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The Late Quaternary pollen sequence of Toll Cave, a palaeontological site with evidence of human activities in northeastern Spain

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ABSTRACT

Palynological investigations of Toll Cave, a carnivore and archaeological cave site in northeastern Spain, are presented. The inferred vegetation reveals the long-term permanence of mixed pine-oak forests through a long period of environmental changes within the interval MIS 4 to MIS 1, and probably before. A relatively high diversity of woody taxa is found, including conifers, mesophytic angiosperms, Mediterranean forest, and xerothermic scrub. The most outstanding findings include the abundance of *Pinus*, evergreen *Quercus*, and *Juniperus*; the continuous occurrences of deciduous *Quercus*, *Acer*, *Castanea*, *Betula*, *Fraxinus*, *Buxus*, *Olea*, *Salix*, and *Erica*, and the presence of *Abies*, *Taxus*, *Carpinus betulus*, *Tilia*, *Populus*, *Celtis*, *Juglans*, *Ulmus*, *Calicotome*, *Cistus*, *Ephedra fragilis*, *Myrtus*, *Pistacia*, *Rhamnus* and *Viburnum*. Together with the pollen record of the nearby Teixoneres Cave, this new data suggest the existence of woodland refugia during the coldest and most arid stages of the upper Pleistocene across this relatively high-latitude region within the Iberian Peninsula. This study also supports the occurrence of forest ecosystems within the Mediterranean-Eurosiberian ecotone of the Iberian Peninsula in the vicinity of *Homo* habitats, including Neanderthals.

1. Introduction

Bringing new palaeobotanical records for the Pleistocene of northeastern Iberia, more specifically for the ecotonal territories between the present-day Mediterranean and Eurosiberian regions, is one of the aims of several ongoing research projects led by this research group (Carrión et al., 2010, 2011, 2013, 2015; González-Sampériz et al., 2010). Lacustrine, peat bog, and offshore pollen records provide valuable information on the changes in the vegetation and climate of the Pleistocene in the extreme south-west of the European continent (Allué et al., 2017a, 2018; Burjachs, 1994; Burjachs and Julià, 1994, 1996; Burjachs et al., 2012; Carrión et al., 2013; Pérez-Obiol, 1988, 1994; Pérez-Obiol and Julià, 1994; Sardella et al., 2019). However, for the study of the past habitats associated with human occupations, palynological records in caves, when successful (sterility is common: Carrión et al., 2009), provide detailed information from the palaeobotanical point of view and a reconstruction closer to the probable local environment in which humans had to exercise their adaptive capacities. Some notorious examples in the region are Teixoneres Cave (López-García et al., 2012; Ochando et al., 2020a), Cova de L'Arbreda (Burjachs, 1987; Burjachs and Renault-Miskovsky, 1992), Abric Romaní (Allué et al., 2017b, Burjachs and Julià, 1994; Val-Peón et al., 2019), Cova del Parco (Bergadà et al., 1999), Balma del Gai (Allué et al., 2007), La Cativera (Allué et al., 2000) and Gabasa (González-Sampériz, 2004; González-Sampériz et al., 2003). In this context, it should be noted the concurrence of pollen on carnivore coprolites (Carrión et al., 1995a, b, 1999, 2004, 2006, 2007, 2008, 2018; Daura et al., 2017; De Porras et al., 2017; Gatta et al., 2016; González-Sampériz et al., 2003; Horwitz and

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Goldberg, 1989; Latorre et al., 2002; Marais et al., 2015; Ochando et al., 2020b, accepted; Scott, 1987, 1994; Yll et al., 2006). Coprolites often complete the palaeobotanical record as they incorporate pollen types strictly entomophilous which can be rarely seen in non-biogenic sediments (Carrión, 2002; Carrión et al., 2018, 2019a, c).

In this work, we present the results of the pollen analysis carried out in Toll Cave palaeontological and archaeological site, adding value and complementing it with a previous study in the adjacent Cova de Teixoneres in the province of Barcelona, northeastern Spain. The findings are substantial to the debate on the distribution of glacial refuges of temperate and Mediterranean woods in the northernmost territories of the northern Mediterranean peninsulas (Bhagwat and Willis, 2008; Giardini, 2007; Lawson et al., 2004; Magri et al., 2017; Margari et al., 2009; Pini et al., 2010; Sadori et al., 2008, 2016; Sinopoli et al., 2018; Tzedakis et al., 2002, 2003; Wagner et al., 2019), and to a theoretical framework for the adaptation of Neanderthals and *H. sapiens* to forested environments of the cold and dry end of the Pleistocene.

2. Physical setting, palaeontological findings and geochronology

Toll Cave (TC) (2° 09′ 02″ E, 41° 48′ 25″ N, 760 m a.s.l.) is located near Moià (Barcelona province, northeastern Spain). The cave is part of a karstic system with a number of galleries (Fig. 1) modelled through autochthonous limestone of Neogene origin, the Collsuspina Formation. The region is located between the Ter River to the north, which connect the inner area of northern Catalonia with the Mediterranean Sea, and the Llobregat River to the south (Rosell et al., 2017). TC, approximately 2 km long, is made up of three main galleries facing south, east and west (Fig. 1). The current entrance is located in the South Gallery gathering most archaeo-palaeontological records (Rosell et al., 2014).

During the 1950s, pioneering researchers highlighted the presence of a well stratified deposit of brown lutites, silt and sand over 9 m thick (Serra et al., 1957; Bergadà and Serrat, 2001). According to them, the sedimentary deposit was formed by a succession of different flooding episodes, which finished with the colmatation of the cave during the Holocene. The upper stratigraphic unit (0.5–1 m thick) contains Bronze Age and Neolithic materials, while the rest of units (up to 12) contain Middle Palaeolithic tools. The Upper Palaeolithic is not represented in the cave, probably due to the aridity of the period and the consequent lack of sedimentation. Regarding to Middle Palaeolithic times, TC is one of the most renowned sites for cave bear (*Ursus spelaeus*) (Serra et al., 1957; Fernández-García and López-García, 2013; Rosell et al., 2012, 2014, 2015).

Unit 1 (0.5–1m thick) may be situated in the MIS 1, Unit 2 (thick sands and gravels, 25–30 cm thick) is most likely MIS 1, but perhaps covers part of MIS 2. Unit 3 (1 m thick, orange lutites rich in faunal remains, mainly cave bears) is MIS 3. Unit 4, formed by brown lutites and sands with significant lateral changes (Serra et al., 1957), is difficult to separate stratigraphically from the underlying deposits. Ongoing excavations are taken Unit 4 as a main goal.

The Pleistocene faunal record of TC is composed mainly by cave bears, suggesting a regular use of the cave for the hibernation of these animals. However, there are also other large predators such as spotted hyaenas (*Crocuta crocuta*), wolves (*Canis lupus*), and lions (*Panthera leo spelaea*), in addition to small carnivores such as badgers (*Meles meles*), lynxes (*Lynx pardina*), foxes (*Vulpes vulpes*) and wild cats (*Felis silvestris*), which shows other uses of the cave, probably carnivore dens. Among ungulates, it is worth mentioning the presence of rhinoceros (Rhinocerotidae indet.), horses (*Equus ferus*), European asses (*Equus hydruntinus*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), aurochs (*Bos primigenius*), chamois (*Rupicapra rupicapra*), wild goat (*Capra*

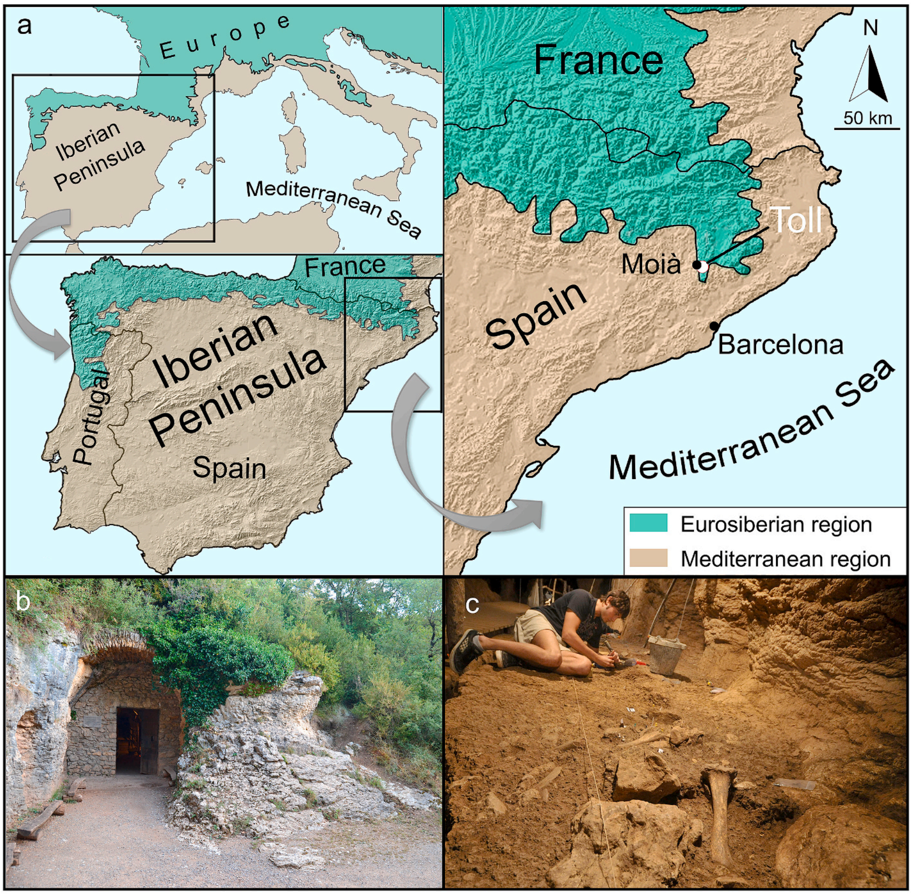

Fig. 1. Toll Cave. a) Location in Mediterranean northeastern Spain near the Eurosiberian region, b) cave entrance, c) excavation area.

pyrenaica), wild boar (*Sus scrofa*) and rabbits (*Oryctolagus cuniculus*) (Serra et al., 1957). Their presence in the cave corresponds, in the majority of the cases, to the accumulations of carnivores. Ramírez-Pedraza et al. (2019) have identified this faunal assemblage as belonging to the Upper Pleistocene, probably associated to a hibernation lair in Unit 4. This assignation is based in the abundance and features of the remains of *Ursus spelaeus*, and the activity of other carnivores as well, such as spotted hyenas and wolves (Rosell et al., 2012, 2014, 2015). At the lowermost Unit 4, Serra et al. (1957) pointed out the presence of hippopotamus (*Hippopotamus* sp.), which would place the base of the sequence at any time in the late Middle Pleistocene.

The chronology of the site is still under scrutiny. Provisional results are based in ^{14}C AMS and amino acid racemization, dating on three teeth and four bone samples (Kromer et al., 2013; Ramírez-Pedraza et al., 2019) (Table 1). Unit 3 is dated in c. 43,130 cal BP. For Unit 4, two bear bone samples were dated outside the ^{14}C range (>49,000 cal BP). The bones of a large-sized ungulate are radiocarbon dated in 47,310 cal BP. Three bear tooth samples dated by amino acid racemization, two of them gave age results between 57,900 (LEB 12757) and 69,800 cal BP (LEB 12756). Another sample (LEB 12755) provided an age of c. 150,000 cal BP, which is considered unrealistic based on the low amino acid concentration (Table 1). In sum, the onset of the sequence is unknown. As we shall see later, it could start at the end of MIS 6 or any stage of MIS 5, but it cannot be categorically discarded that all the sequence is situated between MIS 4 and MIS 1, with clear evidences of MIS 3 accumulation of sediments and biotic remains into the cave. From an archaeological point of view, TC was interpreted in the 1950s as a hibernation lair for cave bears that alternated with dens of other carnivores. However, the location of a lithic industry piece of clear Mousterian manufacture at Unit 4, as well as some bear bones with cut marks, suggested that the cavity could be occasionally used by human groups (Rosell et al., 2014).

Research on the geo- and biochronological context of the TC sedimentary sequence must continue. Strengthening the existing age estimate via the use of complementary extended-range luminescence dating signals (particularly single-grain thermally transferred OSL; e.g., Arnold and Demuro, 2015; Demuro et al., 2019) could be of crucial importance.

3. Modern-day climate and vegetation cover

TC is located in the supramediterranean belt with subhumid ombroclimate and, biogeographically, it belongs to the Pyrenean Province of the Eastern Pyrenean Sector (Rivas-Martínez, 1987; Rivas-Martínez et al., 2007). The area is located in a temperate, oceanic bioclimate, within the upper limits of the Mediterranean Region (Sub--Mediterranean climate) and near the Eurosiberian Region of northern Iberia (Fig. 1). The nearby meteorological station in Moià shows annual rainfall of 749 mm and an annual average temperature of 12.3 °C.

The vegetation of the region is dominated by forests adapted to mild summers and cold winters, patchily altered by disturbances such as overgrazing, fires, and extreme weather events. *Buxus sempervirens*, *Pinus halepensis* and *Quercus pubescens/humilis* are placed in the surroundings of the cave, accompanied by other trees such *Acer campestre/monspessulanum*, *Pinus nigra* subsp. *salzmannii*, *Quercus ilex* and *Quercus petraea* (Fig. 1). These forests also contain a dense woody stratum, with *Crataegus monogyna*, *Daphne laureola*, *Hedera helix*, *Ilex aquifolium*, *Juniperus communis*, *Laurus nobilis*, *Lonicera xylosteum*, *Pistacia terebinthus*, *Prunus spinosa*, *Quercus coccifera*, *Rhamnus saxatilis*, *Rubus ulmifolius*, *Ruscus aculeatus*, *Sorbus torminalis* and *Viburnum lantana*, among other species. It should also be mentioned the presence of a relic beech forest (*Fagus sylvatica*) a few kilometers east of the cave site.

4. Methodology and palynological potential

As recommended for archaeological sediments (Girard, 1975), sampling for pollen was conducted on several stratigraphical profiles within the southern gallery (Units 1–4) (Fig. 2). Preliminarily, one sample per unit was processed to evaluate the palyno-analytical potential of the cave infill. Once this prospective study was completed with success (e.g. good preservation, counts above 100, low number of indeterminable palynomorphs, relatively high palyno-diversity), a more exhaustive sampling was carried out, focusing in the same profiles, approximately 1–14 m from the main entrance: Unit 1, crust Units 1–2, Unit 2, crust Unit 2–3, and Unit 3, were sampled in square Q-14, and Unit 4 in squares P-08, M-01, M-02 and M-03 (Fig. 2). 27 samples were analysed and 25 were found polleniferous (Table 2). Two sterile samples came from Unit 4 (4.20, 4.30). Exposed surface layers of sediment were cleaned back and discarded to a depth of 5–10 cm in Units 1 and 2, and 10–15 cm in the rest of the units, in order to avoid potential sources of contamination by recent bioturbation (Fig. 2).

For the extraction of palynomorphs in the laboratory, we followed the conventional chemical analysis described by Dimbleby (1985) with the modifications proposed by Girard and Renault-Miskovsky (1969). In order to evaluate the quality of the laboratory preparation procedures and identify palynological sterility, we added to each sample three tablets of *Lycopodium* spores of a known concentration. After being treated at the laboratory, the samples were mounted on slides with liquid paraffin. The palynological identification and counting was made by conventional microscopy (400x and 1000x) using a transmitted light optical microscope, and the pollen reference collection of the Department of Plant Biology, University of Murcia. The pollen counts were treated with Tilia Graph 1.7.16 software in order to construct pollen diagrams (Figs. 3–8). A total of 8703 palynomorphs were identified; 6825 pollen grains and 1878 spores. Spores, non-pollen microfossils, and the pollen grains of Asteraceae (Asteroideae, Cichorioideae, *Anthemis* t. and *Centaurea montana* t.) were excluded from the pollen sum assuming over-representation, as a consequence of local over-deposition. The number of pollen taxa is between 5 and 39 per sample, with a total of 66 taxa being recognized. The percentage of indeterminable is lower than 10% (Table 2), and the preservation was generally good. The lowest pollen concentrations were recorded in the lowermost samples of Unit 4, and the maxima were found in the upper sample of Unit 1, perhaps due to compactation of the Holocene sediments. The highest number of taxa are recorded in Unit 1.

Table 1

Geochronological data for Toll Cave. Further details of the ^{14}C AMS can be found in Ramírez-Pedraza et al. (2019).

	Lab. Ref.	Unit	Field ref.	Depth (Z)	Mat.	Taxon	Technique	Dating (cal BP)	Error 1σ (Ka)	Observ.
[b]MPI	S-EVA 27843	3	T′11/3/P17/21	−190	Bone	*Cervus elaphus*	^{14}C AMS	43,130	0,34	
[a]LEB	LEB 12755	4	T′11/4/Q12/19	−174	Tooth	*Ursus spelaeus*	Amino acid racemization	150,000		Low quantity of animo acid
[b]MPI	S-EVA 27845	4	T′11/4/Q12/60	−191	Bone	*Ursus spelaeus*	^{14}C AMS	>49,000		
[b]MPI	S-EVA 27851	4	T′11/3/Q11/44	−199	Bone	*Ursus spelaeus*	^{14}C AMS	>49,000		
[a]LEB	LEB 12757	4	T′11/4/P16/66	−199	Tooth	*Ursus spelaeus*	Amino acid racemization	57,900		
[b]MPI	S-EVA 27850	4	T′11/3/P16/71	−200	Bone	Large sized ung.	^{14}C AMS	47,310	0,54	Cut marks
[a]LEB	LEB 12756	4	T′11/4/P13/29	−203	Tooth	*Ursus spelaeus*	Amino acid racemization	69,800		

[a] LEB: Laboratorio de Estratigrafía Biomolecular (Madrid, Spain).

[b] MPI: Max Planck Institute (Leipzig, Germany).

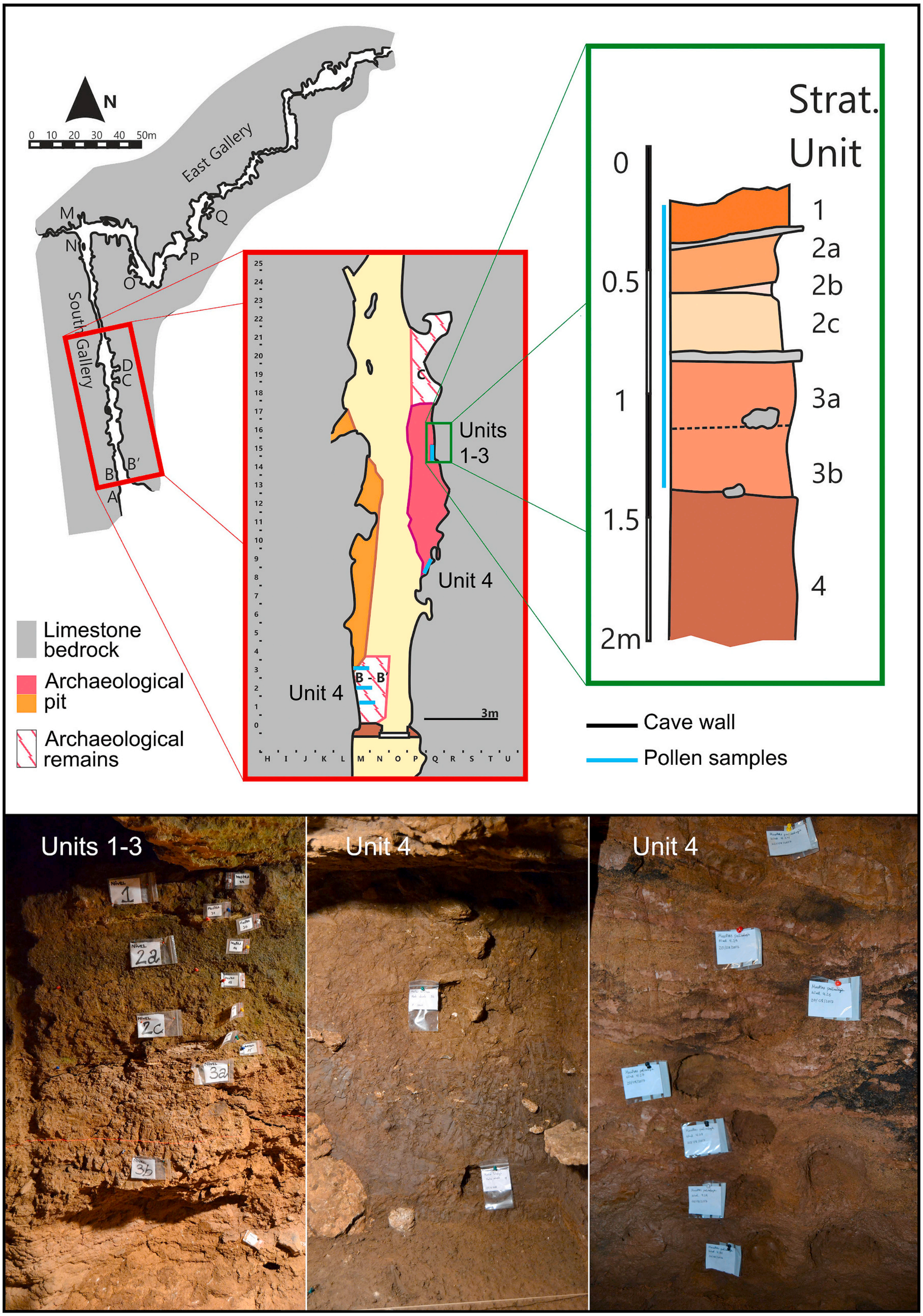

Fig. 2. Stratigrafical units sampled for pollen analysis in Toll Cave.

Table 2
Summary of palynological features of the Toll samples.

Sample	Unit	Nº	Field data	Depth (cm)	Gross Weight (g)	Net Weight (g)	Concentration (grains/g)	Indeterminable (%)	[a]Pollen sum	Number of taxa (Pollen)	Spores sum
1.1	1	1	Q14/ ×=1637;Y=1400	27	81,2	67,8	4638,29	3,97	302	36	58
1.2	1	2	Q14/ ×=1637;Y=1400	30	73,8	56,6	745,05	0,22	456	39	202
Crust 1.2-2a.1	Crust	3	Q14/ ×=1637;Y=1400	34	43,8	43,8	144,55	0,88	341	31	59
2a.1	2	4	Q14/ ×=1637;Y=1400	39	80,8	55,0	3566,62	4,71	318	35	26
2a.2	2	5	Q14/ ×=1634;Y=1395	42	76,3	31,3	1795,46	0,21	469	31	59
2c.1	2	6	Q14/ ×=1637;Y=1400	55	76,8	55,1	851,42	3,43	349	34	23
2c.2	2	7	Q14/ ×=1637;Y=1390	63	74,7	55,5	744,28	0,23	426	27	52
Crust 2c.2-3a	Crust	8	Q14/ ×=1635;Y=1327	70	74,7	74,7	109,45	0,72	416	26	48
3a	3	9	Q14/ ×=1637;Y=1400	100	77,3	61,4	195,13	2,46	203	22	10
3b	3	10	Q14/ ×=1660;Y=1333	125	76,5	70,3	474,74	2,36	212	17	10
4.1	4	11	P08/ ×=1557;Y=642	125	75,3	75,3	3731,31	0,81	491	24	54
4.2	4	12	P08/ ×=1557;Y=634	150	72,4	66,5	2391,97	0,41	487	18	17
4.3	4	13	P08/ ×=1557;Y=682	175	73,2	72,0	2833,61	0,20	495	19	27
4.4	4	14	P08/ ×=1545;Y=694	203	76,8	66,6	470,75	3,79	211	16	30
4.6	4	15	P08/ ×=1545;Y=687	222	78,1	68,7	223,97	4,45	202	16	88
4.8	4	16	M01/ ×=1230;Y=60	244	76,5	49,5	65,62	8,78	205	17	146
4.10	4	17	M02/ ×=1280;Y=108	305	76,4	54,8	158,00	6,47	201	20	197
4.12	4	18	M02/ ×=1248;Y=107	333	78,0	56,5	31,47	8,33	144	26	239
4.14	4	19	M02/ ×=1248;Y=105	361	77,2	75,0	13,46	5,13	39	14	220
4.16	4	20	M02/ ×=1248;Y=105	390	75,7	70,8	24,49	9,52	21	6	0
4.18	4	21	M02/ ×=1270;Y=106	401	76,5	68,1	27,28	6,81	44	10	43
4.20	4	22	M02/ ×=1239;Y=108	426	75,9	41,7	0	0	0	0	0
4.22	4	23	M02/ ×=1239;Y=108	446	76,2	64,6	75,51	9,52	21	5	0
4.24	4	24	M03/ ×=1210;Y=202	486	75,9	47,6	48,73	1,75	57	9	27
4.26	4	25	M03/ ×=1209;Y=202	517	75,1	40,3	44,41	6,38	47	12	234
4.28	4	26	M03/ ×=1217;Y=203	542	77,0	44,4	151,41	5,13	39	7	9
4.30	4	27	M03/ ×=1219;Y=203	569	72,2	64,2	0	0	0	0	0
								TOTAL 6196			1878

[a] Pollen sum column without Asteroideae, Cichorioideae, *Anthemis* type and *Centaurea montana* type.

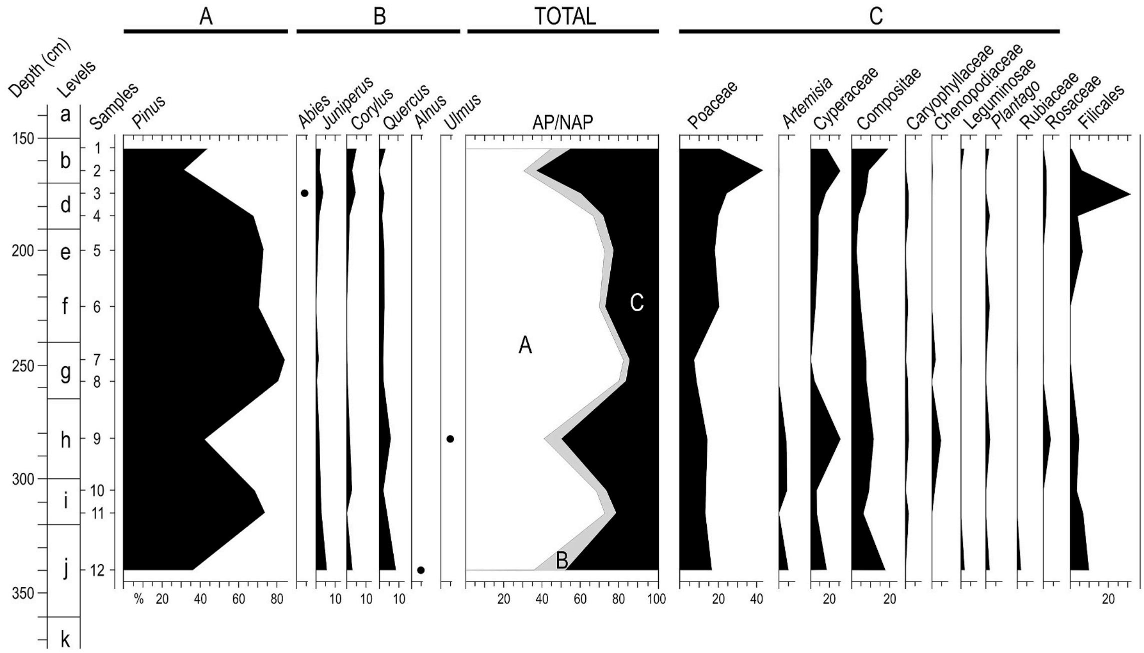

Fig. 3. Pollen diagram from Toll Cave redrawn from Donner and Kurtén (1958).

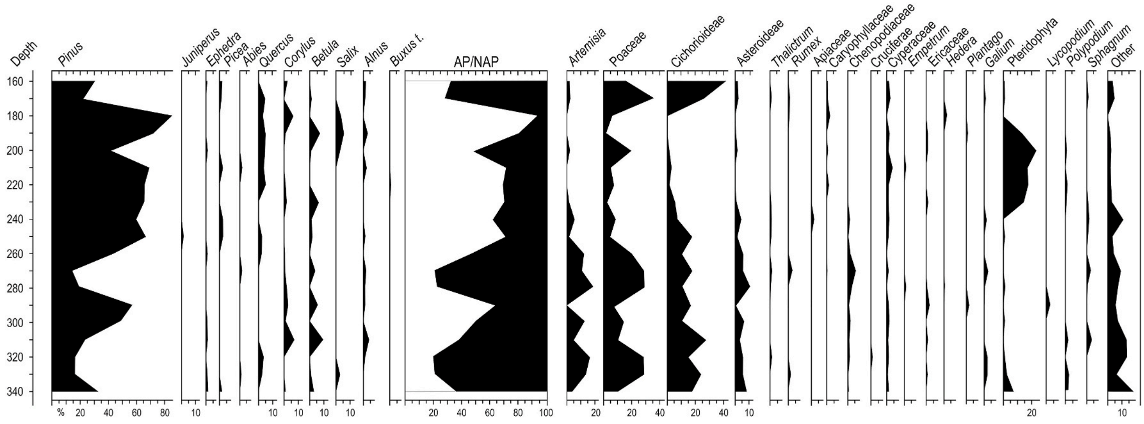

Fig. 4. Pollen diagram from Toll Cave redrawn from Menéndez-Amor and Florschütz (1962).

5. Pollen sequence

5.1. Previous palynological research

Several previous pollen studies have been performed at TC. Donner and Kurtén (1958) analysed 12 pollen samples, at irregular intervals but at specified depth from −155 to −340 cm, collected from the witness section "Sondage B" (Fig. 3) (Serra et al., 1957), situated at the cave entrance. Several years later, Menéndez-Amor and Florschütz (1962), published a second study, allegedly from 19 samples, at 10 cm intervals from −160 to −340 cm, of the same profile (Fig. 4). As mentioned by Butzer and Freeman (1968), it is highly likely that "the two sets of pollen data refer to the same beds of the same section". Allegedly, both studies were aimed at studying the Neolithic vegetational landscapes, and interpreting the potential changes from the Pleistocene to the Holocene as well. Although the AP and NAP curves in both diagrams may be somewhat comparable, there are enough details that allow us to make different palaeobotanical and palaeoecological interpretations. Menéndez-Amor and Florschütz (1962) interpreted the presence of pollen of deciduous arboreal species such as *Quercus*, *Corylus*, *Alnus*, *Betula*, and *Salix* as by long distance transport. In addition, the pollen diagram shows two distinct kinds of alternating pattern: one with high pine values (60–90%) accompanied by grasses, and another one with low pine values (15–45%) together with abundant grasses, *Artemisia* and other Asteraceae (Fig. 4). In contrast, Donner and Kurtén (1958) contend the existence of local broad-leaf trees while their pollen diagram shows less fluctuation in the main pollen contributors (Fig. 3). All these differences could be reflecting on such factors as identification of pollen in poor condition, selective destruction of pollen types through different techniques of sample preparation, and size sample (Butzer and Freeman, 1968). It bears emphasis that both papers (Donner and Kurtén, 1958; Menéndez-Amor and Florschütz, 1962) fail to reckon that most of the cave had been extensively anthropogenically modified by Neolithic groups. Therefore, it means that the first meter below the Neolithic unit, where these authors took the samples, could be mixed with different materials, possibly older. In fact, in more recent excavations, remains of cave bear bones have been found along with ceramics and beads. Some of the criticism made later by Butzer and Freeman (1968), on the work of Donner and Kurtén (1958), and Menéndez-Amor and Florschütz (1962) may be justified by these factors.

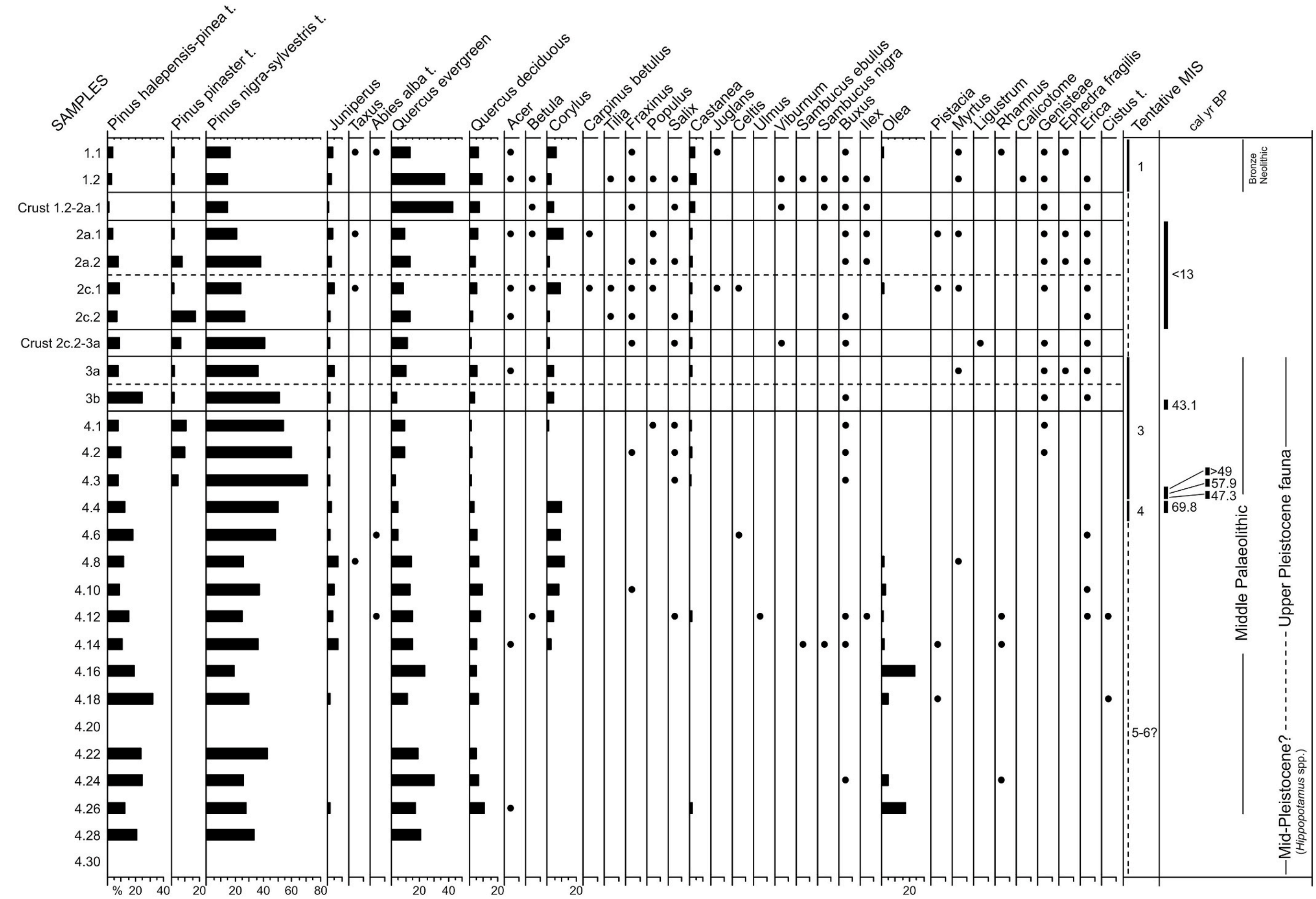

Fig. 5. Pollen diagram of Toll Cave (this paper) including principally the woody component. Asteroideae, Cichorioideae, *Anthemis* type, and *Centaurea montana* type are out from the total pollen sum. Black dots for percentages below 3%. Dashed lines for subdivisions within archaeological units.

5.2. General features of the TC pollen record

Overall, the TC pollen record is characterized by the prevalence and continuity of a *Pinus*-*Quercus* forest, which is in some stages accompanied by *Corylus,* cf *Juniperus* and to a lesser extent, *Castanea* t (type)*, Buxus, Olea, Salix* and *Erica* (Figs. 5–7). The woody component exhibits high cover and noticeable diversity, and includes a combination of mesophytes, such as deciduous trees that feature Eurosiberian temperate forests (*Acer*, *Betula*, *Celtis*, *Fraxinus*, *Juglans*, *Populus*, *Carpinus betulus, Tilia*, *Ulmus*), and Mediterranean taxa in addition to evergreen oaks and pines (*Viburnum, Pistacia, Myrtus, Calicotome*, *Cistus*, *Ephedra fragilis*, *Rhamnus*). The xero-heliophytic component (Poaceae, *Artemisia*, Amaranthaceae, *Ephedra*) is relatively unimportant, with the exception of samples 1.1, 2a.1, 2c.2, crust 2c.2-3a, and 4.28 (Figs. 5–7).

A broad spectrum of non-pollen palynomorphs (NPPs) have been found in TC, including fungal, fern, algal, and moss spores (Fig. 8; Table 3). A majority of the NPPs identified in TC also occur in the vicinity at the Pleistocene sediments of Teixoneres Cave such as *Glomus*, *Diporisporites*, *Hypoxylonites*, *Inapertisporites*, *Microsporonites* and *Monoporisporites* (Fig. 8; Table 3). However, the number of NPPs in Teixoneres is higher, with exclusive taxa such as *Asplenium, Dicellaesporites, Dyadosporites, Fusiformisporites, Uncinulites, Striadiporites, Quilonia*, among others. The taphonomical processes involved in these similarities and differences are unknown to us.

5.3. TC pollen stratigraphy

Unit 4 includes samples from 4.30 to 4.1 (Figs. 5–7) and depicts a palynozone dominated by arboreous pollen (AP), accounting 100% of the total counts in several samples. The frequencies of *Pinus nigra-sylvestris* are c. 19–71%, *Pinus halepensis-pinea* varies between 8 and 32%, with evergreen *Quercus* ranging between 3 and 30%, *Olea* exceeds 23%, deciduous *Quercus* reaches 11%, *Juniperus* is below 8%, and *Corylus* peaks at 12%. Other lesser contributors to AP include *Pinus pinaster*, *Salix*, *Buxus*, *Castanea*, *Pistacia*, *Myrtus*, *Rhamnus* and *Erica*. In the non-arboreous pollen (NAP) category, Poaceae attains relative abundances close to 21% in sample 4.28, *Artemisia* reaches 8% and Amaranthaceae, Cichorioideae, Asteroideae, Fabaceae, *Lotus*, Brassicaceae, Urticaceae and *Plantago lanceolata,* are frequent. Fungal spores abound, especially *Glomus* (1–83%), *Glomus* chlamydospores, *Ctenosporites*, *Hypoxylonites*, and *Monoporisporites*. *Algae* shows maxima above 82% (Fig. 8).

Unit 3 includes pollen samples 3a and 3b (Figs. 5–7) and is also clearly dominated by trees, with AP higher than 81%. The abundance of pines is noteworthy, with a decreasing trend for *Pinus halepensis-pinea* throughout the zone. *Pinus nigra-sylvestris* is consistently high, fluctuating between 36 and 51%, while *Pinus pinaster* does not exceed 1%. *Quercus* shows an increasing trend from 7% (3b) up to 16% (3a). Evergreen *Quercus* ranges from 4 to 10% and deciduous *Quercus* between 3 and 5%. *Corylus* (4–5%), *Juniperus* (2–4%) and *Erica* (1–4%) are noteworthy, as are the occurrence of *Acer*, *Castanea*, *Buxus*, *Myrtus*, *Ephedra fragilis* and Genisteae. *Artemisia* (4–5%) and Poaceae (2–3%) are not abundant, neither are Fabaceae, *Lotus*, Asteroideae, Cichorioideae and *Centaurea montana*. The abundance of *Glomus* is outstanding (50–70%) (Fig. 8). *Dicellaesporites*, *Inapertisporites*, *Multicellites*, *Scleroderma* and Type 209 are frequent, while bryophyte spores abound in 3b (Fig. 8).

In the crust sample 2c.2-3a, AP continues to be dominant, surpassing

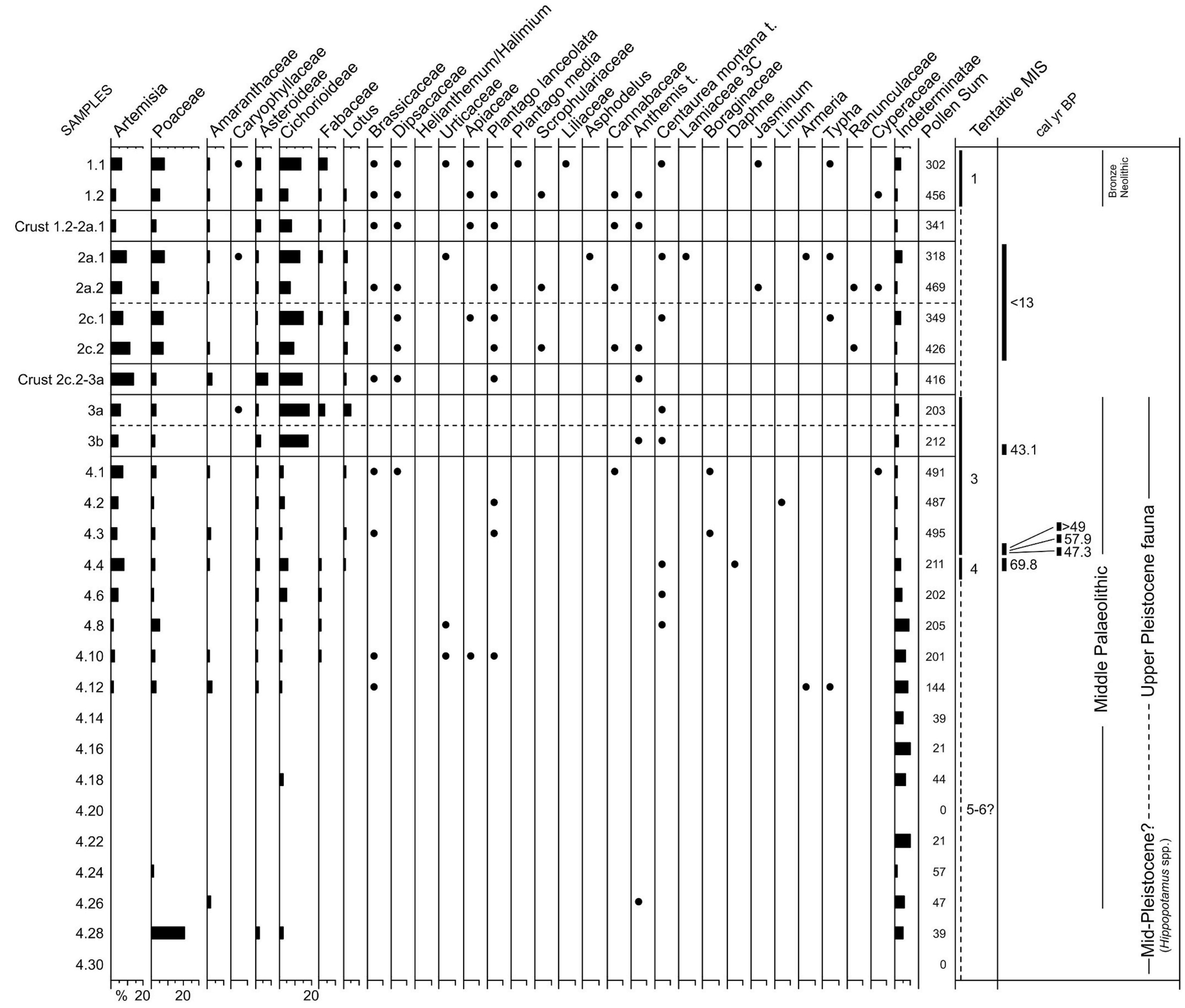

Fig. 6. Pollen diagram of Toll Cave (This paper) including mainly non arboreal elements. Asteroideae, Cichorioideae, *Anthemis* type, and *Centaurea montana* type are out from the total pollen sum. Black dots for percentages below 3%. Dashed lines for subdivisions within archaeological units.

77%. *Pinus nigra-sylvestris* (41%), evergreen *Quercus* (12%), and *Pinus halepensis-pinea* (8%) are noticeable. *Pinus pinaster* is 6% and *Erica* less than 2%. Other AP contributors are *Juniperus*, deciduous *Quercus*, *Corylus*, *Fraxinus*, *Salix*, *Castanea*, and Genisteae. Poaceae does not exceed 3%, while *Artemisia* is more frequent than in Unit 3, exceeding 13%. Among the fungal spores, *Monoporisporites* stands out as being above 48%, and *Glomus*, *Hypoxylonites and Diporisporites* are frequent. The ferns are represented by *Polypodium* (4%) (Fig. 8).

Unit 2 includes samples 2a.1, 2a.2, 2c.1 and 2c.2 (Figs. 3–5). AP is above 73%, with *Pinus nigra-sylvestris* (21–39%), *Pinus pinaster* (1–17%), evergreen *Quercus* (8–13%), *Corylus* (1–11%), *Pinus halepensis-pinea* (3–9%), deciduous *Quercus* (2–6%), *Juniperus* (2–4%), and *Erica* (1–3%) as principal taxa, accompanied by *Taxus, Acer, Betula, Carpinus betulus*, *Fraxinus*, *Salix*, *Buxus*, *Myrtus* and Genisteae. *Artemisia* (6–11%) and Poaceae (5–8%) are dominant within NAP. Amaranthaceae, Asteroideae, Cichorioideae, *Lotus*, Dipsacaceae, *Plantago lanceolata*, Cannabaceae and *Centaurea montana*, are frequent. *Glomus* (39–83%) is abundant, and *Diporisporites*, *Gelasinospora*, *Hypoxylonites*, *Inapertisporites, Monoporisporites* and *Scleroderma*. and fern spores, including *Polypodium*, occur in this zone. The ferns are represented by Triletes and *Polypodium*. Bryophyte spores exceed 9% (Fig. 8).

The pollen sample Crust 1.2-2a.1 shows AP dominant, surpassing 90%. Evergreen *Quercus* (43%), *Pinus nigra-sylvestris* (15%), and deciduous *Quercus* (7%) are noticeable. *Castanea* is 4% and *Salix* less than 4%. Other AP contributors are *Pinus halepensis-pinea*, *Pinus pinaster*, *Juniperus*, *Fraxinus*, *Buxus*, *Erica*, and Genisteae. Poaceae does not exceed 4%, while *Artemisia* is less frequent than in Unit 2, below 3%. Among the fungal spores, *Glomus* stands out as being above 44%, and *Hypoxylonites, Ctenosporites*, *Fractisporonites*, *and Reduviasporonites* are frequent.

Unit 1 includes samples 1.1 and 1.2 (Figs. 3–5). The predominant pollen type continues to be AP, with total values higher than 71%. The abundance of *Quercus* (19–47%) is remarkable, with evergreen *Quercus* ranging between 13 and 38%, and deciduous *Quercus* between 6 and 9%. *Pinus halepensis-pinea* (3–4%) and *Pinus nigra-sylvestris* (14–17%) decrease with respect to the previous units. The relatively high frequencies of *Corylus* (2–7%), *Castanea* (3–5%), *Juniperus* (3–4%), and Genisteae (2–4%) are noticeable. Other lesser contributors to AP include *Pinus pinaster*, *Taxus*, *Acer*, *Fraxinus*, *Viburnum*, *Buxus*, *Myrtus*, *Rhamnus* and *Erica* are well represented. In the non-arboreous pollen (NAP) category, Poaceae attains relative abundances close to 9% in sample 1.1,

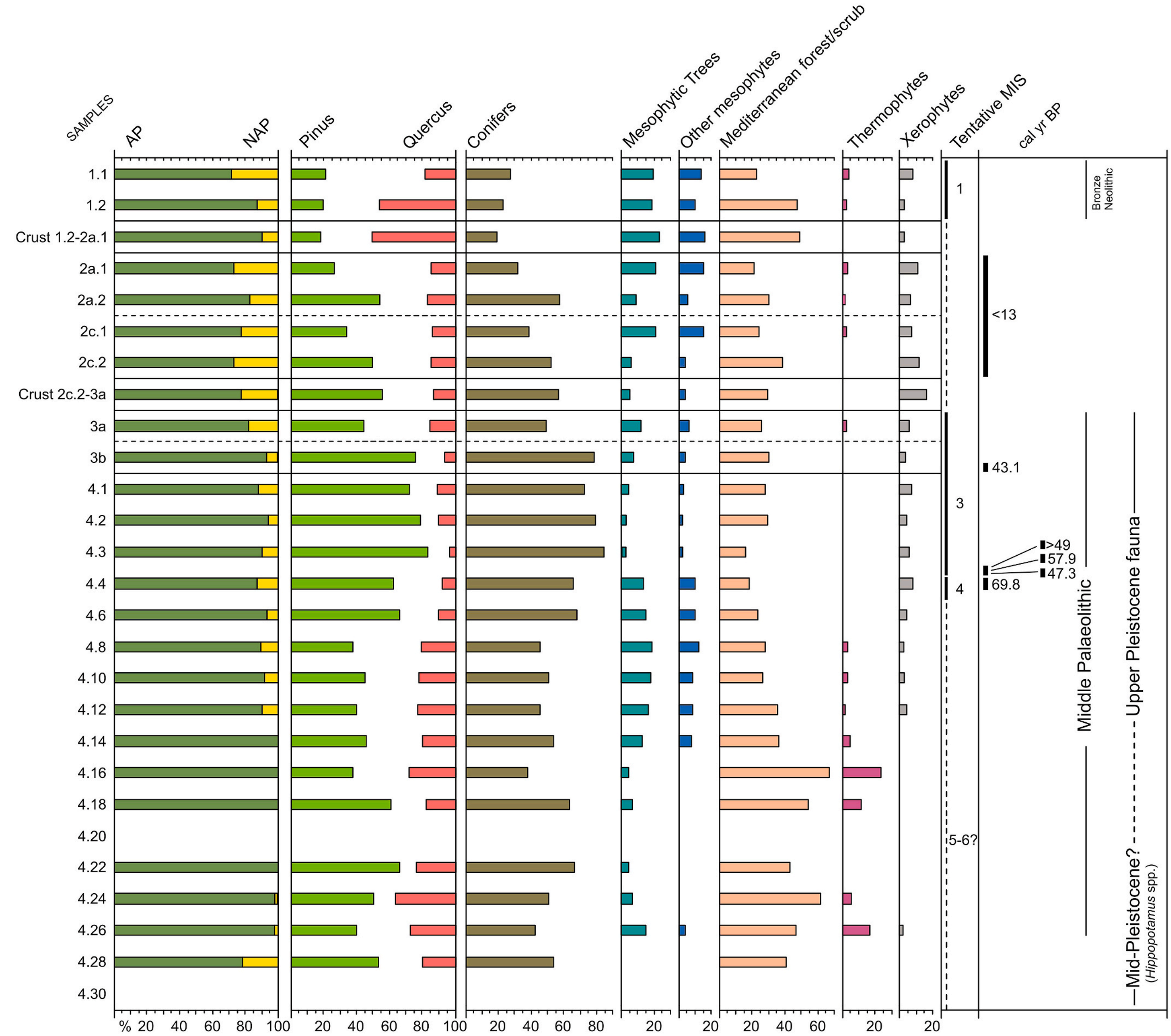

Fig. 7. Synthetic pollen diagram of Toll Cave (this paper) including ecological groups and the main pollen contributors. Conifers include *Pinus*, *Juniperus*, *Taxus* and *Abies*. Mesophytic trees include deciduous *Quercus*, *Acer*, *Betula*, *Corylus*, *Carpinus betulus*, *Tilia*, *Fraxinus*, *Populus*, *Salix*, *Castanea*, *Juglans*, *Celtis*, *Ulmus*, *Sambucus nigra* and *Ilex*. Other Mesophytes comprise mesophytes trees minus deciduous *Quercus*. Mediterranean forest/scrub include evergreen *Quercus*, *Pinus halepensis*, *Pinus pinaster*, *Viburnum*, *Sambucus ebulus*, *Buxus*, *Olea*, *Pistacia*, *Myrtus*, *Calicotome*, *Ephedra fragilis*, *Erica* and *Cistus*. Thermophytes include *Olea*, *Pistacia*, *Myrtus*, *Calicotome*, *Ephedra fragilis*, *Cistus* and *Asphodelus*. Xerophytes include *Artemisia*, Amaranthaceae, *Asphodelus*, Lamiaceae and *Ephedra fragilis*. The dashed lines indicate subdivisions within an archaeological unit.

Artemisia reaches 7% and Amaranthaceae, Cichorioideae, Asteroideae, Fabaceae, *Lotus*, Dipsacaceae and Brassicaceae, are frequent. Fungal spores are abundant, especially *Glomus* (17–62%), *Diporisporites* (10–28%), *Monoporisporites* (3–12%), *Dictyosporites*, and *Inapertisporites*, while bryophyte spores abound in 1.1.

6. Palaeoecological and palaeobotanical remarks

In view of the findings described above, here we postulate in the study area a long-term permanence of forest ecosystems dominated by pines and oaks with an important contribution of *Corylus*, *Juniperus* and *Castanea*, which were continuously accompanied by other trees such as *Abies, Taxus*, *Acer, Betula, Carpinus betulus, Tilia, Celtis, Fraxinus, Juglans, Buxus, Ilex, Populus, Salix*, and *Ulmus*, as well as Mediterranean elements such as *Pistacia, Myrtus, Calicotome*, *Cistus*, *Ephedra fragilis*, *Ligustrum*, *Rhamnus* and *Viburnum* (Figs. 5 and 7). The xero-heliophytic component (*Artemisia*, Poaceae, Amaranthaceae, *Erica*, *Ephedra*) would be relatively unimportant with the exception of some phases (1.1, 2a.1, 2c.2, crust 2c.2-3a, and 4.28) where the landscapes opened somewhat probably as consequence of cold dry spells (Fig. 6). However, the woodland structure and composition would have remained unaltered and both the forest density and the thermophytic component (e.g. *Olea*, *Buxus*, *Pistacia*, *Myrtus*, *Fraxinus*, *Populus*, *Salix, Castanea*) preserved with minor variations (Fig. 7).

Palaeoenvironmental analyses and studies of small mammals (including rodents) in the site also suggests the predominance of local woodlands (Allué et al., 2013; Fernández-García and López-García, 2013; López-García et al., 2012). This inference is supported by isotopic carbon studied by Ramírez-Pedraza et al. (2019) who point out that the average value of $\delta^{13}C$ in *Ursus spelaeus* (only adults) corresponds to

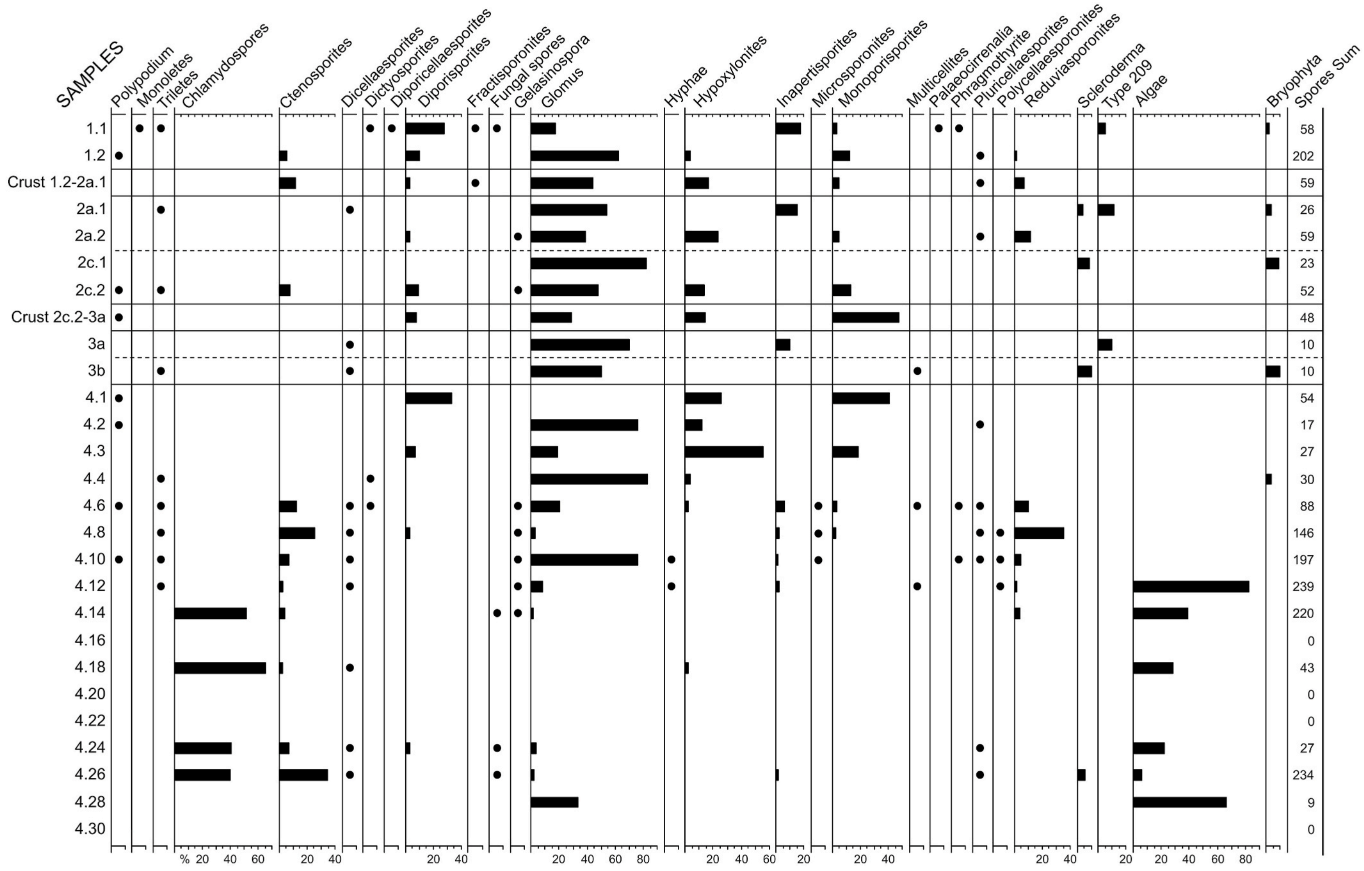

Fig. 8. Palynogram of spore and non-pollen palynomorphs of Toll Cave (this paper). Black dots indicate percentages below 3%. All taxa percentages calculated out from the total pollen sum.

Table 3
Non-pollen palynomorphs from Toll and Teixoneres sequences.

Caves	Toll-Teixoneres	Toll	Teixoneres
Non-pollen palynomorphs	*Polypodium*	*Chlamydospores*	*Asplenium*
	Monoletes	*Palaeocirrenalia*	*Dicellaeporisporites*
	Triletes	*Phragmothyrites*	*Dyadosporites*
	Ctenosporites		*Fusiformisporites*
	Dicellaesporites		*Palambages*
	Dictyosporites		*Quilonia*
	Diporicellaesporites		*Striadiporites*
	Diporisporites		*Trichothyrites*
	Fractisporonites		*Uncinulites*
	Gelasinospora		Type 224
	Glomus		Type 232
	Hyphae		Type 339
	Hypoxylonites		
	Inapertisporites		
	Microsporonites		
	Monoporisporites		
	Multicellites		
	Pluricellaesporites		
	Polycellaesporonites		
	Reduviasporonites		
	Scleroderma		
	Type 209		
	Algae		
	Bryophyta		

animals with a dominant consumption of C_3 plants. δ^{13}C in bear caves are more negative than in the rest of the herbivores and carnivores analysed, and may certainly indicate the presence of a closed forest habitat for this species.

This palaeoenvironmental scenario involves a glacial refugium for woodland ecosystems with relatively dense cover and high species diversity. A pollen study in the nearby Teixoneres Cave confirms this pattern during MIS 3 and MIS 2 (Ochando et al., 2020a). Indeed, the Toll-Teixoneres ecosystems identify a so far unkown, reservoir of angiosperm forest during the Pleistocene in northern Iberia. Similar findings can only be found far southwards within the Iberian Pleistocene such as during the Mid-Pleistocene Bolomor (Ochando et al., 2019), and the Upper Pleistocene Navarrés (Carrión and Dupré, 1996; Carrión and van Geel, 1999; Carrión et al., 1999), littoral of Murcia at Perneras and Sima de las Palomas (Carrión and Dupré, 1994; Carrión et al., 1995a, 2003), and Gibraltar caves (Carrión et al., 2008, 2018), but doubtless, mixed deciduous-evergreen forests are not so manifest in the south. The TC new pollen record in relatively high altitude within Spain must therefore be incorporated to the discussion on glacial refugia for temperate trees in the Mediterranean Peninsulas (Bhagwat and Willis, 2008; Carrión et al., 1999, 2003; Giardini, 2007; González-Sampériz et al., 2010; Lawson et al., 2004; Magri and Sadori, 1999; Magri et al., 2017; Manzano et al., 2017; Margari et al., 2009; Pini et al., 2010; Sadori et al., 2008, 2016; Sinopoli et al., 2018; Tzedakis, 1994, 1999; Tzedakis et al., 2002, 2003; Wagner et al., 2009, 2014; Willis, 1994).

The evidence of evergreen *Quercus* (mainly *Quercus ilex*) during the Quaternary glacial stages indicated limited abundance in northern Iberia (Uzquiano et al., 2016). The presence of deciduous oaks has been nevertheless shown in the ecotonal territories from Mediterranean to Eurosiberian regions (Aranbarri et al., 2016; Blanco-Castro et al., 1997; García-Mijangos et al., 2015; Gil-Romera et al., 2014; González-Sampériz, 2004; González-Sampériz et al., 2004, 2017; Loidi, 2017; Morales-Molino and García-Antón, 2014; Salomón et al., 2016). Pine forests (*Pinus halepensis*, *Pinus nigra* and *Pinus sylvestris*) may have been, however, widespread in the region during the study period, even in cold stages, as shown by a number of palaeobotanical studies (Allué et al., 2007, 2018; Bergadà et al., 1999; Burjachs, 1994, 2009; Burjachs and Julià, 1994; Burjachs and Renault-Miskovsky, 1992; González-Sampériz, 2004; González-Sampériz et al., 2003; Pérez-Obiol and Julià, 1994; Val-Peón et al., 2019; Yll, 1995). *Pinus pinaster* was rather a component of mixed forests with deciduous and evergreen oaks. A critical study at the local scale is by López-García et al. (2012) who analysed charcoals remains in hearths within units II, IIb and III from Teixoneres showing the abundance of *Pinus pinea/pinaster* and *Pinus sylvestris*.

Carpinus betulus is worth commenting because its current distribution in the Iberian Peninsula is restricted (Postigo-Mijarra et al., 2010). *Carpinus* has existed in the Peninsula since the Oligocene (Postigo-Mijarra et al., 2008, 2009), and there are palynological evidences during the Middle Pleistocene (Desprat et al., 2005, 2007; García Antón and Sainz Ollero, 1991). Fossil remains for *Carpinus* are still usual in the late Pleistocene (Postigo-Mijarra et al., 2008, 2009, 2010; Carrión et al., 2013) demonstrating its well-known resistance to cold conditions. Several localities pertinent to this case are Abric Romaní (Burjachs et al., 2012) during MIS 3, Pla de l'Estany-Garrotxa (Burjachs, 1990, 1994) during the Eemian (substage 5e), and Cañizar de Villarquemado record (González-Sampériz et al., 2013; García-Prieto, 2015) during MIS 5. Thereafter during the Holocene, *Carpinus* populations were depleted (Postigo-Mijarra et al., 2008; Magri et al., 2017) leading to its almost complete disappearance. However, its native presence has been confirmed in a few inhabited areas between the Cantabrian Mountains and the extreme west of the Pyrenees (Aizpuru and Catalán, 1984). The increased vulnerability of *Carpinus* communities through glacial-interglacial cycles, together with ecological factors, may have caused the disappearance of this taxon during the Holocene, whose extirpation from the Iberian Peninsula is still poorly understood (Magri et al., 2017). The presence of hornbeam (*Carpinus betulus*) at TC reinforces previous palynological data (Burjachs, 1990, 1994; Burjachs et al., 2012; González-Sampériz et al., 2013; Postigo-Mijarra et al., 2010) that supports the naturalness of the current populations in southwestern Europe.

7. Neanderthals in forest ecosystems

Although the archaeological and palaeontological studies carried out in TC (Ramírez-Pedraza et al., 2019; Rosell et al., 2012, 2014; 2015; Serra et al., 1957) point towards a prolonged use over time of the cave as a hibernation lair for carnivores, the occurrence some of lithic tools of clear Mousterian manufacture at Unit 4, and bear bones with cut marks, suggests that the cavity was occasionally used by Middle Palaeolithic human groups (Rosell et al., 2014). Therefore, the studied pollen sequence site can be directly compared with human and cave bears occupation histories at TC, and the relevant connections between these inhabitants and their ecosystem. Archaeological excavations in TC have shown a broad faunal diversity with species belonging to large and small carnivores, ungulates and small vertebrates (Rosell et al., 2012, 2014; 2015; Serra et al., 1957). At synchronous phases, it is also noteworthy in the nearby Teixoneres site the presence of a wide spectrum of edible plants accessible in the proximity, such as holly oak (*Quercus ilex*), olive (*Olea europaea*), Mediterranean hackberry (*Celtis australis*), elderberry (*Sambucus nigra*), hazelnut (*Corylus avellana*), walnut (*Juglans regia*) and chestnut (*Castanea sativa*).

The idea that Neanderthals were significant inhabitants of woodlands as well has been suggested by several authors (Carrión and Walker, 2019; Carrión et al., 2018, 2019b; Finlayson and Carrión, 2006, 2007; Rosas, 2016; Stewart, 2005; Stewart et al., 2019). Similarly, Nabais and Zilhao (2019) consider that Neanderthals were highly knowledgeable of their environments, integrating small prey in their diet, such as rabbits, turtles and birds since very early (e.g., Blasco, 2008; Blasco and Fernández Peris, 2009;Blasco et al., 2013; Blasco et al., 2014; Blasco et al., 2016; Fiore et al., 2016; Morin et al., 2019). Clearly, Neanderthals adapted to a wide range of environments and were able to develop complex, diverse and successful subsistence strategies in each territory (Spagnolo et al., 2019). Thus, fuel acquisition strategies have been seen on the part of Neanderthals, as well as occupation patterns in the Northwest of the Iberian Peninsula through taxonomic and taphonomic studies with charcoal (Allué et al., 2017a). Nevertheless, the pressures from hunting and predation in difficult terrain will also have led to risks of injury and mortality in even the most favourable environments, as shown by Spikins et al. (2019). Interestingly, Stewart et al. (2019) contend that North European Neanderthals were particularly adapted to the conditions of temperate episodes during which a wooded landscape and rich faunal diversity existed. In this context, the regional palaeovegetation picture shown here has important implications for existing arguments about the habitats and long survival of Neanderthals in the Iberian Peninsula (Carrión, 2004; Finlayson and Carrión, 2007; Higham, 2014; Jiménez-Espejo et al., 2007; Stewart, 2005; Wood et al., 2013; Zilhão et al., 2017).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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