reaches terrace levels at +45 m above the riverbed and yields a radiocarbon age of 32–35 ka (García-García *et al.*, 2016). Thus, both ages (Middle to Late Pleistocene) could fit with the age of the alluvial fan deposition.

Materials and methods

Sedimentary analysis of the outcrop was carried out in the field with special attention to the beds surrounding the fossil bone. Small fragments of the bone as well as the carbonate sedimentary coating were retrieved. The specimen was not retired from the outcrop.

Four thin sections were prepared to analyse the fabric of the carbonate coating with a Leica M205C at the University of Jaén (Spain), with close observation of the texture and the presence of fossil organic microstructures. Some fragments of this carbonate coating were analysed under Scanning Electron Microscopy (SEM), through secondary electron images with a Merlin Carl Zeiss SEM, at the CICT (University of Jaén).

The Schreger lines of two small fragments were studied. These lines were first defined in the early 19th century by Bernhard Gottlob Schreger (1800) as

a peculiar feature of the Proboscidean dentine (see more details in Espinoza & Mann, 1993). Schreger lines are observed in transversal sections of the tusk, constituting a pattern of two different sets of curved lines that intersect, one in a clockwise direction and the other counter-clockwise. These lines form angles among them, and the set of lines and angles constitutes the “Schreger pattern” (Espinoza & Mann, 1993, 1994; Palombo & Villa, 2001; Ferretti, 2003; Trapani & Fisher, 2003; Lambert, 2005; Ros-Montoya, 2010; Agostini *et al.*, 2012). The Schreger pattern for elephants is characteristic of each species, since their angles are different. This makes it possible to discriminate taxa with a very high reliability. Thus, analysis of the Schreger lines lends valuable support for the taxonomic identification of Proboscidean when the bone remains found in the site are not conclusive (e.g. Mausouss *et al.*, 2014).

Primarily two large fragments were selected and photographed with a high-resolution camera, then the angles between lines were measured using Dino-Lite Pro AM4000 and Photoshop CS6 software, to determine their values and relate them to the taxonomic genus.

Results

Sediment

The tusk remain was recorded in detritic sediments made up mainly of conglomerates and coarse sands (Fig. 2). The conglomerates range from pebbles to boulders, locally over 90 cm in size. Conglomerates are commonly constituted by Jurassic and Cretaceous limestones and dolostones. These lithologies are the most common ones in the surrounding reliefs of Sierra Mágina and Sierra de Bedmar. Some sand layers are observed, laterally and stratigraphically eroded by conglomerates. Sands are massive and show slight cross-stratification. The tusk remain was found at the base of a sand layer.

The conglomerate deposits present clast-supported fabric with an erosive base, indicating palaeochannels. Clast imbrication is observed when the clasts are from 3 to 15 cm long. However, grain-size sequences were not identified. An additional fabric in the case of conglomerates is matrix supported —not

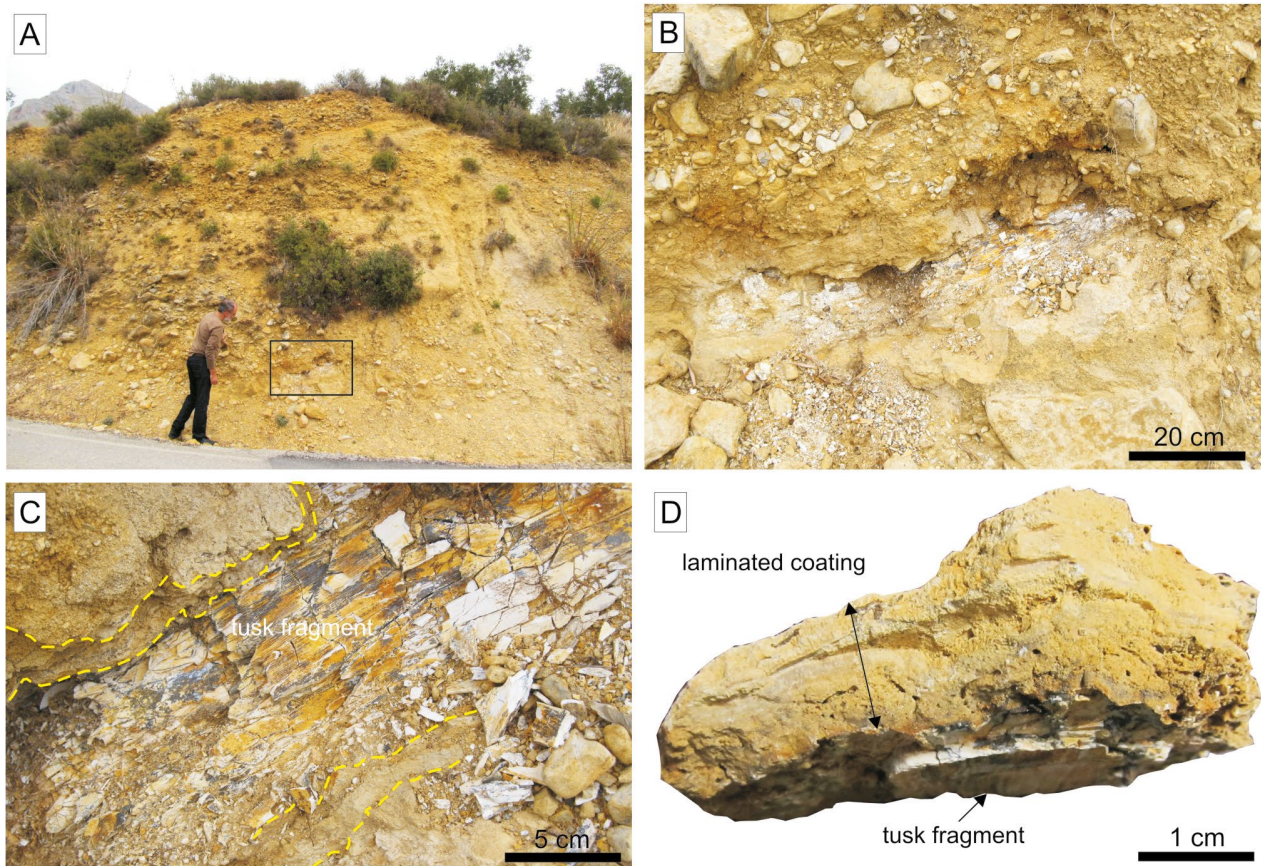


Fig. 2.— Field view of the outcrop and fossil bone remain. A. Talus of the road JV-3222 with conglomerates and the presence of the fossil bone (square is represented in Fig. 2B). B. Close view of the fossil bone in the outcrop. C. Detailed view of the fossil bone with carbonate coating indicated by the yellow line. D. Fragment of fossil bone with the carbonated coat (laminated crust) growing from the surface.

describing bedding, but irregular lens-shaped bodies. These deposits are interpreted as debris flows.

The tusk remains

The studied remain is a straight fragment of proboscidean tusk measuring 74 cm in length and having a diameter ranging from 15.2 to 11.4 cm (Fig. 2B, C). Its preservation in the outcrop is very poor; some parts of the dentine are deteriorated or stained with patches of chalky to chipped appearance. The fossil tusk is coated by a carbonate crust less than 2 cm thick (Fig. 2D). The remain deepens 24° north, at the base of a sandy bed some 40 cm thick.

During their ontogenetic development, elephant tusks progressively form series of dentin cones that intertwine with tubular bundles carrying blood (Fig. 3A). This ivory is easily distinguishable from other groups, for example hippos, since making a transver-

sal cut reveals a pattern of curved lines crossing each other, the Schreger lines. The Schreger pattern of lines and angles is not influenced by palaeoenvironmental factors or linked to the sex of the individual.

Analyses of the Schreger pattern was carried out on two tusk fragments selected from the inner part of the specimen retrieved from the Cuadros outcrop (Fig. 3B and C). The first fragment shows a pattern of lines in the lower left corner, but the fracture is not perpendicular to the axis of the tusk, meaning it is not possible to measure the angle formed by the Schreger lines (Fig. 3D). The other sample shows two sets of lines (Fig. 3C). Several angles were measured on this surface (Fig. 3E), with an average value of 106.5°. The graph in Fig. 3F (modified from Palombo & Villa, 2001), based on more than 200 specimens, shows that the studied specimen corresponds to the genus *Palaeoloxodon*.

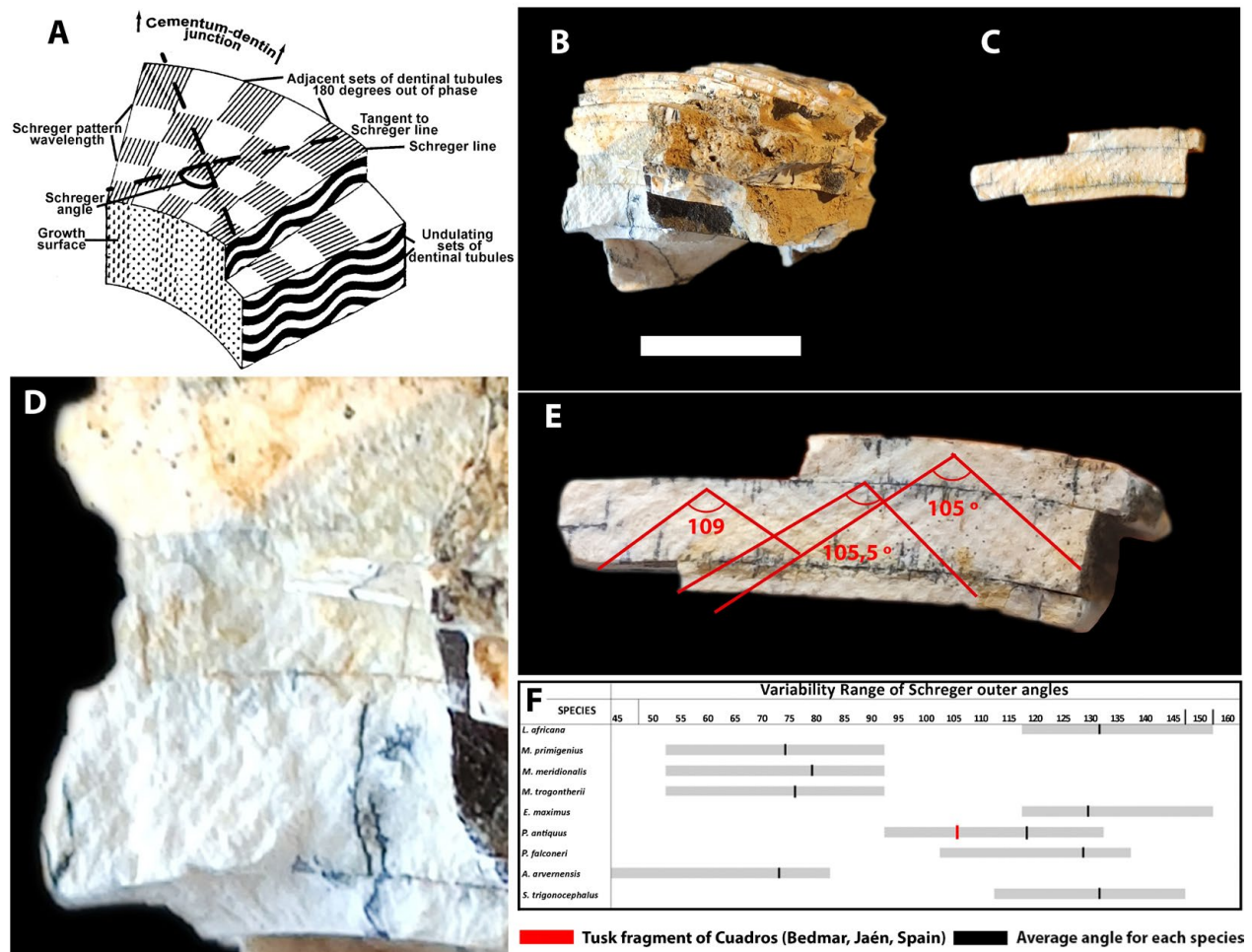


Fig. 3.— A. Schematic diagram showing Schreger pattern (modified from Trapani & Fisher 2002). B and C. Cuadros (Bedmar, Jaén, Spain) tusk fragments (scale bar 2 cm). D and E. Details of the Schreger lines. F. Variability ranges of Schreger inner angles of different Proboscidea (*Loxodonta africana*, *Mammuthus primigenius*, *Mammuthus meridionalis*, *Mammuthus trogontherii*, *Elephas maximus*, *Palaeoloxodon antiquus*, *Palaeoloxodon falconeri*, *Anancus arvernensis* and *Stegodon trigonocephalus*) and the Schreger angle of Cuadros specimen (modified from Palombo and Villa, 2001).

Carbonate coating

A coating of carbonate, with poorly laminated fabric from a macroscopic point of view, surrounds most of the fossil bone (Fig. 2C, D). This coat consists of laminated brownish, creamy limestone with a porous appearance. Porosity is characterized by elongated lamina-parallel pores, but pores arranged 90° with respect to the laminae are also recorded. The total thickness is commonly less than 2 cm. The laminae are more or less continuous, yet of variable thickness. Under petrographic microscopy, lamination is seen to be organized in two types of bands (Fig. 4): porous and compact bands.

The porous laminated bands range from 6 to 10 mm in thickness; they comprise thick laminae (1 to 3.5 mm, average 2 mm) with phytal shrub appearance and high porosity (Fig. 4A-C). These bands constitute laminated bindstones of vegetal remains. In turn, the compact laminated bands, less than 1.3 mm thick, have alternating clear and dark thin laminae (90 to 480 μm thick, average 200 μm) of low porosity. The surface of some porous laminated bands evidences irregularities related to erosion.

The SEM analyses allowed us to identify clusters of multibranching stalks, locally with fan appearance, in the porous bands (Fig. 5). The stalks have a di-

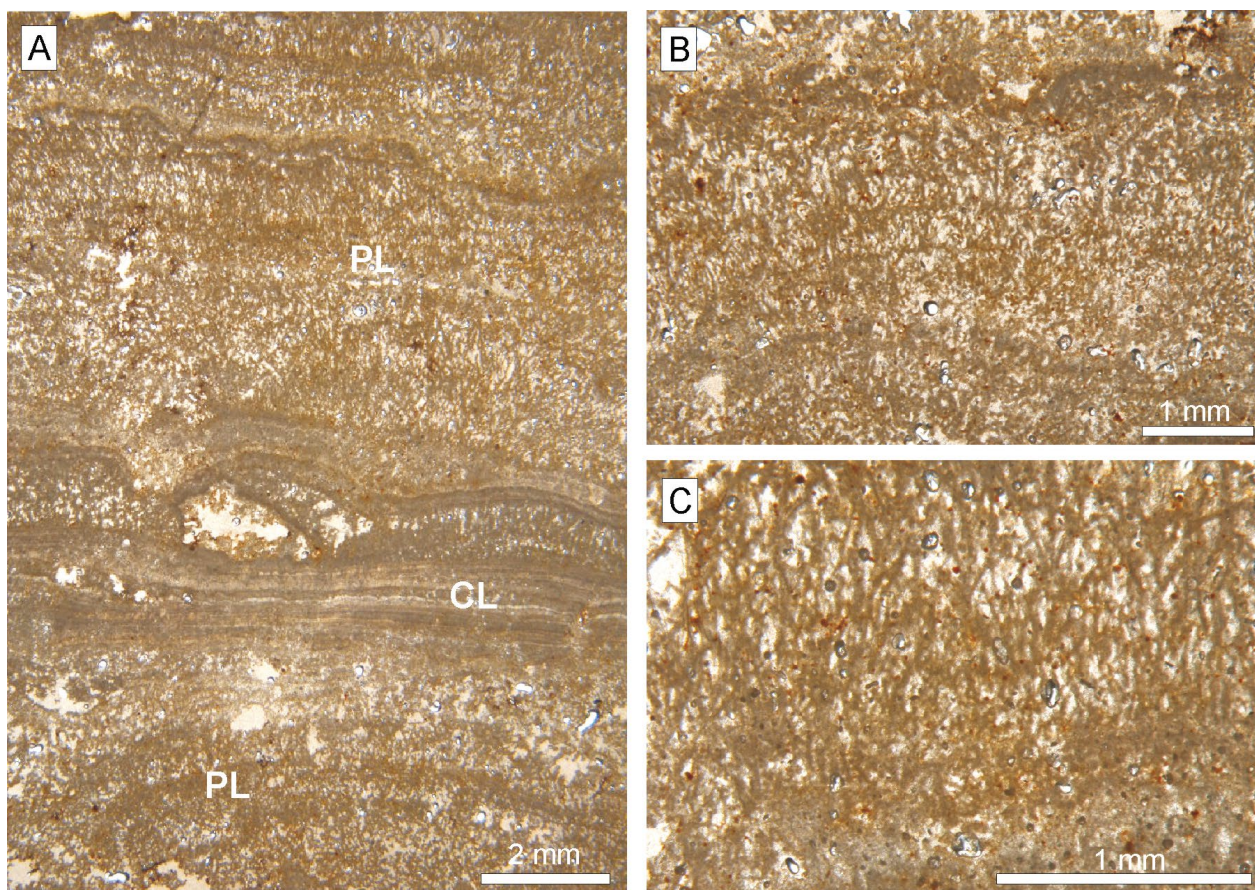


Fig. 4.— Thin section of the carbonate laminated coating. A. Alternating bands with porous lamination (PL) and compact lamination (CL). B and C. Details of the porous lamination having phytal appearance and high porosity.

ameter ranging from 8 to 20 μm , and in detail, are composed by calcite crystals from 1 to 10 μm . The central part of the stalks shows a hollow (2 – 4 μm in diameter) delimited by the calcite crystals.

Discussion

The fossil tusk fragment is recorded in detritic sediments evidencing high energy conditions, given the presence of boulders and debris flow. The environment was probably the proximal part of an alluvial fan that formed surrounding the palaeoreliefs of the Sierra Mágina. The potential presence of scavengers as well as surficial water streams favoured the fragmentation, dispersion and transport of remains. Such scenarios are typical for large corpses of vertebrates from terrestrial environments (e.g. Behrensmeier, 1988). The disarticulated tusk or fragment of tusk would have eventually been transported by the wa-

ter streams feeding the alluvial fan. In this environment, the surface of the tusk was colonized mainly by mosses and thin microbial mats. Water from the karstic carbonate system of Sierra Mágina favoured the precipitation of carbonate upon the mosses. Therefore, the carbonate coating constitutes a phytothermal bindstone, the porous bands of laminated bindstones of bryophytes alternating with compact laminated bands interpreted as microbial mats.

The carbonate coating played an essential role in the preservation of this vertebrate remain. From a tafonomic standpoint, the growth of mosses around the fragment of the elephant tusk, as well as early carbonate cementation, protected the remains from erosion and weathering. The presence of erosive surfaces within the laminae of the carbonate coating is congruent with a local high-energy environment. However, the growth of mosses and the cementation could have been very fast processes, at a seasonal

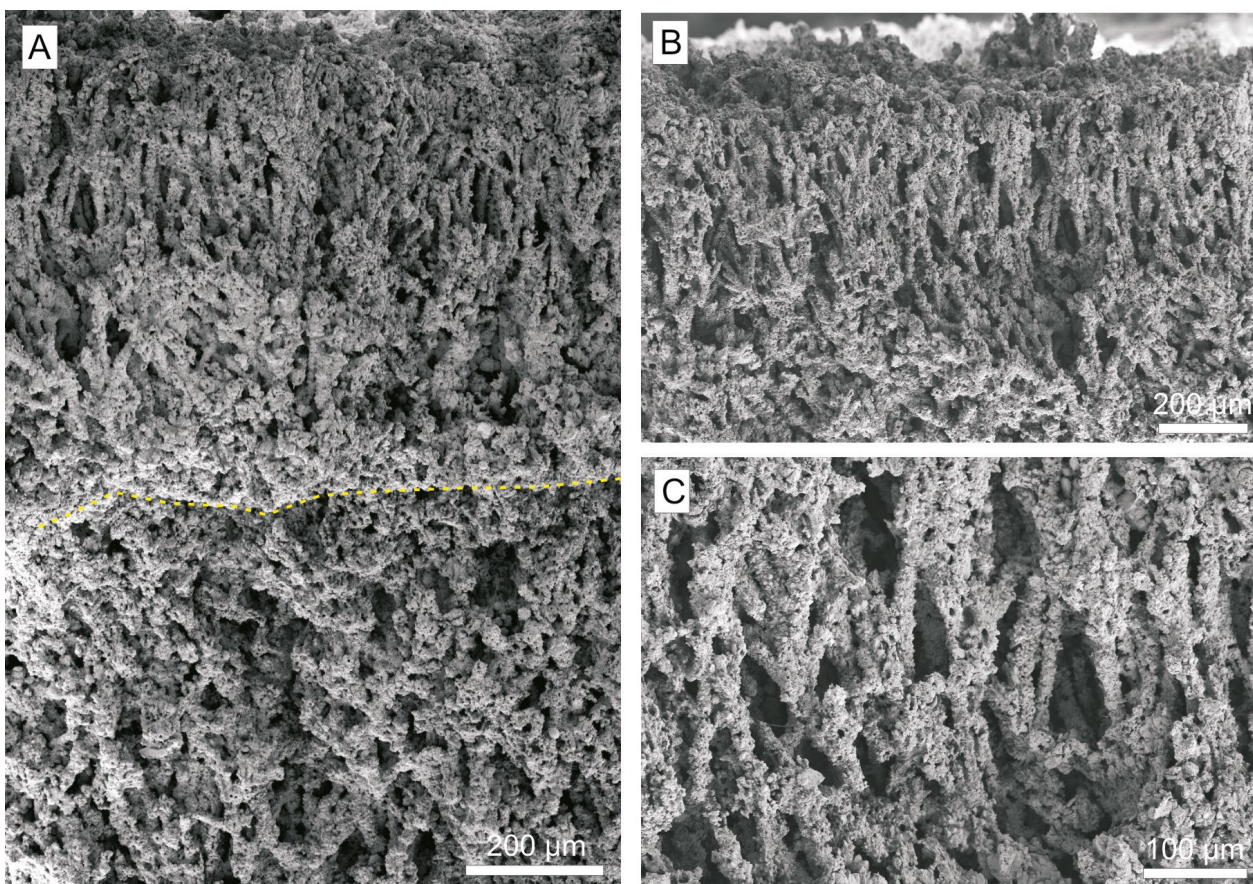


Fig. 5.— Images of porous lamination under SEM with secondary electrons. Note the clusters of multibranching stalks growing up from the surface of the bone. A. Boundary between two porous laminae (yellow dash-line) meaning the interruption of stalk growth. B and C. Details of the multibranching stalks.

scale. Subsequent burial by new input of detrital deposits in the alluvial fan determined the preservation.

In view of the average value (106.5°) of the inner Schreger angles of the Cuadros specimen (Fig. 3) and the model by Palombo & Villa (2001; Fig. 3F), the specimen would coincide with the genus *Palaeoloxodon*.

The genus *Mammuthus* presents inner Schreger angles less than 90° and therefore narrower than in the *Palaeoloxodon* (Fisher *et al.*, 1998; Agostini *et al.*, 2012). The values of the outer Schreger angles of *Mammuthus*, in the dentine-cementum junction, are higher than the inner Schreger angles (Palombo & Villa, 2001, 2007; Trapani & Fisher, 2003; Agostini *et al.*, 2012). Pawłowska *et al.* (2014) found Schreger angles reaching 120° in the dentine-cementum junction for *Mammuthus*. But the Schreger angles measured in the studied specimen are not located at

the dentine-cementum junction; they are inner angles, and therefore taxonomic assignment to the genus *Mammuthus* is discarded.

Analysis of dentinal tubule density for taxonomic determination was discarded due to the fact that the Schreger angles in this case sufficed to identify the genus *Palaeoloxodon*. According to Agiadi & Theodoru (2005), dentinal tubule density would not present a discriminating power between *Mammuthus meridionalis* and *Palaeoloxodon antiquus*, for example. Moreover, previous authors report that the dentinal tubule density may change depending on the distance from the pulp cavity—toward the outer surface of the tusk, the dentinal tubules branch, anastomose and fuse (Agiadi, 2001). Thus, measuring the density of the tubules, at random distances from the pulp would not provide reliable results, just as comparing the Schreger angles of outer and inner

positions in the tusk would be insufficient. The use of inner Schreger angles is therefore held to suffice for identifying the studied sample as *Palaeoloxodon*.

The average value (106.5°) of the inner Schreger angles obtained for the Cuadros specimen (Fig. 3) is coincident with only two different species according to the model proposed by Palombo & Villa (2001; Fig. 3F): *Palaeoloxodon antiquus* and *Palaeoloxodon falconeri*. However, *Palaeoloxodon falconeri* can be discarded as it is a typical island dwarf proboscidean from Sicily (Romano *et al.*, 2019). The tusk fragment found in the Cuadros outcrop can parsimoniously be said to correspond to *Palaeoloxodon cf. antiquus* Falconer et Cautley, 1847.

Palaeoloxodon was a genus of the Order Proboscidea (Family Elephantidae) that originated in Africa in the Early Pleistocene and dispersed throughout Central and Southern Europe to Asia during the latest Early Pleistocene, where it rapidly differentiated into various species (e.g. Larramendi *et al.*, 2020). *Palaeoloxodon antiquus* lived in Europe during the Middle and Late Pleistocene, with a wide distribution and diversification of dwarfed insular descendants (see Larramendi *et al.*, 2020). The earliest occurrence of this straight-tusked elephant in Europe is documented around 600 – 850 Ka (Madurell-Malapeira *et al.*, 2010; Lister, 2015). Its last appearances are post-Eemian, at ~35 ka (Sousa & Figueiredo, 2001; Mol *et al.*, 2007; Palombo *et al.*, 2010; Athanassiou, 2011; Palombo, 2014) but dwarfed species of the genus *Palaeoloxodon* inhabiting Mediterranean islands persisted (~20 ka in Sicily for *Palaeoloxodon ex. gr. mnaidriensis*; Palombo *et al.*, 2020). *P. antiquus* showed a broad ecological adaptation, and has been reported from moderate, humid and warm climates (Garutt & Vangengeim, 1982; Stuart, 1991; Konidaris *et al.*, 2018); it lived in forested areas where it fed on leaves, branches and soft grass (Garutt, 1972, 1986).

According to Maslim & Ridwell (2005) and Clark *et al.* (2006), major climatic changes at a global scale occurred in the latest Early Pleistocene had an important impact on the composition of mammalian assemblages. In the neighbouring Guadix-Baza Basin, numerous sites (Baza-1, Fonelas P-1, Venta Micena, Barranco León, Fuente Nueva-3, Huescar-1) show diverse fauna of the Pliocene to Early

Pleistocene, composed by Hyanidae, Felidae, Canidae, Ursidae, Mustelidae, Cervidae, Bovidae, Elephantidae, Equidae, Giraffidae, Rhinocerotidae, Hippopotamidae and Suidae, as well as numerous micromammals (Arribas & Palmqvist, 1998; Arribas *et al.*, 2009; Martínez-Navarro *et al.*, 2010; Rook & Martínez-Navarro, 2010; Medin *et al.*, 2017; Rodríguez-Gómez *et al.*, 2017; Ros-Montoya *et al.*, 2017, 2018; Espigares *et al.*, 2019). The faunal turnover occurring around the Early/Middle Pleistocene transition in Iberia involved the extinction of most of the Early Pleistocene large carnivoran taxa such as the giant hyena *Pachycrocuta brevirostris*, the sabre-tooth felid *Megantereon whitei*, the jaguar *Panthera gombaszogensis* and the canid *Lycaon lycaonoides*. Herbivores were also affected, including two horse species, *Equus altidens* and *Equus sus-senbornensis* (Martínez-Navarro *et al.*, 2009, 2018). Species of African origin arrived at Europe by this time (Martínez-Navarro & Rabinovich, 2011): the spotted hyena *Crocuta crocuta*, the lion *Panthera leo*, the leopard *Panthera pardus*, the auroch *Bos primigenius* and the straight-tusked elephant (recorded in the Cuadros outcrop) *Palaeoloxodon antiquus*. At the same time, taxa of Asian origin, such as the steppe mammoth *Mammuthus trogontherii*, the deer *Cervus elaphus*, an Indian bovid *Hemibos galerianus*, and the horse *Equus ferus*, among others, reached Iberia (Martínez-Navarro *et al.*, 2009; Madurell-Malapeira *et al.*, 2010).

In comparison with the neighbouring Guadix-Baza Basin, the record of large Middle Pleistocene mammals recorded in the Solana del Zamborino outcrop (Fonelas) comprises Felidae (*Felis*, *Lynx* and *Panthera*), Canidae (*Canis* and *Vulpes*), Cervidae (*Capreolus*, *Cervus*, and *Dama*), Bovidae (*Bison* and *Bos*), Elephantidae (*Mammuthus* and *Palaeoloxodon*), Equidae (*Equus*), Rhinocerotidae (*Stephanorhinus*), Hippopotamidae (*Hippopotamus*), Suidae (*Sus*) and Cercopithecidae (*Macaca*) (Botella-López *et al.*, 1976; de Porta, 1976; Alberdi & Ruiz-Bustos, 1985; Martín-Penela, 1983, 1988).

The Middle Pleistocene examples of *Palaeoloxodon antiquus* in South Spain have been reported from fluvial terraces along the Western Guadalquivir Basin by the localities of La Rinconada, Hornachuelos, and Almodóvar del Río in Sevilla and

Table 1.— Record of the Late Miocene to Pleistocene Proboscidean in Andalusia, South Spain with indication of outcrops and authors.

Outcrop	Turolian	Pliocene	Lower Pleistocene	Middle Pleistocene	Upper Pleistocene	Authors
Alfacar (Granada)	<i>M. borsoni</i> , <i>A. arvernensis</i>					Aguirre (1958, 1974)
Barranco Quebradas Huescar 3 (Granada)		<i>A. arvernensis</i>				Alberdi & Ruiz-Bustos (1989)
San Clemente-1 (Granada)		<i>A. arvernensis</i>				Martínez-Navarro et al. (2006)
Baza 1 (Granada)		<i>M. borsoni</i> and <i>A. arvernensis</i>				Ros-Montoya et al. (2017)
Huélago (Granada)			<i>M. meridionalis</i>			Alberdi et al. (2001)
Fonelas P-1 (Granada)			<i>M. meridionalis</i>			Arribas et al. (2001)
Zújar (Granada)			<i>M. meridionalis</i>			Agustí & Oms (1998)
Láchar (Granada)			<i>M. meridionalis</i>			Aguirre (1974), Ros-Montoya (2010)
Pantano Cubillas (Granada)			<i>M. meridionalis</i>			Aguirre (1974)
Cortijo Sabinas (Granada)			<i>M. meridionalis</i>			Ros-Montoya (2010)
Cortes de Baza (Granada)			<i>M. meridionalis</i>			Aguirre (1958)
Barranco del Paso (Granada)			<i>M. meridionalis</i>			Gibert et al. (1992)
Venta Micena (Granada)			<i>M. meridionalis</i>			Palqvist et al. (1996, 2005)
Barranco León (Granada)			<i>M. meridionalis</i>			Martínez-Navarro et al. (2004)
Fuente Nueva 3 (Granada)			<i>M. meridionalis</i>			Martínez-Navarro et al. (2003)
Huésca 1 (Granada)				<i>M. meridionalis</i>		Ros-Montoya et al. (2018)
Cúllar Baza 1 (Granada)				<i>M. trongontherii</i>		Alberdi et al. (2001)
Cortijo Daimuz (Granada)				<i>M. trongontherii</i>		Ros-Montoya (2010)
Solana del Zamborino (Granada)				<i>M. trongontherii</i> and <i>P. antiquus</i>		Martín-Penela (1988), Ros-Montoya (2010)
Loja (Granada)				<i>P. antiquus</i>		Ros-Montoya (2010)
Cuadros (Jaén)				<i>P. cf. antiquus</i>		This work
Hornachuelos (Córdoba)				<i>P. antiquus</i>		van Made & Mazo (2001)
Almodovar del Río (Córdoba)				<i>P. antiquus</i>		van Made & Mazo (2001)
El Pirulejo (Córdoba)				<i>P. antiquus</i>		Cortés-Sánchez et al. (2017)
La Rinconada (Sevilla)				<i>P. antiquus</i>		van Made & Mazo (2001)
Jarillas (Sevilla)				<i>P. antiquus</i>		Baena-Escudero et al. (2014)
El Padul (Granada)					<i>M. primigenius</i>	Aguirre et al. (1973), Álvarez-Lao et al. (2009)

Córdoba provinces (Van der Made & Mazo, 2001; Baena-Escudero *et al.*, 2014; Table 1). Moreover, Cortes-Sánchez *et al.* (2017) reported this species from the Cave of El Pirulejo (Córdoba province). In the Granada Basin, *P. antiquus* has been identified from the Middle Pleistocene of a Loja outcrop (Ros-Montoya, 2010; Table 1). The eastern record of *P. antiquus* in South Spain pertains to the Guadix-Baza Basin (Granada province) by the Solana de Zamborino outcrop (Table 1; Martín-Penela, 1988). The *P. cf. antiquus* recorded from the Cuadros outcrop is 47 km North of Solana de Zamborino and would be easily connected with the Guadix-Baza Basin through the strait between Sierra Mágina and Sierra de Cazorla relief, which constituted the gateway to the Guadalquivir Basin. Therefore, the record of *Palaeoloxodon cf. antiquus* from the Cuadros outcrop connects the populations of *P. antiquus* from the Western Guadalquivir Basin with those of the Guadix-Baza Basin. Seasonal migrations between low lands of the Western Guadalquivir Basin (outcrops at 10 – 200 m above sea level), and high lands of the Granada Basin (outcrops at 500 – 600 m) or the Guadix-Baza Basin (outcrops at 900 – 1200 m) are not discarded. The studied outcrop, 550 m high, lies potentially along the way from the Guadalquivir Basin to the Guadix-Baza Basin. In this sense, African elephants (*Loxodonta africana*) present seasonal movements related to vegetation dynamics, in turn ruled by dry and wet conditions (e.g. Wittemyer *et al.*, 2007; Wall *et al.*, 2013; Bohrer *et al.*, 2014).

The age of the alluvial fan where the studied tusk remain was recorded is inferred from comparisons with terraces of Guadalquivir and other tributary streams, ranging from 600 to 32 ka (Middle to Late Pleistocene). However, the fact that the record of *P. antiquus* in South Spain is reported exclusively from the Middle Pleistocene in the Western Guadalquivir Basin, Granada Basin and Guadix-Baza Basin (e.g. Martín-Penela, 1988; Van der Made & Mazo, 2001; Ros-Montoya, 2010; Baena-Escudero *et al.*, 2014) leads us to infer a Middle Pleistocene age for the alluvial fan. Still, we cannot totally discard a Late Pleistocene age for this fossil remain.

Conclusions

This work reports the first record of an elephantidae from the eastern sector of the Guadalquivir foreland Basin (Jaén province). The remain was retrieved from conglomerates deposited in the alluvial fans downslope of the outermost mountain front of the Betic Cordillera, more precisely from Sierra Mágina. These fans developed during the Middle to Late Pleistocene, associated with an intense erosive phase of the young reliefs of the mountain front.

The remain is a fragment of a fossil tusk (74 cm length) associated with high energy detritic sediments ranging from coarse sands to boulders, transported by water streams at the foot of the mountains. The fossil bone is mostly coated by a carbonate-laminated crust (< 2 cm). Its detailed analysis under thin section and SEM evidences a porous laminated fabric of phytal appearance (clusters of multibranching stalks). These structures are interpreted as fossil bryophytes. Therefore, the disarticulated tusk would have been transported and probably fragmented by surficial water streams in a high energy context. The surface of the tusk was covered by mosses that cemented early on. This carbonate crust surrounding part of the tusk favoured its preservation in a high-energy environment, while preservation was likewise aided by fast burial.

The analysis of the Schreger lines in the internal structure of the tusk allows us to assign this remain to the straight-tusked elephant *Palaeoloxodon cf. antiquus*. This taxon has been reported from the Middle Pleistocene of the Western Guadalquivir Basin (Sevilla and Córdoba provinces) and neighbouring basins such as Granada Basin and Guadix-Baza Basin (Granada province). Consequently, the specimen studied in the southeastern Jaén province (Eastern Guadalquivir Basin) would connect the populations of *P. antiquus* from the Western Guadalquivir Basin and the Guadix-Baza Basin. Seasonal migrations between low lands of the Western Guadalquivir Basin and high lands of the Guadix-Baza and Granada basins are not discarded.

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