AVIAN EGGSHELL REMAINS IN THE HUMAN BEARING LEVEL TD6 OF THE GRAN DOLINA SITE (EARLY PLEISTOCENE, ATAPUERCA, SPAIN)

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1

Avian eggshell remains in the human bearing level TD6 of the Gran Dolina site (Early Pleistocene, Atapuerca, Spain)

Abstract

The site of Gran Dolina (Atapuerca, Spain) has a 19-meter-thick Lower and Middle Pleistocene infilling, divided into eleven levels. This work is focused on the level TD6 (0.8-0.9Ma), consisting of a succession of debris flow and fluvial facies with a high diversity of vertebrates, including *Homo antecessor*. Here we describe for first time eggshell fragments from Atapuerca, recovered by screen washing of sediments from the excavations. The 22 eggshell fragments recovered are small and poorly preserved, with all material showing signs of abrasion. All eggshells have smooth outer surfaces, densely packed mammillae, and are multi-layered. Thus, they can be identified as avian eggshells. Most fragments were relatively well intact, with no signs of recrystallisation, as evidenced by cathodoluminescence analysis, however the degree of abrasion of the fragments hindered the identification of some ultrastructural characters. Three taxa have been identified: Charadriiformes, Gruidae and Anseriformes (all recorded in the TD6 assemblage by osteological remains). The association supports the presence of water bodies close to the site. The relatively high diversity of ootaxa in the small sample size analysed suggest that a wide range of the nesting species inhabited surrounding areas of Gran Dolina at the moment of accumulation of the TD6 level.

Keywords: eggshells; Aves; Early Pleistocene; Atapuerca; Gran Dolina

2

Introduction

The amniote eggshell

The amniote eggshell is a complex biomaterial composed both of organic (proteins) and inorganic (calcium carbonate) phases (Erben, 1970). Its mineralized composition provides them with a high preservation potential (Hayward, 2000), and as such they are common fossils in many continental paleontological and archaeological sites. Wilhem Von Nathusius performed the first comparative study of avian eggshells at the end of the 19th century (Tyler 1964). The first references of fossil eggshells come from the mid-century 19th (Buckman 1859; Pouech 1859; Meyer 1860), but the exhaustive analysis of the fossil eggshells had to wait almost a century until the first dinosaur eggs were studied in detail (e.g. Andrews 1932). These studies where limited due to the difficulties in assigning eggs to corresponding taxa. Gervais (1877) was the first in thin-sectioning eggshells to solve the taxonomic affinity of Pouech's eggshells, 50 years later Van Stalen (1925) did the same with Mongolian remains. In the second half of the 20th the first parasystematic classifications of the eggs and eggshells appeared (e.g. Zhao 1979). Mikhailov (1991, 1997a, b) reviewed all previous classifications, concerning also extant avian taxa, laying the foundations for paleoology (Mikhailov et al. 1996).

The conservative architecture of the eggshell, especially in the case of avian eggshells, makes difficult the assignation of fossil eggshells to a particular species, and most eggshell attributions are restricted to large clades (Mikhailov 1997a). Nevertheless, despite their limited taxonomic value, eggshells are a source of both paleoethological and paleoenvironmental information, as its calcite composition make eggshell fragments and eggs an ideal source for $\partial^{18}O$ isotopic analyses (Erben et al. 1979; Johnson et al. 1997; Amiot et al. 2017).

Eggshells in Quaternary sites

Quaternary and Holocene ratite eggshells, commonly found in archaeological sites, have been studied in detail (Kai et al. 1988; Texier et al. 2010; Fernández et al. 2016; Lomoschitz et al. 2016; Miller et al. 2016), with some works using eggshells for dating archaeological sites (Clarke et al. 2007). The analyses of non-Ratite eggshells are much scarcer (Keepax 1981; Sidell 1993a, b, Beacham and Durand 2007), because of the difficulties in eggshell preparation and diagnosis (Sidell 1993 a, b). Recently, biochemical

3

approaches have allowed the systematic study of eggshells in archaeological sites (Stewart et al. 2013) but this method is destructive and limited to very recent localities.

Objectives

Eggshells can provide important insights on fauna associations not recorded by other fossil remains yet has rarely been applied to Holocene and Quaternary localities due to the lack of interaction between paleoology (a mineralogical and paleontological discipline) and zooarchaeology (archaeology discipline). In archaeological articles focused in eggshells, only studies dealing with modern eggshells are cited, even when dealing with methodologies and applications of the eggshell studies (e.g. Clarke et al. 2007; Stewart et al. 2013).

This lack of paleoological references further emphasises the need to integrate its approaches to aid in paleoenvironment and paleoethological reconstructions.

Here we present the first paleoological analysis on avian eggshells concerning Quaternary eggshells from the Iberian Peninsula. We discuss the probable avian fauna that laid those eggs and compare the association with the osteological record of the same site in order to ascertain the environment that surrounded the site in the moment of the accumulation of the remains. Also, we provide a taphonomic analysis to explain how these remains were incorporated in the taphocenoses. The application of the paleoology techniques in Quaternary eggshell remains will add a considerable amount of information not only about the avian assemblages of the past, but also concerning the environment, the climate and the use of the cave during the deposit of the archaeo-palaeontological levels.

Geographical and geological settings

The Gran Dolina site

The Gran Dolina is one of the Sierra de Atapuerca archaeo-palaeontological sites, located near to the city of Burgos, Spain (Figure 1(a)). These sites are well known for providing a complete record of Quaternary archaeological, palaeontological, climatic, biodiversity, and anthropological changes spanning over nearly 1.5 million years (Arsuaga et al. 1993, 1997; Carbonell et al. 1995, 2008; Bermúdez de Castro et al. 1997; Rodriguez et al. 2011; Cuenca-Bescós et al. 2016). The sites of Trinchera del Ferrocarril

4

in Atapuerca were exposed during the construction of a railway trench running southeast to northwest through the Atapuerca range (Figure 1(b)). Years later, Trinidad de Torres Perez Hidalgo highlighted the paleontological importance of the sites of Trinchera del Ferrocarril in his quest for fossil bears in the Iberian Peninsula.

The Atapuerca sites are cave infillings, belonging to the Las Torcas karst system which developed in Late Cretaceous marine limestones. The karst is divided into two systems: the one whose caves were exposed by the construction of the railway, called Trinchera del Ferrocarril, and one internal, called the Cueva Mayor System. The Cueva Mayor system includes Galeria del Sílex, Galería Baja, Galería del Silo, Galería de las Estatuas, Portalón and Sima de los Huesos Sites. Trinchera del Ferrocarril includes Gran Dolina (shortened to TD, Trinchera Dolina), Galería (TG) and Sima del Elefante (TE) (Ortega et al. 2013) (Figure 1(b)).

Figure 1 here.

The Gran Dolina (TD) is the longest stratigraphic section in Atapuerca. The site has a 19 meters-thick sequence divided in 11 lithostratigraphic units, numbered from TD1 to TD11 from the base to the top (Parés and Perez-González 1999; Campaña et al. 2017), only levels TD3 to TD11 presents abundant remains. The Lower Pleistocene sediments (TDLOW) from the level TD1 to TD7, have reverse polarity, and the Middle Pleistocene sediments (TDUP) from TD8 to TD11, have normal polarity (Figure 1(c), (d)). The polarity change that marks the boundary (between the levels TD7 and TD8) has been interpreted as the Brunhes-Matuyama boundary (Parés and Pérez-González 1995; Cuenca-Bescós et al. 2016).

The Gran Dolina sediments have yielded ample fossil and archaeological remains: human remains, lithic tools, other vertebrates, as well as scarce pollen and seeds (Carbonell et al. 1995; Sánchez-Marco 1999; Rodríguez et al. 2011; Terradillos-Bernal and Rodríguez-Álvarez 2014; Saladié et al. 2014; Allué et al. 2015; Rodríguez-Hidalgo et al. 2016; Bruner et al. 2017). Small vertebrates have also been analysed to infer environmental and climatic changes, revealing an open landscape and a rather warmer and more humid environment during the deposition of the analysed level in the vicinity of the cave than today (Cuenca-Bescós et al. 1995, 2001, 2005, 2011, 2017; Blain et al. 2008; Lozano-Fernández et al. 2013).

5

The importance of the Gran Dolina site resides in the amplitude of the sequence, covering the time lapse between 1 Ma and 300 ka (Moreno et al. 2015), and also in the recovering of a human fossil collection that enabled the description of the only human species discovered in the Iberian Peninsula, *Homo antecessor* (Bermúdez de Castro et al. 1997).

TD6 settings

The fossil eggshells that are studied here belong to the Early Pleistocene, level 6 (TD6), of the Gran Dolina. This level also contains human remains and evidence of human occupation (Bermúdez de Castro et al. 1997, 2008). The level TD6 have been dated with ESR-OB as between 800 and 900ka (Moreno et al. 2015).

The TD6 level of the Gran Dolina is a 3m-thick deposit divided into three subunits, which are from the bottom to the top: TD6.3, TD6.2, and TD6.1 (Pérez-González et al. 2001, Campaña et al. 2017) (Figure 1(e)). TD6 consist in allochthonous sediments. The TD6.3 (2m) subunit is mainly formed by debris flow facies. TD6.2 (0.5m) is formed by channel and floodplain facies, and it ends at the top with another debris flow layer. The upper TD6 subunit, TD6.1 (0.5m) is formed again by channel facies and floodplains (Campaña et al. 2017).

Taphonomic analysis carried out in the TD6 level points that the large vertebrate fossil remains appear *in situ* (Saladié 2009). The accumulation in the sublevel TD6.3 is the result of the using the cave as a den by hyenas, with sporadic occupations by hominids (Saladié et al. 2017). The TD6.2 level contains human remains that were mainly accumulated along with other large vertebrates by the hominin themselves, which used the cave as a home (Saladié et al. 2011). In addition, this subunit has also provided evidences that the cave was episodically occupied by carnivores (Saladié et al. 2014). The large vertebrate remains of sublevel TD6.1 are related to the presence of hyena latrines within the cave (Pineda et al. 2017). Regarding small vertebrate faunas, the small mammal accumulations are caused primarily by the action of nocturnal birds of prey, as *Strix aluco*, the Tawny owl, and secondarily by mammal carnivores, and transported by flows (Fernández-Jalvo and Andrews 1992; Fernández-Jalvo 1995). Nevertheless, squamate and amphibian accumulation seems to be due to in-situ mortality (Blain et al. 2008). The eggshells analysed in the present work come from the TD6.1 sublevel.

6

Bird remains from the Atapuerca sites have been analysed by several authors (Sánchez-Marco 1987, 1995, 1999, 2004, 2005; Rosas et al. 2001; Núñez-Lahuerta et al. 2016a, b), with level TD6 yielding more than 30 different taxa (Table 1). The avian association in the TD6 level is dominated by open country species and bushland and inland water species (Sánchez-Marco 1999). Same results were given by mammals, amphibian and reptile squamates, which reflected a humid and relatively open environment (Cuenca-Bescós et al. 2005; Blain et al. 2008),

Table 1 here.

Material and Methods

This work represents the first eggshell analysis carried out in the Atapuerca sites. Twenty-two eggshell fragments were recovered during the evaluation of the bird remains on the samples.

Field work

The samples were recovered after washing and sieving the sediments of the Gran Dolina TD6 level extracted during the field campaigns. The preparation of the sediments for the recovery of microfaunal remains is a process that takes place simultaneously to the Atapuerca excavation campaign each year over 1.5 months. Eggshell remains are not usually found in the sediment of these sites; for now, only one sample (12kg) has provided eggshell fragments: TD6.1 G12 680-690; hereafter, further analysis of more samples will be performed.

The sediment samples from the TD6 levels were processed by water and sieving to separate the small fossil remains from the clay matrix. A water motor pump extracts water from the Arlanzon River, and the water is allowed to drop over a sieve platform (superimposed 10.5 mm, 5mm and 0.5mm mesh screens) where the samples are located, allowing the water to remove the matrix. The obtained sample (concentrate) contains fragments from the cave walls and lithic industry as well as complete and partial fossil remains of small vertebrates, large vertebrates and eggshells. When dried, those samples are packed and labelled with the field campaign year, the site, the square and the depth.

7

Laboratory work

The eggshells were recovered by picking out them from the rest of the remains in the Palaeontology Section of the Earth Sciences Department of the University of Zaragoza with the help of an Olympus SZ5 binocular microscope. An analysis protocol for eggshell was applied to these remains: Eggshells where cleaned in an ultrasound bath for five minutes and dried under standard room conditions. The 22 eggshell fragments were mounted, gold-coated and analysed with a JEOL6400 Scanning Electron Microscope (SEM), at the University of Zaragoza, using both secondary and backscattered electrons to obtain images of the shell features. Also X-ray analyses were performed in order to confirm the calcite composition of the eggshells. Backscattered Scanning Microscopy (BSE) and energy dispersive X-Ray spectroscopy (EDS) was used to detect diagenetic alterations in the eggshell (Moreno-Azanza et al. 2016), using Oxford Instruments INCA 300 X-Sight (133 eV a 5.9KeV) attached to the electronic microscope.

Radial sections of the seven best preserved eggshells were prepared at the Preparation of Rock and hard materials Service of the University of Zaragoza following the methodology of Quinn (1994). Every eggshell fragment was adhered to a methacrylate block, and embedded in epoxy resin. The resultant blocks were cut with a diamond saw. The sections were then polished and adhered to the glass which will contain the thin section (as the eggshells were fragile and scarce, only one fragment was placed in each glass). The sample was cut again, with a thin section added to the glass, and a fragment imbued in the methacrylate block. Thin sections were polished with silicon carbide until the thickness was approximately 30 microns, the optimum for the observation. The methacrylate block with the eggshell surplus is stored for future observations (Quinn 1994). The thin sections were analysed under a petrographic microscope (Olympus BX 41) and cathodoluminescence (Cl) analyses were performed using a Nikon Eclipse 50i POL microscope coupled with a cathodoluminescence system (CL8200 Mk5-1) at the Institut Català d´Arqueologia Clàssica in Tarragona, Spain.

All materials are housed at the Museo de Ciencias Naturales de la Universidad de Zaragoza (MPZ) (Canudo 2018).

8

Identification

Eggshell SEM images were studied applying the methodology established by Mikhailov (1997a). Several characters were analysed (Figure 2): presence of recognizable layers, surface ornamentation, pore shape (Figure 2(a)), mammillae diameter and distance between mammillae (between ten and thirty measurements per eggshell fragment, depending on the state of the surface) (Figure 2(b)). Also, the thickness (five measurement per fragment), the ratio between the thickness of the Continuous Layer (CL) and the Mammillary Layer (ML), and the relation between the External Zone (EZ) and the Squamatic Zone (SqZ) were measured using ImageJ Software (Schneider et al. 2012). The obtained data were compared with those provided by Mikhailov (1997b).

Descriptive terminology follows Mikhailov (1991, 1997a) (Figure 2). The comparisons were carried out based on the descriptions and microphotographs provided in the avian eggshell atlas by Mikhailov (1997b) which includes the descriptions of the eggshells of 20 different orders of extant birds. Despite the general recommendations of Mikhailov et al. (1996) we choose not to use a parataxonomic classification of the recovered materials due to the small sample size, which hinders quantification of the intra ootaxonomic variability. The recent age of the materials studied allowed us to compare eggshell characteristics to modern analogues at the genera level.

Figure 2 here.

Results

Systematic palaeontology

The recovered eggshell fragments present smooth outer surfaces. No specimens preserve the cuticle. When pore channels where observed, an angusticanaliculated pore system, with straight, narrow individual pores was observed. The mammillae are densely packed in the inner surfaces (Figure 3(b)), and all the recovered eggshells are multi-layered. Thus, they can be identified as avian eggshells, the shape of the pore system allows discarding also palaeognathae birds as producers (Mikhailov 1997b). Three ootaxa have been identified (Table 2, 3) based on eggshell thickness and relative proportions between the mammillary layer and the continuous layer and between the

9

squamatic zone and external zone. The variability between the eggshells of each ootaxa may be due to intraoospecific variation or to the presence of eggshells of different species within the same order. The analysis of further samples will shed light ~~on this~~.

Table 2 here.
Table 3 here.

Type A

Assignation: Order Charadriiformes Huxley, 1867

Charadriiformes indet.

Figure 3

Material: 12 eggshell fragments.

The ~~E~~eggshell fragments present sings of abrasion, with eroded radial sections, detachment of the external surface and eroded mammillae (Figure 3(a)). Some fragments exhibit secondary ~~precipitations~~ in the outer surfaces. This suggests that some autogenic crystals formed during fossilization.

Outer surfaces are smooth, with scarce round pore openings. Type A eggshells are thin (~~mean 154,5 μm, standard deviation 25,7~~) relative to the other eggshell types recovered. Two eggshell fragments present a thin (10 μm, N=3), highly eroded cuticle (Figure 3(a)). Its altered condition, with several removed patches, hinders further description.

Most of the radial sections are poorly preserved, but in some samples a smooth transition between the mammillae and continuous layer is observed (CL:ML= 4:1). The continuous layer is subdivided in a squamatic zone where prisms and column boundaries cannot be differentiated and a well-developed external zone, with marked prisms. The EZ/SqZ ratio is 0.3 on average. The squamatic zone is well preserved, with individual squamae of up to 5 microns, and presents sub-micron vesicles that are restricted to this zone (Figure 3(c)). An external zone can only be observed in some fragments, with a characteristic vertical crystal splitting that separated each prism. Each individual prism is wide compared to the other types (25-40 μm). The mammillae layer is composed of tightly packed barrel-shaped mammillae (H/W ratio <1).

10

The eggshell sections lacked distinct growth lines and displayed uneven distribution of organic matter through the shell, being most abundant in the mammillary layer and almost absent in the external zone. Under cross polarized light, the eggshells display columnar extinction. There is a relative increase in the width of the prisms towards the outer surface of the eggshell. Noteworthy is that some domains open in large fans towards the outer surface of the eggshell, killing neighbouring domains. Some crystals exhibit zoned extinction in concentric rings and dogtooth spar texture (Figure 3(c, d)).

The inner surfaces show tightly packed, reabsorbed mammillae (mean mammillae diameter 40 µm) (Figure 3(b)).

Figure 3 here.

The presence of a well-developed squamatic ultrastructure is diagnostic of the avian eggshell (Mikhailov 1991). The well-developed external surface allows discarding Passeriformes affinities of the eggshell (Mikhailov et al. 1997b). Thin eggshells with well-developed external zones and 0.3 EZ/SqZ ratios are present in several loosely related avian groups, including Pelecaniformes, Falconiformes, Anseriformes, Gruiformes, Charadriiformes and Cuculiformes (Mikhailov 1997b). Within these groups, the 4:1 CL: ML ratio is shared by only a few families, including Cathardidae (Falconiformes), Anseriformes (some *Cygnus* species), Rhynocheti (Gruiformes) and the suborders Laria and Alcae (Charadriiformes). Type A TD6 eggshells differ from the eggshell of the Anseriformes in having less elongated mammillae and lacking the bifurcating channels observed in some *Cygnus* eggshells (Plate 8F in Mikhailov 1997b). From Rhynocheti, the Type A eggshells differ in the lack of a mosaic pattern in the external surface and a slightly larger CL/ML ratio (Figure 10D in Mikhailov 1997b).

The Type A eggshells from the Gran Dolina level 6 in Atapuerca display the "typical" neognathe condition (Mikhailov 1997b) but with a particularly solid ultrastructure in the external zone. This condition is present in Charadriiformes (Plate 12 in Mikhailov 1997b) and in some falconiforms (Cathardidae; Figure 11 in Mikhailov 1997b). Within Charadriiformes, Lari and Alcae eggshells both present an external surface with a characteristic mosaic pattern, but this character cannot be observed in TD6 eggshells due to the eroded condition of the eggshells.

11

Although it was not possible to differentiate Type A eggshells from those of Catharidae, this family is restricted to the South American continent in the Pleistocene, allowing us to reject this attribution. Within Charadriiformes, the TD6 eggshells mostly resemble those of Lari and Alcae, although they lack the diagnostic mosaic pattern in the outer surface. This, together with the absence of seagull osteological remains in the Sierra de Atapuerca archaeological complex, makes this attribution unlikely. Therefore, we attribute Type A eggshells to Charadriiformes indet.

Type B

Order Gruifomes Bonaparte, 1854

Family Gruidae Vigors, 1825

Gruidae indet.

Figures 4

Material: 3 eggshell fragments

Eggshell fragments present signs of abrasion, with eroded radial sections and mammillae (Figure 4(a)).

Outer surfaces are smooth, with scarce elongated pore openings of around 33 μm in maximum diameter (N=3). Eggshells of the type B are the thickest of the assemblage (mean 340,3 μm, standard deviation 83,7).

There is a smooth transition between the mammillae and continuous layer (CL:ML= :1). The mammillae are significantly larger than in the type A eggshells (H:W=2:1), and some fragments present well preserved bases of the mammillae. An external zone can be observed in some fragments, with well-marked boundaries between prisms. These prisms are wide (25-50 μm). The EZ/SqZ ratio is 0.24 on average. Pore channels are straight and narrow (mean diameter of less than 20 μm) (Figure 4(b)). The channels broaden towards the outer surfaces, resulting in the funnel shaped, slightly elongated pore openings.

Organic matter is evenly distributed through the eggshell thickness. No defined grow lines can be seen in thin sections, but a certain degree of lamination in the organic matter distribution can be observed. The transition between the mammillary and continuous layer is more abrupt than in type A eggshells. Under cross polarized light, the eggshells display columnar extinction. There is a relative increase in the width of the prisms towards the outer surface of the eggshell, although less marked than in type A

12

eggshells. Some crystals exhibit dogtooth spar texture, suggesting that they may be autogenic crystals formed during fossilization (Figure 4(c, d)).

The inner surfaces show packed mammillae (mean mammillae diameter 70 μm).

Figure 4 here.

Up to 500-micron-thick eggshells with similar CL:ML ratios than those seem in Type B eggshells are present in many clades of Aves, including some Ratites, Gaviiformes, Procellariformes, Pelecaniformes, Ciconnidae, Balaenicipites, Falconiformes, Accipitridae, Anseriformes and Gruiformes (Mikhailov 1997b). From all those clades, with the exception of Anseriformes and some Gruiformes, Type B TD6 eggshells differ in the tall mammillae and relative thin external zone. From Anseriformes, the Type B eggshells can be easily differentiated in lacking the typical ratite like general arrangement shown in most Anseriformes (Fig. , Plate 8 in Mikhailov 1997b), with a sharp transition between the mamillary and continuous layer not observed in the Dolina eggshells.

Within Gruiformes, the thin external zone of the Type B eggshells only fits with the Gruidae family. Elongated pores are a diagnostic feature of this clade, as it is a very smooth transition between the squamatic and external zones (Mikhailov 1997b).

Type C

Order Anseriformes Wagler, 1831

 Anseriformes indet.

Figure 4

Material: 5 eggshell fragments

Eggshell fragments present signs of abrasion, with eroded radial sections and eroded mammillae.

Outer surfaces are smooth, and no pore openings can be seen in the studied sample (Figure 4(e)).

The eggshells are thin (mean 186.1 μm, standard deviation 7.0) and show an abrupt transition between a thick mammillary layer and the continuous layer (CL:ML=

13

1:1). The mammillae are tall (H:W ratio >2.1). The continuous layer has a thin, poorly differentiated external zone, although this may be due to a poor preservation. The inner surfaces show packed mammillae (mean mammillae diameter 48 µm).

Type C can be easily distinguished from Type A eggshells by an abrupt transition between a thick mammillary layer and the continuous layer. Thin eggshells with a 1:1 CL:ML ratio are not common in Holocene taxa and are restricted to the clade Anseriformes (Mikhailov 1997b). This clade is also characterised by an abrupt transition. Mikhailov (1997b) also reports 1:1 CL:ML ratios in some Proceralliformes, but no eggshell with this condition is figured in the Atlas. Furthermore, Type C TD6 eggshells further differ from those of the Proceralliformes in the shape of the mammillae, flatter in Proceralliformes (Plate 2 in Mikhailov 1997b) and tall in the Dolina eggshells. The lack of a well differentiated external zone is not congruent with an anseriform attribution, a condition present in all Passeriformes, Strigiformes and Pssittaciformes. Type C eggshells can be easily differentiated from the former by the presence of well-defined mammillae and from Strigiformes (Mikhailov 1997b) and Pssittaciformes (Figure 13 in Mikhailov 1997b) by its unusual CL:ML ratio. All of this, together with the abrasion of the outer surfaces reinforces the idea of a not preserved thin external surface, although additional specimens are needed to support this claim.

Taphonomy

Bioestratinomy

The low number of eggshell fragments recovered (less than two eggshell fragments per kilo); the small size of most of the fragments (less than 4 mm^2) and the clear evidences of erosion and abrasion observed in some fragments are coherent with an allochthonous origin of the fragments. An interesting piece of evidence supporting this is TD6.1 G12-2, an eggshell fragment in which non cratered and cratered bases of the mammillae can be observed (Figure 5(g,h)), suggesting that this fragment belong to an unhatched broken egg, with no signs of embryo that suffer significant transport prior to accumulation (Bravo et al. 2003; Oser and Jackson 2014). A certain amount of transport is also supported by the lack of preserved cuticle in all but two examined specimens. Furthermore, he single specimen that preserved part of the cuticle (Figure 3b) shows clear signs of abrasion.

14

Fossildiagenesis

Cathodoluminescence analyses show that the eggshell fragments here described are non-luminescent (Figure 5). This, together with a homogeneous low magnesian calcite composition determined with x-ray diffraction (Table 4) suggest that the original composition of the eggshells has been preserved unaltered.

Figure 5 here.
Table 4 here.

Nevertheless, the presence of authigenic calcite crystals in some eggshell fragments, evidenced by zoned extinction, dog tooth spar texture and microcrystalline calcite, suggest that a certain degree of alteration took place (Figure 10) (Moreno et al. 2016). No extensive recrystallization occurred, but some crystals may have been overgrown during fossilization. The lack of response to cathodoluminescence can be explained with a pure calcium carbonate composition of the fluids. The karstic nature of the deposit provides a source of such fluid, which partially could be the cause of the alteration of the Gran Dolina eggshells. Interestingly, despite the karstic nature of the cave no other carbonate fossils or crusts are preserved in the assemblage, thus carbonate precipitation has not been intense.

Discussion

Diversity

Despite the small size of the sample (n=22) and the relatively poor preservation of the eggshell fragments, three different eggshell types, were identified as belonging to three common groups of birds in the European Pleistocene. Type B eggshells are easily distinguished from other eggshells in the assemblage based on the high total shell thickness and wide mammillae diameter. Type A eggshells are the thinnest in the assemblage, and present small and tightly packed mammillae and a smooth transition between the mamillary and continuous layers, with clear differentiation between the squamatic and external zones. The columns observed in the external zone are also slenderer than those seen in Type B eggshells, due to a relatively thicker external zone. Finally, Type C eggshells are similar in total shell thickness to Type A and are easily

15

differentiated due to their 1:1 continuous to mammillary layer ratio. Thus, it can be inferred that the eggshell assemblage represents at least three different taxa that nested in the vicinity of the Gran Dolina cave at the moment of the deposition of the TD6 stratum. Also, the presence of more species belonging to the same orders cannot be ruled out.

Attribution to avian taxa and correlation with previous identification of species in TD6

The eggshells have been identified as belonging to Charadriiformes, Gruidae and Anseriformes. These three groups are common in European Pleistocene sites (Tyrberg 1998), and have been also identified in the avian assemblage of the level TD6 in the Gran Dolina (Sánchez-Marco 2005, 2006)

Several Charadriiformes species have been identified within the TD6 bone fossil assemblage in the previous analysis; the Eurasian dotterel (*Charadrius morinuells*), the black-tailed godwit (*Limosa limosa*) and the Eurasian woodcock (*Scolopax rusticola*) (Table 1). Representing the Gruidae family, the Baillon´s crake (*Porzana pusilla*) appears in the fossil bone assemblage recorded in the TD6 fossiliferous level (Table 1). Also, several representatives of the Anseriformes order appear within the bone remains recovered in the TD6 level: *Anas* sp., *Anas crecca* (Common teal*), Anas crecca/querquedula*, *Anas strepera/clypeata* and *Melanitta fusca* (Velvet scoter) (Table 1).

Palaeoenviromental implications

The TD6.1 sedimentary facies comprise wide channels laterally changing change to floodplains. It represents an environment with a stream inside de cave (Campaña et al. 2017). The sedimentological analysis of the sublevel TD6.1 point to a more humid moment in the Sierra de Atapuerca than in previous levels, reflected by the presence of channels. This is congruent with the environmental reconstruction analysis of the small vertebrates, which points to a more humid and warmer conditions (Cuenca-Bescós et al. 2005, 2017; Blain et al. 2008). Also, the taxa identified based on eggshell remains strongly support this reconstruction, as the three groups are related with the presence of water masses in the environments.

Despite the small sample size, we were able to identify eggshells belonging up to three different orders of birds. This is again coherent with an allochthonous origin of the eggshells, which do not represent the debris of a nest or rockery, but instead represent a

16

wider sample of the nesting species of the ecosystem that surrounded the Gran Dolina, covering the upstream of the hydric network of the area. The humid conditions and the presence of streams within the cave favoured the transport of the eggshells from outside to the inside of the cave along with the sediment.

Future eggshell studies in archaeological and paleontological sites

Despite that eggshell fragment are usual in archaeological sites (Stewart 2013) there are scarce studies of eggshells in Pleistocene sites. The study of eggshells from the level TD6 in the Gran Dolina cave represents the first attempt of study these avian remains in the Atapuerca sites.

The combined use of different techniques (SEM, petrography microscopy, cathodoluminescence and others) allows describing the fine architecture of the avian eggshells and assigning them to specific taxa. Also, it allows inferring the processes that lead to its preservation in archaeological sites. This can be a source of valuable information, as eggshells are good palaeobiological indicators (Erben 1979).

There is no major accumulation agent forcing the presence of the eggshells in the sites, although eggs can be sporadically consumed by mammals or birds. For this reason, the avian association inferred by the eggshells is mainly not subject to the predator bias. It also adds information to the avian record of the site, as it only reflects the presence of taxa nesting in the vicinity of the site, discarding migratory taxa that could blur the signal. That could allow giving a much more concrete picture of the landscape of the site in the moment of the accumulation, even giving the possibility of the study of patterns of seasonality.

On the other hand, eggshells could have a major role in the reconstruction not only of the landscape but can also become the source of $\partial^{18}O$ data than can be used for inferring palaeotemperatures.

Conclusions

The study of eggshells from the level TD6 in the Gran Dolina cave represents the first attempts of study these avian remains in the Atapuerca sites. 22 eggshell fragments were recovered from the Gran Dolina site. The fragments were recovered by washing and sieving the sediments from the level 6 of the site, dated 0.8-0.9Ma, in which the remains

17

of *Homo antecessor* were recovered. The sediments of the level 6 are allochthonous to the cave, and represent debris flows and channel and flood plain facies. The analyses performed to the fragments suggest that they were transported to the inside of the cave along with the sediment.

The eggshell association shows a moderate diversity, despite the scarcity of fragments in the site, as only one sample yielded eggshell remains (less than 2 eggshell fragments per sediment kilogram); however, the reanalysis of the site collection is currently underway, and more fragments are expected to be found. The three identified groups fit with Charadriiformes, Gruidae and Anseriformes eggshells. These groups are present in the TD6 assemblage by osteological remains. The eggshell association supports the idea of a humid environment, as the three identified groups are strongly related to water masses.

The preservation of the eggshells, along with the low concentration and the relative high diversity points that the eggshell assemblage is allochthonous to the cave. It does not represent the debris of a nest or rockery within the cave, but instead represent a wider sample of the nesting species of the ecosystem that surrounded the Gran Dolina in the moment of accumulation of the TD6 level.

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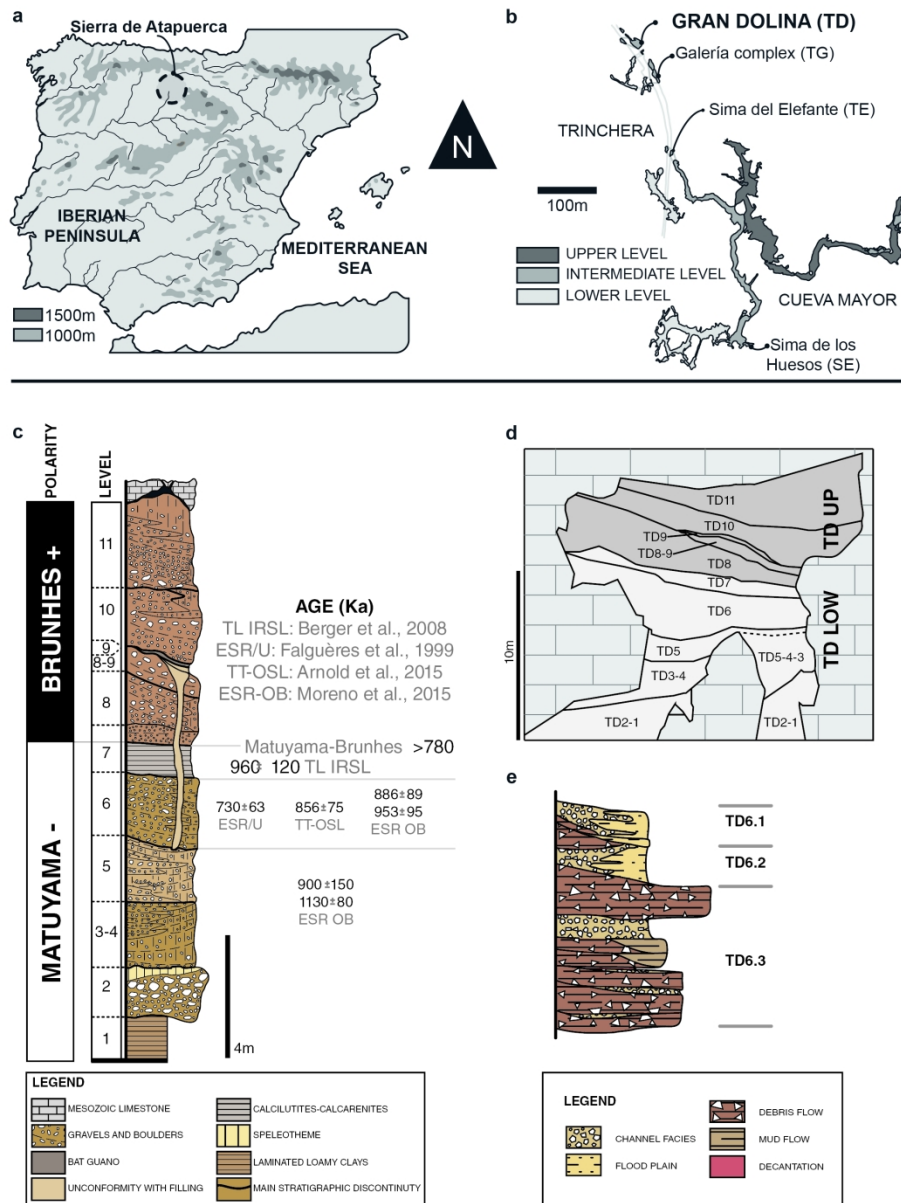
Geological and Geographical context of the Atapuerca complex. (a) location of the Atapuerca sites in Iberian Peninsula. (b) Atapuerca complex map. The dot points the Gran Dolina location. Modified from Ortega et al. 2017. (c) schematic stratigraphic profile of the Gran Dolina infill. Modified from Berger et al. 2008. (d) schematic view of the lithostratigraphic units and cave morphology of the Gran Dolina from the railway trench view. (e) Simplified sedimentary facies column of TD6 level. Modified from Campaña et al. 2017.

196x256mm (300 x 300 DPI)
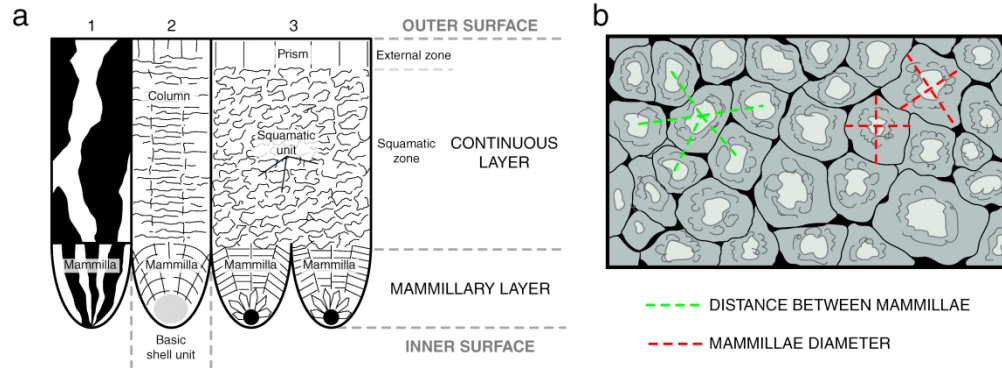
Avian eggshell structure. (a) general avian eggshell structure and nomenclature sensu Mikhailov (1991, 1997a, b). 1: under polarised light, 2: under non-polarised light, 3: electron microscope. (b) scheme of the eggshell inner surface: mammillae diameter and mammillae packaging measurement.
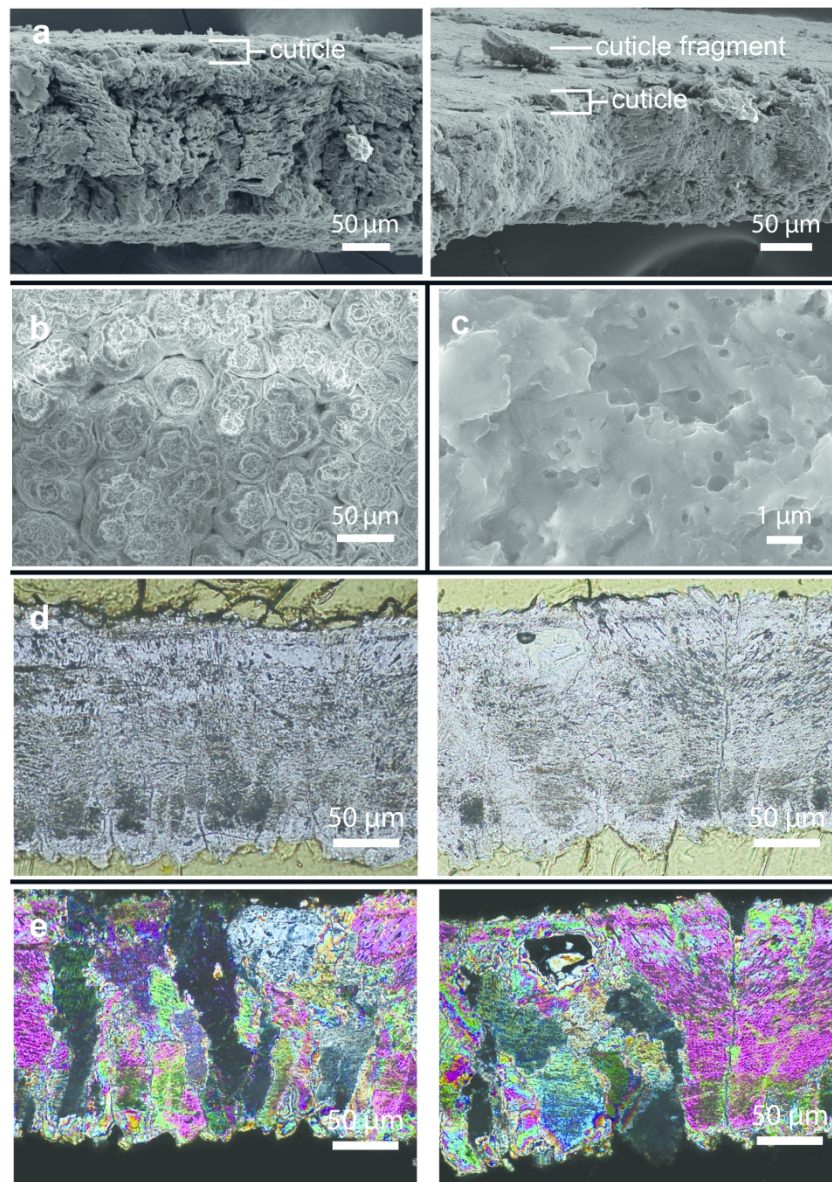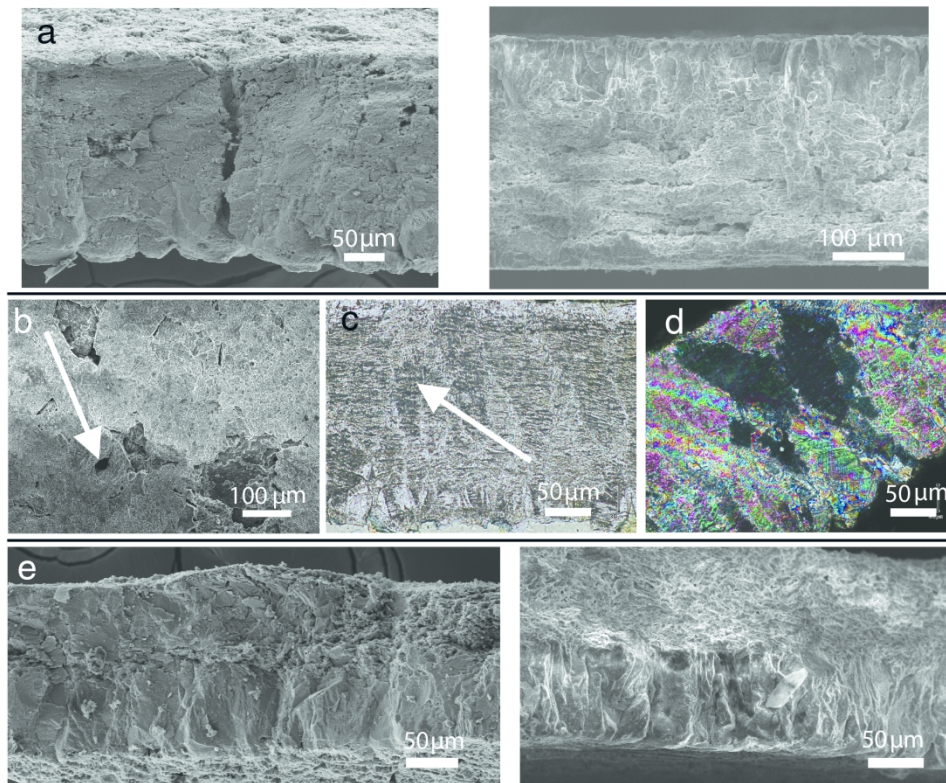
Type A eggshells under secondary-electron microscope (SEM) and petrographic microscope. (a) radial sections showing the ultrastructure of the eggshell (SEM) (TD6.1 G12-7/MPZ 2019/166 at left; TD6.1 G12-8/MPZ 2019/167 at right). (b) inner surface,showing the eroded mammillae (SEM) (TD6.1 G12-18/MPZ 2019/177). (c) Sub-micron vesicles in theSquamatic zone (SEM) (TD6.1 G12-9/MPZ 2019/168). (d) Petrographic microscope with non-polarized light(TD6.1 G12-4/MPZ 2019/163). (e) Petrographic microscope with polarized light. (TD6.1 G12-4/MPZ2019/163).

208x282mm (300 x 300 DPI)

Types B and C eggshells. (a) Type B under electron-microscope (SEM), radial sections showing the ultrastructure of the eggshell (TD6.1 G12-2/MPZ 2019/161 on the left, TD6.1 G12-6/MPZ 2019/165 on the right). (b) Detail of a pore opening in the outer surface (TD6.1 G12-6/MPZ 2019/165). (c) Type B eggshell under petrographic microscope (TD6.1 G12-1/MPZ 2019/160) non-polarized light (arrow points towards lamination of the organic matter). (d) (c) Type B eggshell under petrographic microscope (TD6.1 G12-1/MPZ 2019/160) polarized light. (e) Radial sections of Type C eggshells under secondary-electron microscope (SEM) (TD6.1 G12-14/MPZ 2019/173 on the left, TD6.1 G12-5 /MPZ 2019/164 on the right)

248x222mm (300 x 300 DPI)
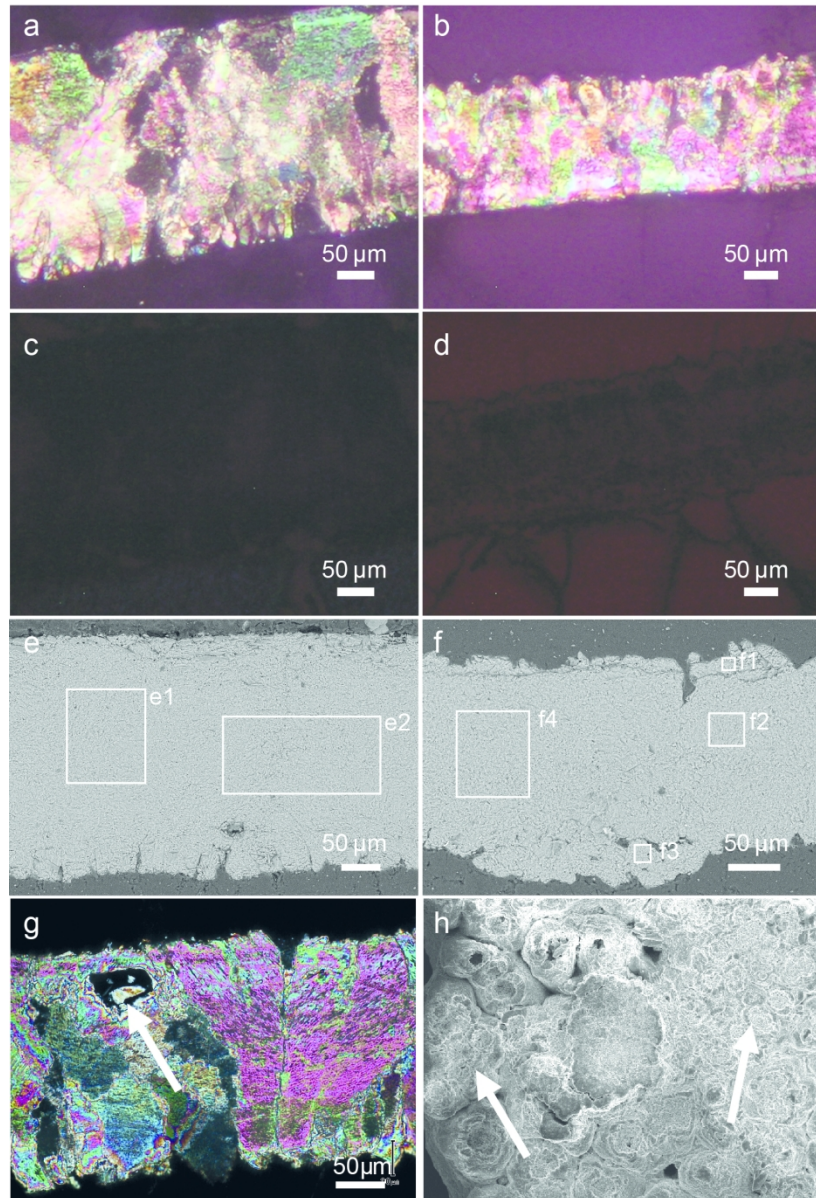
Chemical composition remarks of the analyzed eggshells. (a, b) Cross polarized microphotographs. (c,d) Cathodoluminescence microphotographs. (e, f) Backscattered electron images. See table 4 for energy-dispersive X-ray analysis for atomic composition. The homogeneous dark brown to dark blue luminescence is congruent with a homogeneous low magnesian calcite composition. Silica content is probably due to remains of the silica carbide used during polishing. (a, c, e) TD6.1 G12-6/MPZ 2019/165; (b, d) TD6.1 G12-4/MPZ 2019/163; (f) TD6.1 G12-9/MPZ 2019/168; (g) Radial section of TD6.1 G12-4/MPZ 2019/163 under petrographic microscope and polarize light showing authigenic calcite crystals. (h) Cratered and intact bases of the mammillae in the inner surface of TD6.1 G12-2/MPZ 2019/161.

144x212mm (300 x 300 DPI)

Order
Anseriformes
Falconiformes
Galliformes
Gruiformes
Charadriiformes
Columbiformes
Passeriformes

| Taxa identified in the TD6 assemblage |
|---|
| *Anas* spp., *Anas crecca*, *Melanitta fusca* |
| *Falco naumanni* |
| *Perdix paleoperdix, Coturnix coturnix* |
| *Porzana* sp., *Porzana pusilla* |
| *Charadrius morinellus, Limosa limosa, Scolopax rusticola* |
| *Columba livia/oenas* |
| *Melanocorypha calandra*, *Calandrella* cf. *brachydactyla, Galerida cristata*, *Lullula arborea*, *Alauda arvensis, Eremophila alpestris*, P*tyonoprogne rupestris*, *Hirundo rustica*, *Motacilla flava, Anthus pratensis, Cinclus cinclus, Prunella collaris, Prunella modularis, Turdus merula, Turdus iliacus, Turdus philomelos*, *Fringilla coelebs, Sturnus* sp., *Sylvia hortensis, Muscicapa striata, Emberiza citrinella,* Corvidae indet., *Corvus antecorax* |
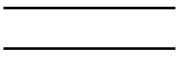
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	TYPE A	TYPE B	TYPE C
Thickness (µm)	150	300	180
CL:ML	4:01	2,5:1	1:01
Ez/Sqz	0.3	0.24	0.3
Intermamillary distance (µm)	36	60	45
Mammillae diameter (µm)	40	70	48

Sample		Type	Taxa
MPZ	Field number		
MPZ 2019/160	TD6.1 G12 1	-	Aves
MPZ 2019/161	TD6.1 G12 2	Type B	Gruiformes
MPZ 2019/162	TD6.1 G12 3	-	Aves
MPZ 2019/163	TD6.1 G12 4	Type A	Charadriiformes
MPZ 2019/164	TD6.1 G12 5	Type C	Anseriformes
MPZ 2019/165	TD6.1 G12 6	Type B	Gruiformes
MPZ 2019/166	TD6.1 G12 7	Type A	Charadriiformes
MPZ 2019/167	TD6.1 G12 8	Type A	Charadriiformes
MPZ 2019/168	TD6.1 G12 9	Type A	Charadriiformes
MPZ 2019/169	TD6.1 G12 10	Type A	Charadriiformes
MPZ 2019/170	TD6.1 G12 11	Type C	Anseriformes
MPZ 2019/171	TD6.1 G12 12	Type C	Anseriformes
MPZ 2019/172	TD6.1 G12 13	Type A	Charadriiformes
MPZ 2019/173	TD6.1 G12 14	Type C	Anseriformes
MPZ 2019/174	TD6.1 G12 15	Type B	Gruiformes
MPZ 2019/175	TD6.1 G12 16	Type A	Charadriiformes
MPZ 2019/176	TD6.1 G12 17	Type A	Charadriiformes
MPZ 2019/177	TD6.1 G12 18	Type A	Charadriiformes
MPZ 2019/178	TD6.1 G12 19	Type A	Charadriiformes
MPZ 2019/179	TD6.1 G12 20	Type A	Charadriiformes
MPZ 2019/180	TD6.1 G12 21	Type A	Charadriiformes
MPZ 2019/181	TD6.1 G12 22	Type C	Anseriformes

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Sample/Analysed area		O	Mg	Si	Ca
TD6.1 G12-6/MPZ 2019/165					
	e1	78.76	-	-	21.24
	e2	78.64	-	0.2	21.16
TD6.1 G12-9/MPZ 2019/168					
	f1	78.74	-	-	21.26
	f2	78.38	0.36	-	21.26
	f3	78.69	-	0.24	21.07
	f4	78.68	0.26	0.14	20.92