Fossils in Iberian prehistory: a review of the palaeozoological evidence

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ABSTRACT: This paper constitutes the first comprehensive review of animal fossils retrieved in Iberian archaeological sites. Out of 633 items from 82 sites, 143 were analyzed and a further 13 assessed and their status clarified by us on 20 sites. Among others, this study is the first one in Iberia to assess the role played by fossil scaphopods and to carry out a systematic description of shark teeth. The relevance of those 156 fossils we assessed through a comparison with all the finds located in the Iberian literature. Failure to report fossils properly did not allow us to warrant such status for 352 items. We believe that the poor record of fossils in Iberian archaeological sites is the result of a combination of methodological and theoretical constraints. For that reason, we contend that the items herein reported probably represent a fraction, however substantial, of the evidence at hand. In light of the contrasted relevance of fossils for addressing cultural issues, some recommendations and a plea for a more systematic and rigorous search of archaeological specimens are made.

KEYWORDS: Fossil, Shells, Scaphopods, sharks, Iberian Peninsula, Upper Palaeolithic, Neolithic, Copper Age, Bronze Age

1. Introduction

Traditionally the term fossil refers to any kind of direct or indirect evidence of organic remains (i.e., including molds and casts) and organic traces, such as trails, footprints and burrows. It includes all types of bodily remains, including bones, shells, teeth, leaves and mineralized plant remains as well as bioconstructions, bioinclusions in amber, remains produced by the activity of ancient organisms such as gastrolites and coprolites and occasionally geological traces related to the fossil (Raup and Stanley, 1978; Benton and Harper, 2009). Descending from theory to practice is not always straightforward and with regard to prehistoric sites, certain remains are readily recognized as fossils, but others are not.

Zooarchaeologists address the study of animal remains from archaeological sites with the proviso in mind that both those evidencing human activities, and those representing background (local) faunas, constitute elements contemporaneous with the human occupation (Reitz and Wing, 2008). Still, the possibility exists that a fraction of any archaeological fauna represents remains from species that lived well before the accumulation was produced (i.e., "fossils", in the broadest sense of the word). Oakley (1975) was the first to address this issue, and Gautier (1987) introduced the taphonomic group of reworked intrusives to take account of fossils found in archaeological deposits.

Though the evidence is scarce and not always devoid of controversy, fossils as testimonies of human collecting behavior have been first recorded on middle Pleistocene archaeological sites associated with pre-*sapiens* hominines. Flakes made from a fossil coral chert at Swanscombe (England) presently qualify as the oldest evidences of use of fossils by pre-sapiens humans, and probably also the bead-like Jurassic crinoid "plates" from Gesher Benot Ya'aqov (Israel) (Oakley, 1973, Edwards and Clinnick, 1980, Goren-Inbar, 1991, verb.com.). Surprisingly, despite the use of shells and feathers as ornaments reported on Mousterian and Chatelperronian sites (e.g., Riparo Fumane, Combe-Grenal, Les Fieux and Gorham´s), no reports exist of fossils being intentionally collected by Neanderthals (Soressi and d'Errico, 2007, Zilhão et al., 2010, Peresani et al., 2011, 2013, Morin and Laroulandie, 2012, Finlayson et al., 2012).

Starting with the Upper Palaeolithic, the practice of collecting fossils appears to become widespread in Europe. From that moment on, one witnesses the establishment of interchange networks that, in addition to raw materials and items such as shells, occasionally evidence long-distance transport of fossils (e.g. Taborin 1993, Eriksen 2002, Simetsberger, 1993, Steininger, 1995, Álvarez, 2009).

During the Holocene, from the latest stages of Prehistory to Classical Antiquity, fossil collecting became widespread in both the Old and New Worlds (Oakley, 1975; Wright, 1994; Colvin, 2011; Fujita and Melgar, 2014; Ramundo, 2011; Todd, 2014; Crook, 2014, with references therein). The Mesoamerican Pre-Columbian populations being a paradigmatic case in point (Lowery et al., 2011, Jiménez, 2017). Evidence of the esteem that fossils reached among Mesoamerican societies is a ca. 1 m long femur, probably a proboscidean from the extinct North American megafauna, that captain Hernán Cortés received as a gift in Tlaxcala (Díaz del Castillo, 1632). Still, it appears that it is only during Greek Classical Antiquity that fossils became deeply embedded within the fabric of society, fostering a number of mythological narratives (e.g. Mayor, 2000, 2010, Solounias and Mayor, 2004).

The Iberian Peninsula, one of the richest European regions in terms of fossil deposits, is noteworthy for the comparatively scarcity of fossils reported on its archaeological sites. The treatment of fossils the Iberian archaeological literature has been for the most part defective, with data scattered throughout the grey literature and protocols for reporting them essentially non-existent (see discussion). This is regrettable given that the record of fossils in Iberian archaeology dates back to the nineteenth century, and the few papers devoted to this subject have yielded outstanding results (e.g. Cáceres et al., 2019).

In this paper we combine a methodologically robust description of novel fossils from 18 sites (Fig. 1, Table 1) with comparison to all other finds previously reported in the Iberian archaeological literature. Geographical and archaeological background, as well as a brief description of the twenty archaeological sites from where 156 fossils are first reported in this paper, is included in the Supplementary Information. This approach allowed us to frame fossils in terms of broader spatio-temporal and cultural trends while critically assessing the fossil status of previous finds (Tables 2 and S1). We contend that the scarcity of fossil in Iberia is a construct due to a combination of factors that reflects a failure to grasp the cultural relevance of fossils.

1.1 *Introduction to identification of fossils for archeologist*

Contrary to established wisdom, with independence of the period and region considered, fossils constitute a recurrent theme in Prehistory. In Iberia several causes can be invoked to explain the scarcity of studies dealing with fossils. The first one, essentially stochastic, contends that this simply reflects the larger number of archaeological sites available for study in other countries (Taborin, 1993; Eriksen, 2002; see also references in Álvarez, 2009, Boyadziev, 2008; Bar-Yosef et al., 2010; Dimitrijevič et al., 2010). More intriguing is the possibility that up until now many archaeological fossils may have passed largely unnoticed. One compelling argument to back up such proposal is the sheer number of fossils that our restricted search on a handful of sites managed to unveil.

The unreliability of published records is one major reason to think that fossils have been regularly overlooked. Indeed, many published items are questionable because of a systematic failure to justify their fossil and taxonomic status, and a substantial number of them could not be found upon request (see discussion). Both problems may simply reflect a failure to grasp the relevance of fossils for archaeological research. The scope of such failure reaches beyond specific categories and links with the humanistic tradition of Iberian archaeology, where natural items are not often a major cause of concern. In our case, this generates data of questionable value, raising doubts over a substantial fraction of the evidence. To address this matter in the future, focus should be laid on implementing protocols to recognizing and reporting data properly.

Identification lies at the very core of this problem, one first issue being how to acknowledge fossil status. This issue may seem trivial but for not well mineralized fossils or others not belonging to readily recognizable groups (e.g. trilobites, ammonites, etc.), a high level of expertise is required to achieve a correct interpretation. The problem is all the more pressing in archaeological deposits, where fossils are scarce, often found in isolation, worked, fragmented and devoid of any archaeological/paleontological context. Matters become more complicated when fossils are phenotypically indistinct from extant species. This would be the case of the Tyrrhenian molluscs in the Mediterranean, frequent in outcrops dotting the Iberian coastlines from Catalonia to the Algarve. These fossils are often members of living species, look strikingly "recent", and, as we will see, are recurrent items on sites from this region. In the absence of discriminating features such as shine, weight or incrustations, and no access to reference collections, analysts need to be aware that specimens they consider as recent might, in fact, represent fossils. Failure to achieve proper identifications often reflect a failure to contact palaeontologists. This eventually translates into gross misinterpretations as would be to consider fossil conch shells evidence of shell-fishing activities or fossil shark teeth the result of fishing (Russ, 2010; Luján, 2016).

On most faunal material, colouration alone may not prove decisive to distinguish fossil from recent. In this way, the distinct green colour of shark teeth from glauconitic-rich deposits is a clue that the tooth is fossil, yet one must be keen to set these green hues apart from those of recent teeth in contact with copper oxides (tools). Likewise happens with black hues produced by thermo-alterations (often recent) and manganese impregnation (fossil), or reds resulting from diagenesis/redox process (fossil) *vs*. contact with iron oxides (tools), etc.

Setting apart fossil from recent may occasionally require specific equipment and techniques. This would be the case of strontium isotopes, only reported in fossil scaphopods, and electronic microscopy analyses that non-destructively monitor whether fluoride content in shark enameloid (fluorapatite) is high in both the root and crown (fossil) or just the crown (recent) (Elderfield, 1986; Shackleton and Elderfield, 1990; Vanhaeren et al., 2004; Bajnóczi et al., 2013, Lübke et al., 2017). For contentious "*Dentalium*" scaphopod beads (see discussion), FT-Raman spectrometry would be a non-invasive way to rapidly set apart recent from fossil.

Identification at the taxonomic level is far more challenging given the wide spectra of groups the fossil record harbours. No analyst feels comfortable identifying specimens whose anatomical disparity exceeds the variability she/he is acquainted with. Ichnofossils, groups whose inter-specific morphological differences are subtle, and fragments, as is so often the case of worked specimens, are particularly troublesome (Cáceres et al., 2019; Vera and Lozano, 2004). Seldom can specialists grant taxonomic status to fragments.

Fragmentation raises the issue of size. Although size is by no means a guarantee of a correct taxonomic identification, size is often a useful diagnostic trait. Even when dealing with complete specimens, and more so in the case of subtle differences among taxa, small size dictates mandatory use of magnifying optical equipment (Vera and Lozano, 2004). Taxonomic identification requires sophisticated equipment when ultrastructure or chemical clues allow for a correct diagnosis, as is the case of ivory (Schuhmacher et al., 2013).

Scaphopods exemplify as few other groups the taxonomic problems that made it difficult for us to accept the fossil status of many specimens in the Iberian literature. Problems here range from a lack of reference collections to unstated assumptions. Tusk-shells most often lack striking features. They are small and being often turned into ornaments implies that most have been altered. Add to it that the Iberian Neogene record, with 24 species from 9 genera (*Paradentalium* [5 species], *Fissidentalium* [1], *Antalis* [8], *Pseudoantalis* [1], *Fustiarias* [3], *Gadilina* [1], *Entalina* [1], *Pulsellum* [1]) and *Cadulus* [3]) is diversified, and one understands why fossil scaphopods are a taxonomist's nightmare. For these reasons, nobody could grant status, let alone taxon, to many of the specimens we studied. To further complicate the issue, the term "*Dentalium*" has been traditionally used in Iberian archaeology in a generic, loose sense to refer to any kind of tusk-shell. However, the extant genus *Dentalium* is only present in the Indo-Pacific region, and all Mediterranean scaphopods formerly labelled as *Dentalium* are currently placed in the genus *Antalis*. Most Iberian scaphopod species, then as now, are rare and quite small, though the Miocene and Pliocene taxa were on the average larger than their Pleistocene equivalents. Since collectors have long focused on the largest specimens, the number of species likely to appear in Iberian sites is restricted to six (i.e. the two *Paradentalium* reported in this paper (see discussion) to which one must add four *Antalis* species (*A. fossile, A. inaequicostatus, A. dentalis,* and *A. vulgare*, of which the latter two still inhabit the Mediterranean Sea). Since all *A. vulgare* we came across were modern, even when certified taxonomically, the fossil status of scaphopods referred to as "*Dentalium*", "*Dentalium* sp.", and "fossil *D. vulgare*" in the Iberian literature will always require confirmation.

Tusk shells also exemplify, as few other groups, the need for good reference collections. A widespread and not recommendable practice in the absence of the pertinent reference specimens is to carry out a best-match exercise with whatever happens to be at hand. This is not new. Indeed, we believe this is how D. de Orueta y Aguirre, in the nineteenth century, came to identify as *Dentalium elephantinum* the *Paradentalium* shells that E.J. Navarro sent him from Tesoro cave (Navarro, 1884). Nearly 20 years later Rev. R.A. Bullen followed suit with the tusk-shells J. Bonsor sent him from Campo Real, exemplifying another "principle" of identification as is following on the footsteps of prestigious colleagues (Bullen, 1905). Use of inappropriate tools, such as field guides and illustrations on the web instead of other reliable sources (i.e, Steiner, 1997; Steiner and Kabat, 2001, 2004) complicate matters further, and often result in all sorts of errors, mistaking serpulid polychaete tubes as scaphopod shells.

Reporting fossils requires not only specifying how identifications were achieved, but also illustrating specimens properly. Illustrations often offer a relible way to verify identification. Although quality is obviously important here, anatomical considerations are equally important to keep in mind. The tendency to depict scaphopods in lateral view, for example, is regrettable because only the external and internal perimeters of the shell, when seen in transversal section, are informative. For bivalves, unless specimens are readily recognizable on account of specific features, both the external and internal faces of the valve should be illustrated. Failure to do so may not allow researchers to certify the fossil nature of a given specimen (e.g., Bosch et al., 2011).

2. Materials and methods

2.1. *Materials*

The studied fossils, numbering 156 (of them 143 studied by us and 13 additional ones assessed from other publications; see Tables 1 and 2) are multifarious in their sources of origin (they have been recovered in 20 archaeological sites). All were taken from geological outcrops and transported to archaeological deposits, with the only exception of Las Aguas cave (see Results).

Fossils can be further separated in two groups:

i) Fossils retrieved on our excavations (e.g. El Juyo, Hoyo de la Mina, Hedionda-IV) and excavations addressed by research projects which some co-authors took part (e.g. La Pileta, El Pirulejo, Tesoro, Altamira, Rascaño, Campo Real) and fossils from archaeofaunal collections we were requested to study (e.g. Aitzbitarte-IV, Peña de la Abuela).

ii) Assessments of fossils described in the literature (e.g. Las Aguas, Reclau Viver, Tossal de les Basses, Les Jovades, Los Alcores, Casal do Pardo) or provided through personal contacts with curators and excavators (e.g. Parpalló, El Oficio, Señorío de Guzmán). It must be stressed that a number of items from the latter group could not be found upon request, and that others, for a variety of reasons, could not be properly studied; all of these are only mentioned in the review section.

2.2. *Methods*

To determine the fossil status of proboscideans we followed Osborn (1942) and Aguirre (1995). Fossil molluscs were identified following criteria provided by Lozano (1999), Vera et al. (1993) and Vera and Lozano (2004), along with A. Morales' reference collection housed at the Universidad Autónoma de Madrid. Shark teeth were compared with material partly collected by one of the co-authors (J.-C.C.) that is now housed at Museo de Ciencias Naturales de Álava. Descriptive terminology and taxonomic nomenclature for sharks follows Cappetta (2012).

Measurements were taken with a digital caliper (estimated error +/-0.1mm). Due to the heterogeneity for reporting fossils in the Iberian literature, both the Number of Identified Specimens (NISP) and the Minimum Number of Individuals (MNI) have been considered (Reitz and Wing, 2008).

Taphonomic and use-wear analyses follow Taborin (1993). A Nikon-SMZ-P00 stereoscope allowed the study of manufacture processes. The criteria for defining Palaeolithic lamps follow Beaune (1987).

The putative non-synchronicity of items was explored via published chronostratigraphic data (see references in the following paragraph). Absolute dates were obtained for the elephant tooth from El Pirulejo (U/Th) and the oyster from La Pileta, (^{14}C/AMS) (Cortés et al., 2016a,b).

Source areas of fossils were explored through field surveys around Hoyo de la Mina (5 km^2), Hedionda-IV (~800 m), and Tesoro (20 km^2) (see Ferrer et al., 2005; Vera and Lozano, 2007). Geologic maps from the Spanish Geological Survey (IGME) and publications were used for the sites of La Pileta, Altamira, Rascaño, El Juyo, El Pirulejo, El Oficio, Los Alcores, Les Jovades and Tossal de les Basses (Aguirre, 1995; Aguirre et al., 2005; Cossmann and Peyrot, 1924; Glibert, 1945; Lozano, 1999; Vera and Lozano, 2004).

3. Results

3.1. Upper Palaeolithic sites

3.1.1. *La Pileta*

An oyster and a bittersweet clam whose fossil nature had passed unnoticed in the 1943 excavation were spotted upon inspection of the collections housed at the Museo de Málaga (Inventory number 232; Fig. 2). The ^{14}C/AMS date of the stalagmitic crust covering the pallial face of the oyster provided an age ~31.8-31.4 cal ka BP, coincident with the Gravettian period (Cortés et al., 2016a). This specimen is an almost complete valve of the common oyster (*Ostrea edulis* Linnaeus 1758) (Fig. 2.2). In southern Iberia, the species first appears in Langhian-Serravallian deposits and reaches to the present day (Lozano, 1999). The yellowish colour and texture of the calcarenite crust covering this large specimen (umbo-pallial diameter: 178.8 mm, antero-posterior diameter: 129.7 mm) (Fig. 2.2A) match those of oysters from the Tortonian deposits of the Ronda basin (Fig. 3).

From a functional standpoint, this oyster was worked into an open channel lamp, the channel here being the portion of the shell underlying the branchial chamber just below the cloacal siphon (Fig. 2.2). The specimen meets three of the criteria to qualifying as a lamp, namely: (1) a marked concavity on the inner surface of the ventral valve with thermoalteration traces (Fig. 2.2C), (2) organic residues in the active zone and borders, and (3) intentional shaping through extractions with a hard hammer, modelling a handle to hold the instrument (Beaune, 1987).

The second fossil from La Pileta is an incomplete valve from a large bittersweet clam *Glycymeris bimaculata* (Poli, 1795) (Fig. 2.1). Local Neogene-Quaternary beds document this species still inhabiting Iberian waters since the Miocene (Lozano, 1999). The fossil does not bear traces of human manipulation, its colour also matching that of fossils from the calcarenitic facies of the Tortonian beds from the Ronda basin (Fig. 3). Bioerosion traces, in this case caused by an encrusting sponge (genus *Entobia*) (Fig. 2.1A), is another distinctive trait of the fossils from the Ronda basin beds. These marine deposits, which are not known to occur more than 15 km away from La Pileta, are the most parsimonious source for these bivalves (Cortés et al., 2016a).

3.1.2. *Las Aguas*

This fossil was used during the Gravettian rock art horizon but does not derive from an archaeological level (Alcalde et al., 1911). It is also the only non-transported fossil described in this paper. The specimen is preserved on the upper Aptian limestone wall of the cave and is a transverse section of a Lower Cretaceous rudist of the genus *Pseudotoucasia.* It was decorated with red dot motifs to highlight it from the walls of the cave chamber (Fig. 4). Despite its taxonomic confirmation pending permission for study, the most likely candidate is *P. santanderensis* (Doubillé, 1889), a species frequent in the Urgonian limestones that crop out between the nearby localities of Comillas and Santander (Mengaud, 1920; Ramírez del Pozo and Portero, 1976).

3.1.3. *Parpalló*

Brief notice of the discovery of fossils from Parpalló cave first appeared in Pericot (1942), who mentioned an "*ammonite*", a "*madrepore*", and four unspecified fossil "shark teeth". The teeth, retrieved in Solutrean and unspecified Upper Palaeolithic levels, are now on display at the Museu de Prehistòria de València (inventory nos. MPV-45906-45909) but the present whereabouts of the invertebrates are unknown. Soler (1990: 40-fig. 2) schematically depicted the shark teeth and identified them as *Carcharodon carcharia* (sic). All the material is assigned here to *Cosmopolitodus hastalis* (Agassiz, 1843) (Fig. 5), which ranges from the

Burdigalian to Piacenzian and is considered to have a cosmopolitan distribution (Cappetta, 2012). In Spain the species is known from the Miocene to the Pliocene (Bauza et al, 1963), with abundant specimens being collected in the Miocene of Alicante, distant ca. 70 km from Parpalló (Jiménez, 1917).

A fossil bittersweet clam identified as *Glycymeris* sp. was later reported on the Solutrean levels (Soler, 2015: 18; fig. 2.8). That figure illustrates a fossil *Glycymeris nummaria* (Linnaeus, 1758) that still thrives in Iberian waters. A previous paper from this author reported a specimen of *Turritella turris* Basterot, 1825 without the author noticing that this is a fossil taxon (Soler, 2001: 375). The pigmentation on what appears to be the remnants of the conchiolin layer does not suggest fossilization, thus it would prove safer to leave this marine snail identified as *Turritella* sp.

3.1.4. *Reclau Viver*

A group of 50 fossils, worked to form the beads of a necklace, was depicted by Avezuela and Alvarez (2012: 328) (Fig. 6A). The quality of that illustration allowed us to recognize 49 thick scaphopod shells whose circular inner section, hexagonal external section and six prominent primary ribs, reaching up to 48 towards the base, coincide with the diagnostic characters of the species *Paradentalium sexangulum* (Gmelin, 1790). The necklace also included a turritellid snail which, lacking a view of the stoma, could be either *Protoma cathedralis* (Brongniart, 1856) or *P. obeliscus* (Grateloup, 1822). The gastropods are upper Miocene taxa whereas the tusk-shell occurs in Pliocene outcrops. They could most parsimoniously derive from local basins, the Miocene featuring outcrops in the Vallès Penedès and the Camp de Tarragona, and the Pliocene on the Alt Empordá, Baix Llobregat and Baix Ebre. Originally on display at the Museu Arqueològic de Banyoles, no more data can be provided for these specimens since the necklace could not be found upon request.

3.1.5. *Altamira*

Three fossil shark teeth, whose relevance was overlooked at the time, were retrieved in the 1924-25 excavations (Breuil and Obermaier, 1935:188). Of them one could not be found upon request and the other two are housed at the Altamira National Museum and Research Center (ANMR) with inventory numbers CE00727 and CE58223. The ^{14}C dating of this Solutrean level provided an age 20.6 cal ka BP (Heras et al., 2013). A fourth tooth

(CE42523), presumably also Solutrean, was retrieved during excavations conducted by P. Rasines del Río in 2006 in the spoil heap of the 1920s excavation.

Specimens CE00727 and CE42523 (Fig. 7.1-4 and 7.5-8, respectively) belong to the otodontid shark *Cretolamna borealis* (Priem, 1897). The former is an incomplete anterolateral tooth measuring 26.9 x 13.4 x 8.1 mm (height, width, depth; HWD hereafter). Its crown exhibits a high, slender cusp with a recurved apical part in lateral view. Only one triangular cusplet is preserved. The cutting edge is continuous. The labial and lingual faces of the cusp are slightly flattened and convex, respectively, with smooth enameloid. A lingual neck occurs along the crown-root boundary. The root is bilobed, with a marked lingual bulge with a bi-pointed nutritional foramen. CE42523 is a relatively small lower lateral tooth (HWD: 11.9 x 11.5 x 3.0 mm) whose crown is labiolingually compressed with a greenish smooth enameloid on its labial and lingual faces. The main cusp is slender, distally bent and gradually widens towards the base. Mesially, it is flanked by a wide triangular cusplet. The cutting edge is continuous. A shallow depression is located central on the medio-basal part of the labial face of the cusp. The root is short and bilobate. The ends of the lobes feature recent fractures.

CE58223 (Fig. 7.9-12) is assigned to *Anomotodon hermani* Siversson, 1992 (HWD: 28.9 x 13.4 x 7.5 mm) and derives from the files of the jaw. The crown has a tall and erect triangular cusp, sigmoid in profile, that broadens basally. The cutting edge is continuous from apex to base. Both lingual and labial faces are convex. The fine, sinuous vertical folds on the lingual face of the crown in *A. hermani* teeth are not visible on the photographs due to poor preservation of the enameloid. A clear lingual furrow separates crown and root. The latter has two diverging lobes which are broken off at both ends. The labial root face has a V-shaped notch, and the lingual root protuberance is abraded. The enameloid on the crown exhibits surface pitting and striations. Such weathering on teeth reflects prolonged open-air exposure (J.C.C., pers. obsv.). Had this been the case, the specimen lied unnoticed on a surface for a prolonged period before being collected.

C. borealis and *A. hermani* are documented in western Europe from the Santonian to Campanian (Guinot et al., 2013; Siversson et al., 2015; Corral, 2018). Campanian records appear in Sweden, Belgium, northern and western France and in the Basque-Cantabrian Region (Corral, 2018) (Fig. 8).

A natural incorporation into the archaeological deposits is ruled out since Altamira was formed on Middle-Upper Cenomanian limestones (Ramírez and Portero, 1976). The most likely source area for these specimens is Punta Ballota, in Tagle, ca. 7 km on a straight line from Altamira, whose coastal cliffs exhibit a Campanian rock formation similar to that in Alava where both species are common (Corral, 2018). Less likely would be localities near Santander Bay (~30 km) and the nearby (~2 km) inland Campanian deposits at Vispieres since fresh rock surfaces in the latter are less accessible than in the coastal zone. The least likely alternative would be transport from other Campanian localities in western France.

3.1.6. *Aitzbitarte-IV*

This specimen was found on a Solutrean level from this cave and illustrated and reported as "shark" by Avezuela and Álvarez (2012). Based on the figure these authors provide, this is a medium-sized incomplete tooth with a triangular enameloid crown and a small portion of the root. Cutting edges are irregularly serrated and basal folds are present on the labial side of the crown. This morphology matches that of two SW European extinct Lamniformes (Table 3): *Palaeocarcharodon orientalis* (Sinzow, 1899) and *Carcharocles* cf. *sokolowi* (Jaekel, 1895).

C. cf. *sokolowi* was reported from the lower Eocene outcrops near Dax (southern Aquitaine basin) (Adnet, 2006) and the genus *Carcharocles* also occurs on the Upper Eocene beds of the Pamplona Basin in the neighboring province of Navarre (JCC, pers. obs.), which lie ca. 80 km to the south. Likewise, *P. orientalis,* whose serrated teeth occasionally show folded ornamentation on the labial side of the crown, is the nearest species. In addition, it is known to occur in the Paleocene limestones of the Urbasa Range, Navarre (60 km away from the site).

The tooth had been side-notched and grooved to allow hanging.

3.1.7. *Rascaño*

The 1974 excavations on an "*archaic*" (sic) Magdalenian deposit (level 5: 19.7 cal ka BP) yielded a fossil shark tooth (ANMRC-Inventory number CE11599) (Fig. 7.13-16). The specimen (HWD: 25 x 10 x 4 mm) was first reported by González and Barandiarán (1981: 101) who mentioned "shark" without further specifications. Corchón (1986: 337) refers to (lit.): "*a simple shark-tooth… non-worked pendant?*" without remarking its intensive abrasion and peculiar colouration. No marks or man-made features exist that could elucidate a function for this fossil.

The tooth consists of a broad triangular cusp with a remnant of the root. The labial face is flat and the lingual convex. The enameloid is smooth on both crown faces. Viewed laterally, the cusp is thin and straight, its apex recurved labially. The cutting edges are continuous. The poor preservation and absence of diagnostic characters does not permit identification below the order level of the Order (Lamniformes indet.).

No conclusive evidence exists to decide whether abrasion is due to biostratinomic reworking or to a natural tumbling in water prior to collection. The specimen, as the Altamira teeth, exhibits the greenish colouration typical for glauconite-rich rock deposits formed in the shallow continental margins of northern Iberia during the Upper Cretaceous (Corral, 2018). Since Rascaño was formed in an Urgonian facies of the Aptian marine limestone (Portero and Ramírez, 1978), the possibility of a fossil falling from the cave wall into the archaeological deposit is discarded. The imprecise taxonomic status does not allow much speculation about potential source areas. Still, the Campanian coastal outcrops of Santander Bay, some 20-25 km away from Rascaño, seem as the most parsimonious source of origin for this specimen (Fig. 8).

3.1.8. *El Juyo*

Along with common Magdalenian ornaments, the excavators reported a specimen of the fossil tower shell *T. turris* (ANMRC-CE54420, Fig. 9) on level 4 (~17.1 cal ka BP) (Barandiarán et al., 1985). Although *T. turris* features a geographically variable sculpturing, its most diagnostic characters are the round whorls seen on profile and the deeply excavated sutures (Basterot, 1825). In the European Atlantic and *Paratethys* this tower shell ranges from the Aquitanian to the Tortonian.

This 35 mm long x 15 mm wide specimen was abraded, so that most of its sculpturing was lost. The shell featured *ca.* 5 whorls with a round contour and was deeply excavated at the level of the suture; the apex and initial whorls of the spire were missing, the sculpture consisting of alternating thin and thick equidistant and slightly projecting flattened spiral cords.

No marine Neogene outcrops exist in the Cantabrian region or the neighbouring Upper Meseta. The nearest source areas for *T. turris* appear on the SW French basins of Aquitaine, Dax and Adour (Fig. 8) on deposits that range from the Aquitanian-Burdigalian to the Tortonian (Lozouet et al., 2001). Although more distant Tortonian and Burdigalian-Langhian outcrops occur in Catalonian localities, the sculpturing of the El Juyo snail best matches that of French specimens (Batllori, 1995; Navas et al., 1996). The documented connections of the Cantabrian region with SW France during prehistoric times (Sauvet et al., 2008; Tarriño, 2006), along with the matching morphology, reinforces the hypothesis of this fossil reaching the site from one of the French basins (Fig. 8).

An in-depth analysis is required to determine the agent that drilled the outermost whorl of this shell, although the regularity of the rim hints to human agency rather than the radulae of driller snails (Fig. 9).

3.1.9. *El Pirulejo*

An 86.5 mm long x 91.0 mm wide molar of a proboscidean now housed at the Museo Histórico Municipal of Priego (Inventory number-2008/44) was retrieved in level P/2, contextually dated to the final Magdalenian (~14-13 cal ka BP) (Cortés et al., 2016b). This left M^3 from a senile individual retained five plates corresponding to the central portion of the tooth, all of whom exhibited marked wearing (Fig. S1). Enamel loops featured clear loxodont sinuses, the enamel proper being intensively folded (Fig. S1.2). Enamel thickness ranges from 2.3-4.5 mm (mean: 3.31 mm). All these are diagnostic features of the straight-tusked elephant, *Elephas* (*Palaeoloxodon*) *antiquus* (Falconer and Cautley, 1848).

From a taphonomic standpoint, the molar featured a carbonate crust that partly covered its occlusal surface. Intentionally fractured on its oral and aboral ends (Figs. S1.4); the fractures are perfectly perpendicular to the occlusal surface and exhibit identical colouration. This contrasts with the remaining faces and suggests synchronicity. The patches of ochre and scratches on the fractures hint at its function as an anvil (Cortés et al., 2016b). The presence of thermo-alterations and charcoal on the root and lower portions of the buccal wall of the crown suggest prolonged contact with a heat source (Fig. S1.1).

U/Th dates provided an average of 185.15±13 ka BP years, corresponding to MIS6 (Cortés et al., 2016b). The date fits the conventional 800-70 ka BP range of a species whose most recent Iberian records date ca. 33 ka BP (Ros, 2010; Stuart, 2005). For such reason, although the fossil status of our specimen seems valid, pre-Gravettian finds in archaeological deposits would require absolute dating to certify fossil status (Martín, 1988; Stuart, 2005; Mol et al., 2007).

The Magdalenians from El Pirulejo could have collected this molar on any of the Quaternary outcrops around the cave (Fig. 10). *E. antiquus* is frequent on most of the fossil localities dotting the basins of the infra-Baetic arch (Guadix, Solana de Zamborino and Loja) (Ros, 2010) and the fluvial terraces of the Guadalquivir river (La Rinconada, Hornachuelos and Almodóvar del Río) (Made and Mazo, 2001).

3.2. Upper Palaeolithic to Neolithic sites

3.2.1 *Hoyo de la Mina*

Ornamental molluscs were found throughout the chronostratigraphic sequence on the site. Among them, 15 fossil scaphopod worked as beads were retrieved in Magdalenian, Epipalaeolithic and Neolithic levels (Simón et al., 2005). Two species, *Paradentalium sexangulum* and *P. inaequal*e (Bronn, 1831) have been recognized. The latter species features a thick shell with an inner circular and an outer hexagonal section due to the six well marked primary ribs that thicken and flatten towards the base, plus 12 diagnostic secondary ribs, set in pairs between the primary rib, towards the apex. The more regular striation pattern of the outer shell of *P. inaequale* also allows to set it apart from *P. sexangulum*. At Hoyo de la Mina, in addition to two specimens of unknown provenience, *P. inaequal*e was retrieved in Magdalenian (NMI=1), Epipalaeolithic (NMI=3) and Neolithic deposits (NMI=2) but *P. sexangulum* only occurs in the Epipalaeolithic (NMI=3) and the Neolithic (NMI=4) (Fig. 6D).

The gathering of fossil scaphopods for ornamental purposes at Hoyo de la Mina was sustained through millennia (Table 2). Although in southern Iberia both species are documented since the Tortonian, *P. sexangulum* reaches only to the Pliocene whereas *P. inaequale* becomes extinct in the Piacenzian (Aguirre, 2000). These fossils are frequent in Messinian deposits of the Almanzora basin and on the Upper Zanclean grey marls of the basins of Vélez-Málaga, Málaga, Mijas and Estepona (Vera et al., 1993; Vera and Lozano, 2004). Although a prospection on ca. 5 km^2 area around Hoyo de la Mina failed to spot any Pliocene outcrops (Ferre et al., 2005), we believe the lower Pliocene beds of the Málaga coast were the most likely source areas of these specimens. Those beds range from less than 10 km (basin of Málaga) to ca. 20 km from the site (basin of Vélez-Málaga) (Fig. 3; Aguirre, 1995, 2000; Aguirre et al., 2005). *P. inaequale* is frequent in the basin of Vélez-Málaga yet unknown in the basins of Mijas and Estepona. If one were to take the similar proportions of both species at Hoyo de la Mina as a reflection of those in the source area, then the basin of Vélez-Málaga would be the most likely place of collection (Vera et al., 1993; Vera and Lozano, 2004).

3.3. Neolithic sites

3.3.1. *Hedionda-IV*

Sector 8, featuring ceramics and organic remains, yielded a 29 mm long x 25 mm wide shark tooth (Fig. 11A). The perforations on the root were probably made with a drill or a flint borer and suggest an ornamental use. Although the piece was slightly eroded, there were neither traces of serrated edges on the crown nor of accessory cusplets. This morphology matches that of *C. hastalis*. In the province of Málaga, *C. hastalis* is only documented in Pliocene outcrops (Bauzá et al., 1963), occurring in a Zanclean outcrop of the Manilva basin, lying <1 km from Hedionda-IV.

The second fossil is a lower (i.e. left) valve of the spoon oyster *Neopycnodonte cochlear* (Poli, 1795). Documented in the Malaga coast since the Miocene, it still thrives in the NE Atlantic and Mediterranean (Lozano, 1999; Poppe and Gotto, 1993). The shell has an umbo-pallial diameter of 73 mm and an antero-posterior diameter of 47 mm. In addition to natural or man-made polished surfaces, trace analyses revealed modifications hinting at a tool. These include percussed notches on its right and left margins and intensive pecking of the dorsal surface (Fig. 11B). Apparently, these marks aimed at securing the specimen onto a handle. From a functional standpoint, the oyster might have served as a container (presumably a spoon).

The fossil nature of the oyster was presupposed on account of its deep-water habits (bathymetric range: 60-500 m, Van Rooij et al., 2010; Wisshak et al., 2010), and because in the aforementioned Manilva basin outcrop where *C. hastalis* is found, spoon oysters of similar colouration to this specimen are frequent.

3.3.2. *Peña de la Abuela*

Our study of the mollusc collection revealed 154 fragments of *P. sexangulum,* representing no less than 23 individuals on the Middle Neolithic (Vth millennium cal BC) deposit. Of these, eight featured clear indications of processing. Documented from the Tortonian of Portugal until the Zanclean-Astian in the Mediterranean and southern Iberian basins, the species is alien to the region. Indeed, the nearest source areas are located on the Baix Llobregat basin, ca. 450 km away (Álvarez et al., 2003).

3.3.3. *Tesoro*

From a historiographic standpoint, the tusk shells Navarro recognized as fossils constitute the earliest record of fossil pieces worked as ornaments in Iberian prehistory and one of the earliest records in Europe (Navarro, 1884). This collection made part of a 6-7th millennium cal BP necklace incorporating stone beads. It is housed at the Museum of Altamira (ANMRC-Inventory number-00492) and we found it after an exhaustive search in the literature (Fig. 6E). Despite fragmentation and anthropic modification, 17 of the 26 specimens worked as beads still retained the outer polygonal perimeter, diagnostic for many Iberian fossil scaphopods. Although all were originally misidentified as belonging to the living Indo-Pacific species *Dentalium elephantinum* L., 1758 (Navarro, 1884), our analyses recognized 15 as belonging to *P. sexangulum* and other 11 representing *P. inaequale* (out of the latter, 9 being small discs). Given that all discs had an identical diameter, and in scaphopods shell width increases from the apex to the base, each bead must represent a different individual. Such meticulous search for uniformity is the first instance ever documented beyond question in Iberian sites. An ongoing study will determine their fossil provenance.

3.3.4. *Other Neolithic sites*

Two Neolithic cave sites (Fig. 1), Tossal de les Basses (Luján and Rosser, 2013: fig. 4.3) and Les Jovades (Pascual, 1993: 86, fig. 6.3), depict two specimens of conch shells these authors identify either as "*Strombus*" or *Srombus* sp. The quality of the illustrations allowed us to identify them as *Persististrombus latus* (Gmelin, 1791). This is a species first recorded in Tyrrhenian deposits that reached to the Pleistocene, its most recent records coinciding with the last interglacial (~80 ka BP). New studies are required to determine their fossil provenance.

3.4. Copper age sites

3.4.1. *Grave 5-Señorío de Guzmán*

Among the grave goods documented in this site, one necklace made of perforated pebbles and cowries (*Trivia* sp.) included a large scaphopod. Originally identified by López et al. (2015) as *Dentalium,* our analysis proved the specimen to represent a *P. inaequale* (Fig. 6B). An ongoing study will determine its fossil provenance.

3.4.2. *El Oficio*

Scaphopod beads were spotted by one of the authors (MCS) on a bracelet with an assortment of shell, bone, serpentine and copper items, on display at the Museo Arqueológico Nacional in Madrid. This bracelet (MAN-inventory number-C1276), was first reported and illustrated by Siret and Siret (1890: fig. 63) (Fig. 6C). Our subsequent study revealed three fossil scaphopods including two specimens of *P. sexangulum* and one *P. inaequale*. An ongoing study will determine its fossil provenance.

3.4.3 *Los Alcores*

A conch shell identified as *Srombus* sp. (García, 1980) is here confirmed as *Persististrombus latus* (Gmelin, 1791).

3.4.4 *Other Copper Age sites*

Two Copper Age sites with fossils are Campo Real, with two specimens of *P. sexangulum noe (SI/PC/56A/1.* Casa Museo Bonsor), and Casal do Pardo (Gonçalves et al., 2018), where one *Pecten maximus* and three shark teeth were recovered. The latter were originally identified as *Prionace* sharck, but the quality of the illustrations allowed us to identify two of them as *Isurus* (or *Cosmopolitodus*) sp. and *Hemipristis serra* (Agassiz, 1843).

3.5. Final remarks

Our collection of 143 items is dominated by scaphopods (83.2%), with an anecdotal contribution of mammals (0.7%) -the only fossils of continental origin-, and secondary contributions of sharks (9.1%), gastropods (4.2%) and bivalves (2.8%) (Table S3).

In terms of cultural periods, the Solutrean (accounting for 39.6% of the items and ~17% of the sites) and the Neolithic (~40% of the items and 21.7% of the sites) constitute the bulk of the records, all other periods being secondary when not anecdotal (Table S4). Taking the data at face value, no temporal trend in terms of items or sites increasing with time emerges since their contributions appear to fluctuate throughout the sequence. Still, this phenomenon would require further analysis given that not only are Palaeolithic periods significantly longer-lasting (anywhere from 5 to 12 ka) than later ones (1 to 2.8 ka), but also because stochastic phenomena, as has been the finding of a necklace with fossils, can heavily bias samples when these are small.

4. Discussion

4.1. *Fossils in the Iberian archaeological record*

A total of 490 fossils from 62 additional Iberian sites were detected in the literature and compared with our records (143 fossil and 20 sites). That process took several years due to the difficulties of locating sources and specimens (Tables 2 and S2). The published records, representing 82 sites and 100 deposits, range from the Gravettian to the Bronze Age (~34 to 4 cal ka BP). Their geographical location and the items recorded on them appear in Table S1 and Figure 12.

Combined, our study has now raised the Iberian record of archaeological fossils by more than 20% in terms of sites and by ~24% (+40% when fragments are excluded) in terms of items. Even though our research was grounded on sound protocols and serendipity played a role, the decisive driver in the process of locating items was the one-finds-once-one-learns-what-to-look-for exercise. This substantial increase in numbers suggests that equivalent searches on other periods and "contexts" should foster an equally significant increase of records.

4.1.1. *Upper Palaeolithic*

No fossils have been thus far reported in Iberian Aurignacian deposits. Gravettian fossils are scarce and restricted to Cantabrian (northern Spanish) sites (Fig. 12, Table 2). These include three nerite snails of the species *Neritina picta* (Férussac, 1823), from the cave of Aitzbitarte III (Level III) and a fourth one from level E at La Garma (Álvarez, 2011;

Álvarez and Avezuela, 2013). The snails were perforated, presumably to allow hanging, and are reported to derive from lower-middle Miocene deposits on the Aquitaine basin (Álvarez and Avezuela, 2013). The Aitzbitarte specimens could not be found upon request.

In addition to those from Parpalló and Aitzbitarte IV (sections 3.3 and 3.6), another Solutrean fossil shark is the tooth of *Otodus (Megaselachus) megalodon* (Agassiz, 1843) found at Higueral de Valleja (Table 3). This nowhere depicted specimen featured (lit. trans.) "*…clear traces of use on its edges"* (Giles et al., 2012: 42).

Breuil and Obermaier (1935: 207) reported "*Cidaris spines*" as deriving from "*…the rock of the cave...*" in the Solutrean levels at Altamira. Interestingly, the most recent cartographic survey of Altamira failed to spot any fossils on the cave walls. For this reason, the Solutrean fossil invertebrates that the Museum of Altamira houses (i.e. 18 cidarid spines [ANMRC-CE04172], two echinoid test of Holectypidae [ANMCR-CE00935] and a brachiopod inner cast of Rhynchonellidae [ANMCR-CE00933]), could most parsimoniously derive from nearby Upper Cretaceous strata. Finally, a marine cephalopod nautiloid (Mesozoic-Cenozoic) [ANMCR-CE01478] has been described but its stratigraphic provenance remains unclear. Although some of these unpublished specimens are beautifully illustrated at http://ceres.mcu.es/, not being able to study them forces us to leave their taxonomic status determined to family level only.

The Magdalenian is the only Upper Palaeolithic period where megafaunas are documented. In addition to the elephant from El Pirulejo (section 3.9), the unspecified bone from a rhinoceros of the genus *Stephanorhinus* was retrieved in an Upper Magdalenian level at the cave of El Castillo and ^{14}C/AMS dated to ~36.2 cal ka BP. This bone was collected (lit.trans.): "*…as something special or as a trophy*" (Bernaldo et al., 2006: 457). On level IIIA from Gorham's cave, Gibraltar, the fragment of an upper molar from the steppe rhinoceros *Dicerorhinus* cf. *hemitoechus* (Falconer, 1868), an invalid synonym for *Stephanorhinus hemitoechus* (Falconer, 1868) was retrieved (Riquelme et al., 2011). Since the species is found in the middle-upper Pleistocene fossiliferous breccias of Gibraltar and the Mousterian deposits of Gorham's and Genista caves and presumably went extinct around 40 ka BP, the find must represent a fossil (Currant et al., 2012). Still, given the narrow temporal window existing between the Magdalenian and the postulated extinction of the species, an absolute date or geochemical analysis would be required to certify the fossil status of this specimen beyond question.

Magdalenian invertebrate fossils previously published include the ammonite from Parpalló (present whereabouts unknown) and a coral from Las Caldas cave that had been worked into a pendant (Pericot, 1942; Corchón and Ortega, 2017). Unpublished invertebrates are reported by González and Freeman (2015: 42) on the Lower Magdalenian (ca. 14 cal ka) "*Santuario de la máscara*" funerary context from El Juyo, where they mentioned "*…a collection of Cretaceous marine molluscs that are normally embedded in the limestone walls of this cave and which by virtue of their capricious forms must have called the attention of the hunters from El Juyo. In the restricted space of the graves, 21 of these items were collected"*. On this sanctuary González and Freeman (2015: 53) also reported "*…fossils (some of very large size)…*" in a foundation well. Of these, two brachiopods from the genus *Rhynchonella,* that for the moment should more safely be left at the level of the Order (i.e. Rhynchonellida), are housed in the Museum of Altamira and lack catalogue numbers. The Museum of Altamira houses two additional unpublished specimens of this same brachiopod from the Upper-Final Magdalenian levels at the cave of La Pila which also lack catalogue numbers (Gutiérrez et al., 2000). Not having had access to any of these 25 specimens, we need to leave open most issues revolving around them.

4.1.2. *Neolithic*

The earliest confirmed records of fossils in Portuguese sites are shark teeth found in silos from the Late Neolithic-Early Copper Age necropolis of Aljezur (Algarve) (Fig. 12B, Table 2). These include a tooth from the extinct tiger shark *Galeocerdo aduncus* (Agassiz, 1843), another from the weasel shark *Hemipristis serra* and two others from the lamniform *Otodus* (*M.*) *megalodon* (Cardoso and Antunes, 1995). In Spain, two fragmentary shark teeth indistinctly referred to as *Isurus* sp. or *Hisurus* (sic) *hastalis* were retrieved in the Early (MF612348) and Late Neolithic (MF64694) levels from the 1991-1994 excavations at Los Castillejos (Pau and Cámara, 2019: 71, 81). Although the pictures do not allow a reliable identification, when confirmed fossil, they should be referred to the genus *Cosmopolitodus* according to the updated taxonomy (Cappetta, 2012).

In addition to the 57 scaphopods previously mentioned, Spanish Neolithic sites refer 33 putative fossil molluscs (Table S2). At La Bernarda, these include (lit.) "*...a cephalopod…"* and three *Glycymeris* sp. clams (Pascual, 1998: table 6). This would also be the status of 20 cockles (family Cardiidae) and 7 conchs (*Strombus* sp., nowadays

Persististrombus sp.) at Cova de les Cendres, one of the latter turned into an anvil, despite the author failing to provide evidence to support their fossil status (Pascual, 2009). This drawback applies also to in two unspecified gastropods from the caves of Benámer and Tossal de les Basses (Barciela, 2011; Luján, 2016).

4.1.3. *Copper Age*

In the Iberian Copper Age (Fig. 12C, Table 2) elsewhere referred to as the Chalcolithic, fossils become more frequent due to a recurrent presence of ivory objects from tusks of *E. antiquus*. This ivory has been reported at Camino de las Yeseras, Leceia, Señorío de Guzmán and Matarrubilla, Los Algarves and Los Millares (Schuhmacher et al., 2013; Liesau and Moreno, 2013; Schuhmacher and Cardoso, 2007; Almagro and Arribas, 1963). It can hardly be considered a coincidence that it is at this time when modern Asian and African elephant ivories first appear on Iberian sites, evidencing trade links with the Eastern Mediterranean and northern Africa.

The distribution of recent ivory fits a pattern that contrasts that of the fossil ivory. In this way, tusks from the Indian elephant have been mostly documented in SE Iberia, whereas those from its African relative are retrieved mostly on Portuguese sites, the Guadalquivir river constituting a border of sorts. In the case of fossil ivory, no such spatial segregation is documented. Instead, one finds a correlation existing between the distance of any given site to outcrops where fossil ivory is found and the presence/abundance of fossil ivory on that site (Fig. 10, Banerjee et al., 2012; Schuhmacher et al., 2013). Fossil ivory is no trivial item. During the Bell Beaker Horizon, half of the items executed on ivory derive from fossil specimens (Schuhmacher and Cardoso, 2007). This has been taken to reflect an increase in the demand but also that fossil ivory is easier to work than recent one when soaked/dampened in water (Christensen, 1999:176). In Copper Age societies, the data additionally hint at a close link existing between the presence of ivory and a development of metallurgy that fostered an increase in the number and kinds of manufactured items. More intriguing is that fossil ivory concentrates in low-rank sites, including peasant communities, whereas recent ivory dominates in high status centers (Fig. 12C).

The Copper Age is the heyday of fossils in Portugal (Fig. 12C). With the exception of those reported at the Dolmen of Soto (Obermaier, 1924), only Portuguese sites, in particular communal graves on coastal Estremadura, feature fossil crinoids. Taxonomically undetermined and less frequently reported on the Alentejo hinterland, the earliest finds were documented at Pedra do Douro (NMI=27) by Leisner and Schubart (1966). Later finds appeared at Carasca (NMI=10), Cova da Moura (NMI=6), Lapa do Suão (NMI=1), tholoi of Charrino (NMI=13), Sizandro (NMI=1) and Poço Velho (NMI=1) (Thomas, 2014), along with an unspecified number of specimens from Vila Nova de São Pedro (Valera, 2002) (Table 2). Except for Sizandro, neither the descriptions nor the illustrations allow one to confirm taxonomic status. At tholoi of Charrino, for example, "…*unworked crinoid stems are found alongside finished crinoid beads, suggesting the fossilized crinoid stems essentially functioned as either cylindrical beads or hollow pencil-like bead performs for bead production*" (Thomas, 2014: 192). Figure 99 from this monograph depicts 28 putative crinoid beads whose stalk morphology allowed us to confirm crinoid *columnaria*. Included here are the 9 specimens from the lower row, the last specimen to the right on the upper row, and the antepenultimate and last specimens to the right on the middle row. We remain unsure about the organic nature of the remaining 16 items. Still, given the sealed nature of the tholoi, if the unworked specimens (drafts) are crinoids, the 13 specimens Thomas reports (2014: table 8), probably underestimate the real number therein depicted.

Although isolated *columnaria* do not allow for a precise taxonomic identification, the only fossiliferous outcrops likely to yield crinoids in the Portuguese Estremadura are Jurassic formations where the genus *Pentacrinus* is frequent (López, 1987). Jurassic deposits also represent a substantial part of the substrate in the Algarve and it is for this reason that the crinoids from Dolmen de Soto may suggest direct contact between this region and western Andalusia.

Another fossil echinoderm reported on the Chalcolithic village of Outeiro de Sao Mamede is the regular echinoid of the genus *Cidaris* (Linnaeus 1758), not uncommon in the Jurassic outcrops around that site (Cardoso and Carreira, 2003). The Late Neolithic/Copper Age site of Fontainhas (Algarve) reported a specimen of the living SE Atlantic butterfly cone, *Conus pulcher* Lightfoot, 1786 (Pereira da Costa, 1867). The illustration allowed us to re-classify it as *C. antiquus* Lamarck, 1810, an upper Tortonian species with a characteristic flat apex, found in Miocene beds throughout the Algarve. The nearest outcrops to Fontainhas featuring this cone are those of Foz de Rego and Cacela.

The Iberian Copper Age provides the earliest and most striking cases of ichnofossils being used as construction materials in European archaeology (Cardoso and Boaventura, 2011). Castro (1961) was the first to call attention to the orthostat slabs with ichnofossils of

Thalassinoides isp. that lined the walls of dolmens (megalithic graves) in the Portuguese Estremadura. At Anta da Estria these slabs were placed on the center of the funerary chamber, and at Anta da Monte Abrão in the corridor leading into that chamber. In both cases, a relevant funerary role was evident. Neogene calcareous sandstones featuring ichnofossils of *Ophiomorpha* isp., *Scolicia-Cardioichnus* isp. and *Gastrochaeonolites* isp. were "*deliberately chosen to highlight specific decorative or symbolic aspects*" of the tholoi of Matarrubilla and La Pastora on the archaeological megasite of Valencina (Cáceres et al., 2019). The sandstones from La Pastora also featured embedded oysters and evidences of bioerosion by "*lithophagous bivalves*" (sic) (Cáceres et al., 2019: 19).

The fossil status of published Iberian scaphopods often remains contentious due to a failure to justify identifications (Table S2). This is the case of the "fossil *Dentalium"* (accepted genus name today is *Antalis*) from Los Millares and Cuesta del Negro (Almagro and Arribas, 1963; Cámara, 2001). In the Mediterranean Sea, *Antalis* includes two large and living species with a robust shell (*A. vulgare* and *A. inaequicostatum*) used as pendants during Prehistory. Although morphology and larger size suggests that some of the Los Millares specimens may represent fossils. This also applies to the 67 specimens reported as "*Dentalium/limestone*" on this site. On the communal grave at Covacha de la Presa, five *Dentalium costatum* (Sow, 1814), a non-Mediterranean fossil species, are reported (Carrasco et al., 1977). Contentious also is the status of six putative fossil scaphopods "*…most often perforated, but otherwise unmodified shell beads made a wide variety of fresh and marine species from the Dentalium*" reported at Cova da Moura (Thomas, 2014). The circular section of the only depicted specimen from that site represents a recent *Antalis dentalis* (Linnaeus, 1758), calling into question the status of others in the lot (Thomas, 2014: fig. 36). Lastly, "*unspecified scaphopods*" are mentioned at La Presa and Fuente Álamo.

Due to inadequate reporting, doubts also arise about the fossil status of other molluscs. These include those from Cuchillo cave (referred to as "*fossil mollusc*"), Loma del Tio Ginés ("*two fossilized shells*"), Mesa/Mera cave (*"perforated shell from the fossiliferous outcrops of Caprés*"), El Argar ("*fossil shell*"), Cuartillas ("*fossil shells*"), and La Bernarda ("*rings of fossil Cerastoderma*") (Table S2). The fossil "*Strombus*" (nowadays *Persististrombus*) from Los Alcores and Les Jovades, were mistakenly interpreted as recent (García, 1980; Pascual, 1993).

Thirteen fossil shark teeth derive from Copper Age sites (Table 3). The most common species, and the only one recorded in Spain is *C. hastalis* which was originally reported as

Lamnidae/Carchariidae at Dolmen de Soto (Obermaier, 1924). The species is confirmed on the Portuguese sites of Leceia and tholos of Marcela (Obermaier, 1924; Cardoso and Antunes, 1995) (Table 3). At Casal do Pardo, two *Isurus* or *Comopolitodus* and one *Hemipristis serra*, that could most parsimoniously derive from local, shark-rich outcrops of the lower-middle Pliocene Huelva Sandstone Formation were by Ruiz et al. (1997). Los Castillejos reports an *Isurus* sp. tooth (catalogue number MF186) from the 1946-1947 excavations (Altamirano, 2014), and a second specimen (MF61860) from the 1991-1994 excavations (Pau and Cámara, 2019). The latter is an almost complete tooth with serrated cutting edges. In case these do not represent damage due to natural agents, the specimen needs re-assessment for neither *Isurus* nor the closely related *Cosmopolitodus* feature dental serrations. A tooth of the weasel shark *H. serra* and another from *O.* (*M.*) *megalodon* seem to be confirmed at Leceia, and two additional teeth from the latter species on the megalithic grave at Dolmen de Nora.

At Vila Nova de São Pedro, failure to provide details on the fossil nature of two teeth from the sandtiger shark *Carcharias taurus* (Rafinesque, 1810) is regrettable as the species still lives in Iberian coastal waters (Cardoso and Antunes, 1995). One last fossil shark tooth, which requires confirmation which could not be found upon request, was reported at Los Tiestos cave (Table S2).

4.1.4. *Bronze Age*

During the Bronze Age (Fig. 12D, Table 2) the use of fossil ivory is reported at Las Peñuelas, El Oficio and El Argar (Schuhmacher et al., 2013; Liesau and Moreno, 2013; Schuhmacher and Cardoso, 2007). Shark teeth, without specifying whether fossil or recent, were first reported at the cave of Los Toyos (Siret and Siret, 1890). One *C. hastalis* tooth from Fuente Álamo is illustrated by Driesch et al. (1985) and a tooth without taxonomic assignment is reported at La Pedrera (Navarro, 1982). In Portugal, the grave at Vale de Carvalho yielded 5 teeth of *C. taurus,* which is an extant taxon, and because of this their fossil status would require confirmation (Cardoso and Antunes, 1995). The extant species *Dentalium vulgare* is reported as fossil at Fuente Álamo, Cerro de la Encina and El Argar (Friesch, 1987: 104). One *Isurus* sp. tooth (catalogue number MF3280), reported on a Copper Age level at Los Castillejos (Altamirano, 2014: 35, fig. 16), has been now assigned to the Early Bronze Age (Pau and Cámara, 2019). This specimen is an incomplete crown that, when confirmed fossil, should switch to the genus *Cosmopolitodus*.

Ten Iberian sites report fossil molluscs of doubtful status. These include the Neolithic sites of La Draga (lit. trans.: *Glycymeris* and/or *Cerastoderma glaucum*), L'Avi (*Strombus/Charonias*), San Sadurni ("*fossil gastropod*"), Costamar (*Spondylus gaederopus* Linnaeus, 1758), Quintanet (*Glycymeris* sp.), Barranquet ("*1 oyster, 1 bivalve, 1 shell and 8 shell fragments*"), Les Cendres (sic "*discs of fossil Cerastoderma"*), and Nerja ("*fossil mollusc*") (Table S2).

Out of the 444 paleozoological items the Iberian archaeological record has thus far yielded, 245 are small fragments whose taxonomical and fossil status is difficult to certify (Tables S3 and S4). The remaining 199 items, roughly a third (NMI=63) remain doubtful and 137 -of which 13 were assessed for this study- seem valid. In light of it, our 143 fossils substantially expand the Iberian dataset (+30% of published finds, +70% in case fragments are excluded) although such increase is far from homogeneous (Table S3). In this way, only 3 items were added to the Copper Age collections, whereas our Magdalenian and Solutrean samples significantly raise both the number of deposits (a three-fold and four-fold increase, respectively) and items (~99% of the Iberian Solutrean fossils derive from this study, the Magdalenian exhibiting a five-fold increase) (Table S4). The increase is also significant in the case of the Neolithic (+25% for sites and +20% for items), less so for the Gravettian (+33% sites and items) and slight for the Bronze Age (~6% of both sites and items) (Tables S3 and S4).

Striking differences emerge when the published dataset is compared with our samples. Although the Neolithic appears to repeat as the dominant period in terms of items, its contribution diminishes drastically when fragments are excluded (~59% vs. 9%) (Table S4). The Copper Age, as seen, is the dominant period both in terms of sites (42%) and items (28.8%), more so when fragments are excluded (~62%). The Solutrean, along with the remaining Upper Palaeolithic periods, constitutes a marginal moment, both in terms of sites (1.6%) and items (2%). More crucial perhaps is the fact that the Iberian dataset witnesses a rise in fossils and sites through time. This coincides with a general trend in Iberia and elsewhere of archaeological sites becoming more frequent as one approaches recent times.

Striking differences also emerge when the contributions of faunal groups are confronted. Our samples lack crinoids and ivory, the latter minimizing the contribution of mammal elements in our samples when compared with the Iberian record (0.7% vs. ~13.6%). Our samples score lower for bivalves (2.8% vs. ~10.1%), yet shark teeth frequencies (9.1% vs. 6.3%) and those of gastropods (4.2% vs. ~4.5%) are similar. Only scaphopods score significantly higher in our samples (83.2% vs. 10.7%). Although the contributions of groups in the published datasets would change if fragments were to be excluded (Table S3), a more rigorous search for fossils in our case may help explain the abundance of small-sized specimens in our case.

4.2. *Fossil use and provisioning*

In terms of source of origin, and except for the sites of Peña de la Abuela and El Juyo, the fossils reported in this paper could most parsimoniously derive from outcrops located in the neighborhoods of the sites (i.e. ≤20 km, often ±2 km, Table 4). These data suggest that local provisioning, rather than trade, constituted the main way to obtain fossils

Provisioning at the local/regional level is confirmed when our data are confronted with published finds. This is most evident for fossil ivory and crinoids but was also clear for the remaining groups. As a corollary, one may surmise that the variety of fossils found at any given site might be more a reflection of availability rather than choice. Indeed, the reported dominance of marine Neogene taxa in our studied sites merely reflects the contingency that most of them cluster along the eastern and southern Spanish coasts where those fossils abound. Still, local provisioning may bear wider implications if local fossils were preferentially selected as markers of cultural identity, as described for other European sites (Moreau, 2003, Vanhaeren et al., 2004, Bajnóczi et al., 2013). For the Iberian Peninsula this is an issue that future studies will need to address.

Fossils transported over long distances often have wider implications. This would be the case of the tower shell from el Juyo. Indeed, in northern Belgium, the Magdalenian constitutes the only period when *Turritella* fossils are documented in the archaeological record (Moreau, 2003). These are taken to signal the northwards expansion of a cultural tradition previously restricted to southern Belgium (Otte, 1990; Straus and Otte, 1996). Could the specimen from El Juyo be taken to signal an equivalent expansion of SW French hunters-gatherers or traditions into more southern latitudes?.

Most of the molluscs and shark teeth from our samples constituted ornaments, tools being only documented in two cases, the oyster lamp from La Pileta and the elephant tooth anvil from El Pirulejo. For such reason, one would surmise that hunter-gatherer and agrarian societies alike prized fossils more for symbolic reasons, whether ornamental, funerary or as markers of cultural identity, than for utilitarian ones. This hypothesis seems validated on account of published finds. In this case, only symbolic uses, both ornamental and funerary, have been documented on fossils. Still, given that as of this writing most published records remain mute as to their function; future research is needed to confirm the trend.

5. Conclusions

In this paper, in addition to significantly raising the Iberian archaeological fossil record, we offered a critical overview of published finds. By doing so, glimpses about issues fossils may help one address over which conventional faunas remain mute, emerged. These issues include social aspects dealing with mobility, stratification and long-distance-trade, and ideological issues addressing identity and funerary practices, so crucial to reach a more faithful understanding of past societies. As is the case in palaeontology, one could try to use fossils as “guides” to probe further into these questions but only when abundant, good quality and well contextualized evidence becomes available. Failure to acknowledge that relevance will make the notion of “fossils as trivia” to persist, hampering rigorous studies on the subject.

From a strictly quantitative standpoint, fossils constitute a minor fraction of the natural objects found in archaeological deposits. But the “*bigger is better*” inertia to grant importance to items exclusively on quantitative terms, itself a result of a narrow processualist approach to archaeology, applies best to the economic (i.e. productive) realm. In the social and ideological domains, frequency needs not equate with “importance”. In fact, very often the opposite holds. Because fossils happen to be items of nil significance in terms of subsistence, we need to frame their study solely in terms of social and ideological meaning, domains where quantification is far less important than contextualization.

To frame the search, one needs to be aware that identification is the cornerstone upon which the interpretive building rests. As Reitz and Wing (2008: ix) so aptly state: “*theoretical interpretations are no better than the methods used to develop supporting data. It is as necessary to be well-grounded in the basics as it is to be guided by good theory*”. Indeed, identification of fossils is more difficult to achieve than that of modern faunas because, among others, archaeozoologists have not been trained to work with them. Challenging also is their restricted informative value when de-contextualized, as is so often the case in archaeological deposits. Under these circumstances, no single reference collection and no single specialist will suffice. Collaboration, along with some acquaintance about the fossils one may expect in the area where an excavation is going to take place, are required. However humble, this no-brainer is probably the major take-home message to keep in mind for future developments on the subject.

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Figure captions

Figure 1. Location of the archaeological sites studied in this paper.

Figure 2. Fossil bivalves from La Pileta. 1, *Glycymeris bimaculata,* valve in lateral (A) and internal (B) views; 2, *Ostrea edulis* left valve in external (A), internal (B) and internal-oblique (C) views, and close-up of the pallial area (D).

Figure 3. Archaeological sites studied in this paper (black stars) from the Betic Cordillera with location of the main Neogene-Quaternary basins. (BSB) Lower Segura; (CB) Cartagena; (FB) Fortuna; (GB) Granada; (G-BB) Guadix-Baza; (GFB) Guadalquivir; (HB) Huércal; (MB) Málaga; (NB) Níjar; (RB) Ronda; (SB) Sorbas.

Figure 4. Palaeolithic at Las Aguas cave. Red dots was placed on a natural section of a large rudistid mollusc of the genus *Pseudotoucasia (*probably *P. santanderensis*) cropping our in the Aptian limestone of the wall. This fossil is the only one described in this study non-transported into archaeological levels by *H. sapiens*.

Figure 5. Neogene shark teeth of *Cosmopolitodus hastalis* from Parpalló Cave. (1) Upper anterior tooth, MPV-45907; (2) upper anterior tooth, MPV-45906; (3) lower lateral tooth, MPV-45909; (4) lower anterior tooth, MPV-45908. All in lingual and labial views, from left to right, respectively. Photographs: Alfred Sanchís (Museu de Prehistòria de València).

Figura 6. (A) Necklace from Reclau Viver cave with *Paradentalium sexangulum* and *Protoma obeliscus*/*P. cathedralis* (taken from Avezuela and Alvarez, 2012: 328); (B) necklace from Señorío de Guzmán/Grave-5; (C) necklace of fossil scaphopods and stone beads from El Oficio; (D) scaphopods from Hoyo de la Mina cave: (1–3) *Paradentalium inaequale*; (E) scaphopods from Tesoro cave: (4–10, 12–14, 16–18) *P. sexangulum*, (11, 15) *P. inaequale*. Pi: *P. inaequale*; Ps: *P. sexangulum*.

Figure 7. Upper Cretaceous selachian teeth from Upper Palaeolithic caves in Cantabria. (1–12) Altamira cave: (1–4) *Cretolamna borealis*, lower (?) anterolateral tooth in distal, lingual, labial and mesial views, CE00727; (5–8) *Cretolamna borealis*, lower lateral tooth in mesial, labial, lingual and distal views, CE42523; (9–12) *Anomotodon hermani*, anterior tooth in mesial, labial, lingual and distal views, CE58223. (13–16) Rascaño cave: Lamniformes indet. in mesial, labial, lingual and distal views, CE11599. Dental views from left to right. Photographs: A. Prada (Altamira National Museum and Research Centre).

Figure 8. Northern Spanish and Western French sedimentary basins. Arrows depict the most direct routes that the El Juyo turritellid presumably followed to reach this cave from its nearest source areas (Map modified from Lozouet, 2014).

Figure 9. Pierced fossil of the gastropod *Turritella turris* in lateral view from El Juyo cave.

Figure 10. Location of geologic deposits with attested presence of *Elephas* (*Palaeoloxodon*) *antiquus* and archaeological sites featuring ivory use from this species. (1) Llanera; (2) Silluca; (3) Buelna; (4) Castillo; (5) Torralba; (6) Ambrona; (7) Madrid; (8) Aranjuez; (9) Pinedo; (10) Cova Negra; (11) Bolomor; (12) Solana del Zamborino; (13) Ángel; (14) Genil (fluvial terraces); (15) Guadalquivir (fluvial terraces); (16) La Rinconada; (17)

Guadalete (fluvial terraces); (18) Figueira Brava (*Elephas* or *Mammuthus*); (19) Foz de Enxarrique, Copper Age sites with *Elephas* (*Palaeoloxodon*) *antiquus* remains; (20) Camino de las Yeseras; (21) Leceia; (22) Señorío de Guzmán; (23) Matarrubilla; (24) Los Algarbes 5; (25) Las Peñuelas 9-10; (26) El Oficio; (27) Los Millares-7; (28) Santa Cruz; (29) Santo Antão do Tojal; (30) Casal do Campo; (31) Casal do Torcato; (32) Grutta da Furninha; (33) Algés; (34) Meirinha; (35) Conínbriga; (36) Condeixa-a-Vehla; (37) Mealhada.

Figure 11. Fossils from Hedionda-IV cave. (A) Pierced shark tooth of *Cosmopolitodus hastalis* in lingual view; (B) left valve of the oyster *Neopycnodonte cochlear* in (from left to right), internal, profile and external views.

Figure 12. Distribution of the Iberian archaeological sites featuring animal fossils. (A) Upper Palaeolithic-Epipalaeolithic; (B) Neolithic; (C) Copper Age; (D) Bronze Age.


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-0°
44°
42°
40°
38°
36°
BAY OF BISCAY
ATLANTIC OCEAN
MEDITERRANEAN SEA
El Juyo
Las Aguas
Altamira
Rascaño
Aitzbitarte
Reclau Viver
Peña de la Abuela
Parpalló
Casal do Pardo
Les Jovades
Los Alcores
Tossal de les Basses
Señorío de Guzman
Grave 5
El Pirulejo
Campo Real
El Oficio
La Pileta
Hoyo de la Mina
Tesoro
Hedionda-IV
200 km


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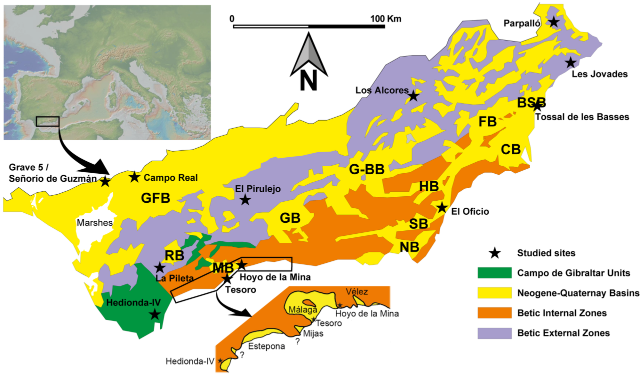

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100 Km
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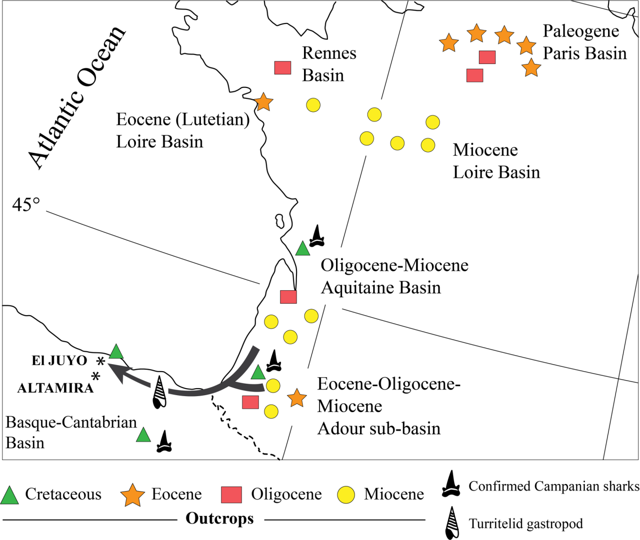
Parpalló
Les Jovades
Los Alcores
BSB
Tossal de les Basses
FB
CB
G-BB
HB
El Oficio
SB
NB
GB
El Pirulejo
GFB
Grave 5 / Señorío de Guzmán
Campo Real
Marshes
RB
La Pileta
MB
Hoyo de la Mina
Tesoro
Hedionda-IV
Vélez
Málaga
Hoyo de la Mina
Tesoro
Mijas
Estepona
Hedionda-IV
Studied sites
Campo de Gibraltar Units
Neogene-Quaternay Basins
Betic Internal Zones
Betic External Zones


0
5 cm

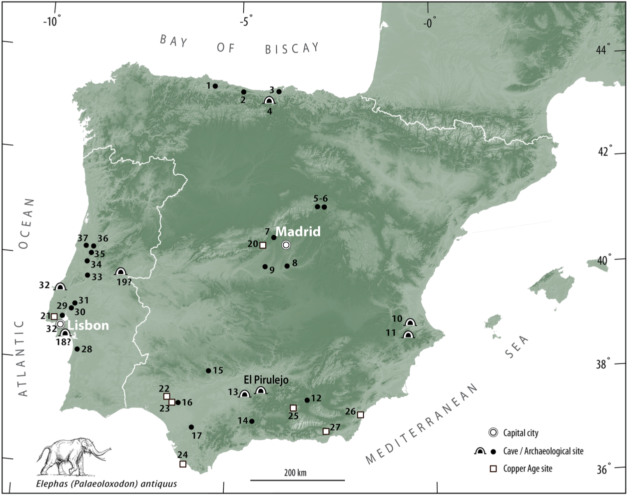

1
2
0 1cm
3
4

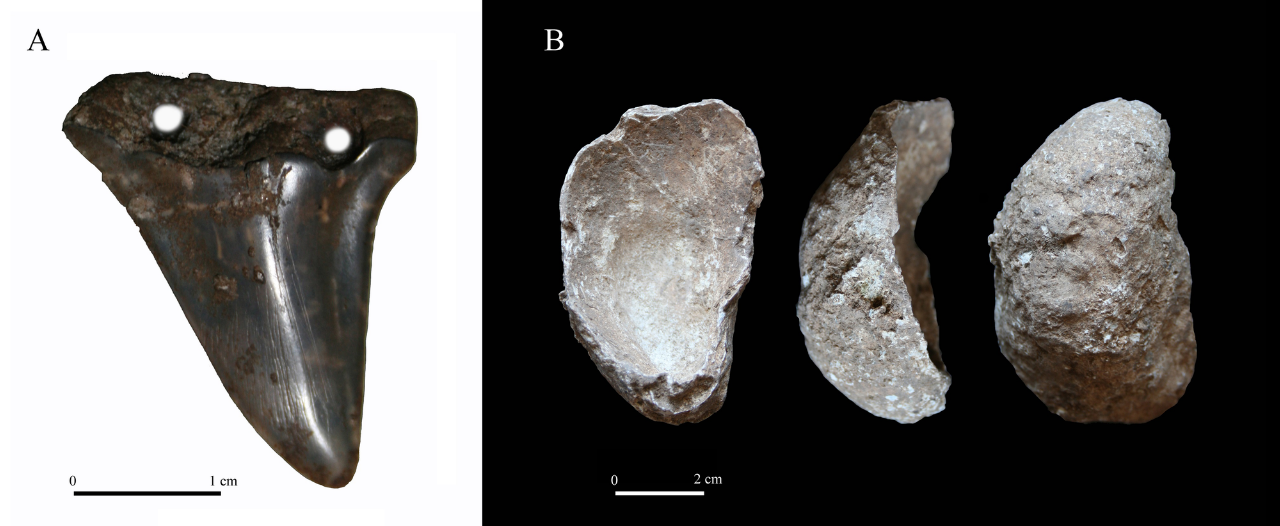

A
B
Pi
C
Pi
Ps
Ps
E
4
5
6
7
8
9
0 1cm
1
D
F
19
2
3
10
11
12
13
14
15
16
17
18

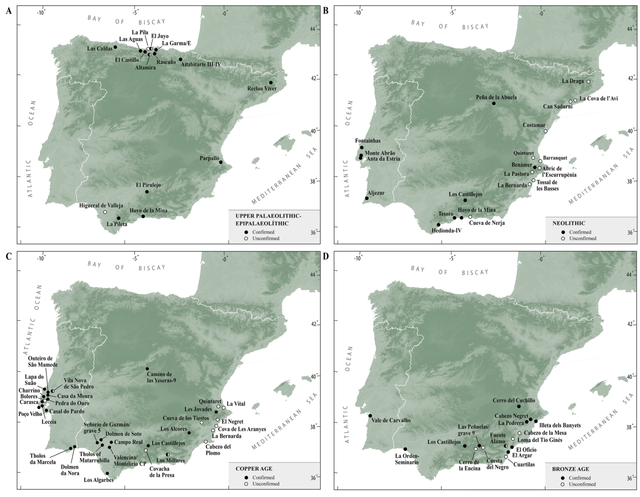

1
2
3
4
0
1cm
5
6
7
8
0
1cm
9
10
11
12
0
2 cm
13
14
15
16
0
2 cm


Atlantic Ocean
Rennes
Basin
Paleogene
Paris Basin
Eocene (Lutetian)
Loire Basin
Miocene
Loire Basin
45°
Oligocene-Miocene
Aquitaine Basin
El JUYO
ALTAMIRA
Eocene-Oligocene-
Miocene
Adour sub-basin
Basque-Cantabrian
Basin
Cretaceous
Eocene
Oligocene
Miocene
Outcrops
Confirmed Campanian sharks
Turritelid gastropod


0
1cm


-10°
-5°
-0°
44°
42°
40°
38°
36°
BAY OF BISCAY
ATLANTIC OCEAN
MEDITERRANEAN SEA
Madrid
Lisbon
El Pirulejo
1
2
3
4
5-6
7
8
9
10
11
12
13
14
15
16
17
18?
19?
20
21
22
23
24
25
26
27
28
29
30
31
32
32
33
34
35
36
37
200 km
Capital city
Cave / Archaeological site
Copper Age site
Elephas (Palaeoloxodon) antiquus


A
0
1 cm
B
0
2 cm


A
B
C
D
BAY OF BISCAY
ATLANTIC OCEAN
MEDITERRANEAN SEA
-10°
-5°
-0°
44°
42°
40°
38°
36°
UPPER PALAEOLITHIC-EPIPALAEOLÍTHIC
NEOLITHIC
COPPER AGE
BRONZE AGE
Confirmed
Unconfirmed
Las Caldas
Las Aguas
La Pila
El Juyo
La Garma/E
El Castillo
Altamira
Rascaño
Aitzbitarte III-IV
Reclau Viver
Parpalló
El Pirulejo
Higueral de Valleja
Hoyo de la Mina
La Pileta
La Draga
La Cova de l'Avi
Can Sadurní
Peña de la Abuela
Costamar
Fontainhas
Monte Abrão
Anta da Estria
Quintaret
Barranquet
Benàmer
Abric de l'Escurrupènia
La Pastora
La Bernarda
Tossal de les Basses
Aljezur
Los Castillejos
Tesoro
Hoyo de la Mina
Cueva de Nerja
Hedionda-IV
Outeiro de São Mamede
Lapa do Suão
Vila Nova de São Pedro
Charrino
Bolores
Carasca
Casa da Moura
Pedra do Ouro
Poço Velho
Casal do Pardo
Leceia
Camino de las Yeseras-9
Quintaret
La Vital
Les Jovades
Cueva de los Tiestos
El Negret
Cova de Les Aranyes
La Bernarda
Cabezo del Plomo
Los Alcores
Señorío de Guzmán/ grave 5
Dolmen de Soto
Campo Real
Los Castillejos
Tholos da Marcela
Dolmen da Nora
Tholos of Matarrubilla
Valencina/ Montelirio CP
Covacha de la Presa
Los Millares
Los Algarbes
Cerro del Cuchillo
Vale de Carvalho
Cabezo Negret
La Pedrera
Illeta dels Banyets
Las Peñuelas/ grave 9
Cabezo de la Mesa
Fuente Álamo
Loma del Tío Ginés
Los Castillejos
El Oficio
El Argar
La Orden-Seminario
Cerro de la Encina
Cuesta del Negro
Cuartilas

Archaeological Site	MM	SH	GA	BI	SC	TOTAL	Cultural stage	Cal ka BP
Cave of La Pileta	-	-	-	2 1 Lamp 1 Unknown use	-	2	Gravettian	31.8-31.4
Cave of Las Aguas	-	-	1 +Rock art	-	-	1		31.8-31.4
Cave of Parpalló	-	2 Unknown use	-	1 Ornament?	-	3	Solutrean	24.7-13.6
	-	2 Unknown use	-	-	-	2	Unspecified Upper Palaeolithic	-
Cave of Reclau Viver	-	-	1 Hole. Pendant	-	49 (Pendant)	50	Middle Solutrean	20-19
Cave of Altamira	-	3 Unknown use	-	-	-	3	2 Solutrean+1Solutrean?	19-16.5
	-	-	-	-	-	1	Unspecified (Upper Palaeolithic)	-
Cave of Aitzbitarte-IV	-	1 Unknown use	-	-	-	1	Solutrean	19-16.5
Cave of Rascaño	-	1 Unknown use	-	-	-	1	Early Magdalenian	16.5-14
Cave El Juyo	-	-	1 Hole. Pendant	-	-	1		16.5-14
El Pirulejo (travertine rosckshelter)	1 Anvil+ochre	-	-	-	-	1	Final Magdalenian	15-12.8
Cave of Hoyo de la Mina	-	-	-	-	1 Pendant	1	Upper Magdalenian	13.5-11
	-	-	-	-	6	6	Epipalaeolithic	11-8

					Pendant			
	-	-	-	-	2 Pendant	2	Unspecified (Upper Palaeolithic-Neolihic)	-
	-	-	-	-	6 Pendant	6	Neolithic	7-6
Cave Hedionda-IV	-	1 Holes. Pendant	-	1 Ladle?	-	2		7-6
Peña de la Abuela (Open-air site, Grave)	-	-	-	-	23 Pendant	23		7-6
Tossal de les Basses (Open-air site)	-	-	1 (Unknown use)	-	-	1		7-6
Cave of El Tesoro (Multiple grave)	-	-	-	-	26 Pendant	26		6-5
Casal do Pardo (Grave. Artificial cave)	-	3 Unknown use	-	-	-	3	Copper Age	4.2-3.9
Campo Real (Open-air settlement)	-	-	-	-	2 Pendant	2		4.2-3.9
Les Jovades (Open-air site)	-	-	1 Unknown use	-	-	1		4.2-3.9
Cave Los Alcores (Grave)	-	-	1 Hole. Pendant	-	-	1		4.2-3.9
Señorío de Guzmán/5 (Tholos)	-	-	-	-	1 Pendant	1		4.2-3.9
El Oficio (Grave 269. Open-air settlement)	-	-	-	-	3 Pendant	3	Bronze Age	3.8-3.3
20 Sites	**1**	**13**	**6**	4	**119**	**143**		

Table 1. Fossil finds studied in this paper. Absolute dates specify the age of the level where fossils were retrieved. Fossil codes as follows: MM (Large mammal), SH (Shark tooth), GA (Gastropod), BI (Bivalve), SC (Scaphopod).

Period (Time slot)	SITE	MM	SH	GA	BI	SC	CR	OT	TOTAL	REF
Gravettian 4 sites, 7 items (ca. 10 ka)	**La Pileta**	-	-	-	**2**	-	-	-	2	1
	Aitzbitarte III	-	-	3	-	-	-	-	3	2
	La Garma/E	-	-	1	-	-	-	-	1	3
	Las Aguas			**1**					1	1
Solutrean 4 sites, 59 items (ca. 5ka)	**Parpalló**	-	**2**	-	**1**	-	-	2	5	4, 1
	Reclau Viver	-	-	**1**	-	**49**	-	-	50	5, 1
	Altamira	-	**3**	-	-	-	-	-	3	1
	Aitzbitarte-IV	-	**1**	-	-	-	-	-	1	5, 1
Magdalenian/ 6 sites, 6 items (ca. 9ka)	**Rascaño**	-	**1**	-	-	-	-	-	1	1
	El Juyo	-	-	**1**	-	-	-	-	1	1
	El Pirulejo	**1**	-	-	-	-	-	-	1	1
	Hoyo de la Mina	-	-	-	-	**1**	-	-	1	1
	Castillo	1	-	-	-	-	-	-	1	6
	Caldas	-	-	-	-	-	-	1	1	7
Epipalaeolithic 1 site, 6 items (ca. 3ka)	**Hoyo de la Mina**	-	-	-	-	**6**	-	-	6	1
Unspecified layer 3 sites, 5 items	**Altamira** (UP)	-	-	-	-	-	-	**1**	1	1
	Parpalló (UP)	-	**2**	-	-	-	-	-	2	1
	Hoyo de la Mina(UP-N)	-	-	-	-	**2**	-	-	2	1
Neolithic 11 sites, >66 items (ca. 2.8 ka)	Benámer	-	-	1	-	-	-	-	1	8
	Hoyo de la Mina	-	-	-	-	**6**	-	-	6	1
	Hedionda-IV	-	**1**	-	**1**	-	-	-	2	1
	Peña de la Abuela	-	-	-	-	**23**	-	-	23	9
	Tesoro	-	-	-	-	**26**	-	-	26	1
	Tossal de les Basses	-	-	**1**	-	-	-	-	1	10, 1
	Aljezur	-	4	-	-	-	-	-	4	11
	Fontainhas	-	-	-	1	-	-	-	1	12
	Estria	-	-	-	-	-	-	IC	IC	28
	Monte Abrão	-	-	-	-	-	-	IC	IC	28
	Los Castillejos	-	2*	-	-	-	-	-	2	13
Copper Age 24 sites, >105 items (ca. 1 ka)	**Les Jovades**	-	-	**1**	-	-	-	-	1	14, 1
	Dolmen of Nora	-	2	-	-	-	-	-	2	11
	Tholos de Marcela	-	1	-	-	-	-	-	1	11
	Vila Nova de São Pedro	-	2	-	-	-	-	-	2	15
	Pedra do Ouro	-	-	-	-	-	27	3	30	16

	Carasca	-	-	-	-	-	10	-	10	16
	Cova da Moura	-	-	-	-	-	6	-	6	16
	Lapa do Suão	-	-	-	-	-	1	-	1	16
	Tholos do Charrino	-	-	-	-	-	13	-	13	16
	Poço Velho	-	-	-	-	-	1	-	1	16
	Casal do Pardo	-	**3**	-	1	-	-	-	4	30, 1
	Camino de las Yeseras-9	9	-	-	-	-	-	-	9	17
	Leceia	1	3	-	-	-	-	-	4	11
	Valencina/Montelirio CP	1	-	-	-	-	-	-	1	17
	Señorío de Guzmán/G5	1	-	-	-	**1**	-	-	2	17, 1
	Tholos Matarrubilla	6	-	-	-	-	-	-	6, IC	17, 29
	Los Algarbes	1	-	-	-	-	-	-	1	17
	Los Millares/grave VII	1	-	-	-	-	-	-	1	17
	Los Castillejos	-	2*	-	-	-	-	-	2	13
	Dolmen de Soto	-	1	-	-	-	+	-	1	18
	Tholos La Pastora	-	-	-	-	-	-	-	IC	29
	Campo Real	-	-	-	-	**2**	-	-	2	1
	Los Alcores	-	-	**1**	-	-	-	-	1	19, 1
	Outeiro de São Mamede	-	-	-	-	-	1	-	1	20
Bronze Age 12 sites, 30 items (ca. 1.2 ka)	Los Castillejos	-	1*	-	-	-	-	-	1	13
	Cabezo Negret	-	-	1	-	-	-	-	1	21
	Cerro del Cuchillo	-	-	-	1	-	-	-	1	22
	Illeta dels Banyets	1	-	-	-	-	-	-	1	23
	Las Peñuelas/grave 9	3	-	-	-	-	-	-	3	24
	Fuente Álamo	-	1	-	-	-	-	-	1	25
	El Argar	1	-	-	-	**8***	-	-	9	17, 1
	El Oficio/grave 158	-	-	-	-	**3**	-	-	3	1
	El Oficio/grave 265	1	-	-	-	-	-	-	1	24
	La Pedrera	-	1	-	-	-	-	-	1	26
	Vale de Carvalho	-	5	-	-	-	-	-	5	11
	La Orden-Seminario	-	-	-	3	-	-	-	3	27
	58 sites (61 deposits)	28 **(1)**	38 **(10+5*)**	12 **(6)**	10 **(5)**	127 **(117+10)**	59	7	281 **(139+15*)**	
	%	10%	13.5%	4.3%	3.6	45.2%	21%	2.5%	100%	

Table 2. Fossils reported in Iberian archaeological sites (bold: finds first reported in this paper), NISP (Number of identified specimens). (*): published items confirmed for this review). Fossil codes as follows: MM (Large mammal), SH (Shark tooth), GA (Gastropod), BI (Bivalve), SC

(Scaphopod), CR (Crinoid), OT (Other), IC (ichnofossil). Reference codes as follows: (1) This paper, (2) Álvarez, 2011, (3) Álvarez and Avezuela, 2013, (4) Pericot, 1942, Soler, 1990, 2015, (5) Avezuela and Álvarez, 2012, (6) Bernaldo et al., 2006, (7) Corchón and Ortega, 2017, (8) Barciela, 2011, (9) Álvarez et al., 2003, (10) Luján and Rosser, 2013, (11) Cardoso and Antunes, 1995, (12) Cardoso and Guerreiro, 2002, (13) Pau and Cámara, 2019, Altamirano, 2014, (14) Pascual, 1993, 15) Varela, 2002, (16) Thomas, 2014 (with references), (17) Schuhmacher et al., 2013, (18) Obermaier, 1924, (19) García, 1980, (20) Cardoso and Carreira, 2003, (21) Barciela et al., 2012, (22) Barciela, 2006, (23) Barciela, 2015, (24) Schuhmacher and Cardoso, 2007, (25) Driesch et al., 1985, (26) Navarro, 1982, (27) Martínez and Vera, 2014, (28) Cardoso and Boaventura, 2011, (29) Cáceres et al., 2019, (30) Gonçalves et al., 2018. UP (Upper Palaeolithic), N (Neolithic).

PERIOD	SITE	NISP	TAXA	REF
Upper Palaeolithic (5 sites, 11 items)	**Parpalló**	**4**	***Cosmopolitodus hastalis***	1, 2
	Altamira	4(**3**)°	**2 *Cretolamna borealis*** **1 *Anomotodon hermani***	1
	Aitzbitarte-IV	**1**	***Palaeocarcharodon orientalis* /** ***Carcharocles* cf. *sokolowi***	3, 1
	Rascaño	**1**	**Lamniformes indet.**	1
	Higueral de Valleja	1	*Otodus* (*Megaselachus*) *megalodon*	4
Neolithic (3 sites, 7 items)	**Hedionda-IV**	**1**	***Cosmopolitodus hastalis***	1
	Aljezur	4	*Galeocerdo aduncus* *Hemipristis serra* 2 *Otodus* (*Megaselachus*) *megalodon*	5
	Castillejos	2	*Isurus* sp.	6
Copper Age (7 sites, 14 items)	Dolmen of Nora	2	*Otodus* (*Megaselachus*) *megalodon*	5
	Tholos de Marcela	1	*Cosmopolitodus hastalis*	5, 1
	Vila Nova de São Pedro	2	*Carcharias taurus*	7
	Leceia	3	*Otodus* (*Megaselachus*) *megalodon* *Cosmopolitodus hastalis* *Hemipristis serra*	6
	Castillejos		*Cosmopolitodus hastalis*	7, 1
	Dolmen of Soto	1	Lamnidae?	8

	Casal do Pardo	**3**	2 *Isurus/Cosmopolitodus* 1 *Hemipristis serra*	9, 1
Bronze Age (4 sites, 8 items)	Castillejos	1	Isurus / Cosmopolitodus	6, 1
	Fuente Álamo	1	*Cosmopolitodus hastalis*	10
	La Pedrera	1	Unspecified shark	11
	Vale de Carvalho	5	*Carcharias taurus*	5
	17 sites	**40**		

Table 3. Overview of fossil shark teeth from Iberian archaeological sites. (1) This paper, (2) Pericot, 1942, (3) Avezuela and Álvarez, 2012, (4) Giles *et al.,* 2012, (5) Cardoso and Antunes, 1995, (6) Varela, 2002, Schuhmacher and Cardoso, 2007, (7) Pau and Cámara, 2019, Altamirano, 2014, (8) Obermaier, 1924, (9) Gonçalves et al., 2018, (10) Driesch *et al.,* 1985, (11) Navarro, 1982. (º) one tooth not found.

Archaeological Site	**Taxon**	**Lower Cretaceus**	**Upper Cretaceous**	**Paleocene/ Eocene**	**Miocene**			**Pliocene**	**Pleistocene**
		Aptian	**Campanian**		**Aquitanian–Burdigalian**	**Langhian-Serravallian**	**Tortonian**		
La Pileta	*Glycymeris bimaculata*	–	–	–	–	–	Ronda < 15 km	–	–
	Ostrea edulis	–	–	–	–	–		–	–
Las Aguas	*Pseudotoucasia santanderensis*?	*In situ*	–	–	–	–	–		
Parpalló	*Cosmopolitodus hastalis* *Glycymeris nummaria*	–	–	–	–	–	Basin of Valencia (Miocene–Pliocene) ≥15 km		–
Reclau Viver	*Protoma* sp.	–	–	–	–	–	Catalonian Miocene–Pliocene basins < 20 km		–
	Paradentalium sexangulum	–	–	–	–	–			–
Altamira	*Cretolamna borealis*	–	Basque-Cantabrian region <7.5 km	–	–	–	–	–	–
	Anomotodon hermani	–		–	–	–	–	–	–
Aitzbitarte-IV	*Paleocarcharodon orientalis/ Carcharocles* cf. *sokolowi*	–	–	Basque-Cantabrian region (<60km)/ Aquitaine (≥80km)	–	–	–	–	–

Rascaño	Lamniformes indet.	–	Basque-Cantabrian region <25 km	–	–	–	–	–	–
El Juyo	*Turritella turris*	–	–	–	Aquitaine/Dax > 250 km			–	–
El Pirulejo	*Elephas antiquus*	–	–	–	–	–	–	–	Guadalquivir basin/ karstic deposit?: km?
Hoyo de la Mina	*Paradentalium inaequale*	–	–	–	–	–	–	Málaga <10km Vélez <20km	–
	Paradentalium sexangulum	–	–	–	–	–	–		–
Hedionda-IV	*Cosmopolitodus hastalis*	–	–	–	–	–	–	Estepona <1km	–
	Neopycnodonte cochlear	–	–	–	–	–	–		–
Peña de la Abuela	*Paradentalium sexangulum*	–	–	–	–	–	–	Baix Llobregat ≥450km	–
Tosal de les Basses	*Persististrobus latus*	–	–	–	–	–	–	–	Tyrrenian Mediterranean deposits 0.25km
Tesoro	*Paradentalium inaequale*	–	–	–	–	–	–	Málaga <5km	–
	Paradentalium sexangulum	–	–	–	–	–	–		–
Les Jovades	*Persististrobus latus*	–	–	–	–	–	–	–	Tyrrenian Mediterranean deposits 34km
Los Alcores	*Persististrobus latus*	–	–	–	–	–	–	–	Tyrrenian Mediterranean deposits 100km
Señorío de Guzmán/ Grave 5	*Paradentalium inaequale*	–	–	–	–	–	Guadalquivir Miocene-Pleistocene basin <1km		–
Campo Real	*Paradentalium sexangulum*								
El Oficio Grave 158	*Paradentalium inaequale*	–	–	–	–	–	–	Cuevas del Almanzora <5km	–
	Paradentalium sexangulum	–	–	–	–	–	–		–
Casal do Pardo	*Pecten maximus* *Isurus/Cosmopolitodus* *Hemipristis serra*	–	–	–	–	–	–	Lisboa	–

Table 4. Biostratigraphic provenance of fossils studied in this paper and their nearest presumptive source areas.