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RESEARCH

The fallow deer *Dama celiae* sp. nov. with two-pointed antlers from the Middle Pleistocene of Madrid, a contemporary of humans with Acheulean technology

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Abstract

We describe fossils of a new species of fallow deer, *Dama celiae*. It is the end member of the lineage *Dama farnetensis–D. vallonnetensis–D. roberti–D. celiae*, which reduced the number of points of the antler from four to two, while the parallel lineage leading to the living fallow deer evolved more complex and palmate antlers. The fossils are from localities Pedro Jaro I and Orcasitas in the + 25–30-m terrace of the Manzanares river, which is correlated to MIS9 (337–300 ka) and which also yielded fossils of *Megaloceros matritensis*, a recently named species, end member of a lineage that survived longer than previously believed. A younger terrace of the Manzanares yielded remains of *Haploidoceros*, a rare deer known from two older localities in southern France and one younger locality in Spain. So many rare deer species in this valley indicates either endemism and a very special environment or that the record of fossil deer is much less known than generally assumed. Until recently, the European Middle Pleistocene record of deer had only one middle-sized species at a time. Now, it appears that there were up to three contemporaneous species of the size of a fallow deer. Acheulean lithic assemblages have been documented from the same sites as *Dama celiae*. This species was contemporaneous to Neanderthals with Acheulean culture. Cut marks suggest that it was consumed by them and probably was hunted.

Keywords New species · Cervidae · Evolution · Manzanares valley · Cut marks

Introduction

Traditionally, it was considered that the diversity of Cervidae in the later part of the Middle Pleistocene of Europe was low with only one species at a time that had the size of a fallow deer (e.g., Kurtén, 1968; Faure & Guérin 1992; Delpech & Guérin 1996; Van der Made 1999). More recently, the existence of a new genus with a species of this size in the Middle and Late Pleistocene of Europe became accepted (Croitor et al. 2008; Sanz et al. 2014; Van der Made & Mazo 2014) and descendant of the giant deer *Megaloceros savini* was shown to have survived into the later part of the Middle Pleistocene of the Manzanares valley with the species

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Megaloceros matritensis (Van der Made 2019). Here, we describe another new species of deer from the same terraces of the Manzanares valley, Madrid, which adds to the cervid diversity and contributes to our understanding of the evolution of the fallow deer.

There is consensus that the living species, *Dama dama* and *Dama mesopotamica*, are closely related to the fossil species (or subspecies) *Dama clactoniana*. All of them have palmate antlers. But when tracing the ancestry further back, consensus disappears. Different authors trace the palmate fallow deer back to some of about ten Early Pleistocene European named species or subspecies of similar size, with branching antlers (e.g., Fig. 1). These or other authors placed these species in the genera *Dama*, *Cervus*, *Axis*, *Rusa*, *Pseudodama*, or *Euraxis*. Part of the problem is that the early Middle Pleistocene and late Early Pleistocene record of fallow deer is less dense. Many species of fallow deer have been named, quite some of them being synonyms, but the species from this period were among the last ones to be named (Table 1). These are *Dama vallonnetensis* (Lumley et al. 1988) and *Dama roberti* (Breda & Lister 2013). Several models of the evolution of the fallow deer have been published, which differ in the position of these species, either directly ancestral to the palmate species or on a side branch.

It is the aim of this paper to (1) describe and name the fallow deer from the sand pits Pedro Jaro I and Orcasitas in the Manzanares valley, Madrid; (2) discuss the phylogenetic position of this species and of *D. vallonnetensis* and *D. roberti* relative to the fallow deer with palmate antlers; and (3) present the Acheulean archaeological sites of Pedro Jaro I and Orcasitas.

Different models of the evolution of the Dama-like deer

As stated above, many different models of the evolution of the fallow deer have been proposed. Pfeiffer (1999) presented cladograms in which *Dama rhenana*, *Dama nestii*, *Dama clactoniana*, *Dama mesopotamica*, and *Dama dama* form a group of progressively more derived species. *Axis* is

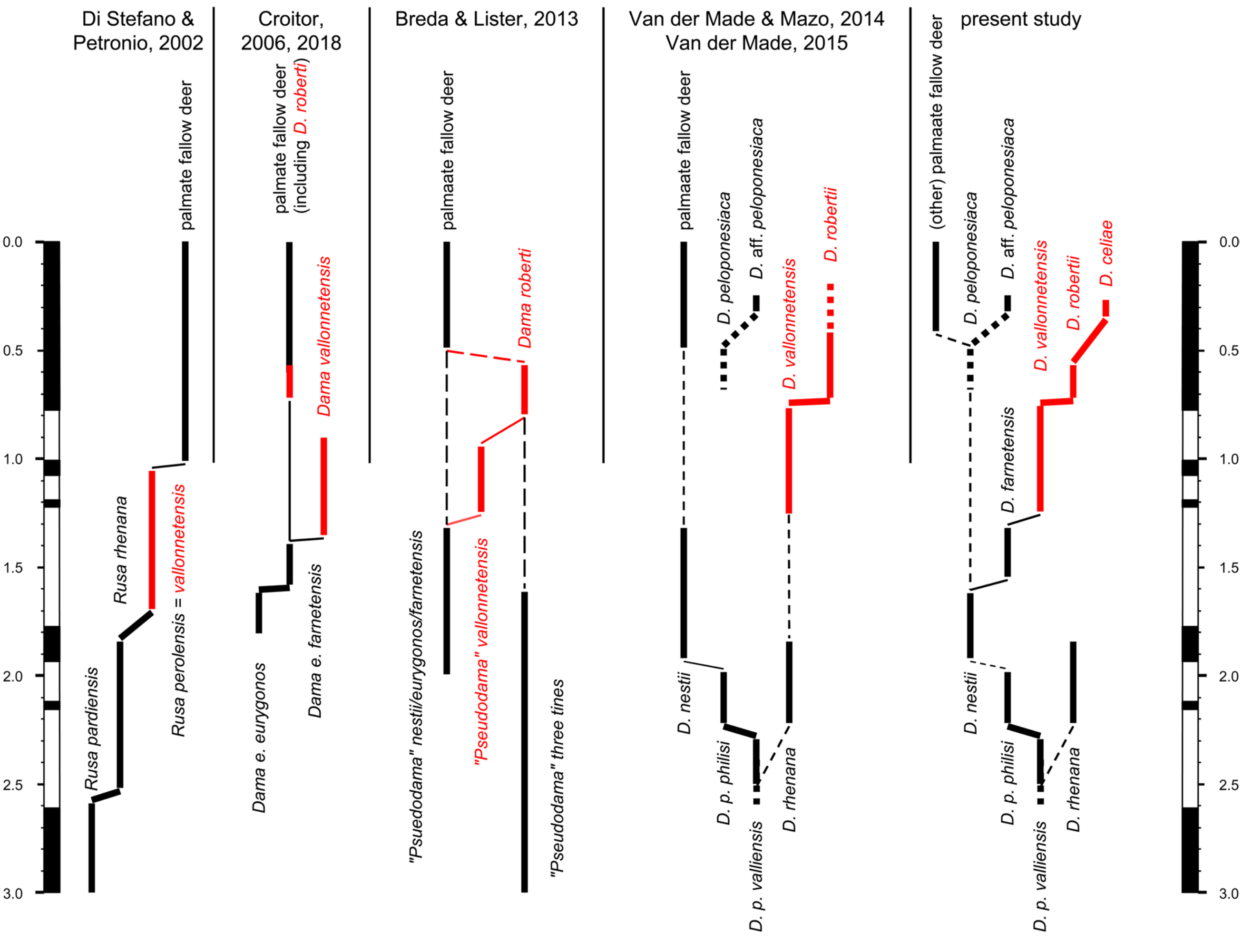

Fig. 1 The position of *Dama vallonnetensis* and *Dama roberti* in the different published phylogenies and the new proposal

Table 1 The most relevant named fallow deer species as originally named

Species/subspecies and author	Type locality	Approximate age of the type locality
Dama dama Linnaeus, 1758	Sweden	Recent
Cervus somonensis Desmarest 1820	Abbeville (Menchencourt)	Late M Pleistocene
Cervus clactonianus Falconer 1868	Clacton	MIS11
Dama mesopotamica (Brooke, 1875)	Luristan, Iran	Recent
Dama nestii Azzaroli 1948	Upper Valdarno	≈ 2–1.7 Ma
Cervus rhenanus Dubois 1904	Tegelen	Olduvai/Renunon Chron
Cervus philisi Schaub 1941	Senèze	2.11 Ma
Dama nestii eurygonos Azzaroli 1948	Upper Valdarno	
Cervus philisi valliensis Heintz 1970	St. Vallier	2.5 Ma
Cervus (s. l.) *peloponesiacus* Sickenberg 1976	Megalopolis	
"*Cervus*" (s.l.) *nestii vallonnetensis* Lumley et al 1988	Vallonnet	Jaramillo, 1 Ma/Cobb Mountain, 1.2 Ma
Pseudodama lyra Azzaroli 1992	Ponte a Elsa	≈3.5–2.6 Ma
Pseudodama farnetensis Azzaroli 1992	Sand pit Cava Liberatori near Farneta	1.6–1.4 Ma
Dama clactoniana mugharensis Di Stefano 1996	Tabun E	213 ± 46 ka/MIS7
Dama dama tiberina Di Stefano & Petronio 1998	Ghiaie di Ponte Molle Formation at Ponte Molle, Rome	MIS7—Di Stefano & Petronio 1998 550–450 ka—Mecozzi et al. 2021
Cervus abesalomi Kahlke 2001	Dmanisi	1.8–1.7 Ma
Dama dama geiselana Pfeiffer 1998	Neumark Nord	MIS7
Dama roberti	Pakefield Solheilac	MIS17 MIS15
Dama aff. *peloponesiaca* Van der Made 2015	Azokh 1 unit V	MIS9/MIS8

more closely related to this group than *Cervus*, *Megaloceros*, *Praemegaceros*, and *Eucladoceros*. No tree in a temporal context was presented.

Di Stefano and Petronio (2002) considered the palmate species of *Dama* to be descendants of a lineage with species with three-pointed antlers (here: points or tines A, B, C), which they placed in *Rusa* (Fig. 1). They placed a parallel lineage in *Axis*, which acquired a fourth point (here: A, B, C, D), and then gave rise to *A. farnetensis*, which survived till about 500 ka.

Croitor (2006, 2018) believed that the *Dama e. eurygonos–D. e. farnetensis* lineage gave rise to three lineages, leading to *D. vallonnetensis* and the two living species (Fig. 1), which implies the loss of the middle tine (point B) in *D. vallonnetensis*, while the palmate species retained it. In his opinion, *D. roberti* is based on juvenile antlers of *D. clactoniana*. He believed most of the Early Pleistocene European fallow deer-sized species not to be closely related to palmate *Dama* and placed them in *Cervus* and *Metacervoceros*.

Breda and Lister (2013) presented a model in which the palmate species of *Dama* evolved passing through a three-pointed stage and a four-pointed stage, lost the middle tine (or tine B) (in *"P." farnetensis*, *D. vallonnetensis*, *D. roberti*), and regained it in the palmate species. They also suggested the alternative that *D. roberti* evolved directly from a species with three points (A, B, C) or that the palmate species evolved directly from a species retaining the middle tine.

Van der Made and Mazo (2014), Van der Made (2015), and Van der Made et al. (2017) considered *Dama vallonnetensis* and *Dama roberti* to be on a lineage that reduced the tines and that the palmate species evolved from *Dama nestii* or *Dama nestii farnetensis*. Van der Made (2015) and Van der Made et al. (2016, 2017) recognized the palmate species *Dama peloponesiaca* and *D.* aff. *peloponesicaca*, not recognized by the other authors (Fig. 1).

Nomenclatorial issue

One of the species discussed here is *Dama roberti*. Its nomenclatorial status has given rise to some discussion. Robert (1829) described two skeletons under the name "*Cerv. Dama Polignacus*": one of a large individual and one of a small individual and ended his description with the question whether these size differences indicated two different species or two races of the same species and stated that new finds will allow to decide. He did not formally indicate a holotype. Pomel (1853) introduced the new name *Cervus roberti* for fossils previously described by Robert under the name *Cervus Dama polignacus*. Pomel did not indicate whether he referred to the large or small skeleton, but his description included two features that are present in the antler of the small deer and that are different in the antler of the large deer and one feature that Robert (1829) indicated to be present in the large deer, but not in the small one. It is not clear whether Pomel (1853) believed there were two species and named the second one, or that he intended to introduce a replacement name and for what reason.

Pomel's (1853) name was used only a few times. Scrope (1858, p. 224) reproduced Pomel's (1853) faunal list, including *Cervus roberti*, but did not comment on this species. Lydekker (1885) merely mentioned it as a synonym of *C. polignacus*. De Stefano (1914) stated that the fossils of *Cervus roberti*, *C. polignacus*, and other species were too incomplete and fragmentary to know whether some of them are synonyms. Azzaroli (1953) unambiguously applied Robert's (1829) name *Cervus polignacus* to the large skeleton and Pomel's (1853) name *Cervus roberti* to the small skeleton. This seems to satisfy article 74.5 of the ICZN for the selection of a lectotype for each of the two species.

Breda and Lister (2013) named a species *Dama roberti* in honor of two persons named Robert, Robert Mutch, who collected the holotype from Pakefield, and Félix Robert, who collected the paratype from Soleilhac. Van der Made et al. (2017) noted (1) that there was already a species called *Cervus Dama roberti*, that according to Azzaroli (1953), was based on the specimen, that Breda and Lister (2013) later designated paratype of their *D. roberti*, and (2) the correct name for a species named in honor of both persons called Robert would be *Dama robertorum*. Lister and Breda (2016) indicated that the ICZN (1999, article 33.2) does not allow correcting an incorrectly latinized name. They also opted for the interpretation that *C. roberti* was meant to be a replacement name of *C. D. polignacus* and that thus both have the same type specimen (ICZN 1999, article 72.2). Whatever the interpretation of the nomenclatorial rules, the name *Dama roberti* applies to the deer from Soleilhac and Pakefield.

Here, we describe and name the new species *Dama celiae*, which we believe to be the descendant of *D. roberti* and which was found in two Acheulean archaeological sites from Madrid.

The paleontological and archaeological sites

Geomorphological and chronological framework

The Pedro Jaro I and Orcasitas sand quarries were located in the SE of Madrid, in the valley of the Manzanares, in the South Sub-plateau of the Iberian Peninsula. The Manzanares, tributary of the Jarama, which flows again into the Tagus river, is a low-sinuosity river embedded in an asymmetrical valley in which two terrace systems can be distinguished (Pérez-González and Uribelarrea 2002). Isostatic rising, block adjustment, and litological structured controls (Alia 1960; Pérez-González 1971, 1980, 1994; Silva et al. 1988a and b) or climatic and eustatic fluctuations (Silva et al. 2017) interfered with their formation. In the upper course of the Manzanares River valley, up to 13 stepped terraces can be distinguished (between + 4–5 and + 95 m), with thicknesses of up to 6–7 m (Pérez-González 1994). In the lower course of the Manzanares river, downstream of the district of Villaverde and until the confluence with the Jarama, the terraces (+ 25–30 m, + 18 + 20 m, and + 12–15 m) are affected by synsedimentary subsidence because of the substratum of evaporitic rocks, which gives rise to a thickening of the alluvial deposits (Uribelarrea 2008), known as the Complex Terrace of Butarque (Goy et al. 1989). Lithic industry and faunal assemblages have been found in the sand and gravel bars, as well as in flood plain facies of the stepped terraces and mainly in the Complex Terrace of Butarque, resulting in one of the largest concentrations of Paleolithic sites known in Europe (Santonja and Villa 1990, 2006; Santonja and Pérez-González 2000–2001; Rubio-Jara et al. 2016; Rubio-Jara and Panera 2019; Yravedra et al. 2019a).

The Pedro Jaro I and Orcasitas sand quarries (Quero 1994; Gamazo 2002) were located at the stepped terrace + 25–30 m of the Manzanares River valley (Fig. 2) (Rubio-Jara and Panera 2019), which has an equivalent morphological position to Unit Arganda I at the Arganda Complex Terrace (≈T + 30–32 m) of the Jarama River, dated between MIS11 and MIS9 according to AAR analysis and biostratigraphy (López Martínez 1980; Sesé et al. 2011a and b; Panera et al. 2011), and probably within MIS9 according to ESR dating (Moreno et al. 2019). Likewise, the T + 25–30 m of the river Tagus valley has been dated to the end of the MIS9 or early MIS8 by IRSL (López-Recio et al. 2015).

Arenero de Pedro Jaro I

The Arenero (= sandpit) Pedro Jaro I was located in the neighborhood of Los Rosales, on the left of the road from Madrid to Andalucía at km 7.3 (Gamazo 2002: 374). It is situated in deposits of the + 25–30-m terrace of the river Manzanares (Fig. 2). The same person owned also another sandpit, situated between km 4 and 5 of the road to San Martín de la Vega (Gamazo 1982, Fig. 1, number 14; Gamazo 2002: 375). This one is now called Arenero de Pedro Jaro II and should not be confused with number I.

Sesé and Soto (2002b) gave a faunal list under the heading Pedro Jaro, but this is of the other sandpit (Pedro Jaro II). The faunal list of Pedro Jaro I includes caballoid horse *Equus* cf. *ferus*, *Equus* cf. *hydruntinus*, Rhinocerotidae cf. *Stephanorhinus hemitoechus*, *Dama celiae*, cf. *Megaloceros matritensis*, and Bovini indet. (Fig. 3). The identification of these species, other than *Dama celiae*, is tentative and thus not indicative of a precise age.

The finds preserved in the Museo Arqueológico Nacional (hereinafter MAN) and Museo de San Isidro

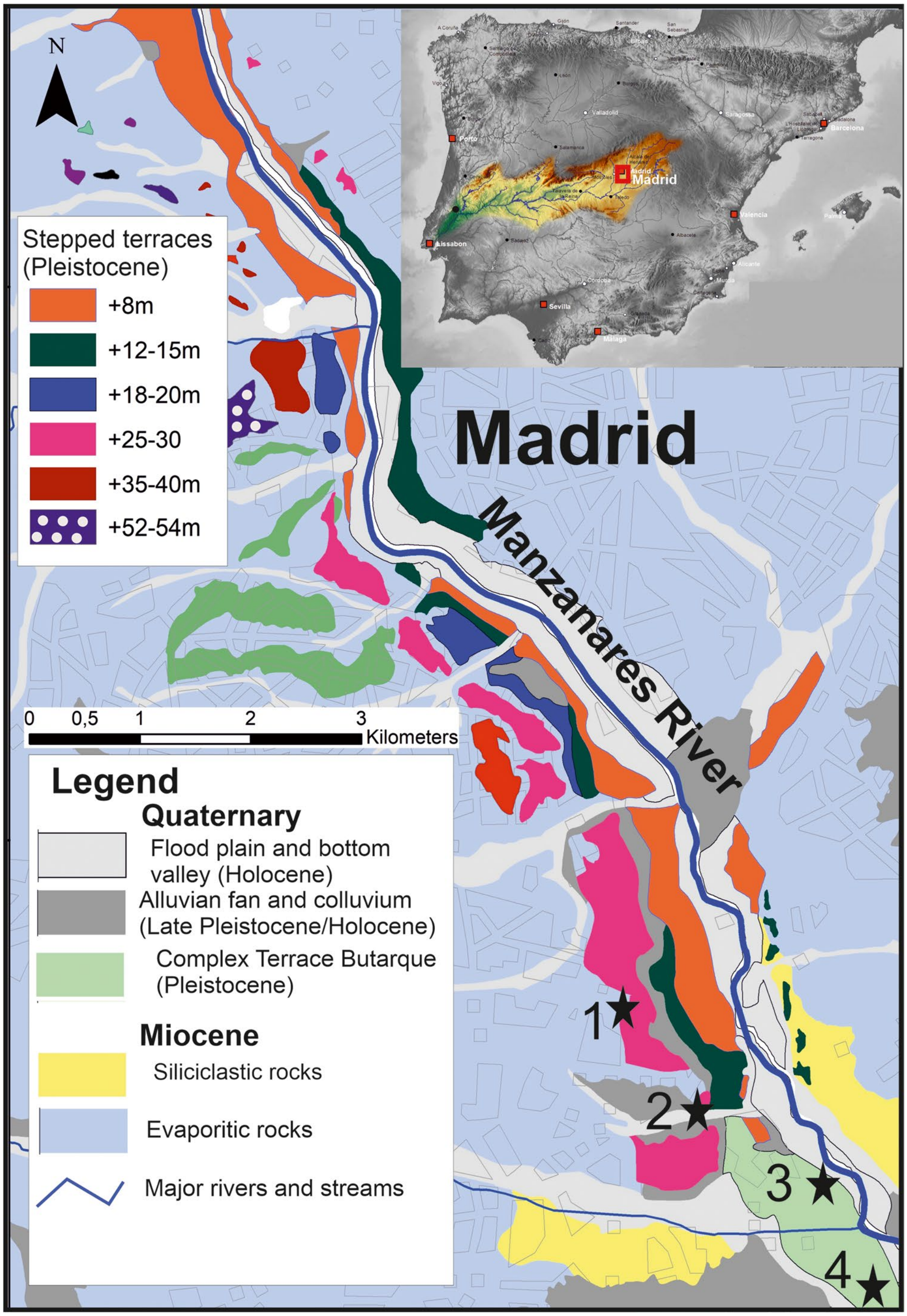

Fig. 2 Map of the Manzanares valley with the localities Orcasitas (1), Pedro Jaro I (2), Tafesa (3), and Arenero de Soto (4) (modified from Instituto Geológico y Minero de España, IGME-CSIC)

(hereinafter MSI) have been virtually unpublished until this study. The lithic industry (448 pieces) is ascribed to the Acheulean technocomplex, because of the presence of handaxes, choppers, and flakes with lengths of over 10 cm and because levallois is rare (Fig. 4). The presence of pieces of all the technological groups that constitute the operative chain proves that the collection of lithic elements on site was not selective but systematic (Table 2).

The best-represented technological group is that of flakes, 61.5% of the total series, of which 16.5% are retouched, although the relevant presence of large cutting tools (LCTs)–20%–stands out.

Among the cores (average dimensions 89 × 74 × 41 mm), the dominant reduction processes are the elementary ones with 20 pieces, some of them opportunists. There is also the presence of some pieces with polyhedral bifacial and

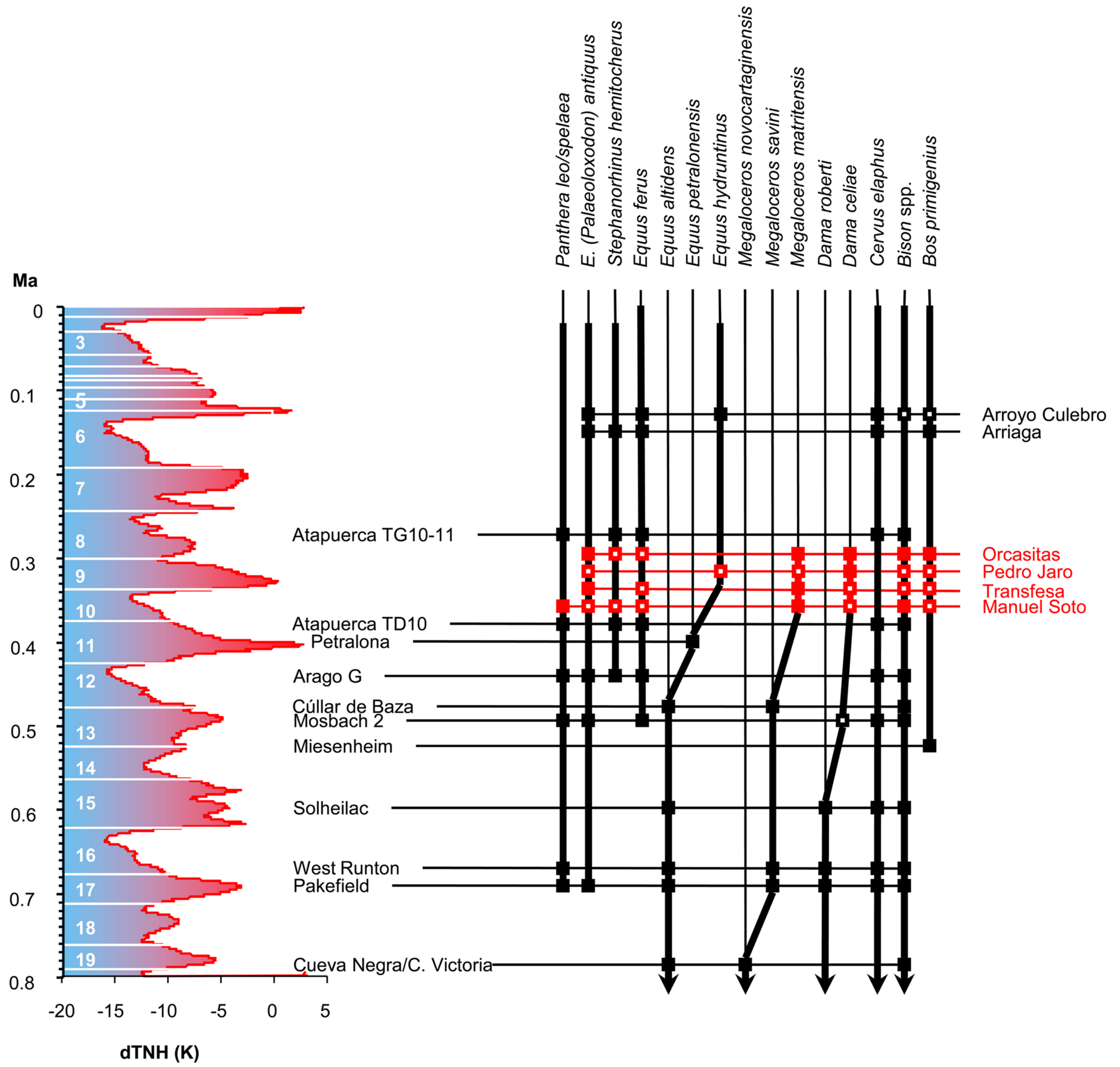

Fig. 3 The temporal distribution of relevant species of large mammals discussed in the text. On the left, the temporal scale in millions of years (Ma), the difference in Northern Hemisphere air temperature with the present (dNHT in Kelvin), after Van de Wal et al. (2011), and the Marine Isope Stages (MIS). On the right, temporal distribution of the species (thick lines) and their presence in selected localities (solid squares) or possible presence (open squares). The selected localities are preferentially those with a first or last occurrence (left; save if this is latest Pleistocene or Holocene) and in the Manzanares sandpits (on the right)

multifacial schemes. However, a significant presence of cores with organized reduction processes (13) is documented, fundamentally from the discoid group, and to a lesser extent peripheral monopolar debitage or Quina concept (cf. Turq 2000: 316), characterized by the secant or perpendicular exploitation of a main surface which may be cortical or débitage. Although its presence might seem rare for the Acheulean, at the Thiongo Korongo site, with a chronology of 1.3. Ma, there is a high percentage (20%) of these cores from the Lower Floor (Santonja et al. 2014), and they were also recorded at TKSF (Rubio-Jara et al. 2017). Approximately 5% of the total of the complete flakes are from centripetal or discoid cores.

The flake tools have average dimensions of 59 × 50 × 17 mm and all of them are made on flint, except two pieces of quartzite. The best-represented types are

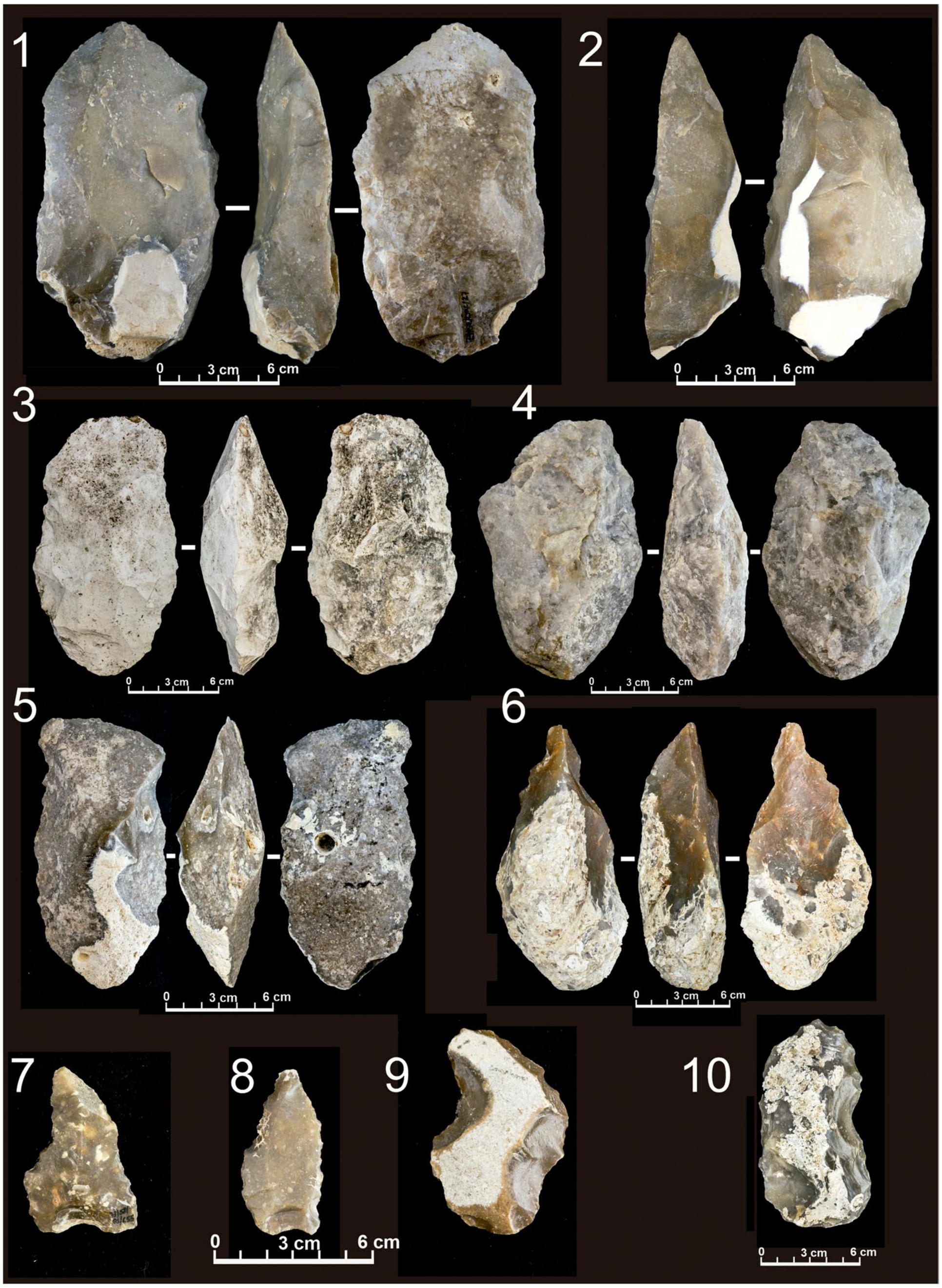

Fig. 4 Lithic industry from Orcasitas (1–2) and Pedro Jaro I (3–10). Cleavers on flake (1, 4, 5); heavy-duty tool (2); handaxe on large flake (3); trihedral pick (6); denticulates (7, 9); Mousterian point (8); and notch (10). All pieces made on flint except number 4 on quartz

scrapers and retouched flakes (the two add up to 60% of the flake tools). Among the scrapers, the transverse ones are outstanding, and are followed by the convergent ones, both simple and double. The group of retouched elements is completed with denticulates, notches, and awls.

The predominance of convergent scrapers and the presence of two Mousterian Points show the presence of symmetrical points in the toolkit.

Among the handaxes (average dimensions 139 × 79 × 42 mm), the most commonly used support is flint flakes, although in five pieces (of which three have flake as support) the raw material is quartzite. Thick handaxes (virtually 90%), dominate over the flat ones. A good deal of the first ones (12) are partial handaxes with sparse bilateral and bifacial shaping, which tends to concentrate on the apical area to create pointy tips, whereas others (actually, 10) have been shaped by means of broad invasive removals, with more intense bilateral and bifacial shaping, giving rise to amygdaloid silhouettes, oval in some cases, with edges sometimes retouched and pointy tips, and in four pieces, straight edges. The flat handaxes, all made on flint and mainly crudely made, show subtriangular silhouettes with pointy tips. The intention

Table 2 Main technological groups in the lithic series of Pedro Jaro I

Technological groups	*n*	%
Pebble	4	0.89
Hammerstone	1	0.22
Flake	134	29.91
Large flake	8	1.79
Flake fragment	61	13.62
Core	36	8.04
Core fragment	13	2.90
Chunk	16	3.57
Flake tool	74	16.52
Handaxe	37	8.26
Handaxe preform	5	1.12
Trihedral pick	17	3.79
Cleaver on flake	6	1.34
Heavy-duty tool	24	5.36
Waste	12	2.68
Total	448	100

Table 3 Main techonological groups in the lithic serie of Orcasitas

Technological groups	*n*	%
Flake	51	53.13
Flake fragment	16	16.67
Core	2	2.08
Core fragment	2	2.08
Flake tool	7	7.29
Large flake	4	4.17
Handaxe	4	4.17
Trihedral pick	2	2.08
Cleaver on flake	4	4.17
Heavy-duty tool	4	4.17
Total	96	100

of creating pointed pieces can also be observed in the shapping of the trihedrals (average dimensions 144×71×48 mm), which are well represented in the series. Generally, shapping is less invasive, and they are made on large flint flakes, except for one piece on quartzite. The cleavers on flake (average dimensions 144×93×50 mm), although fewer (6), are also significant. They are grouped into types II and V (Tixier 1956; Inizian et al., 1995: pp. 55–57), and show symmetrical silhouettes, transverse straight of slightly convex edges, and bilateral shapping aimed to thin down thicker areas. Finally, the large number of heavy-duty tools (24 pieces) made from large flint flakes (average dimensions 111×95×38 mm) with shapping aimed to obtaining pointy tips, sometimes with handaxe-like morphologies, together with edges that shape macrotools assimilable to scrapers, denticulates, or broad backed knives, is outstanding.

Arenero de Orcasitas

The sand quarry of Orcasitas was located at km 7 along the road from Madrid to Andalucía (Quero 2002) and very close to the Pedro Jaro I sandpit (Fig. 2), but today, the site corresponds to number 10 in the street Menas Albas of the neighborhood Orcasitas of Madrid. It is in deposits of the + 25–30-m terrace of the river Manzanares valley (Pérez-González and Calvo 1989).

In 1959, an elephant skull was found and excavated. The excavation also yielded Acheulean and, from a different level, Bronze-age lithichs and pottery (Quero 1994). Mazo (1994) described the skull. Sesé and Soto (2002b) gave the following faunal list: *Elephas antiquus*, Rhinocerotidae indet., *Equus caballus*, *Cervus elaphus*, *Dama* sp., and *Bos primigenius*. Van der Made (2019) described part of the deer fossils as a new species: *Megaloceros matritensis*. None of the deer fossils are now assigned to *Cervus elaphus*. The fossil collection includes part of the skull of *Bos primigenius*. However, metacarpal MSI O/62 7925 has a morphology that goes better with *Bison*. Several partial skulls of *Bos primigenius* are known from the Manzanares terraces, though a photograph from 1935 by Royo in the collections of the Museo Nacional de Ciencias Naturales (MNCN) attests that a *Bison* skull from the “arenero del Barbas” existed, but the specimen was accidentally lost (Sesé & Soto 2002b). The presence of both *Bos* and *Bison* is thus possible. The updated faunal list includes *Elephas (Palaeoloxodon) antiquus*, *Equus* cf. *ferus*, Rhinocerotidae, *Bos primigenius*, *Bison* sp., cf. *Capreolus*, *Dama celiae*, and *Megaloceros matritensis* (Fig. 3). Some subrecent teeth in the MAC belong to *Bos taurus* (domestic cattle) and very probably do not derive from the + 25–30-m terrace. This terrace is correlated to MIS9. This is not contradicted by the fauna, but most of the species existed well before and after MIS9 (Fig. 3). An exception is *Megaloceros matritensis*, which is the last member of a lineage and occurs in about 10 localities or levels in the + 25–30-m terrace of the Manzanares. No younger occurences are known, but then the species was recognized only recently. The species is a descendant of *Megaloceros savini*, still present in Cúllar de Baza 1 (Van der Made 2019), dated to 476 ± 24 ka (Ortiz et al. 2000). This supports an age for Orcasitas that is much younger than that of localities with *Dama roberti*.

The 96 pieces of lithic tool from Orcasitas studied in this paper are unpublished and are deposited at MAN. These lithic tools can be ascribed to the Acheulean technocomplex, and consist mainly of flakes, which add up to 81.26% of the whole, including retouched flakes (Table 3). The limited presence of cores (just two) may be due to a selective collection of the finds. One is a bipolar unifacial core on flake, and the other a centripetal bifacial retouched core.

The group of flake tools consists of seven flint pieces: five retouched flakes—in one of them the support is a large flake, a notch, and a retouched notch. Among the LCTs (average dimensions 140 × 86 × 42 mm), there are four handaxes: one of flint and a fourth one, very rounded, of quartzite. The supports used consist of large flakes in two cases, one of quartzite and the other one a flint cobble-slab. The handaxes are thick, with little bilateral and bifacial shapping, made by means of wide removals aimed at shapping a pointed end, except in one piece that has a fractured tip. The bifacial shapping extends to the bases, which are sharp, except in one case that is cortical. The silhouettes are amygdaloid, except in one piece that is oval. One of the handaxes was intensely retouched. The four cleavers, all made on large flint flakes, show suppressed butts and removals, in some cases with bifacial shapping, in the thicker areas that result in regular and symmetrical silhouettes. Two of those are type II cleavers, one with use retouch in the edge, and the other two are of types V and VI, the last one on kombewa flake (classification of Tixier 1956; Inizan et al. 1999). There are four heavy-duty tools, three of which are large flakes with pointed tips. The same happens with the two trihedrals, one made on an angular flint cobble and the other one on a highly cortical quartzite flake. The scarce shapping is focused on the apical third of the object to create a point. This is an Acheulean association because of the presence of handaxes, choppers, and flakes with lengths of over 10 cm and because levallois is absent (Fig. 4).

Transfesa

A few specimens from Transfesa are tentatively assigned to *Dama celiae*. TRANSFESA (later called TAFESA) near Villaverde (Fig. 2) was an enterprise dedicated to transport and logistics. In 1958, the skull of an elephant was found on the terrain of this company (Meléndez 1958). In addition to the skull, other remains of mammals were excavated at a higher stratigraphic level (De Andrés & Aguirre 1975) and pollen was sampled from sediments associated to the skull and from a core (Menéndez Amor & Florschütz 1963). An excavation at a level 6 m above the elephant skull and at about 75 m distance was carried out in 1996. The materials collected during the first excavations are kept in the Museo Nacional de Ciencias Naturales (hereinafter MNCN), and those of the later excavation in the Museo Arqueológico Regional (hereinafter MAR) and were described in a monograph (Baena & Baquedano Beltrán, 2010).

The pollen comes from a level that has been called Mz0, the elephant skull comes from Mz1, the excavation in 1996 was in Mz2, and the other early excavations in Mz3 (Silva et al. 2010). Theese units form part of the + 25–30-m terrace of the Manzanares (Rubio et al. 2016), which is correlated to the + 30–32-m terrace of the Jarama, which is dated and correlated to MIS10-9 (Panera et al. 2011; Moreno et al. (2019);.

Aguirre (1989) classified the fossils from Mz1 as *Elephas antiquus*, *Sus* cf. *scrofa*, and Cervidae indet., and from Mz3 as *Dolichodoryceros savini* and *Equus* sp. A skull fragment of a deer from Mz3 was described in detail as *Praedama* (De Andrés & Aguirre 1975). Sesé and Soto (2002b) gave the faunal list (for Mz1 and Mz3): *Elephas (Palaeoloxodon) antiquus plathyrhinchus*, *Equus caballus*, *Sus* cf. *scrofa*, "*Cervus*" sp., *Praemegaceros* sp. (= *Praedama* sp.), and Bovidae indet. The fossils collected from Mz2 were assigned to cf. *Elephas antiquus*, *Megaloceros savini*, *Bos/Bison*, *Microtus* sp., *Oryctolagus cuniculus*, and cf. *Mauremys leprosa* (Mazo 2010; Sesé, 2010). We do not know on which fossils the mention of *Sus* was based, while part of the deer fossils became type specimens of a new species and the remaining deer fossils were assigned to a fallow deer (Van der Made 2019). The updated faunal list is *Elephas (Palaeoloxodon) antiquus*, *Equus* cf. *ferus*, *Megaloceros matritensis*, *Dama celiae*?, *Bos/Bison*, *Microtus* sp., *Oryctolagus cuniculus*, and cf. *Mauremys leprosa* (Fig. 3). The pollen was interpreted as indicative of a steppic environment (Menéndez Amor & Florschütz 1963). These species do not contradict correlation of the terrace to MIS10-9, but most of them are not informative with this precision. The deer fossils were initially assigned to *Megaloceros savini*, which led to an overestimation of the age of site, but when it was recognized that these fossils represented *M. matritensis*, a descendant of *M. savini*, nothing contradicted a correlation to MIS9-10 (see Van der Made 2019).

The lithics from unit Mz1were interpreted as middle Acheulean (Aguirre 1989), and those from unit Mz2 were described and figured in detail and classified as Acheulean (Baena et al. 2010b, a). The substantial presence of cobbles (36%) in the assemblage of unit Mz2, which consists of 651 pieces, is remarkable. These are mainly made on quartz but also on quartzite. Only six of them show percussion marks, which suggest their use as hammerstones. The presence of these raw materials contrasts with the hegemonic use of flint (92%) in the knapping items. The flake production is focused mainly on bifacial and multifacial operative schemes, and to a lesser extent on orthogonal and discoid schemes, with no presence of Levallois, suggesting an expeditious assemblage. Macrotools (20%) and other tools on flake (30%), among which denticulates dominate followed by scrapers, notches, and becs, are well represented. There are only two cleavers on flake, in contrast with the 22 handaxes and trihedral-picks present, which are thick, with sinuous edges and barely symmetrical profiles.

Arenero de Manuel Soto

A fragment of a metatarsal from the sandpit of Manuel Soto could belong to *Dama celiae*. As sandpits changed owners and the same person may have owned more than one sandpit, there may be some confusion with the names. Gamazo (1982, Fig. 1) indicated the position of sandpits under the names Arenero de Manuel Soto (number 3), another one also called Arenero de Soto, Arenero de Ramón Soto, or Arenero de Nicomedes (number 19), and a third one under the name Arenero de Adrián Rosa, Aporta o Nicomendes (no. 24). Gamazo (2002) indicated that the sandpit of Manuel or Ramón Soto or Nicomedes (near km 1.6 of the road to San Martín de la Vega) corresponds to number 19 and has the code AM, that Arenero de Soto (near km 1.5 of the same road and should be no. 3) has codes ASO and CASO, while she gave no code for number 24. Fossils in the MSI with code AN are indicated to come from Arenero de Nicomedes and should correspond to no. 24.

We identified other fossils with the code AM (corresponding to no. 19) as *Panthera leo* (or *P. spelaea*), *Equus* cf. *ferus*, Rhinocerotidae indet., *Bison* sp., *Dama celiae*?, and *Megaloceros matritense* (Fig. 3), and from Arenero de Nicomedes with code AN as *Megaloceros matritensis* (= "*Cervus* sp.") and Bovini indet. However, Sesé and Soto (2002b) gave a faunal list for Manuel Soto (no. 3): Carnivora indet., cf. *Elephas (Paeoloxodon) antiquus*, Rhinocerotidae indet., *Equus caballus*, *Cervus* sp., *Dama* sp., and Bovidae indet. cf. *Bos/Bison* and Arenero de Nicomedes (no. 19): *Equus caballus*, *Cervus elaphus*, and cf. *Dama* sp. This gives the impression that our list for no. 19 and Sesé and Soto's (2002b) list for no. 3 are based on the same fossils. Note that both include a carnivore and only two of the sandpits of the Manzanares yielded carnivores: Manuel Soto and Mayoral. Possibly, our list for no. 24 (code AN) corresponds to Sesé and Soto's list for 19.

The fossil which concerns us here is labeled to come from Arenero de Manuel Soto and has a collection number including the code AM and should be from sandpit number 19, but we cannot exclude number 3. Sandpit no. 19 is in the stepped terraces, while no. 3 is in the Complex Terrace of Butarque and its age is more difficult to assess on the basis of geomorphology. In any case, the association with code AM includes both the fallow deer metatarsal and *Megaloceros matritensis*, which otherwise is only known from the + 25–30-m terrace, correlated to MIS9-10.

Material and methods

The fossils from Arenero de Pedro Jaro I are stored in the MAN and MSI, and those from Arenero de Orcasitas are stored in the MSI, MAN and a few specimens in the MAR. The lithics from Pedro Jaro I and Orcasitas, analyzed in this paper, come from archeopaleontological interventions carried out during the monitoring and control of the exploitation of the Manzanares sand quarries during the 1950s and 1960s, and have never been published before. The specimens from Transfesa are stored in the MNCN and MAR, and those from Manuel Soto in the MSI. The fossil specimens are compared with others, both recent and fossil indicated in Table 4. The acronyms of the collections where those specimens were studied are indicated in Table 5. The methods of study of the Cervidae and the way of measuring (Table 6) are similar to those used by Van der Made and Tong (2008). The measurements in the figures and in Tables 7 and 8 are in millimeters.

Taxonomy and description

Family Cervidae.

Genus *Dama* Frisch, 1775.

Species *Dama celiae* sp. nov.

Holotype MAN 73/58/PJ-39, 73/58/PJ-21, 73/58/PJ-26 and associated fragments forming the left antler and MAN 73/58/PJ-24 and associated fragments forming part of the main beam of the right antler of the same individual.

Type locality and horizon Arenero de Pedro Jaro I, Manzanares valley, Madrid, Spain. Late Middle Pleistocene, probably MIS9-10.

Derivatio nominis The species is named in honor of Celia Casado Sarrión.

Diagnosis Middle-sized Cervidae. Males with antlers with large upwards-directed brow tines and main beams directed backwards and curving laterally and again backwards, without important upward curvature and without signs of further bifurcation, important flattening or palmation. The bifurcation between brow tine and main beam is situated low above the burr.

Differential diagnosis *Dama celiae* differs from *Dama roberti* and other species of *Dama* in having a long main beam without bifurcation or the flattening that preceedes such a bifurcation (or if it would have had such a bifurcation, it would be situated much further from the burr). *Dama celiae* differs from *Haploidoceros* in that the bifurcation between brow tine and main beam is situated much lower above the burr and that the main beam does not curve upward and then foreward. *Dama celiae* differs from *R. eldii* in that the main beam of the antler does not curve upward in its distal part and in not having minor tines.

Material

MAN 73/58/PJ-39, 21, 26—three fragments of a left antler that fit together: basal part (39), main beam (21, 26) from Pedro Jaro I. Figure 5 (1).

MAN 73/58/PJ-24—part of the main beam of the right antler (same individual as above) from Pedro Jaro I. Figure 5 (2).

Table 4 Provenance of the data. Either the acronym of the collection where the material was studied is indicated, or a reference from where the data are taken. In the case that the material is known to be stored in a different place than where it was studied, this is indicated between brackets

Species	Locality	Collection/reference
Dama? lyra	Ponte a Elsa	IGF
	Montopoli	IGF
Dama rhenana	Tegelen	NBC, TMH, NMM
Dama phylisi	Senèze	IQW
Dama nestii	Upper Valdarno	IGF
	Il Tasso	IGF
	Casa Frata	IGF
	Solava	IGF
Dama nestii erygonos	Upper Valdarno	IGF
Dama abesalomi	Dmanisi	GSM
Dama farnetensis	Cava Liberatori, Persignano near Farneta	IGF
	Selvella	IGF
	Val di Chiana	IGF
	Casa Palazzi	IGF
	Cava dell'Erba	IGF
Dama vallonnetensis	Vallonnet	MPRM
Dama roberti	West Runton	NHM
	Bacton	NHM
	Soleilhac	MCP
Dama celiae	Arenero de Orcasitas	MAN
	Arenero de Pedro Jaro I	MAN
Dama peloponesiaca	Megalopolis	NCUA, BGR
Dama aff. *peloponesiaca*	Azokh V	MUB
Dama clactoniana	Bilzingsleben	FBFSUJ
	Petralona	AUT
	Clacton	NHM
	Swanscombe	NHM
	La Calera de Uclés	Studied before deposition in an institute
	Atapuerca TG10-11	CENIEH
Dama dama geiselana	Neumark Nord	FBFSUJ (LVH)
Dama dama	Gimbsheim, Eich, Brühl	NMM
	Lehringen	HMV
	Pinilla del Valle	UCM (MAR)
	Can Rubau	CIAG, MACG
	Recent	EBD
Dama mesopotamica	Kebara	HUJ
	Recent	HUJ, SAPM
Dama? sericus	Loc. 52	Teilhard de Chardin & Trassaert 1937
Axis? perolensis	Peyrolles	NHM
Cervus elaphus	Vogtstedt	IQW
	West Runton	NHM
	Mauer	SMNK
	Bilzingsleben	FBFSUJ
	Murr	SMNS
	Steinheim	SMNS
	Azokh V	MUB, ASMHCS
	Neumark Nord	LVH
	Can Rubau	CIAG
Haploidoceros mediterraneus	Lunel Viel	MNPE
	Preresa	MAR
Rucervus eldii	Recent	AMNH, ZICAS

Table 5 Acronyms of the collections

Acronym	Collection
AMNH	American Museum of Natural History, New York
ASMHCS	Artsakh State Museum of History and Country Study, Stepanakert
BGR	Bundesanstalt für Geowisenschaften und Rohstoffe, Hannover
CENIEH	Centro Nacional de Investigación de La Evolución Humana
CIAG	Centre d'Investigacions Arqueològiques de Girona
EBD	Estación Biológica de la Doñana, Sevilla
FBFSUJ	Forschungstelle Bilzingsleben, Friedrich Schiller Universität Jena
GSM	Georgian State Museum, Tbilisi
HMV	Historisches Museum, Verden
HUJ	Hebrew University, Jerusalem
IGF	Istituto di Geologia, now Museo di Storia Naturale, Firenze
IQW	Institut für Quartärpaläontologie, Weimar
LPTUP	Laboratoire de Prehistoire de Tautavel, Université de Persignan
LVH	Landesmuseum für Vorgeschichte, Halle
MACG	Museu d’Arqueologia de Catalunya, Girona
MAN	Museo Arqueológico Nacional, Madrid
MAR	Museo Arqueológico Regional, Alcalá de Henares
MCP	Musée Crozatier, Le Puy-en-Velay
NHM	Natural History Museum, London
MNPE	Musée national de Préhistoire, les Eyzies
MPRM	Musée de Préhistoire Régionale, Menton
MSI	Museo de San Isidro, Madrid
MUB	Medical University, Baku
NBC	Naturalis Biodiversity Center, Leiden
NCUA	National and Capodistrian University of Athens
NHM	Natural History Museum, London
NMMaa	Natuurhistorisch Museum, Maastricht
NMMai	Naturhistorisches Museum, Mainz
SAPM	Staatssammlung für Anthropologie und Paläoanatomie, München
SMNK	Staatliches Museum für Naturkunde, Karlsruhe
SMNS	Staatliches Museum für Naturkunde, Stuttgart
TMH	Teylers Museum, Haarlem
UCM	Universidad Complutense, Madrid
ZICAS	Zoological Institute of the China Academy of Sciences, Beijing

MAN 73/58/PJ-25, 27, 33, 34, 35, 75—minor fragments belonging to the previous two antlers from Pedro Jaro I.

MAN 3/58/ORC-1—right frontal and antler with brow tine and initial part of the main beam from Orcasitas. Figure 5 (5).

MAN 73/58/ORC-3—left shed antler with complete brow tine and initial part of main beam from Orcasitas. Figure 5 (4).

MAN 73/58/ CA K7/7–8—left frontal, antler broken of just above the burr, right frontal of the same individual with basal part of the antler, various fragments, none of them being palmate, from Orcasitas. Figure 5 (3).

MAN 19/68/CA K7/5—part of the left main beam, fits on MAN 73/58/ CA K7/7.

MAN 19/53/CA K7/4—part of the left main beam, fits on MAN 73/58/ CA K7/8.

MAN 19/58/CA K7/10—tip of the left brow tine, belongs to MAN 73/58/ CA K7/8, but there is no connection.

MAN 73/58/ORC/4—left shed antler, basal fragment from Orcasitas. Figure 5 (7).

MSI 1962/13/32—left frontal and antler base from Orcasitas. Figure 5 (6).

MSI 1962/13/33—fragment of brow tine from Orcasitas; same individual as no. 32. Figure 5 (6).

MAR 96/79/XIII/13/4/488—a left scapula from Transfesa unit Mz3.

MAR “nivel superficial” —a left scapula from Transfesa unit Mz3.

MNCN 62,332—a proximal and a distal fragment of a left radius from Transfesa unit Mz1.

Table 6 Acronyms of measurements

Acronym	
	Antlers and skull
DTsbc	Transverse diameter (width) of the skull at the brain case just below the pedicles
DTsped	Smallest width of the skull, measured at the pedicles
Lp	Length of the pedicles
DAPp	Antero-posterior diameter of the pedicles, just below the burr
DTp	Transverse diameter of the pedicles, just below the burr
DAPr	Antero-posterior diameter of the burr
DTr	Transverse diameter of the burr
DAPb	Antero-posterior diameter of the antler, just above the burr
DTb	Transverse diameter of the antler, just above the burr
Hint1	Height of the first bifurcation, measured at the medial side and from below the burr
Hint2	Height of the first bifurcation, measured at the medial side and from the upper surface of the burr
Hext1	Height of the first bifurcation, measured at the lateral side and from below the burr
Hext2	Height of the first bifurcation, measured at the lateral side and from the upper surface of the burr
Hmid	Height of the middle tine measured from the middle of the lower side of the burr till the bifurcation
Hback	Height of the back tine measured from the middle of the lower side of the burr till the bifurcation
	Scapula
DAPd	Distal antero-posterior diameter
DAPdf	Antero-posterior diameter of the distal articular surface
DTd	Distal transverse diameter
DAPn	Antero-posterior diameter of the "neck," the narrowest part of the bone
DTn	Transverse diamere of the "neck"
	Radius
DAPd	Distal antero-posterior diameter
DAPdf	Antero-posterior diameter of the distal articular surface
DTd	Distal transverse diameter
DTdf	Transverse diameter of the distal articular surface
	Metatarsal
DAPp	Proximal antero-posterior diameter
DAPpf	Antero-posterior diameter of the proximal articular surface
DTp	Proximal transverse diameter
DTpf	Transverse diameter of the proximal articular surface
DTm	Minimal transverse diameter

Table 7 Measurements of the antlers of *Dama celiae* (in mm)

No	s/d	DTsbc	Lp	DAPp	DTp	DAPr	DTr	DAPb	DTb	Hint1	Hint2	Hext1	Hext2
73/58/PJ-39	s	≈ 110	11.6	51.2	40.4	75.8	61.0	70.6	48.3	55.0	45.6	49.8	44.6
73/58/ORC-1	d		11.5	54.8	41.4	73.9	59.7	70.7	45.8	61.6	55.8	51.5	45.3
73/58/ORC-3	d					68.3	53.8	68.8	53.7	51.2	47.3	47.3	42.9
C-37/V-6	s	≈ 94	18.3	12.5	23.5	> 51	38.9	≈ 52	32.1	36.3	32.1	34	28.6
C-37/V-6	d		≈ 19	> 28.4	24.2								
73/58/ORC/4	s							42.2	28.8	40.1	34	35.5	31.8
1961/13/32	s	≈ 107.6	15.0	41.8	32.1	67.6	51.5	64.5	43.1				

Table 8 Measurements of the bones tentatively assigned to *Dama celiae*

Scapula	s/d	DAPd	DAPdf	DTd	DAPn	DTn
MAR 96/79/XIII/1314/488	s	54.9	39.7	37.0	31.4	20.0
MAR “nivel superficial”	s	–	36.8	35.5	30.0	–
Radius	s/d	DAPd	DAPdf	DTd	DTdf	
MNCN 62,332 (=5265)	s	27.7	23.3	41.0	38.4	
Metatarsal	s/d	DAPp	DAPdf	DTp	DTpf	DTm
MSI AM/61–3877	d	> 29,4	> 27.0	27.7	≈ 27.7	17.6

Fig. 5 Antlers of *Dama celiae* sp. nov. (1) MAN 73/58/PJ/39 + 21 + 26—left antler holotype from Pedro Jaro I: (a) left lateral view, (b) anterior view, (c) dorsal view. (2) MAN 73/58/PJ/24 main beam of right antler of the same individual: dorsal view, placed symmetrically with respect to the left antler. (3) MAN C37/V6—left frontal and basal antler and right frontal with pedicle from Orcasitas: (a) medial view of left antler, (b) lateral view of left antler, and (c) frontal view of both. (4) MAN 73/58/ORC-3—left shed antler from Orcasitas: (a) anterior, (b) lateral, and (c) dorsal views. (5) MAN 73/58/ORC-1—right antler of *Dama celiae* fom Orcasitas: (a) lateral and (b) medial views. (6) MSI 1962/13/32 + 33—left frontal and antler base + brow tine from Orcasitas. Figure 4 (6). (7) MAN 73/58/ CA K7/7–8—left shed antler from Orcasitas: (a) lateral view, (b) section. Scale bar approximate

MSI AM61/3877—proximal fragment of a right metatarsal from Arenero de Manuel Soto.

Description and comparison

The specimens from Orcasitas and Pedro Jaro I share the following morphologies: massive and long upward–curving brow tine, initial parts of the brow tine and main beam in a straight line or with a very obtuse angle, bifurcation between the brow tine and main beam very low above the burr, and regular pearling of the burr and groves on the surface as in *Dama* (the latter feature as described by Lister 1996), long main beam without bifurcation, directed backwards and then curving outwards without any tine originating at this place. The similarities between these specimens and the difference with other species indicate that they belong to the same species.

In some cases, half the width of the skull below the pedicle could be measured, allowing to estimate the approximate width. It is about 10 cm (Table 7). This is a middle-sized species.

The pedicle of the antler is situated close to the posterior half of the orbital (Fig. 53a). This is a common position in the Cervinae, while in the Capreolinae, the pedicle is situated further back above the brain case. The suture between frontal and parietal is situated just behind the pedicle and is directed transversely. The pedicles are oriented parallel (Fig. 53c), while in *Haploidoceros*, they tend to be divergent.

The burr has a very regular "pearling." This is more like in *Dama* than in *Cervus*, where the pearling may be more irregular. The surface of the antler has shallow groves, but no pearling, and resembles more that in *Dama* than in *Cervus* (Lister 1996).

The left antler from Pedro Jaro I, the holotype (Fig. 5 (1)), is a nearly complete antler. The main beam is long without any sign of bifurcation and is directed backwards and curves outward and then again backward. The preserved part is 58 cm from the middle of the burr, measured in a straight line and 62 cm along the outer curvature. A long part of the beam of the right antler, which is identical in its curvature, is also preserved. Its length is 62 cm, measured along the curvature, and 59 cm in a straight line. Its lower part is already some distance of the burr, suggesting that at about 64 cm from the burr there was still nothing to be seen of the flattening that preceedes a bifurcation. At this place, the diameters of the section become smaller, suggesting that the tip would be close. Fragments of the main beam that fit on MAN C37/V6 from Orcasitas show an identical outward curvature. There is no important upward curvature in the preserved part. At some distance from the burr, the section of the main beam is oval with a clearly wider transverse than antero-posterior or dorso-ventral section. There is no indication of any bifurcation save for that of the brow tine. *Haploidoceros mediterraneus* (Fig. 6 (2) is one of the few deer with a long not bifurcated main beam, but it is directed more upward and curves forward. The angle between brow tine and main beam is much sharper and the bifurcation placed much higher above the burr (Fig. 6). *Rucervus eldi* (or *Panolia eldi*; Fig. 6 (3) has a long main beam, but with minor tines coming off and with a distal upward curvature. It is similar to the specimens from Madrid in that the bifurcation of the brow tine and main beam is situated very low above the burr and that they make a very obtuse angle (Fig. 6).

The middle-sized to large deer like *Metacervoceros pardinensis*, *Praeelaphus perrieri*, and *Axis? perolensis* (Fig. 6 (1) have branching antlers with three or four points (Heintz 1970). The latter differs from the fallow deer from Madrid in having a much higher bifurcation (Fig. 6). Azzaroli (1992) named the species *Pseudodama lyra*, and the holotype is a frontal with both complete antlers with tree points from Ponte a Elsa. The antlers are of a general primitive type, which occurs also in other species of this age that are no fallow deer, and we are not aware of any associated dental or postcranial specimens that allow the confirmation of the generic classification. It differs from the deer from Madrid in having three points and a high first bifurcation with a sharp angle between brow tine and main beam. In these features, it is similar to *D. rhenana*.

The *Dama*-like deer are a very large group and include species with three points. This is the case with *Dama rhenana*, *Dama philisi* (Fig. 7 (1) and (2), *Dama philisi valliensis* (Heintz 1970), which differ from the deer from Pedro Jaro I and Orcasitas in having a high first bifurcation (Fig. 8) with a sharp angle.

Dama nestii, *Dama nestii eurygonos*, and *Dama abesalomi* have branching antlers with four points (Fig. 7 (3, 4); Azzaroli 1948, Fig. 5 (1). In addition, they differ from the fallow deer from the Manzanares valley in that they have first bifurcations with sharper angles that are positioned higher above the burr (Fig. 8).

The type of *Dama farnetensis* has three points on one side and four on the other, differing thus from the deer from Pedro Jaro I and Orcasitas. The species has a first bifurcation with an obtuse angle (Fig. 7 (5)) and in some specimens a bifurcation that is proportionally as low as in the deer from Madrid (Fig. 8).

We do not know the number of points of the antler of *Dama vallonnetensis* in its type locality Vallonnet, but this species has antlers with a bifurcation as low as in the deer from Madrid (Fig. 8) and with a similar very obtuse angle (Fig. 9 (1)). The deer from TE9 was assigned to *Dama vallonnetensis* (Rosas et al. 2001; Van der Made 2013). This antler has a long main beam, which becomes flattened and still more distally bifurcated. It has three points, but it is similar to those from Madrid in the shape and position of the first bifurcation.

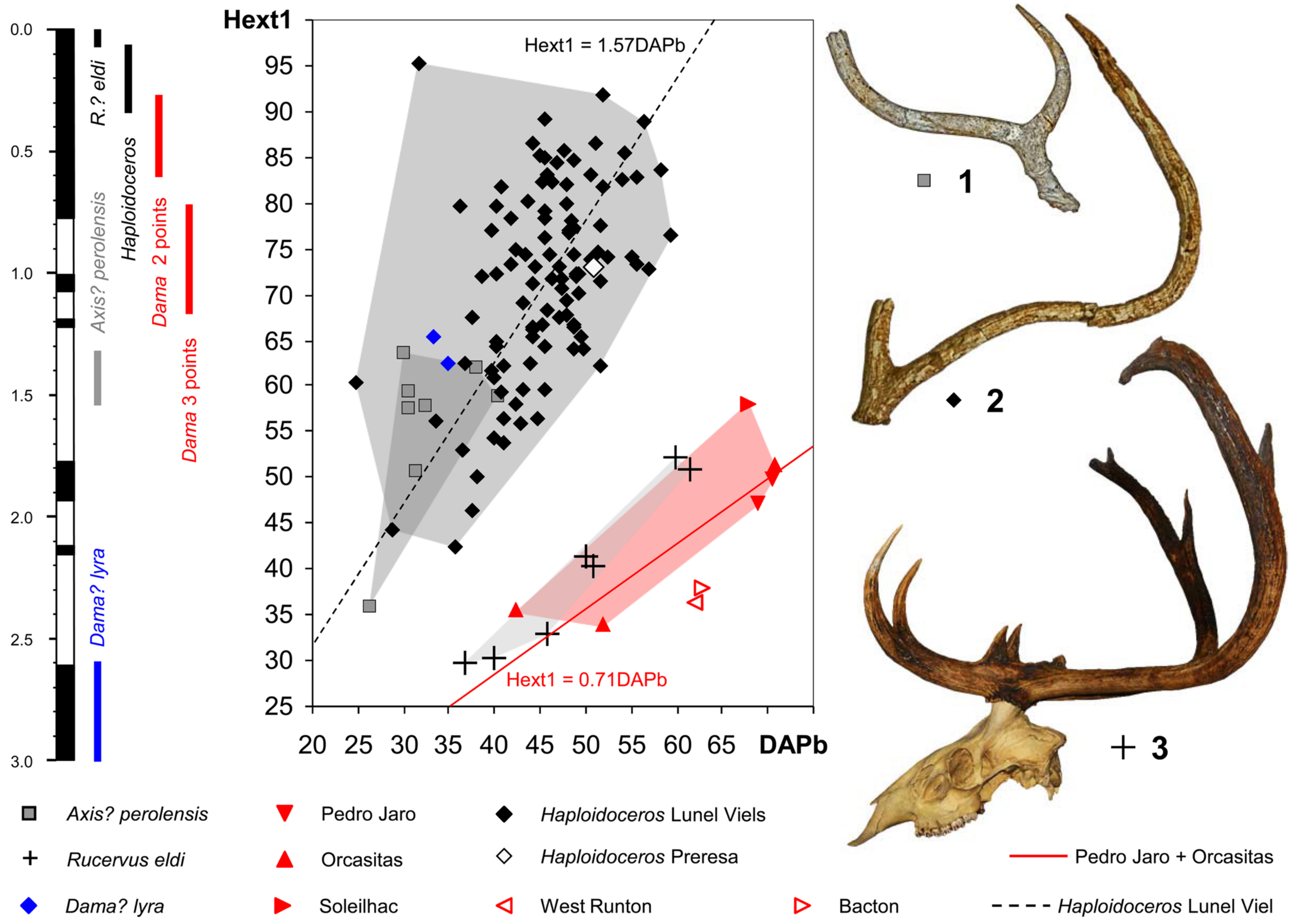

Fig. 6 Bivariate diagram of the antero-posterior diameter of the antler just above the burr (DAPb) and height of the first bifurcation, measured at the lateral side and including the burr (Hext1) comparing *Dama celiae* from Pedro Jaro I and Orcasitas with other species and samples of deer, predominantly those not closely related to *Dama*. Provenance of data as indicated in Table 2. Approximate temporal distribution of the different species. Photographs: (1) NHM 34,526—left antler of *Axis? perolensis* from Peyrolles, medial view. (2) MNPE LVI-15728—right shed antler, syntype of *Haplodoiceros mediterraneus*, medial view. (3) AMNH 54,557—skull with antlers of recent *Rucervus eldi*

The main beam of *D. roberti* from Pakefield becomes flattened at some distance of the burr (Fig. 8 (9)), as the antler from TE9, but there is no second bifurcation. In a specimen from Soleilhac (Fig. 8 (10)), there is a similar flattening and then a narrowing and the main beam ends in a single point. This is a two-pointed antler, but the specimens from Pakefield and Soleilhac differ from those from Pedro Jaro I in having a marked flattening. Antlers of this species from Soleilhac, West Runton, and Bacton assigned to this species (Fig. 9 (2, 3)) have a bifurcation with a low position above the burr and a variable angle. The main beam of the antler from Soleilhac is straight, and the ones from Pakefield are only slightly curved, but the antler from Pedro Jaro I curves strongly outward and then backward again.

The remaining species of *Dama* differ from the deer from Madrid in having palmate antlers (Figs. 7 (8, 9, 11) and 9 (6, 7); Melentis 1966a, plate III Fig. 4). While *D. peloponesiaca* and *D.* aff. *peloponesiaca* (Fig. 9 (6, 7)) tend to have the bifurcation in much higher poisitions, relative to the size (DAPb) of the antler than the deer from Madrid (Fig. 9). *Dama clactoniana* and *Dama dama* have the first bifurcation in a position similar to that of the deer from the Manzanares valley (Fig. 8). The curvature of the main beam in the deer from Madrid is similar to that in the living fallow deer, in curving outward and then again more parallel to the median plane. *Dama clactoniana* and *D. dama* have the origin of the middle tine where the main beam curves backward and the origin of the back tine close to the place where the antler curves upward and well after the place where the main beam starts to widen into what becomes the palmation. In the specimen from Pedro Jaro I, there is no middle tine at the position where the antler curves backward and the preserved pard does not include a back tine, palmation, or upward curvature. The preserved part of the main beam is long, and if

Fig. 7 Antlers of fallow deer. (1) NBC St28148—left antler, holotype of *Dama rhenana* from Tegelen: lateral view. (2) NMB Se1843—skull fragment and antlers of *Dama philisi* from Senèze, left-frontal view. (3) IGF 363—skull fragment with both antlers, type of *Dama nestii* from the Upper Valdarno, anterior view. (4) GSM 1495—left antler, holotype of *Dama abesalomi* from Dmanisi, (a) anterior and (b) lateral views. (5) IGF 194v—skull fragment with both antlers, holotype of *Dama farnetensis* from Cava Liberatori, Persignano near Farneta, left-anterior view. (6) CENIEH Ata06/TE9c/J-30/70—antler of *Dama vallonnetensis* from Atapuerca TE9. (7) NCM 2004.831.12–14—skull fragment and antlers, holotype of *Dama roberti* from Pakefield: left lateral view. (8) HUJ 7722—left antler of recent *D. mesopotamica*, lateral view. (9) NHM no number—right antler of *D. clactoniana* from Swanscombe, medial view. (10) MCP 2003–4-390-SOL—right antler of *Dama* from Soleilhac: lateral view. (11) LVH 27–6-89′13—right antler of *D. dama geiselana* from Neumark Nord, medial view. Not to scale

there would be a second bifurcation, the resulting Hm or Hback would be > 58 cm in a straight line and > 62 cm along the curvature and much higher than in species with a similar low first bifurcation (Figs. 10 and 11).

The brow tine is large in all specimens from Pedro Jaro I and Orcasitas; it is long and has a large diameter. It is initially horizontal and then curves up very much and even backwards. The point may be directed medially (Fig. 5 (4a, 4c)). Also, *Dama roberti* has such large brow tines in Pakefield (Fig. 7 (7)), Soleilhac (Figs. 7 (10) and 9 (4, 5)), and Bacton (Fig. 9 (2)) and this is also the case in *Dama vallonnetensis* (Fig. 9 (1)). *Dama farnetensis* has a long brow tine, but it is directed more outwards and less upwards (Fig. 7 (5)). All these species tend to have low first bifurcations. The palmate species also have low first bifurcations, but their brow tines tend to be smaller, shorter, and with smaller diameters at the base. This is so in *Dama peloponesiaca* (Fig. 9 (6) is just one out of many specimens) and *Dama* aff. *peloponesiaca* (Fig. 9 (7)). *Dama clactoniana* (Fig. 7 (9)) and *D. d. geiselana* (Fig. 7 (11)) may have large brow tines, but the upward curved part is not as long as in Pedro Jaro and Orcasitas. Recent *Dama dama* tend to have much smaller and less cuved brow tines and *Dama mesopotamica* has the brow tine very reduced or completely lost (Fig. 7 (8)) and the first large tine that can be seen is homologous to the second tine in *Dama dama*.

Two scapulas from Transfesa were too small for *Megaloceros matritensis* (Van der Made 2019, Fig. 18). The best preserved specimen (Fig. 12 (2)) has a tuberosity that is pointed in lateral view, as in *Dama*, with a nearly straight anterior edge, and slightly hooked in distal view. The articular surface is slightly flattened at the lateral

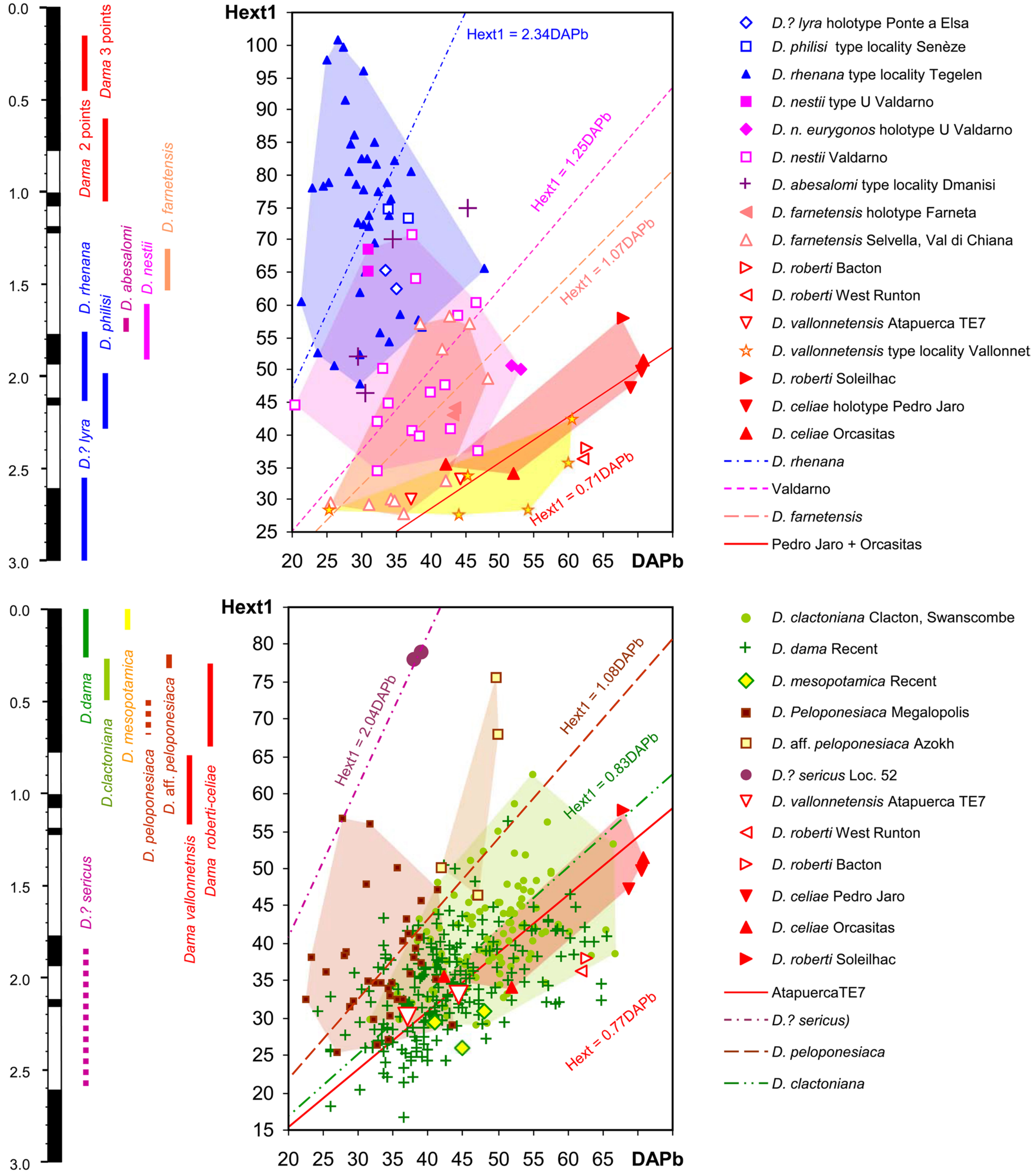

Fig. 8 Bivariate diagrams of the antero-posterior diameter of the antler just above the burr (DAPb) and height of the first bifurcation, measured at the lateral side and including the burr (Hext1), comparing *Dama celiae* from Pedro Jaro I and Orcasitas and *D. roberti* with species and samples of *Dama*-like deer with branching antlers (above) and with palmate antlers (below). Provenance of data as indicated in Table 4. Approximate temporal distribution of these species

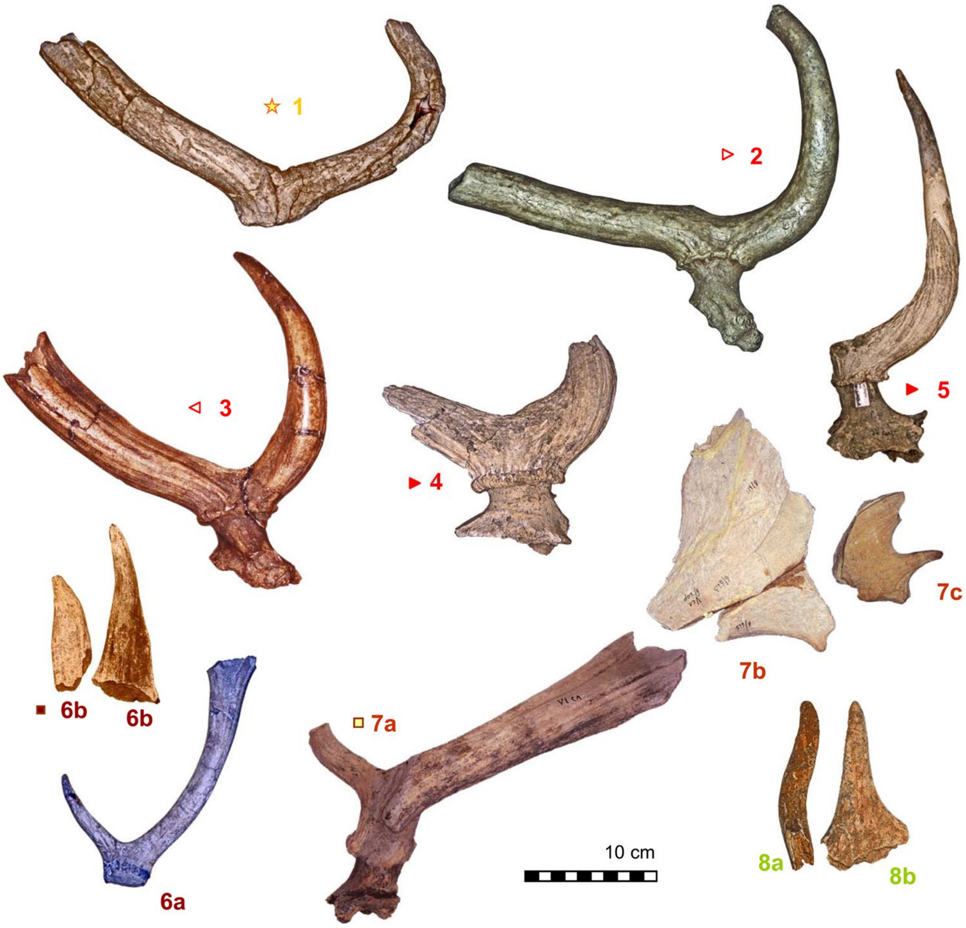

Fig. 9 Antlers of fallow deer. (1) MPRM B7/C/10170—left shed antler of *D. vallonnetensis* from Vallonnet, medial view. (2) NHM M18182—right antler of *Dama roberti* from Bacton: lateral view. (3) NHM M18181—right antler of *Dama roberti* from WestRunton: lateral view. (4) MCP 2003–4-288-SOL—left antler of *Dama roberti* from Soleilhac: medial view. (5) MCP 2003–4-387-SOL—left antler of *Dama roberti* from Soleilhac: medial view. (6) *Dama peloponesiaca* from Megalopolis: (a) NCUA 8—left antler, lateral view, (b) NCUA no number—flattened tine, NCUA no number—flattened tine. (7) *Dama* aff. *peloponesiaca* from Azokh Cave 1, level V: (a) MUB 1/206—right antler, medial view, (b) MUB 6/623—fragment of left (?) palmation, (c) MUB 4/406—fragment of palmation. (8) *Dama clactoniana* from Atapuerca TD10: CENIEH Ata15/TD10-3/I21/87—flattened tine, two views. Letters A, B, C, and D refer to tine positions; for the explanation, see text

side. Lister (1996) used these features to distinguish between *Cervus* and *Dama*. These specimens have the right size for *Dama*. In side view, the scapulas have a constriction just above the articulation. In *Dama* and the specimens from Transfesa, the diameter there (DAPn) is relatively less compared to the other measurements, than in *Cervus elaphus*, *Haploidoceros*, and *Megaloceros matritensis* from Orcasitas (Fig. 12). The transverse diameter at this place is not clearly different between the species. This morphological feature confirms that the scapulas belong to *Dama*. A radius from Transfesa (Fig. 12 (1)) is smaller than the radii of *Cervus elaphus*, and its size fits *Dama* (Fig. 12). The edge between the facets for the lunar and ulnar is angled as in *Dama* (a feature described by Lister 1996). A proximal metatarsal from Arenero de Manuel Soto is of cervid morphology and the approximate size of a fallow deer (Fig. 12). The proximal articular surface is damaged. If these remains belong to *D. celiae*, they suggest a large body weight, comparable to that of *D. clactoniana* and (on average) more than *D. d. geiselana* and considerably more than the living *Dama dama* and *D. mesopotamica*, which weigh 35–80 kg and 70–140 kg, respectively (Wilson & Mittermeier, 2011).

Taxonomic discussion

The origin of the pedicle is not so far posterior as in the Capreolinae. The main beam is much longer than in the Muntiacinae and primitive Miocene species of deer, which are smaller (as seen by the diameter of the pedicle or estimated skull width). This leaves the Cervinae. The low first bifurcation (compared to other measurements of the antler) is well documented in the specimens from Madrid. It is lower than in most of the European Cervinae (*Haploidoceros*, *Eucladoceros*, *Croizetoceros*, *Arvernoceros*, *Praeelaphus*, *Metacervocerus, Cervus*) and living species from Asia, *Axis*, *Rusa*, *Elaphurus*, and *Rucervus* (with the exception of *R. eldi*). Such a low first bifurcation occurs only in the Cervinae in some species of *Dama* (Fig. 7), *Megaloceros*, *Megaceroides*, and *Rucervus eldi* (or *Panolia eldi*). The species of *Megaloceros* and *Megaceroides* are much larger (as can be seen in the diameters of the pedicle or the estimated width of the skull). *Rucervus eldi* (Fig. 6 (3)) is different in that the main beam of the antler curves much upward in its distal part and in that it has very small points situated on the posterior side of the main beam. These comparisons show the deer from Madrid to be different from all

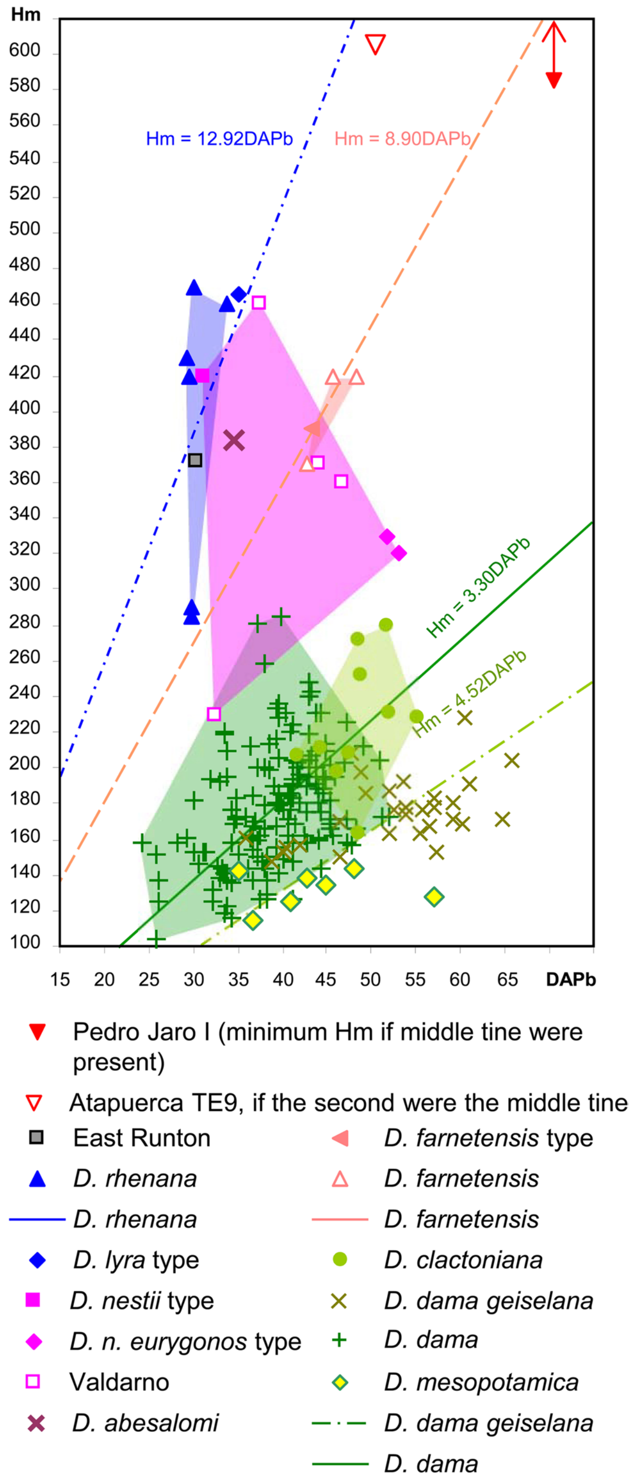

Fig. 10 Bivariate diagram comparing the height of the middle tine above the lower side of the burr (Hm) to the antero-posterior diameter of the antler just above the burr (DAPb) in various species and samples of *Dama*. Provenance of data as indicated in Table 4. The lines indicate average proportions

Pleistocene deer of Europe, save for some species of *Dama*. The specimens from Pedro Jaro I and Orcasitas have the perlation of the burr and the regular shallow groves on the brow tine and main beam as in *Dama* (Lister 1996) and also the parallel pedicles. They share the low first bifurcation with *Dama vallonnetensis*, *D. roberti*, *D. clactoniana*, and *D. dama*, as well as *D. farnetensis* in part.

The deer from Madrid does not have a second bifurcation closer than 58–64 cm to the burr, while at this place, the diameters of the main beam decreased and started the formation of a point. *D. clactionana* and *D. dama* have the second bifurcation at 10–30 cm from the burr (Fig. 10). *Dama vallonnetensis* from type locality Vallonnet is not known in this respect, but from Atapuerca TE9 (Fig. 8 (6)), a second bifurction is known. In TE9, it occurs about 60 cm from the burr, but some 20 cm lower at about 40 cm from the burr, the main beam starts to widen (in antero-posterior direction). There is no sign of this in the specimens from Pedro Jaro I. There is also no sign of a palmation, which occurs in *Dama clactoniana*, *D. dama*, *D. mesopotamica*, and *D. peloponesiaca* (Figs. 8 (8, 9, 11) and 9 (6, 7); Melentis 1966a, plate 3, Fig. 4). There is no sign of a flattening of the distal part of the main beam as seen in *D. roberti* (Fig. 7 (7, 10)).

We can reasonably assume that the deer from the Manzanares valley is different from the other known species of Cervidae. Therefore, we give this species the new name *Dama celiae*. A reconstruction of how a male of the species may have looked like is given in Fig. 13.

Discussion

Evolution of the fallow deer

In a broad sense, the evolution of the fallow deer has been seen as the increase of complexity of the antler, with an increase from three points (as in *Dama rhenana* and *D. philisi*) to four points (as in *D. nestii*) and then part of the antler developing into a palmation. However, to know more precisely how this evolution occurred, it is necessary to know which tine is which and what happened to each tine.

The different species of fallow deer with branching antlers have mostly three or four points (or tines coming off the main beam). The lower one is called brow tine (A) and the second may be the middle tine (B), but this depends on the situation. Early species have three tines (positions A, B, C) and some later species have an additional distal tine, making four (A, B, C, D in Fig. 9), while some later species have again three tines. Breda and Lister (2013) discussed several

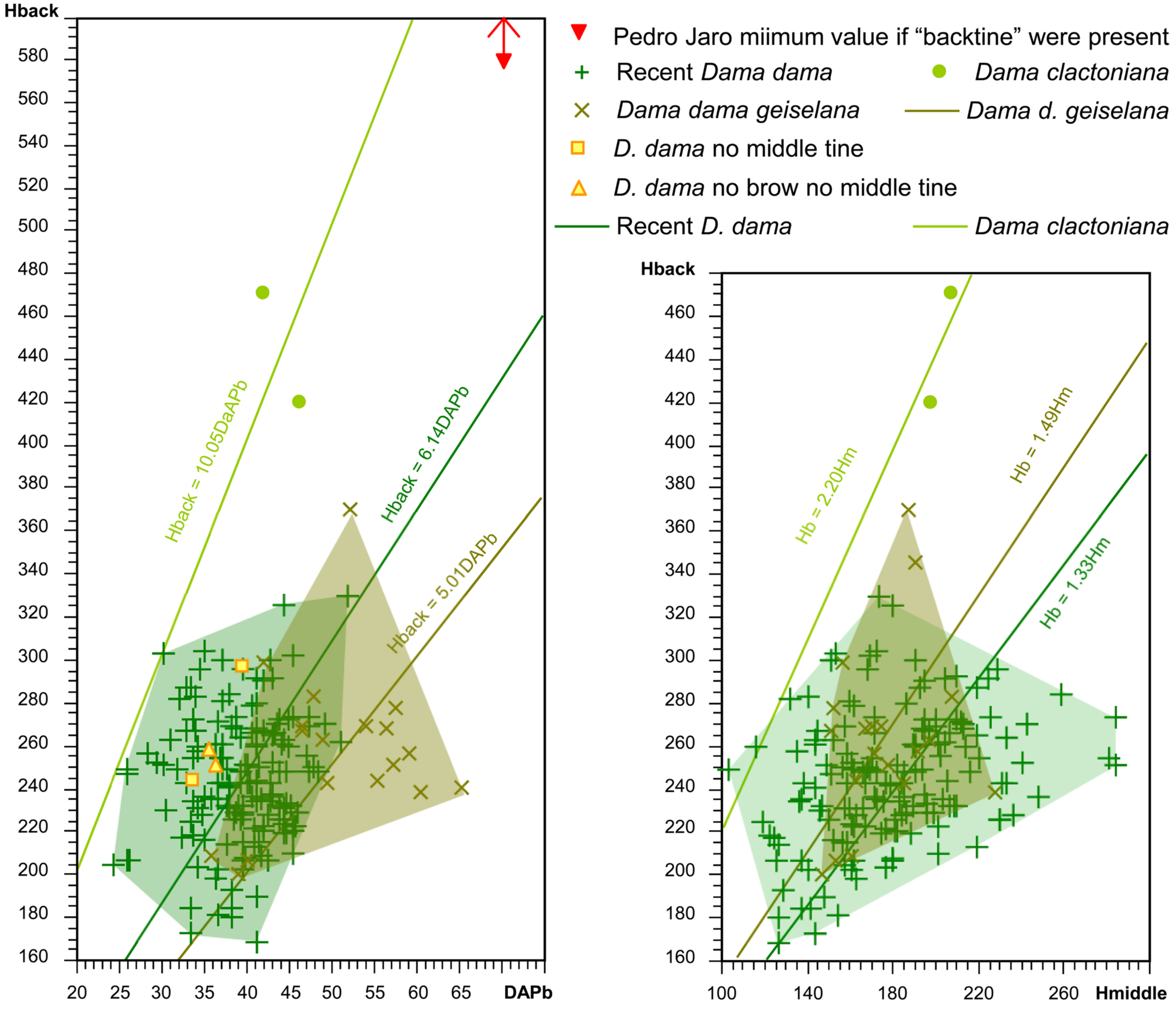

Fig. 11 Bivariate diagrams comparing the height of the "back tine" above the base of the burr (Hback) to the antero-posterior diameter of the antler just above the burr (DAPb) and the height of the middle tine above the base of the burr (Hmiddle) in *Dama clactoniana*, *Dama dama geiselana* from Neumark Nord, and recent *Dama dama*. The lines indicate average proportions. Provenance of data indicated in Table 4. For Pedro Jaro I, the minimum height is given in the hypothetical case that it would have had a "back" tine

scenarios of the evolution of the fallow deer and mentioned the possible reduction of the middle tine, and that the type specimen of *D. farnetensis* has four tines on the right side and three on the left side. The second tine on the right side (B) is small, and on the same place on the left antler, there is no tine at all. So, the left antler has tines on positions A, C, and D. Biometry and morphology provide some additional arguments for the identification of the middle tine.

The position of a middle tine is not random, but is proportional to the rest of the antler. As we can see in Figs. 6 and 7, the position of the brow tine varies much between species, but within each species, the variation is much more limited. We can observe that there is a tendency for the successive species to have the brow tine in progressively lower positions. This is a common evolutionary tendency in the Cervinae and has been documented for *Dama* (Van der Made 1999; Van der Made et al. 2016, 2017), *Megaloceros*, and *Sinomegaceros* (Van der Made & Tong 2008; Van der Made 2015, 2019) and is also known from *Megaceroides* (*Praemegaceros*), while in *Eucladoceros* there is no clear tendency, but the different species differ in this feature (Van der Made & Dimitrijevic 2015). Though there are fewer data on the position of the middle tine (B) than on the brow tine (A), in successive samples or species, it also tends to originate in a progressively lower position. This is documented in *Megaloceros* (Van der Made & Tong 2008), but

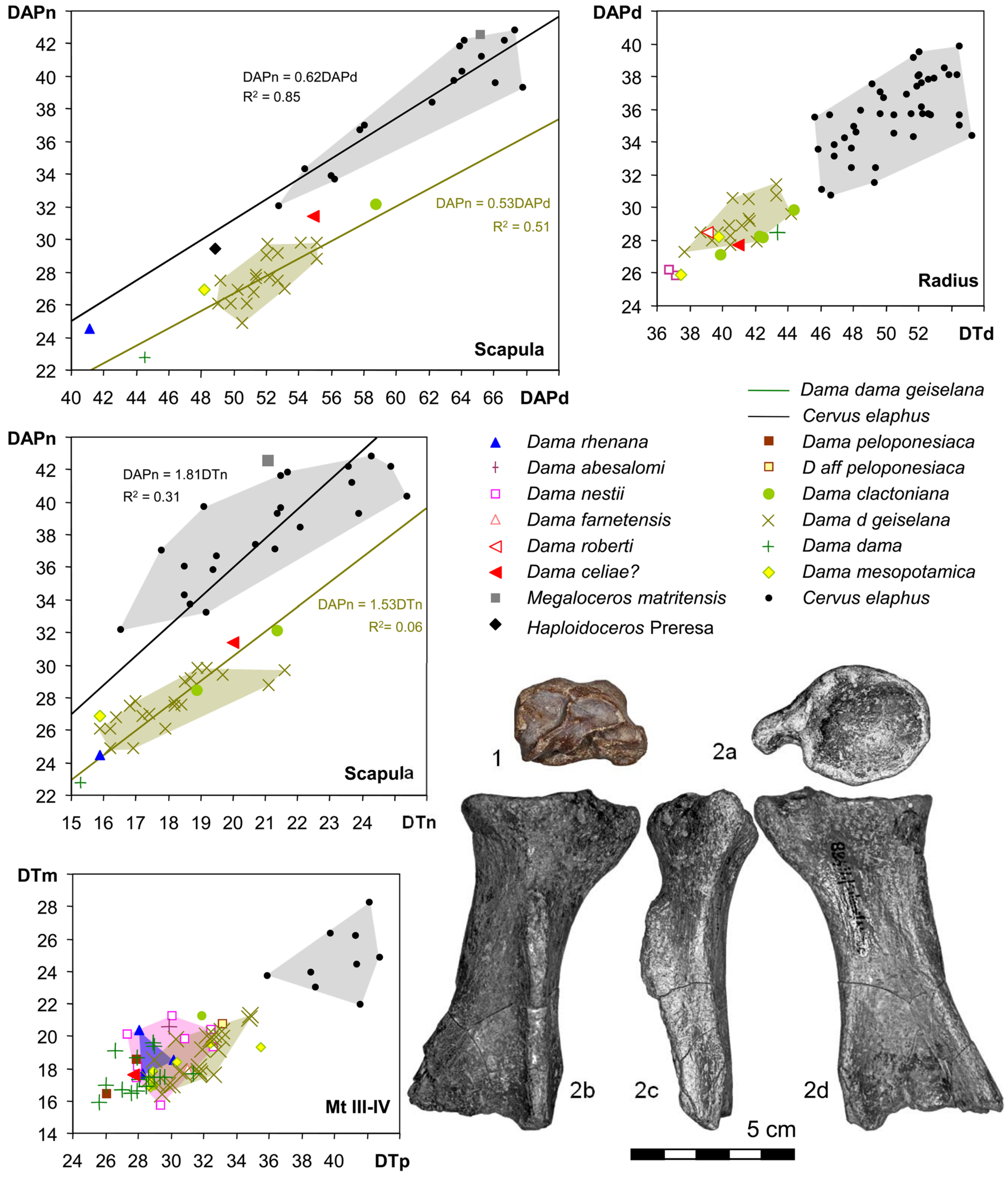

Fig. 12 Bivariate diagrams comparing antero-posterior (DAPn) and transverse (DTn) diameters of the "neck" and distal antero-posterior diameter (DAPd) of the scapula, distal antero-posterior (DAPd) and transverse (DTd) diameters of the radius, and proximal (DTp) and minimum (DTm) widths of the metatarsal. *Cervus elaphus* from Neumark Nord, West Runton and Burgtonna (Mt), Neumark Nord, Bilzingsleben and Can Rubau (radius), Neumark Nord, Voigtstedt, Mauer, Bilzingslegen, Steinheim, Murr, Azokh V, and Can Rubau (scapula). Provenance of data indicated in Table 2. Lines indicate the average proportions. Photographs of *Dama celiae*? from Transfesa: (1) MNCN 62,332—left radius: distal view; (2) MAR 96/79/XIII/1314/488—left scapula: (a) distal, (b) lateral, (c) anterior, and (d) medial views

Fig. 13 Reconstruction of *Dama celiae* (by J.J. Rodríguez-Alba)

it occurs also in *Dama*. The positions in which the different tines originate from the main beam are not independent but are related: if the brow tine originates lower, the middle tine also originates lower (compare Figs. 8 and 10). The antler of *Dama vallonnetensis* from Atapuerca TE9 has suffered post-depositional deformation, but the approximate position of the second bifurcation could be estimated and is indicated in Fig. 10. Given the low position of the brow tine in TE7 and TE9 (Fig. 8), we would expect the position of the middle tine to be as low as in *Dama clactoniana* and *Dama dama*, or at least as low as in *Dama farnetensis*. Nevertheless, the bifurcation is much higher than the bifurcation that marks the origin of the middle tine in any of the other species and it seems much more likely that the middle tine is lost and the second bifurcation in TE9 is homologous to the third bifurcation in *Dama nestii*.

Morphology supports the idea that the middle tine (B) is reduced: the origin of this tine is situated near to the place where the main beam curves from an outward direction to a posterior or upward direction. In any case, the middle tine is not situated more distally than this curvature. Such a curvature is not observed in the specimen from Atapuerca TE9, which could be due to taphonomical processes involving deformation and this may also be the case in Soleilhac. In Pakefield, such a curvature is observed, though it is not very pronounced (Breda & Lister 2013, SI Fig. 3), while in Pedro Jaro I, it is very pronounced. In none of the two cases is there any sign of a middle tine (B) at this place.

A middle tine may occasionally be absent. It is a possibility that by chance, the middle tine is absent in the antlers from Atapuerca TE9, Pakefield, Soleilhac, and Pedro Jaro I, but that it was present in the majority of the individuals of these populations. This is possible, but is it also probable? In the living *Dama dama*, the middle tine (B) may be lacking. Of 155 measured recent antlers from Doñana, two lack the middle tine (EBD 11–3-89, A5 and EBD 2649 M, S27, 1981), and two shed specimens of the same individual lack the middle tine and brow tine (EBD A44), but have the backward-directed tine at the beginning of the palmation. These four are about 2.5% of the sample, and the two which lack only the middle tine are about 1.3%. If the proportion of antlers with a lacking middle tine was more or less similar in the fossil species, it seems unlikely that all the antlers from Atapuerca TE9, Pakefield, Soleilhac, and Pedro Jaro I, which are sufficiently preserved to expect a middle tine, lack it just for chance.

Morphology, biometrics, and statistics favor the first explanation offered by Breda and Lister (2013): the evolutionary loss of the middle tine (B) in *Dama vallonnetensis* and *D. roberti*, but also in *D. celiae*. The other proposal they made is that the flattening near the end of the antler from Soleilhac and in the antlers from Pakefield evolved into the palmation of *Dama clactoniana* and the living species. This, however, seems to be a reversal of the evolution that led to the *D. roberti* antler.

The antler of *Dama vallonnetensis* from Atapuerca TE9 is complete, though it is deformed (Fig. 8 (6)). The two distal tines (C and D) diverge at a very sharp angle and the area between them is a bony plate till the two tines are at a distance. The divergence of the tines is noted approximately 20 cm below the actual bifurcation and roughly at 40 cm from the burr. Just below the separation, the bony plate is over 10 cm wide. The two tines are also flattened at their base. The posterior tine measures 36.6 × ≈ 24 mm at a short distance above the bifurcation. The sections of these tines become more circular near the tips. These tines have lengths from the bifurcation of 46 and 48 cm. *Dama roberti* from Soleilhac has a main beam with a length of 57 cm. It becomes wide (up to 67 mm) and flat near the tip and then round again without bifurcating (Breda & Lister 2013). This widening may have started at a similar height as in TE9. It seems likely that the morphology of the antlers of *Dama roberti* evolved from the morphology of the antler from TE9 by shortening the anterior tine (C) from 48 to about 10 cm and by completely reducing the posterior tine (D). An evolution from the antler of *Dama roberti* to the one of *Dama celiae* would involve the continuation of the trend of reduction of tines and the loss of the flattened part.

Many of the antlers of *Dama clactoniana* do not have a wide palmation but do have several branches. It is easy to imagine the perfectly palmate antlers of *Dama dama* to have originated from filling in the spaces between these branches by bony plate or by a palmate structure growing from the back of tine C. In the more developed *Dama clactoniana* antlers (as in the skull from Swanscombe), many long flat tines may originate from the palmation, while in *Dama dama*, the predominant situation is that the tines originating from the palmation are very short. An evolution from *D. roberti* to *D. clactoniana* and *D. dama* would require that after these tines were reduced (in *D. roberti*), they started again to grow from the flattened area (in *D. clactoniana*) and then, when the palmation increased in size, they decreased again (in *D. dama*). These are repeated reversals.

The antler from Pedro Jaro I does not have a palmation, at least not in the part that is preserved. Could there have been a more distal palmation? The anterior edge of the palmation in *Dama dama* and *Dama clactoniana* is smooth, but at the back there are little points or not so little flattened tines. The most proximal of these is separate from the palmation and is tine D. In German, it is called *Dorn* or *Sporn* (Ueckermann & Hansen 2002) or *Wolfssprosse* (Pfeiffer 1999, Fig. 14) and in English "back tine." The base of this tine can be easily and objectively identified, and its distance to the burr (Hback) can be measured as an indication of the beginning of the palmation. Figure 11 shows the position of the "*Dorn*" relative to other measurements of the antler. It is interesting to note that *Dama clactoniana* has different proportions from *Dama dama* and that the palmation starts in a clearly higher position. This is a little surprising, since the brow and middle tines are in a similar position in both species. In any case, even in *Dama clactoniana*, the palmation starts closer to the burr than what could be possible in Pedro Jaro I.

The most likely scenario is of an evolution of a three-pointed (A, B, C) *Dama* (*D. rhenana*, *D. philisi*, *D. valliensis*) to the four-pointed (A, B, C, D) *Dama nestii* and then the starting reduction of the middle tine (B) in *Dama farnetensis*, complete lack of middle tine in *D. vallonnetensis* (retaining A, C, D), reduction of the most distal tine (D)

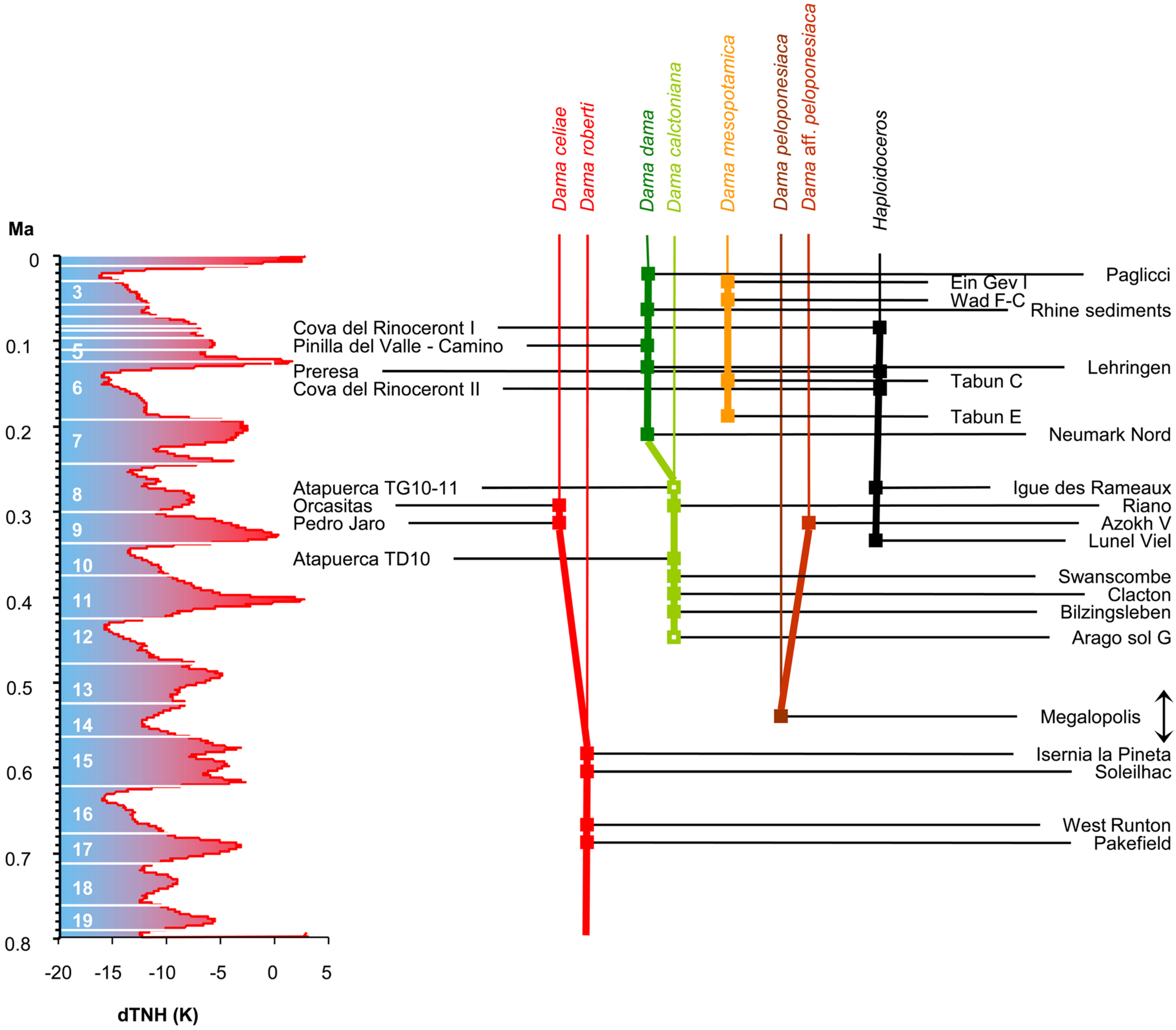

Fig. 14 Temporal distribution of the Middle Pleistocene species of *Dama*. Scale in millions of years (Ma) and dTNH and MIS as in Fig. 3. Localities from Spain on the left, from the rest of Europe on the right. Presence of a species in a locality indicated by a solid square

in *D. roberti* but retention of a flattened area, and finally a simple main beam with out flattening or bifurcation in *Dama celiae* (retaining A and C). The tines moved to a lower position in this lineage, and this is particularly so for the brow tine (A). It seems palmation evolved (from the back of C) in parallel to this reduction and was present already in *Dama peloponesiaca* before *D. clactoniana* appeared. In these species of *Dama*, the first bifurcation, and possibly other structures as well, moved toward the burr and the brow tine (A) reduced (in *D. dama*) or nearly completely disappeared (in *D. mesopotamica*).

Diversity of fallow deer–sized species in the Middle Pleistocene

Until recently, the predominant idea was that there were few *Dama*-sized deer in the Middle and Late Pleistocene of Europe. The living fallow deer were considered to have evolved from *Dama clactoniana* (or *D. dama clactoniana*), which was preceded by *Dama nestii*, whether related or not (e.g., Kurtén, 1968; Faure & Guérin 1992; Delpech & Guérin 1996; Van der Made 1999). In general, *Dama clactoniana* was traced back till the beginning of the Middle Pleistocene or even earlier. With one species at a time, this is a very low diversity of deer of this size, but the idea of a simple lineage or succession of few species started to change (Fig. 1) and various models were published in which species of *Dama* or of this size were contemporaneous and even sympatric (Figs. 1, 14).

Dama clactoniana

If *Dama clactoniana* is not a direct descendant of *D. roberti* or *D. vallonnetensis*, and if there is no directly ancestral form known from W Europe, then it seems that it evolved outside this area and dispersed into it later. The date of the appearance of *Dama clactoniana* varies widely according to the authors and is given as Holsteinian (about MIS9-11) (Sickenberg 1965), possibly before the Holsteinian (Kurtén, 1968), zone 21 (750–600 ka, Cromerian; Guérin 1982; Faure & Guérin 1992), and 1.3 Ma (Di Stefano & Petronio 2002). Lister (1986) considered the first appearance of *Dama dama* (including *D. d. clactoniana*) to be in the early Cromerian and perhaps Beestonian. Croitor (2006, 2018) considered the antlers from Soleilhac and Pakefield (on which the species *D. roberti* is based) as juveniles of *Dama clactoniana*, which implies a first appearance not later than MIS17 (712–676 ka). In the scenario that *D. clactoniana* evolved from *D. roberti* (Breda & Lister 2013), the transition must be after Soleilhac (MIS15, 563–621 ka) and older records are discarded. *Dama clactoniana* is present in Clacton, Swanscombe, and Bilzingsleben (Fig. 14). Flattened tines from Atapuerca TD10 (Fig. 9 (8)) show the species was present in Spain between 400 and 300 ka, but many other sites with remains of a fallow deer, but without a clear palmation or middle tine, are dubious now.

Dama peloponesiaca

Melentis (1966a) described the deer fossils from Megalopolis, which had been excavated in 1902, and assigned part of them to *Cervus (Dama) somonensis*. Instead of this name, today, the name *Dama clactoniana* is used (Sickenberg 1965). The material includes a part of a palmation (Melentis 1966a, Pl. 3, Fig. 4). Sickenberg (1975) named *Cervus* s.l. *peloponesiacus* on the basis of material collected from the same basin. This species was ignored for a long time. There is much more material of this species in the University of Athens than described by Melentis and includes also flattened tines, which appear to have originated at the back of a palmation (Fig. 9 (6b–c)) and many antler bases, with a first bifurcation that is higher than in *Dama dama* or *D. clactoniana* (Fig. 8). The latter difference was given importance, and the species *D. peloponesiaca* was recognized as valid (Van der Made 2011, 2013, 2015; Van der Made et al. 2014, 2016, 2017; Van der Made & Mazo 2014).

The age of the older collections is not well known. Melentis (1966a, b, c) indicated the deer and *Equus abeli* come from a locality near the village of Mussakla, while the rhinos come from a site near the village Issoma Karyon. Of other remains (*Sus scrofa*, *Hippopotamus*, Bovini), the exact provenance was not indicated. The *Equus* is of the caballoid type, and this type appeared around 600 ka in Europe. The *Cervus elaphus* is smaller than in Voigtstedt and Süssenborn, pointing to a similar maximum age (for size changes in *Cervus elaphus*, see Van der Made et al. 2014, 2016). The fossils described by Sickenberg (1975) come from different sites in the Marathousa Beds, and the faunal list he gave includes *Mammuthus meridionalis*, *Praemegaceros verticornis*, and *Bubalus marathousae*. The proboscidean would suggest an age of 700 ka or older. *Bubalus murrensis* is known to have dispersed to Europe during MIS11, 9, and probably 5 (Von Koenigswald et al. 2019). Alternatively, *Bubalus marathousae* is the same as *Bos galerianus* or *Hemibos galerianus* (Petronio & Sardella 1998; Martínez-Navarro & Palombo 2004), implying that *Bubalus* dispersed even earlier to Europe and that the age of at least part of the Sickenberg collection may be older than MIS11. Material recently excavated was described as *"Cervus" peloponesiacus*, and its age was assumed to be early Middle Pleistocene (Athanassiou 2018). The Marathousa member was deposited during various 100-ka eccentricity cycles covering a period from at least 900 to 300 (Van Vugt et al. 2001; Okuda et al. 2002).

A similar but larger species is present in Azokh level V, dated to around 300 ka or less and correlated to MIS9 (Van der Made et al. 2016; Fernández-Jalvo et al. 2016), perhaps MIS8 is also possible for this level (Fig. 14). Fallow deer of this type may have lived for a long time in SE Europe or the Middle East.

Haploidoceros mediterraneus

Bonifay (1967) named *Euctenoceros mediterraneus* on the basis of material from Lunel Viel. For a long time, this species was ignored, until much more material was published and it was placed in a different genus (Croitor et al. 2008). Now it is recognized from several other localities including Preresa in Manzanares Valley (Fig. 14; Croitor et al. 2008; Sanz et al. 2014; Van der Made & Mazo 2014). This is a species which is not closely related to *Dama*, but it is of similar size. Its first appearance is either at Lunel Viel or Igue des Rameaux, which have estimated ages of 350–300 ka, and the last appearance is at Cova del Rinoceront, which is slightly older than 83.8 ± 5.9 ka (Sanz et al. 2014).

Dama mesopotamica

This species has been proposed to be a descendant of *Dama clactoniana* (Di Stefano 1995, 1996), and this seems plausible. The oldest dated and certain *Dama mesopotamica* is from Tabun E, dated to 213 ± 46 ka and correlated to MIS7, while still older remains are of uncertain specific identification (Di Stefano 1995). Di Stefano (1996) named the subspecies *Dama clactoniana mugharensis*, based on fossils from Tabun E, and classified the living mesopotamian fallow deer as *D. clactionana mesopotamica*. Here, we prefer to classify *D. clactionana* and *D. mesopotamica* as different species.

Dama vallonnetensis-roberti-celiae

The long lineage leading to *Dama celiae* was found in Spain in localities of different ages (Atapuerca TE7, TE9, Chaparral, Cueva Victoria, Pedro Jaro I, Orcasitas), and its presence may have been continuous. The impression is that this was a widespread lineage living in what is now the UK, France, Italy, and Spain, but that the geographic distribution contracted, with the last records being Spanish. However, this changes if *D. celiae* is recognized elsewhere. *Dama clactoniana* was described from Aridos, just outside the Manzanares valley (Soto, 1980). The antler has the beginning of a large brow tine, but it is not known whether there was a middle tine or palmation. Fallow deer from Torralba and Ambrona have been classified as *Dama* sp., *Dama* cf. *clactoniana*, and *Dama* cf. *dama* (see Sesé & Soto 2005). They have large upward-curving brow tines, but the distal part of the antler does not seem to be known. It is of interest to note that Sardella et al. (1998), Di Stefano and Petronio (2003), and Mancini et al. (2006, 2008) believed that *"Pseudodama"* survived till about 450 ka, because of antlers with large upward-curving brow tines. Again, the distal part of the antlers is not known. *Dama clactoniana* is cited from Arago. There are several specimens (LPTUP F13/FEJ12M/341, I18/IJAJ/36693670) with brow tines that recall those of *Dama roberti* and *D. celiae*, but we do not know whether the middle tine or palmation is documented there. There is a large antler of *Dama* from Mosbach (IQW Mosbach 159); perhaps, it is from Mosbach 2, but it is only the basal part.

Number of contemporaneous/sympatric species.

Dama clactoniana was present in Atapuerca TD10 and probably also Atapuerca TG10-11 at a distance of about 220 km, as the crow flies, from Orcasitas. These lineages overlapped during 150–100 ky. Though the two lineages may have been ecologically exclusive, they must have lived geographically very close. Both lineages overlap in time with *Haploidoceros*, which is known of this time from the south of France, while the Spanish records of this genus (in Preresa in the Manzanares valley and Cova del Rinoceront in Catalonia) are coeval to those of *Dama dama* (in Pinilla del Valle in the north of the province of Madrid). This means a maximum of three coeval lineages in the south of France and North and Central Spain during MIS9 and a prolonged presence of at least two lineages from at least 400 ka till 85 ka. These lineages coincide in time with the *D. peloponesiaca* lineage in the Middle East and also Greece and afterwards with the *D. mesopotamica* lineage. This means that there may have been up to four coeval *Dama*-sized species in western Eurasia. This is a much greater diversity than previously believed.

Recently, the species *Megaloceros matritensis* was described from terraces of the Manzanares River (Van der Made 2019). It is the end of a lineage, which was believed to have gone extinct when *Megaloceros giganteus* appeared in Europe, around 400 ka. However, this lineage survived longer and both species were contemporary. The fossils of this species come from the same terrace as *Dama celiae*. In both cases, a lineage survived longer, resulting in a higher known biodiversity in Spain.

The landscape of the Manzanares valley

The landscape, in which *Dama celiae* lived, started to form many millions of years earlier. During the Miocene, the Madrid basin was endoreic; it had no connection to the sea, and any runoff was toward the center of the basin, where the water evaporated, forming thick gypsum deposits (Calvo Sorando et al., 2004). Not later than the Early Pleistocene, the Tagus cut back as far as the Madrid basin, connecting it with the Atlantic Ocean (Silva et al. 2017). The lower part of the Manzanares River cuts into the sediments that were deposited in the Miocene: gray clays and gypsum and massive gypsum, forming steep walls. The terraces are mostly on the right side and in the distal part are mostly made of sands, marls, and clays. Pollen preserved in terraces of this age (Gil-García et al. 2018) permits the reconstruction of the vegetation. Close to the river grew willow (*Salix*), alder (*Alnus*), and elm (*Ulmus*), as well as birch (*Betula*), hazel (*Coryulus*), chestnut (*Castanea*), and evergreen oak (*Quercus*). In oxbow lakes or wet areas on the floodplain, there were *Epilobium*, *Typha*, *Myryophillum*, Ranunculaceae, Juncaceae, and Nymphaeceae. *Pinus* and Cuprecsaceae grew in the higher and drier areas like the previous terraces and Miocene sediments. Steppe herbs, such as *Artemisia*, grew on the higher flats. Gypsophile plants grew on the areas where the Miocene gypsum was exposed. A large part of the Madrid basin had similar environments along the Jarama, Henares, Tajuña, and Tajo (Tagus) rivers and the high flats between them.

The species of large mammals that were contemporaries of *Dama celiae* (Fig. 3) include the ubiquitous species *Elephas (=Palaeoloxodon) antiquus*, *Equus ferus*, and *Bos primigenius*. They are common in sites in the Manzanares and Jarama valleys, such as Áridos 1 and 2 (Villa 1990; Yravedra et al. 2010, 2019b) and Tafesa/Transfesa (Sesé & Soto 2002 a, b; Mazo 2010; Yravedra 2010; Yravedra et al. 2019b), but also in sites of similar age from the Central Iberian Peninsula, such as Torralba (Shipman & Rose 1983; Villa 1990) and Ambrona (Shipman & Rose 1983; Villa et al. 2005). The species that lived in the Manzanares valley at the time of *Dama celiae* (Fig. 3) used different parts of the habitat of the Manzanares valley. The wild boar *Sus scrofa*, auerochs *Bos primigenius* (very well represented by fossils), and caballoid horses (*Equus torralbae* or *E. ferus torralbae*) may have used predominantly the floodplains, while bisons (probably *Bison schoetensacki*) and *Equus hydruntinus* may have used predominantly the higher and drier areas between the river valleys. The steppe rhinoceros *Stephanorhinus hemitoechus* has recently been interpreted to be less of a grazer than its vulgar name suggests (Van Asperen & Kahlke 2015) and may have used the floodplains and also the open areas between them. The straight-tusked elephant *Elephas antiquus* is known from many fossils from the Manzanares terraces and was a prominent member of the fauna of that time. A lion (*Panthera leo/spelaea*) was part of this fauna and possibly also a small wolf (*Canis mosbachensis*?). Several of these species appear in Fig. 15, a reconstruction of the environment, close to the river, where all species may have occurred, if only for drinking. Which of the different environments of the valley and higher plain was used preferentially by *Dama celiae*?

Not only *Dama celiae*, but also *Megaloceros matritensis* was only recently recognized as a distinct species. Both come from the same area and date to the period between 365 and 295 ka. Both are end members of a lineage; one lineage was believed to be extinct several hundred thousands of years earlier, and the other was believed to have evolved into a different species. There are two possible explanations for the fact that these species are not known from other areas in Europe: they became known only recently and therefore have not yet been detected in other areas, or their distribution had become very restricted. The time around 300 ka is particularly well known from many fossil localities in Europe, and in view of this, it is strange that these species were not detected earlier. *Dama clactoniana*, *Cervus elaphus*, and *Megaloceros giganteus* are common and well known from localities of this age, but the first is not known from the Manzanares valley and the latter two species are only known from the younger terraces. A similar case is *Haploidoceros mediterraneus*, which is also known from a restricted area from the south of France to Spain. Though already published in 1967 (Bonifay 1967), it was not detected from other parts of Europe during more than half a century. Perhaps, the environments of SW Europe or perhaps of Mediterranean Europe were so different from the rest of Europe to have three endemic species of deer.

Fig. 15 Reconstruction of *Dama celiae* in the Manzanares valley. Other species present are *Anas platyrhynchos*, *Equus ferus*, *Elephas* (*Palaeoloxodon*) *antiquus*, *Mauremys leprosa*, *Bison* sp., *Bos primigenius*, and *Stephanorhinus hemitoechus*. (By J. Gamarra)

Megaloceros matritensis is known from ten localities or levels, and *Dama celiae* is known from two or perhaps four localities in the Manzanares valley and must have been common elements of the fauna of that time and place. This might suggest that these two species were adapted to the particular environment of this area and were rare in environments better suited to *D. clactoniana*, *C. elaphus*, and *Megaloceros giganteus*. *Megaloceros matritensis* has many peculiar masticatory adaptations, which raised the question, whether they might be adaptations to particular environments of the Madrid basin (Van der Made 2019), such as the areas with steppic or gypsophyle plants. We do not know the masticatory apparatus of *Dama celiae* and cannot know its masticatory adaptations, but their co-occurrence suggests that it might have used the peculiar habitats in the Madrid basin as *M. matriteneis*. Dental wear or stable isotope analysis might contribute information that helps to resolve some of these questions.

Acheulean activities

Pedro Jaro I and Orcasitas add up to the not-very-rich list of Middle Pleistocene open-air sites that have provided lithic industries associated with faunal remains (Santonja et al. 2016). These two unpublished assemblages, preserved in the MAN, can be described as Large Flake Acheulean lithic industries on flint (Tables 2 and 3, Fig. 4), and were developed in a moment of expansion of the Acheulean techno-complex throughout the peninsular interior. In the Manzanares valley, this techno-complex is characterized by the hegemonic use of flint, which in Pedro Jaro I and Orcasitas is over 96%, with residual presence of quartzite and anecdotical of quartz, raw materials mainly used for shaping large cutting tools (LCTs). The preference for flint in the industries of the Middle Pleistocene of the Manzanares valley, with a generalized use of large flakes for the elaboration of macro-tools, is a singular characteristic within the panorama of the peninsular Acheulean where the macro-tools are mainly made of quartzite. The selection of flint represented in the lithic assemblages does not seem to be justified in the fluvial loads of the river Manzanares as those consist mainly of quartz. Also, the sizes of these large flakes do not fit the percentiles of the flint located in the gravel and cobble bars that constitute the fluvial loads of the river Manzanares (Goy et al. 1989). They would more likely come from Miocene outcrops found in the interfluvium of the rivers Manzanares and Jarama, about 10 km away from the concentration of sites in the Manzanares valley (Bárez et al. 2016). In Pedro Jaro I and Orcasitas, where the LCTs are well represented, the selection of flint supports could be determined by functional criteria with a macro-tool that presents some variability: pointed handaxes with straight edges, cleavers on flake, heavy-duty tools, and trihedrals. Nevertheless, both in the pieces with little and in those with intense shaping, the search for pointed ends predominates. This characteristic can be observed among the handaxes, in the tools shaped on large flakes, and in the frequent trihedral picks of Pedro Jaro I. The shaping of points is sometimes carried out by selecting supports with already preconfigured morphologies, as can be seen in the handaxe preforms and in several trihedrals from Pedro Jaro I. LCTs with re-shaped tips are also present. In general, those characteristics are shared with other lithic assemblages of the same terrace, such as Tafesa (Baena & Baquedano, 2010) and Transfesa. In the management of raw materials in Pedro Jaro I and Orcasitas, the use of recycled supports is also detected, again an element that can be extended to many deposits in the Manzanares valley, as well as the elemental reduction processes that coexist with other organized of discoid and centripetal types.

Interaction with humans?

The finds from Pedro Jaro I and Orcasitas analyzed here have not been retrieved from a systematic excavation, and therefore, the available information is limited. Both lithic artifacts and fossils have been recovered, but the way they are associated is not known. Only 11% of the lithic artifacts from Pedro Jaro I show edges and surfaces with intense rounding. The faunal remains of the two sites do not present alterations related to fluvial transport such as abrasion, polishing, or rounding on bone surface, so fluvial transport was null or played a minor role in the formation of the bone assemblage of both sites. No carnivore tooth marks have been documented on any of the faunal remains at the two sites. However, cut marks have been documented that evidence anthropic activity on a rhinoceros femur (probably *Stephanorhinus hemitoechus*) from Pedro Jaro I (Yravedra et al. 2019a), and in addition, ten cut marks have been found on a mandible of *Equus* cf. *ferus* from this site. Seven cut marks have been found on the external face of a fragment of a medium-sized deer rib from Orcasitas, attributable to *Dama celiae* or *Megaloceros matritensis* (Fig. 16).

In any case, medium-sized ungulates, like most cervids, fall within the trophic spectrum of humans and *D. celiae* was a meat resource that was exploited by the Middle Pleistocene humans with Acheulean technology in the same way as other medium-sized ungulates. At this time, spears existed already as several were found at Schöningen (Thieme 1997). These specimens were made of the stem of small trees of *Picea* and *Pinus* (Thieme 1998), and *Pinus* grew not far from Pedro Jaro I and Orcasitas (Gil-García et al. 2018). In their features, these spears resemble those for females in Olympic contests (220 m long, 600 g weight) and a copy has been tested. It could be used to throw straight, hitting with great force, or long distance (> 60 m) with a curved trajectory. With an average impact speed of 85 km/h, the spear penetrated 23 cm in a gelatine block with a consistency resembling the body of an

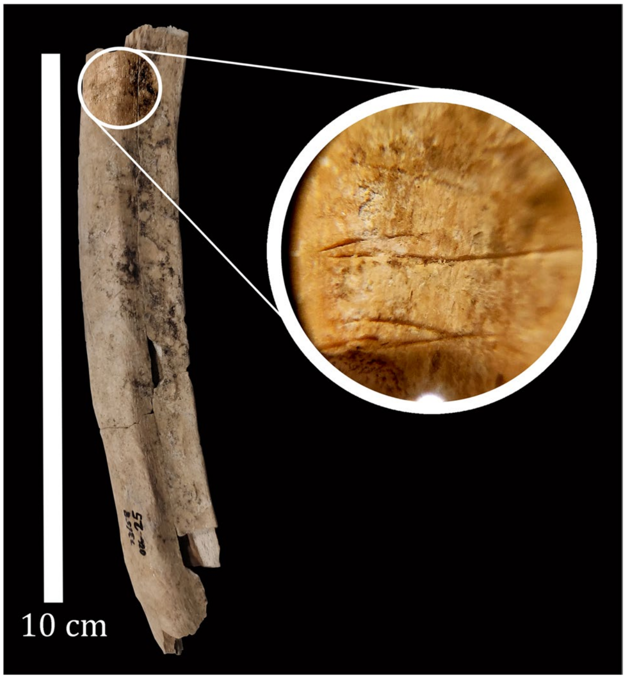

Fig. 16 Medium-sized deer rib, possibly of *Dama celiae*, from Orcasitas with several cut marks

animal (Rieder 2000). Such spears probably formed part of the Acheulean culture, while propulsors, arrows, and bows form part of the Upper Paleolithic (Cattelain 1997) and were not present at this time. An alternative possibility is the use of lithic spear points for hunting, which are documented from other Middle Paleolithic sites (Shea 1988; Shea et al. 2001; Villa et al. 2009), and we have observed some Mousterian Points and convergence scrapers in Pedro Jaro I.

We cannot be sure whether the cut-marked rib from Orcasitas derives from a hunted or a scavenged individual. However, the presence of cut marks (which are associated to filleting) and the absence of carnivore activity in the site suggest hunting by early Neanderthals like in other open-air Middle Pleistocene localities such as Cuesta de la Bajada (Domínguez-Rodrigo et al. 2015), Estanque Tormentas (Yravedra et al 2019a, b), and Tafesa (Yravedra 2010). The technique used in the hunting of these animals could be using spears like those from Schöningen (Thieme 1997) or lithic spear points similar to other regions with mousterian points or convergent scrapers (Shea 1988; Villa et al. 2009); however, only detailed micro wear studies could allow moving forward on this line of interpretation.

Conclusions

The study of fallow deer fossils from the valley of the Manzanares led to the following conclusions:

- The fossils from the sandpits of Pedro Jaro I and Orcasitas belong to a new species, which we call *Dama celiae*.
- This species is characterized by two-pointed antlers with a bifurcation between the brow tine and main beam with a blunt angle and a low position above the burr. The brow tine is large and curves upward. The main beam is very long, directed backwards, and curves outward and then backward again; it has no flattened area as in *D. roberti*.
- This morphology is the result of a reduction of the points of the antler in the lineage *Dama farnetensis–D. vallonnetensis–D. roberti–D. celiae*.
- *Dama celiae* lived more or less around 300 ka and was contemporary to *Haplodoiceros*, which also had two-pointed antlers, and the palmate *Dama clactoniana*. The diversity of deer of this size was greater than previously believed.
- The occurrence of *Dama celiae*, *Megaloceros matritensis*, and *Haplodoiceros* in the Manzanares valley, while they are not known or rare in the rest of Europe, raises the question whether they were endemic and adapted to the particular environment and climate of this area, or whether their fossils have not yet been detected in other parts of Europe.
- *Dama celiae* was also contemporary to the Neanderthals and acheulean culture and probably was hunted by them.

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Data Availability The fossils and lithics analyzed in this article are deposited in the National Archaeological Museum of Madrid, (Spain) and can be reviewed there.

Declarations

Ethical approval Not applicable.

Competing interests The authors declare no competing interests.

References

Aguirre, E., (1989) Vertebrados del Pleistoceno continental. In A. Pérez-González, P. Cabra & A. Martín-Serrano (eds.) Mapa del Cuaternario de España. Escala 1:1.000.000. Madrid: Instituto Tecnológico GeoMinero de España: 47–69.

Alia M (1960) Sobre la tectónica profunda de la fosa del Tajo. Notas y Comunicaciones Del Instituto Tecnológico y Geominero De España 58:125–162

Athanassiou A (2018) Pleistocene vertebrates from the Kyparíssia lignite mine, Megalopolis Basin, S. Greece: Rodentia, Carnivora, Proboscidea, Perissodactyla. Ruminantia Quaternary International 497:198–221

Aulagnier, S., Haffner, P., Michell-Jones, A. J., Moutou F., Zima, J., (2009) Guía de los mamíferos de Europa, del norte de África y de Oriente Medio. Lynx - Barcelona: 270 pp.

Azzaroli, A., (1948) Revisione della fauna dei terreni fluvio-lacustri del Valdarno Superiore, 3. I cervi fossili della Toscana con paricolare riguardo alle specie Villafrnchiane. Palaeontographia Italia, 43: 45–81, pls. 7–9.

Azzaroli A (1953) The deer of the Weybourn Crag and forest bed of Norfolk. The Bulletin of the British Museum (natural History) 2(1):3–96

Azzaroli A (1992) The cervid genus *Pseudodama* n. g. in the Villafranchian of Tuscany. Palaeontographica Italica 79:1–41

Baena, J., Baquedano Beltrán, I., (Eds.), (2010a) Las huellas de nuestro pasado. Estudio del yacimiento de pleistoceno madrileño de Tafesa (Antigua Transfesa). Zona Arqueológica 14. Museo Arqueológico Regional. Alcalá de Henares.

Baena, J., Baquedano, I., Beneítez, P., Cañaveras, J.C., Carrión, E., Lario, J., Martín-Escorza, C., Mazo, A., Millán, A. Sánchez, S. Sanz, E., Sesé, C., Silva, P. B., Yravedra, J., (2010b) Síntesis: Interpretación general del yacimiento de TAFESA (Madrid). In: J. Baena & I. Baquedano Beltrán (eds) Las huellas de nuestro pasado. Estudio del yacimiento del Pleistoceno madrileño de TAFESA (antigua TRANSFESA). Zona Arqueológica, 14: 189–202.

Baena J, Conde Ruiz C, Gamazo M, Sesé C, Soto E (2002) Repertorio de yacimientos paleolíticos en el Manzanares y Jarama. Zona Arqueológica 1:460–491

Bárez S, Baena J, Pérez-González A, Torres C, Pérez IR, de Miguel JV (2016) Acheulian flint quarries in the Madrid Tertiary basin, central Iberian Peninsula: first data obtained from geoarchaeological studies. Quatern Int 411:329–348

Bonifay MF (1967) Principales formes caracteristiques du Quaternaire moyen du sud-est de la France (Grands Mamiferes). Bulletin Du Musee D' Antropologie Prehistorique De Monaco 14:49–62

Breda M, Lister AM (2013) Dama roberti, a new species of deer from the early Middle Pleistocene of Europe, and the origins of modern fallow deer. Quatern Sci Rev 69:155–167

Cattelain, P. (1997) Hunting during the Upper Paleolithic: bow, spearthrower, or both? In: Knecht, H. (eds) Projectile technology. Interdisciplinary contributions to archaeology. Plenum Press, New York and London: 213–240 https://doi.org/10.1007/978-1-4899-1851-2_9

Croitor R (2006) Early Pleistocene small-sized deer of Europe. Hellenic Journal of Geosciences 41(1):89–117

Croitor, R., (2018) Plio-Pleistocene deer of western palearctic: taxonomy, systematics, phylogeny. Institute of Zoology of the Academy of Sciences of Moldova - Chisinau: 139 pp.

Croitor, R., Bonifay M.F., Brugal, J.P., (2008) Systematic revision of the endemic deer *Haploidoceros* n. gen. *mediterraneus* (Bonifay, 1967) (Mammalia, Cervidae) from the Middle Pleistocene of Southern France. Paläontologische Zeitschrift, 82/3: 325-346.

Delpech F., Guérin, C., (1996) Famille des Cervidae. In: C. Guérin and M. Patou-Mathis (eds.). Les grands mammifères Plio-Pléistocènes d'Europe. Masson - Paris, Milano, Barcelona: 47–62.

De Andrés I, Aguirre E (1975) Un molde endocraneano de Praedama (Cervido) del Pleistoceno medio de Madrid. Quaternaria 18:303–330

Desmarest, A.G., (1820) Mammalogie ou description des espèces de mammifperes. Madamme veuve Agasse – Paris : 556 pp.

Dawkins, W.B., (1868) On a new species of fossil deer from Clacton. The Quarterly Journal of the Geological Society of London, 24: 511–516, pl. 18.

De Stefano G (1914) I cervi e le antilopi fossili attribuiti al Quaternario dell'isola di Pianosa. Atti Della Società Italiana Di Scienze Naturali 52:105–155

Di Stefano, G., (1995) Il daino pleistocenico dell'Eurasia. PhD thesis Università consorziate Modena, Bologna, Firenze, Roma: 1–219, pls. 1–25.

Di Stefano G (1996) The Mesopotamian fallow deer (*Dama*, Artiodactyla) in the Middle East Pleistocene. Neues Jb Geol Paläontol Abh 199(3):295–322

Di Stefano G, Petronio C (1998) Origin of and relationships among *Dama*-like cervids in Europe. Neues Jb Geol Paläontol Abh 207(1):37–55

Di Stefano G, Petronio C (2002) Systematics and evolution of the Eurasian Plio-Pleistocene tribe Cervini (Artiodactyla, Mammalia). Geol Romana 36:311–334

Domínguez-Rodrigo M, Barba R, Soto E, Sesé E, Santonja M, Pérez-González A, Yravedra J, Galán AB (2015) Another window to the subsistence of Middle Pleistocene hominines in Europe: a taphonomic study of Cuesta de la Bajada (Teruel, Spain). Quat Sci Rev 126:67–95

Dubois E (1904) Over een equivalent van het Cromer Forest Bed in Nederland. Verslagen van de gewone vergaderingen der wis- en natuur- kundige afdeeling. Koninklijke Nederlandse Akademie Van Wetenschappen 13:243–251

Falconer, H. (1868) XV. Notes on fossil species of *Cervus*, including a description of a remarkable fossil antler of a large species of extinct *Cervus* in the collection of the rev. John Gunn, Irstead. In Ch. Murchinson (ed.). Palaeontological memoirs and notes of the late Hugh Falconer, A.M., D.M. Volume 2. Robert Hardwicke - Lodon: 471–480, plate 37.

Faure M, Guérin C (1992) La grande faune d'Europe occidental au Pléistcène moyen et supérieur et ses potentialités d'informationen préhistoire. Mémoires De La Société Géologique De France 160:77–84

Fernández-Jalvo, Y., Ditchfield, P., Grün, R., Lees, W., Aubert, M., Torres, T., Ortíz, J.E., Díaz Bautista A., Pickering, R., (2016) Appendix: Dating methods applied to Azokh Cave sites. In: Fernández-Jalvo, Y., T. King, P. Andrews & L. Yepiskoposyan (eds). Azokh caves and the transcaucasian corridor. Springer - Dordrecht: 321–339.

Gamazo M (1982) Prospecciones en las terrazas de la margen derecha del río Manzanares (Getafe y Ribas-Vaciamadrid). Noticiario Arqueológico Hispánico 14:7–148

Gamazo, M., (2002) Las colecciones paleolíticas del Manzanares y del Jarama del Museo de San Isidro. In: Panera, J., Rubio-Jara, S. (Eds.), Bifaces y elefantes. La investigación del Paleolítico Inferior en Madrid. Museo Arqueológico Regional de la Comunidad de Madrid. Zona Arqueológica 1: 358–381.

Gil-García MJ, Ruiz-Zapata MB, Rubio-Jara S, Panera J, Pérez-González A (2018) Landscape evolution during the Middle and Late Pleistocene in the Madrid basin (Spain) vegetation dynamics and human activity in the Jarama-Manzanares rivers (Madrid) during the Pleistocene. Quatern Int 520:39–48

Goy, J.L., Pérez-González, A., Zazo, C., (1989) Cartografía y Memoria del Cuaternario y Geomorfología, Hoja de Madrid (559). Mapa Geológico de España. Escala 1:50.000. 2ª Serie (MAGNA). IGME. Servicio de Publicaciones del Ministerio de Industria. Madrid.

Guérin C (1982) Première biozonation du Pléistocène européen, principal résultat biostratigraphique de l'étude des Rhinocerotidae (Mammalia, Perissodactyla) du Miocène terminal au Pléistocène Supérieur d'Europe occidentale. Geobios 15(4):593–598

Heintz, E., (1970) Les Cervidés villafranchiens de France et d'Espagne. - Memoires du Museum national d'Histoire naturelle, série 5, sciences de la terre, 32: 1–303, 319 figures, 313 tableaux, 40 planches.

ICZN (International Commission on Zoological Nomenclature), (1999) International code on zoological nomenclature. Fourth edition. International Trust for Zoological Nomenclatuere - London: 1–306.

Inizan, M.L., Reduron-Ballinger, M., Roche, H., Tixier, J., (1999) Technology and terminology of knapped stone (Préhistoire de la Pierre taillé 5). Nanterre: Cercle de Recherches et d'Études Préhistoriques.

Kahlke, H.D., (2001) Neufunde von Cerviden-Reste aus dem Unterpleistozän von Untermassfeld, In: R.D. Kahlke (ed.) Das Pleistozän von Untermassfeld bei Meinigen (Thüringen), Teil 2. Römisch-Germanisches Zentralmuseum Forschungsinstitut für Vor- und Frühgeschichte. Monographiën, 40(2): 461–482, pls 72–76.

Kurtén, B., (1968) Pleistocene mammals of Europe. Weidenfeld & Nicolson - London: 1–317.

Leonardi G, Petronio C (1976) The fallow deer of the European Pleistocene. Geol Romana 15:1–67

Lister AM (1986) New results on deer from Swanscombe, and the stratigraphical significance of deer remains in the Middle and Upper Pleistocene of Europe. J Archaeol Sci 13:319–338

Lister AM (1996) The morphological distinction between bones and teeth of fallow deer (*Dama dama*) and red deer (*Cervus elaphus*). Int J Osteoarchaeol 6:119–143

Lister AM, Breda M (2016) Validity of the name *Dama roberti* Breda & Lister, 2013, a small European Pleistocene deer, and the status of *Cervus polignacus* Robert, 1829 and *Cervus roberti* Pomel, 1853. Bulletin of Zoological Nomenclature 73:81–82

López Martínez, N., (1980) Los micromamíferos (Rodentia, Insectivora, Lagomorpha y Chiroptera) del sitio de ocupación achelense de Áridos-1 (Arganda, Madrid). In: Santonja, M., López Martínez, N., Pérez-González, A. (Eds.). Ocupaciones achelenses en el Valle del Jarama (Arganda, Madrid). Arqueología y Paleontología I, 161–202. Diputación Provincial de Madrid.

López-Recio, M.; Silva, P.G.; Roquero, E.; Cunha, P.P.; Tapias, F.; Alcaraz-Castaño, M.; Baena, J.; Cuartero, F.; Morín, J.; Torres, T.; Ortiz, J.E.; Murray, A.S.; Buylaert, J.P., (2015) Geocronología de los yacimientos achelenses de Pinedo y Cien Fanegas (Valle del Tajo) e implicaciones en la evolución fluvial en el entorno de Toledo (España). Estudios Geológicos 71 (1), e029. http://dx.doi.org/https://doi.org/10.3989/egeol.41816.340

Lumley, H., de, Kahlke, H.-D., Moigne, A.-M., Moullé, P.-E., (1988) Les faunes de grands mammifères de la grotte du Vallonnet Roquebrune-Cap-Martin, Alpes-Maritimes. L'Anthropologie, 92 (2): 465-469.

Lydekker, R., (1885) Catalogue of the fossil Mammalia in the British Museum (Natural History). Part II Containing the order Ungulata, suborder Artiodactyla. London, 324 pp.

Made, J. van der & V. Dimitrijevic, (2015) *Eucladoceros montenegrensis* n. sp. and other Cervidae from the Lower Pleistocene of Trlica (Montenegro) Quaternary International, 389: 90–118.

Made, J. van der & A.V. Mazo, (2014) Los grandes mamíferos del yacimiento de Preresa. En: I. Baquedano Beltrán & C. Laplana (eds) Haploidoceros mediterraneus una nueva especie de ciervo en el Pleistoceno Ibérico. Museo Arqueológico Regional - Alcalá de Henares: 39–53.

Made, J. van der, Torres, T., Ortiz, J. E., Moreno-Pérez, L., Fernández Jalvo, Y. (2016) The new material of large mammals from Azokh and comments on the older collections. In: Fernández-Jalvo, Y., T. King, P. Andrews & L. Yepiskoposyan (eds). Azokh caves and the transcaucasian corridor. Springer - Dordrecht: 117–162.

Mancini M, Palombo M-R, Petronio C, Sardella R, Bedetti C, Bellucci L, Di Canzio E, Giovinazzo C, Petrucci M, Trucco F (2006) Middle Pleistocene vertebrate-bearing fluvial deposits of the Ceriti Mts Area (Latium coast, central Italy). Geol Romana 39:27–38

Mancini M, Bellucci L, Petronio C (2008) Il Pleistocene Inferiore e Medio di Nettuno (Lazio): stratigrafia e mammalofauna. Geol Romana 41:71–85

Martínez-Navarro B, Palombo M (2004) Occurrence of the Indian genus Hemibos (Bovini, Bovidae, Mammalia) at the Early -Middle Pleistocene transition in Italy. Quatern Res 61:314–317

Mazo AV (1994) El cráneo de Elephas antiquus (Proboscidea, Mammalia) de Orcasitas (Madrid). Estudios De Prehistoria y Arqueología Madrileñas 9:17–24

Mazo, A., (2010) Los Macrovertebrados del Pleistoceno medio del yacimiento de Tafesa (Madrid). In: Baena, J., Baquedano, I. (Eds.), Las huellas de nuestro pasado. Estudio del Yacimiento del pleistoceno madrileño de Tafesa (Antigua Transfesa). Museo Arqueológico Regional de la Comunidad de Madrid, Zona Arqueológica, vol. 14, pp. 155–176.

Mecozzi B, Iannucci A, Mancini M, Sardella R (2021) Redefining Ponte Molle (Rome, central Italy): an important locality for Middle Pleistocene mammal assemblages of Europe. Alpine and Mediterranean Quaternary 34(1):131–154

Meléndez, B., (1958) Hallazgo del esqueleto casi completo de un elefante fosil en las inmediaciones de Madrid. Estudios geológicos, 14: 63, plate VI.

Melentis, J.K., (1966a) Die pleistozänen Cerviden des Beckens von Megalopolis im Pelopones (Griechenland). Annales Géologiques des Pays Helleniques, 16: 52–92, pls. 1–12.

Melentis, J.K., (1966b) Die pleistozänen Nashörner des Beckens von Megalopolis im Pelopones (Griechenland). Annales Géologiques des Pays Helleniques, 16: 363–402, pls. 73–77.

Melentis, J.K., (1966c) Studien über fossile Vertebraten Griechenlands 8. Über *Equus abeli* aus dem Mittelpleistozän des Beckens von Megalopolis im Pelopones (Griechenland). Annales Géologiques des Pays Helleniques, 17: 158–168, pls. 1–2..

Menéndez Amor, J., Florschütz, F., (1963) Sur les éléments steppiques dans la végétation Quaternaire de l'Espagne. Boletín de la Real Sociedad Española de Historia Natural. Sección Geológica, 61/1: 123–133.

Moreno D, Duval M, Rubio-Jara S, Panera J, Bahain JJ, Shao Q, Pérez GA, Falguères C (2019) ESR dating of Middle Pleistocene archaeo-paleontological sites from the Manzanares and Jarama river valleys (Madrid basin, Spain). Quatern Int 520:23–38

Okuda M, van Vugt N, Nakagawa T, Ikeya M, Hayashida A, Yasuda Y, Setoguchi T (2002) Palynological evidence for the astronomical origin of lignite detritus sequence in the Middle Pleistocene Marathousa Member, Megalopolis, SW Greece. Earth Planet Sci Lett 201:143–157

Ortiz JE, Torres T, Llamas JF, Canoira L, García-Alonso P, García de la Morena M, Lucini M (2000) Datación de yacimientos paleontológicos de la cuenca de Guadix-Baza (sector de Cúllar-Baza, Granada, España) y primera estimación de la edad dela apertura de la cuenca mediante el método de racimzación de aminoácidos. Geogaceta 28:109–112

Panera J, Torres T, Pérez-González A, Ortiz JE, Rubio-Jara S, Uribelarrea D (2011) Geocronología de la Terraza Compleja de Arganda en el valle del río Jarama (Madrid, España). Estud Geol 67(2):495–504

Patte E (1953) Remarques sur quelques daims fossiles. Bulletin De La Société Geologique De La France 3(6):657–666

Pérez-González A (1971) Estudio de los procesos de hundimiento en el valle del río Jarama y sus terrazas (nota preliminar). Estudios Geológicos XXVII 4:317–324

Pérez-González, A., (1980) Geología y estratigrafía de los yacimientos de Áridos en la llanura aluvial de Arganda (Madrid). In: Santonja, M., López-Martínez, N., Pérez-González, A. (Eds.), Ocupaciones achelenses en el valle del Jarama. Arqueología y Paleontología I. Diputación Provincial de Madrid, 49–61

Pérez-González A (1994) Depresión del Tajo. In: Gutierrez E (ed) Geomorfología de España. Editorial Rueda, Madrid, pp 389–436

Pérez González, A. & J.P. Calvo Sorando (eds), (1989) Mapa geológico de España E. 1:50.000 Madrid segunda sieri-primera edición. Explicative booklet. Centro de Publicaciones - Ministerio de Industria y Energía - Madrid: 1–71.

Pérez-González, A., Uribelarrea, D., (2002) Geología del Cuaternario de los valles fluviales del Jarama y Manzanares en las proximidades de Madrid. In: Panera, J., Rubio-Jara, S. (Eds.), Bifaces y elefantes. La investigación del Paleolítico Inferior en Madrid. Museo Arqueológico Regional de la Comunidad de Madrid. Zona Arqueológica 1: 303–317.

Pérez González, A., Calvo Sorando J. P. (eds.), (2004) Mapa geológico de España Escala 1:50.000 Segunda serie – Segunda edición. Madrid. Instituto Geológico y Minero de España – Madrid: map & booklet (pp. 1–72).

Petronio C (1980) *Dama nestii eurygonos* Azz. di Cpena (Roma). Geol Romana 18:105–125

Petronio, C., Sardella, R, (1998) *Bos galerianus* n. sp. (Bovidae, Mammalia) from the Ponte Galeria Formation (Rome, Italy). Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, 1998(5): 269–284.

Pfeiffer T (1998) Die fossilen Damhirsche von Neumark-Nord (Sachesen-Anhalt)- *D. dama geiselana* n. ssp. Eiszeit Gegenw 48:72–86

Pfeiffer T (1999) Die Stellung von *Dama* (Cervidae, Mammalia) im system pleisometacarpaler Hirsche des Pleistozäns. Phylogenetische Reconstruktion e Metrische Analyse. Cour Forschungsinst Senck 211:1–218

Pomel, A., (1853) Vertébrés fossiles découvèrts dans le bassin hydrographique supérieur de la Loire, et surtout dans la vallée de son affluent principal l'Allier. J.B. Baillière - Paris: 1–193.

Quero, S. (2002) La investigación del Paleolítico en Madrid durante el franquismo. In: Panera, J., Rubio-Jara, S. (Eds.), Bifaces y elefantes. La investigación del Paleolítico Inferior en Madrid. Museo Arqueológico Regional de la Comunidad de Madrid. Zona Arqueológica 1: 168–193

Quero Castro S (1994) La excavación del elefante de Orcasitas (Madrid). Estudios De Prehistoria y Arqueología Madrileñas 9:11–16

Rieder H (2000) Die altpaläolithischen Wurfspeere von Schöningen, ihre Erprobung und ihre Bedeutung für die Lebensumwelt des *Homo erectus*. Praehistoria Thuringica 5:68–75

Robert, F., (1829) Mémoire sure les Ossemens fossiles des environs de Cussac, commune de Polinac (Haute Loire). Annales de la Société d'agriculture, sciences, arts et commerce du Puy: 68–88, pls

Roger, O., (1882) Verzeichnis der bisher bekannten fossilen Säugetiere. 162 pp. Regensburg.

Rosas A, Pérez-González A, Carbonell E, van der Made J, Sánchez A, Laplana C, Cuenca-Bescós G, Parés JM, Huguet R (2001) Le gisement pléistocène de la "Sima del Elefante" (Sierra de Atapuerca, Espagne). Anthropologie 105(2):301–312

Rubio-Jara S, Panera J (2019) Unravelling an essential archive for the European Pleistocene. The human occupation in the Manzanares valley (Madrid, Spain) throughout nearly 800,000 years. Quatern Int 520:5–22

Rubio-Jara S, Panera J, Rodríguez de Tembleque J, Santonja M, Pérez-González A (2016) Large flake Acheulean in the middle of Tagus basin (Spain): middle stretch of the river Tagus valley and lower stretches of the rivers Jarama and Manzanares valleys. Quatern Int 411:349–366. https://doi.org/10.1016/j.quaint.2015.12.023

Rubio-Jara S, Panera J, Santonja M, Pérez-González A, Yravedra J, Domínguez-Rodrigo M, Bello P, Roja R, Mabulla A, Baquedano E (2017) Site function and lithic technology in the Acheulean technocomplex: a case study from Thiongo Korong (TK), Bed II, Olduvai Gorge. Tanzania Boreas 46(4):849–917. https://doi.org/10.1111/bor.12275

Santonja, M., Pérez-González, A., (2000–2001) El Paleolítico inferior en el interior de la Península Ibérica. Un punto de vista desde la Geoarqueología. Zephyrus 53–54: 27–77

Santonja M, Panera J, Rubio-Jara S, Pérez-González A, Uribelarrea D, Domínguez-Rodrigo M, Mabulla A, Bunn HT, Baquedano E (2014) Technological strategies and the economy of raw materials in the TK (Thiongo Korongo) lower occupation, Bed II, Olduvai Gorge, Tanzania. Quatern Int 322:181–208

Santonja, M., Pérez-González, A., Panera, J., Rubio-Jara, S., Méndez-Quintas, E., (2016) The coexistence of Acheulean and Ancient Middle Palaeolithic technocomplexes in the Middle Pleistocene of the Iberian Peninsula. Quaternary International 411 (B): 367–377. https://doi.org/10.1016/j.quaint.2015.04.056

Santonja M, Villa P (1990) The Lower Paleolithic of Spain and Portugal. J World Prehist 4:45–94

Santonja M, Villa P (2006) The Acheulian of Western Europe. In: Goren-Inbar N, Sharon G (eds) Axe age. Acheulian Tool-making from Quarry to Discard. Equinox Publishing, London, pp 429–478

Sanz M, Daura J, Brugal JP (2014) First occurrence of the extinct deer *Haploidoceros* in the Iberian Peninsula in the Upper Pleistocene of the Cova del Rinoceront (Castelldefels, Barcelona). CR Palevol 13(1):27–40

Sardella R, Caloi L, Di Stefano G, Palombo MR, Petronio C, Abbazzi L, Azzaroli A, Ficcarelli G et al (1998) Mammal faunal turnover in Italy from the Middle Pliocene to the Holocene. Mededelingen Nederlands Instituut Voor Toegepaste Geowetenschappen TNO 60:499–519

Schaub S (1941) Die kleine Hirschart aus dem Oberpliozän von Senèze. Eclogae Geol Helv 34(2):264–271

Scrope, G.P., (1858) The geology and extinct volcanos of Central France. J. Murray - London: 1–336.

Sesé C (2010) Micromamíferos del yacimiento del Pleistoceno Medio de TAFESA (Madrid). Zona Arqueológica 14:135–139

Sesé C, Panera J, Rubio-Jara S, Pérez-González A (2011a) Micromamímeros del Pleistoceno Medio y Pleistoceno Superior en el Valle del Jarama: yacimimientos de Valdocarros y HAT (Madrid). Estud Geol 67(2):131–151

Sesé C, Rubio-Jara S, Panera J, Pérez-González A (2011b) Micromamíferos del Pleistoceno Superior del yacimiento de PRERESA en el valle del Manzanares y su contribución a la reconstrucción paleoambiental de la cuenca de Madrid durante el Pleistoceno. Estud Geol 67(2):471–494

Sesé, C. & E. Soto, (2002a) Catálogo de los yacimientos de vertebrados del Pleistoceno en las terrazas se los ríos Jarama y Manzanares. In: J. Panera Gallego & S. Rubio Jara (eds.) Bifaces y Elefantes, Museo Arqueológico Regional: 430–457.

Sesé, C., Soto, E., (2002b) Vertebrados del Pleistoceno del Jarama y Manzanares. In: Panera, J., Rubio-Jara, S. (Eds.), Bifaces y elefantes. La investigación del Paleolítico Inferior en Madrid, Museo Arqueológico Regional de la Comunidad de Madrid, Zona Arqueológica, vol. 1: 318–337.

Sesé C, Soto E (2005) Mamíferos del yacimiento del Pleistoceno Medio de Ambrona (Soria, España): Análisis faunístico e interpretación paleoambiental. Zona Arqueológica 5:258–280

Shea JJ (1988) Spear points from the Middle Paleolithic of the Levant. J Field Archaeol 15:441. https://doi.org/10.2307/530046

Shea J, Davis Z, Brown K (2001) Experimental tests of Middle Palaeolithic spear points using a calibrated crossbow. J Archaeol Sci 28:807. https://doi.org/10.1006/jasc.2000.0590

Shea JJ (2006) The origins of lithic projectile point technology: evidence from Africa, the Levant, and Europe. J Archaeol Sci 33(6):823–846. https://doi.org/10.1016/j.jas.2005.10.015

Shipman P, Rose J (1983) Evidence of butchery and hominid activities at Torralba and Ambrona; an evaluation using microscopic techniques. J Archaeol Sci 10(5):465–474. https://doi.org/10.1016/0305-4403(83)90061-4

Sickenberg O (1965) *Dama clactoniana* (Falc.) in der Mittelterrasse der Rhume-Leine bei Edesheim (Landkreis Northeim). Geol Jahrb 83:353–396

Sickenberg, O., (1976) Eine Säugetierfauna des tieferen Bihariums aus dem Becken von Megalopolis (Peloponnes, Griehenland). Anales géologiques des Pays Helleéniques, series 1, 27: 25–73, pls. 6–10.

Silva PG, Goy JL, Zazo C (1988a) Neotectónica del sector centro-meridional de la Cuenca de Madrid. Estud Geol 2:133–136

Silva, P.G., Goy, J.L., Zazo, C., Hoyos, M., Alberdi, M.T., (1988b) In: El valle del Manzanares y su relación con la depresión Prados-Guaten durante el Pleistoceno inferior (Madrid, España). II Congreso geológico de España. Comunicaciones, vol. 1 (Granada, 1988b), pp. 403–406.

Silva PG, Roquero E, López-Recio M, Huerta P, Martínez-Graña AM (2017) Chronology of fluvial terrace sequences for large Atlantic rivers in the Iberian Peninsula (Upper Tagus and Duero drainage basins, Central Spain). Quatern Sci Rev 166:188–203

Silva, PG, Lario J, Cañaveras JC, Sánches Moral S, Sanz E (2010) Geología, geomorfología y sedimentología de los depósitos cuaternarios del yacimiento de TAFESA (Madrid). Zona Arqueológica 14:15–35

Teilhard de Chardin, P., Trassaert, M. (1937) The Pliocene Camelidae, Giraffidae, and Cervidae of South Eastern Shansi. Palaeontologia Sinica, new series C, 1(102): 1–56, Pls. 1–6.

Thieme H (1997) Lower Palaeolithic hunting spears from Germany. Nature 385:807–810

Thieme H (1998) Altpaläolitische Wurfspeere von Schöningen, Niedersachsen. Praehistorica Thuringica 2:22–31

Tixier, J., (1956) Le hachereau dans l'Acheuléen Nord-Africain. Notes typologiques. Congrès Préhistorique de France, XVème sesión (Poitiers), pp. 914–923

Turq, A., (2000) Paléolithique inférieur et moyen entre Dordogne et Lot. Paléo (Supplément 2), 454.

Ueckermann, E. & P. Hansen, 2002. Das Damwild. Biologie, Hege und Jagd. 4th edition. Kosmos - Stuttgart: 327 pp.

Uribelarrea, D., (2008) Dinámica y evolución de las llanuras aluviales de los ríos Manzanares, Jarama y Tajo, entre las ciudades de Madrid y Toledo. PhD. Universidad Complutense de Madrid. Facultad de Ciencias Geológicas. Departamento de Geodinámica. p. 396.

van Asperen EN, Kahlke RD (2015) Dietary variation and overlap in Central and Northwest European *Stephanorhinus kirchbergensis* and *S. hemitoechus* (Rhinocerotidae, Mammalia) influenced by habitat diversity. Quatern Sci Rev 107:47–61

van de Wal RSW, de Boer B, Lourens LJ, Köhler P, Bintanja R (2011) Reconstruction of a continuous high-resolution CO2 record over the past 20 million years. Climate of the past 7:1459–1469

van der Made J (2011) Biogeography and climatic change as a context to human dispersal out of Africa and within Eurasia. In Carrion J.S., Rose J., Stringer C. (editors): Ecological scenarios for human evolution during the early and Middle Pleistocene in the western palaeartic. Quatern Sci Rev 30:1353–1367

van der Made J, Tong HW (2008) Phylogeny of the giant deer with palmate brow tines *Megaloceros* from west and *Sinomegaceros* from east Eurasia. Quatern Int 179:135–162

van der Made J (2013) First description of the large mammals from the locality of Penal, and updated faunal lists for the Atapuerca ungulates - *Equus altidens*, *Bison* and human dispersal into Western Europe. Quatern Int 295:36–47. https://doi.org/10.1016/j.quaint.2012.03.001

van der Made J, Stefaniak K, Marciszak A (2014) The Polish fossil record of the wolf Canis and the deer Alces, Capreolus, Megaloceros, Dama and Cervus in an evolutionary perspective. Quatern Int 326–327:406–430

van der Made J (2015) The latest Early Pleistocene giant deer *Megalcoeros novocarthaginiensis* n. sp. and the fallow deer *Dama* cf. *vallonnetensis* from Cueva Victoria (Murcia, Spain). Mastia 11–13:269–323

van der Made J, Rosell J, Blasco R (2017) Faunas from Atapuerca at the Early-Middle Pleistocene limit: the ungulates from level TD8 in the context of climatic change. Quatern Int 433:296–346

van der Made J (2019) The dwarfed "giant deer" *Megaloceros matritensis* n.sp. from the Middle Pleistocene of Madrid - a descendant of *M. savini* and contemporary to *M. giganteus*. Quatern Int 520:110–139. https://doi.org/10.1016/j.quaint.2018.06.006

van der Made J (1999) Ungulates from Atapuerca-TD6. J Hum Evol 37:389–413

van Vugt N, Langereis CG, Hilgen FJ (2001) Orbital forcing in Pliocene-Pleistocene Mediterranean lacustrine deposits: dominant expression of eccentricity versus precession. Palaeogeography, Palaeoclimatology, Plaeoecology 172:193–205

Villa P (1990) Torralba and Aridos: elephant exploitation in Middle Pleistocene Spain. J Hum Evol 19(3):299–309. https://doi.org/10.1016/0047-2484(90)90071-i

Villa P, Boscato P, Ranaldo F, Ronchitelli A (2009) Stone tools for the hunt: Points with impact scars from a Middle Paleolithic site in southern Italy. J Archaeol Sci 36:850. https://doi.org/10.1016/j.jas.2008.11.012

Villa P, Soto E, Pérez-González A, Santonja M, Mora R, Parcerisas Q, Sese C (2005) New data from Ambrona (Spain): closing the hunting versus scavenging debate. Quatern Int 126–128:223–250

von Koenigswald W, Schwermann AH, Keiter M, Menger F (2019) First evidence of Pleistocene *Bubalus murrensis* in France and the stratigraphic occurrences of *Bubalus* in Europe. Quatern Int 522:85–93

Wilson, D.E., Mittemeier, R. A. (eds) (2011) Hand book of the mammals of the world. 2 Hoofed mammals. Lynx Edicions – Barcelona: 1–885.

Yravedra, J., (2010) Estudio tafonómico y zooarqueológico de los macromamíferos del yacimiento arqueológico de Tafesa (Villaverde Bajo, Mabrid). In: Baena, J., Baquedano, I. (Eds.), Las huellas de nuestro pasado. Estudio del Yacimiento del pleistoceno madrileño de Tafesa (Antigua Transfesa). Zona Arqueológica, vol. 14: 155–176.

Yravedra J, Domínguez-Rodrigo M, Santonja M, Pérez González A, Panera J, Rubio-Jara S, Baquedano E (2010) Cut marks on the middle Pleistocene elephant carcass of Aridos 2 (Madrid Spain). J Archaeol Sci 3:2469–2476

Yravedra J, Rubio-Jara S, Panera J, Martos JA (2019a) Hominins and Proboscideans in the Lower and Middle Palaeolithic in the Central Iberian Peninsula. Quatern Int 520(20):140–156. https://doi.org/10.1016/j.quaint.2017.12.002

Yravedra J, Rubio-Jara S, Panera J, Pérez-González A, Gallego N, González I (2019b) Zooarchaeology and taphonomy of a new site, ETB-H02, of the middle Pleistocene in Estanque Tormentas in the Manzanares River (Madrid, Spain). Quat Int 520(20):99–109. https://doi.org/10.1016/j.quaint.2018.03.014