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Faunal dynamics during the Mid–Pleistocene revolution: What implications, if any, does this have for the appearance of the Acheulean in southwestern Europe?

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ABSTRACT

New data from Europe, putting back the appearance of tools showing affinities or belonging to the Acheulean technocomplex to the late Early Pleistocene, open new questions about the onset of handaxe-making behaviour in the North Mediterranean region. This research aims to provide some clues to the debate by analysing at regional and local scale the main characteristics of the large mammalian fauna before and around the time of the first appearance of Large Cutting Tools in SW Europe. The database consists of 110 large mammal taxa from 58 local faunal assemblages (LFAs), ranging in age from about 1.6 to 0.5 Ma. Results obtained indicate that at the time of the Mid–Pleistocene Revolution the dynamics of large mammal fauna was mainly regulated by discrete dispersal events triggered by major climate changes. The environmental changes, removing keystone species and merging previously independently evolved taxa into new palaeo-communities, altered their internal equilibrium, giving rise to new inter-guild and intra-guild dynamics. The Lower local Stratigraphical Occurrence (LlSO) of various large mammals in key European Early and early Middle Pleistocene sites indicates that the change in taxonomical composition and structure of the fauna was a gradual process, caused by neither “turnover pulse” nor “migratory wave” events. Nonetheless, the evidence of multiple, discrete dispersals of large mammals may support the hypothesis that a few, poorly recorded dispersal events involving small human groups carrying a new technology led culturally different populations to coexist for a while in Europe during the late Early Pleistocene. The similarity degree among the ecological structure of LFAs, bearing or not evidence of human presence, shows on one hand that LFAs sharing a similar functional diversity were sparsely distributed over time, sometimes irrespectively of the age of sites and poorly affected by their geographic position. On the other, results obtained suggest that the relative amount of ecological groups related to the habitat preference and trophic behaviour of species, and the prey/predator relationships were among the factors that mainly controlled the human presence/absence at any site. Conversely, the presence of large predators does not seem to have had any particular relevance in controlling human dispersal and settlement. Based on available data, the hypothesis that the appearance of large cutting tools in Spain may more likely represent either the result of a local technological evolution or a different activity facies than a technological behaviour brought by newcomer populations seems to be the most parsimonious.

1. Introduction

Recent discoveries as well as the increased knowledge on the chronology of various key sites put back the appearance in Europe of tools showing affinities or belonging to the Acheulean technocomplex to the late Early Pleistocene. Evidence from El Forn and Pit 1 localities at Barranc de la Boella (Tarragona, Catalonia, Spain) (Lozano-Fernández et al., 2014; Vallverdú et al., 2014; Pineda et al., 2015; Mosquera et al., 2015a,b) challenges the long lasting concept that in the European Early Palaeolithic, Mode 1 technology seen as a prerogative of *Homo* sp. and *Homo antecessor* humans, predates the appearance of Mode 2 technology believed to be brought by *Homo heidelbergensis*.

Acheulean tool types (i.e Large Cutting Tools, LTCs, a cleaver-like tool and a pick) are first recorded in Europe in a period, the so-called Mid–Pleistocene Revolution (MPR) (Maslin and Ridgewell, 2005) or Mid–Pleistocene Transition (MPT) (Clarket al., 2006),

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during which a new global climatic regime/system had been developing (Berger and Jansen, 1994; Mudelsee and Stattegger, 1997; Head and Gibbard, 2005; Maslin and Ridgewell, 2005; Head et al., 2008; Maslin and Brierley, 2015). At that time, the modification in the temperature and precipitation regime triggered progressive changes in the structure of ecosystems (e.g. inter alios Brugal and Croitor, 2007; Bertini et al., 2010; Croitor and Brugal, 2010; Kahlke et al., 2011; Leroy et al., 2011). Evidence from terrestrial fossil plants and vertebrates indicates that during the post-Olduvai Early Pleistocene open and somehow dry environments progressively expanded in South Europe, although at different geographic and temporal scale across the focal region (see e.g. Magri and Palombo, 2013; Sadori et al., 2013; Palombo, 2015a, and references therein). The increased amplitude of glacial–interglacial cycles engendered long-term changes in vegetation patterns by causing repeated expansions and contractions of plant populations, fragmentation of geographical distributions and progressive, locally slightly dyachronous, extinction of taxa. The dynamics of large mammals in SW Europe at the time of the appearance of Acheulean-like tools indicate that a progressive restructuration of large mammal communities occurred in a period of marked climatic upsetting. Moreover, it highlights that cause-and-effect relationships between climatic oscillations and faunal changes result from the cumulative responses of individual, species and community to physical and biotic environmental changes (e.g. Palombo, 2014 and references therein).

To what extent such environmental changes may have influenced the behaviour, survival opportunities, and settlements of human populations in South Europe it is difficult to ascertain. Nonetheless, the rather unpredictable climatic changes humans had to face, the changing spectrum of trophic resources, the reconfiguration of mammalian fauna structure and the altered competition dynamics among secondary consumers may have affected humans in different ways, maybe promoting the development of new behaviour and strategies to adapt to/take advantage of these environmental changes (see inter alios Foley, 1994, 2002; Dennell, 1998, 2003; Petraglia, 2005; Blasco et al., 2011, 2013; Dennell et al., 2011; Potts, 2012a,b; Preece and Parfitt, 2012; Rodríguez et al., 2012, 2014; Rodríguez-Gómez et al., 2013; Barsky et al., 2013 and references therein; van der Made, 2014). Accordingly, some questions arise, in particular as whether: i) factors promoting ecosystem changes had any role in the appearance of the Acheulean technology in Europe; ii) changes in ecosystems and particularly in the structure of mammalian palaeocommunities contribute to shape the times and modes of human population dynamics and/or had any influence on human behaviour; iii) the dispersal pattern of large mammals supports the hypothesis that the appearance of the early Acheulean was related to the arrival of humans bringing a new technology, who dispersed toward Europe during a "migratory wave" event that involved, among others, some mammals of African origin.

This research aims to provide some clues to the debate by analysing, at a regional and local scale, the main characteristics of the large mammalian fauna shortly before and around the time of the first appearance of Large Cutting Tools to the time of the spread of the Acheulean technology in Western Europe (from about 1.5 to 0.6–0.5 Ma, from V5a to G2b partim Faunal Complexes, FCs, as in Palombo, 2014).

2. Material and methods

2.1. Data set

The database consists of taxonomically revised lists of 110 large mammal taxa from 58 selected Iberian, French and Italian local faunal assemblages (LFAs) ranging in age from the post-Olduvai Early Pleistocene to the beginning of the early Middle Pleistocene (from about 1.6–1.5 to 0.6–05 Ma, from V5a to G2b-1 FC). Besides to the SW European LFAs, a few W European LFAs, having a particular relevance for a better understanding of changes in the fauna structure at the Early to Middle Pleistocene transition, were added to the analysis (Table 1). The list was compiled by revising and updating those resulting from previous studies on the Pleistocene mammals from SW Europe (see e.g. Palombo, 2014, 2015a,b an references therein). Small Mustelidae and Lutrini were not included in the study because of the scantiness and the disproportion of their fossil record in time and space across the studied region. To provide a uniform baseline for the studied material (crucial, for instance, in any cluster analysis), the identification of species was based on a taxonomical uniform view even for species/specimens whose taxonomy, systematics, and identification are controversial (Supplementary information 1). The chronological ordering of the 58 LFAs is mainly based on absolute radiometric dates and palaeomagnetic events (Table 1). The LFAs were gathered in Faunal Complexes (FCs) following standard biochronological principles and according to the results of cluster analysis (cf. Palombo, 2014, Fig. 1 and Supplementary information therein). The attribution of some LFAs to one rather than to another FC is questionable because of unresolved questions concerning either the taxonomic identification of the material or the chronology of the fossiliferous layer/s, therefore it has to be regarded as provisional.

2.2. Turnover indexes

The faunal renewal was estimated as the change in the taxonomic composition at the transition between faunal complexes belonging to two successive biochrons as well as by the number of taxa that appeared (origination rate, OR) and disappeared (extinction rate, ER) during the time slice of a single biochron. The effect on appearance/disappearance events on the composition of a fauna was evaluated as per-taxon-Origination (OR) and per-taxon-Extinction (ER) rates in each unequal time slice as $OR = [(NFL + NFt)/Ntot]/\Delta t$ and $ER = [(NFL + NbL)/Ntot]/\Delta t$, where NFL is the number of taxa that exist only in the focal interval, Nbl is the number of taxa that originate before the interval but go extinct within it, NFt is the number of taxa that originate in the interval and persist beyond it; Δt is the time extent of the interval (see Foote, 2000).

Three turnover indexes were calculated for a better appraisal of the faunal dynamics at the transition between successive biochrons. In the Global Turnover Index (g-TI), both in situ speciation and per dispersal new appearances were treated as First local Historical Appearances (FlHA, Palombo, 2009) and extinctions as Last local Historical Appearances (LlHA). In the "per-dispersal Turnover Index" (d-TI) only the first appearance caused by dispersal (d-FlHA) were taken into account, while in the "per-in-loco-origination (speciation) Turnover Index" (o-TI) only the first appearance due to speciation events in locally evolving phyletic lineages (o-FlHA) were considered. TI was calculated as $TI = \%\ FC_{n+1}$ First local Historical Appearance (FlHA) + % FC_n Last local Historical Appearance (LlHA) where $\%\ FlHA = FlHA/RM \times 100$; $\%\ LlHA = LlHA/RM \times 100$; RM (running mean) $= N/((FlHA + LlHA)/2)$ and N = number of species in FC_n + number of species in FC_{n+1} − number of species crossing the FC_n- FC_{n+1} boundary.

2.3. Ecological groups

To analyse and compare functional traits of the studied LFAs, I have followed the classification of species into functional groups as proposed by Palombo (2015a, and supplementary information