Investigating the Mid-Brunhes Event in the Spanish terrestrial sequence

Hugues-Alexandre Blain[1*], Gloria Cuenca-Bescós[2*], Iván Lozano-Fernández[1*], Juan Manuel López-García[1*], Andreu Ollé[1*], Jordi Rosell[1*], and Jesus Rodríguez[3*]

[1]IPHES (Institut Català de Paleoecologia Humana i Evolució Social), c/ Escorxador s/n, 43003 Tarragona, Spain, and Àrea de Prehistòria, Universitat Rovira i Virgili (URV), Avinguda de Catalunya 35, 43002 Tarragona, Spain
[2]Área de Paleontología, Departamento de Ciencias de la Tierra, Facultad de Ciencias, Universidad of Zaragoza, 50009 Zaragoza, Spain
[3]CENIEH (Centro Nacional de Investigación sobre la Evolución Humana), Avenida de la Paz 28, 09004 Burgos, Spain

ABSTRACT

In the Mediterranean area, which is climatically stressed by limited water resources and extremes of heat, climate variations are known to play a crucial role in the ecosystems and environment. Investigating how climate has changed in the past may help us to understand how it may change in the future and its consequences on temperature and water resources. The Gran Dolina sequence (north-central Spain) provides a unique long paleontological and archaeological record spanning the Mid-Brunhes (ca. 450 ka) climatic transition. A fossil amphibian- and squamate-based reconstruction of temperature and precipitation shows marked peaks that have been related to various interglacial peaks in accordance with numeric dates and paleomagnetic and biochronological data. An analysis of climate and herpetofaunal assemblage changes during the interglacial periods reveals that (1) post-Mid-Brunhes Event (MBE) interglacials were warmer than pre-MBE interglacials, (2) pre-MBE interglacials were warmer than present day, and (3) there were lower levels of rainfall in post-MBE interglacials than in pre-MBE interglacials. The climate trend in the Mediterranean area was found to be congruous with global climate changes as reconstructed from ice and sea-surface temperature records over the past million years.

INTRODUCTION

The Mid-Brunhes Event (MBE) is a climatic transition between marine oxygen isotope stages (MIS) 13 and 11 that separates two climatic modes: (1) early-middle Pleistocene interglacials (780–450 ka), which are characterized by only moderate warmth, and (2) middle and late Pleistocene interglacials (occurring after 450 ka), which are characterized by greater warmth consistent with, or warmer than, the Holocene. This event is observable in a variety of long-term climate records such as the Mapping Spectral Variability in Global Climate Project (SPECMAP) and the European Project for Ice Coring in Antarctica (EPICA) (EPICA community members, 2004; Jouzel et al., 2007), many records of sea-surface temperature (Lisiecki and Raymo, 2005; Becquey and Gersonde, 2002), and some long-term speleothem records (Winograd et al., 1997), but its effect on terrestrial systems is poorly understood due to the absence of detailed long-term records of environmental change (Tzedakis et al., 2006, 2009; Candy et al., 2010). Through their examination of the British terrestrial sequence, Candy et al. (2010) showed that interglacial climates during the early-middle Pleistocene were as warm as those that occurred during the late-middle and late Pleistocene, suggesting that the MBE was not a global climatic transition, but was restricted to specific regions, in particular to higher latitudes of the Southern Hemisphere. Because climate projection models suggest that greater climate changes would be expected under warming conditions at higher latitudes, we would also expect many intracontinental and Mediterranean fringe regions to display considerable temperature increases and precipitation decreases (e.g., Sanderson et al., 2011). In this work we investigate this climatic transition in the long-term terrestrial sequence of Gran Dolina cave (Atapuerca, Burgos, north-central Spain), which spans the MBE transition, by means of the mutual climatic range technique using the amphibian and squamate fossil assemblages.

GEOLOGICAL AND CHRONOLOGICAL SETTING

The Sierra de Atapuerca is ~1080 m above sea level, dominating the now-flat landscape of the Castilian grain-growing plains irrigated by the River Arlanzón near the village of Ibeas de Juarros, located 14 km east of the city of Burgos (Fig. 1).

The ongoing archaeological and paleontological excavations in Gran Dolina, or Trinchera Dolina (TD), cave have been conducted every year since 1976, and have revealed a long, culturally and paleontologically rich sequence dated as between ca. 1 Ma and 250 ka by means of biostratigraphy, electron spin resonance, electron spin resonance on optically bleached quartz dating, U-series, thermoluminescence, infrared-stimulated-luminescence analysis, and paleomagnetic dating (see Appendix DR1 in the GSA Data Repository[1]).

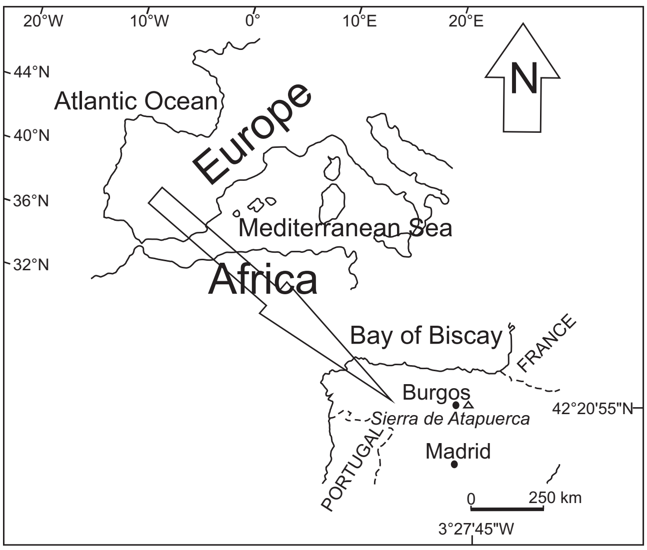

Figure 1. Location of Sierra de Atapuerca (Burgos, Spain).

*E-mails: hablain@iphes.cat; ilozano@iphes.cat; jmlopez@iphes.cat; aolle@iphes.cat; jordi.rosell@urv.cat; cuencag@unizar.es; jesus.rodriguez@cenieh.es.

[1]GSA Data Repository item 2012296, Appendices DR1 and DR2, Figure DR1, geological and chronological setting of Gran Dolina cave, and Table DR1, is available online at www.geosociety.org/pubs/ft2012.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

GEOLOGY, November 2012; v. 40; no. 11; p. 1051–1054; Data Repository item 2012296 | doi:10.1130/G33427.1 | Published online 22 August 2012

MATERIAL AND METHODS

The small-vertebrate fossil remains used for this study consist of disarticulated bone fragments collected by means of water screening during work on the test excavation (~9 m^2) that comprises level TD5 at the bottom to level TD10 at the top (see Appendix DR1). The excavation was divided into ~10-cm-thick excavation layers (T). The small vertebrates have been processed and studied according to these excavation layers (Cuenca-Bescós et al., 2005, 2010, 2011). A total of 5596 kg of sediment was processed, corresponding to 76 samples. The amphibian and squamate assemblage contains ~40,000 fragments corresponding to a minimum of 6145 specimens, representing at least 20 taxa, including newts, toads and frogs, amphisbaenians, lacertids, anguids, and snakes (Blain, 2005; Blain et al., 2008, 2009).

The taphonomic patterns of the herpetofaunal accumulations were discussed in Blain et al. (2008, 2009). Taphonomic observations on the collections of small vertebrates at Gran Dolina suggest, based on the type of digestion evidence and the fractures in the fossils, that the remains were mostly the prey of nocturnal birds such as the eagle owl (*Bubo bubo*), an opportunist that hunts a wide range of prey (Bennàsar Serra, 2010).

Paleoclimatic Reconstruction

Because most amphibians are water dependent and most reptiles are temperature dependent, the climatic and/or environmental parameters in their immediate environment mark their distribution. Paleoclimatic interpretations are based on the presence of herpetofaunal species from each of the excavation layers. The mutual climatic range (MCR) method is used to quantify paleotemperature and paleoprecipitation (see Blain et al., 2009), specifically, mean annual temperature (MAT), mean temperature of the warmest month (MTW), mean temperature of the coldest month (MTC), mean annual precipitation (MAP), and winter (DJF, December-January-February) and summer (JJA, June-July-August) precipitation. Analysis of the MCR in each T layer is based on the distribution atlas of Iberian herpetofauna (Pleguezuelos et al., 2004), divided into 10 × 10 km UTM (Universal Transverse Mercator) squares. Climatic parameters have been estimated for each 10 × 10 km UTM square, using various climatic maps from the Iberian Peninsula (Font Tullot, 1983, 2000). The chronology of the interglacial peaks was assigned by means of numeric dates, and by paleomagnetic and biochronological data as shown in Appendix DR1.

Environmental Reconstruction

Two paleoenvironmental parameters were used in this study: (1) the representation of amphibian and squamate taxa associated with woodland and woodland-edge areas, and (2) the representation of small mammal taxa inhabitants of open-dry environments (dry meadows, steppes, and rocky areas). These two variables were inferred from the paleoenvironmental data for the amphibian and squamate assemblages obtained by Blain et al. (2008) and small mammal assemblage data obtained by Cuenca-Bescós et al. (2005).

RESULTS AND DISCUSSION

On the basis of the paleoherpetological associations, paleoclimatic parameters were estimated relating to MAT, MTC, and MTW months, winter (DJF) and summer (JJA) precipitation, and MAP (Appendix DR2). According to the ΔMAT curve (representing the deviation from the present values), our results first suggest that only warm periods (i.e., interglacials) are evident in the TD sequence. The general trends of the curve (ΔMAT in Fig. 2), in accordance with the numeric dates and paleomagnetic and biochronological data, show three distinct peaks in the time interval represented by level TD10 (T0 to T22): a first small peak (T1) ca. 244 ± 26 ka (Berger et al., 2008) identified as MIS 7; then two higher peaks between 0.33 and 0.40 Ma (Falguères et al., 2001; Moreno García, 2011), which have been correlated with MIS 9 (T9) and MIS 11 (T17). After these, the numeric estimations obtained for the upper part of TD9 (0.42 Ma; Moreno García, 2011) suggest a probable correlation with MIS 13, due to the high values obtained in the lowermost part of TD10 (T21). Level TD8 (T24–T27) certainly corresponds to MIS 15 or MIS 16 with a numeric estimation of 0.60 Ma (Moreno García, 2011). Unfortunately, the low number of herpetofaunal remains in this level does not permit its climatic conditions to be reconstructed. Nevertheless, the occurrence of the amphisbaenian *Blanus cinereus* in T27, slightly north of its current distribution in Spain (Blain, 2005), suggests that this layer corresponds to climatic conditions that were warmer than or similar to those of today. The Brunhes-Matuyama boundary located between levels TD7 and TD8 yields an age close to 780 ka for the lower part of level TD8 and consequently, the highest temperature correlates to MIS 19 (T28). The following succession of high values

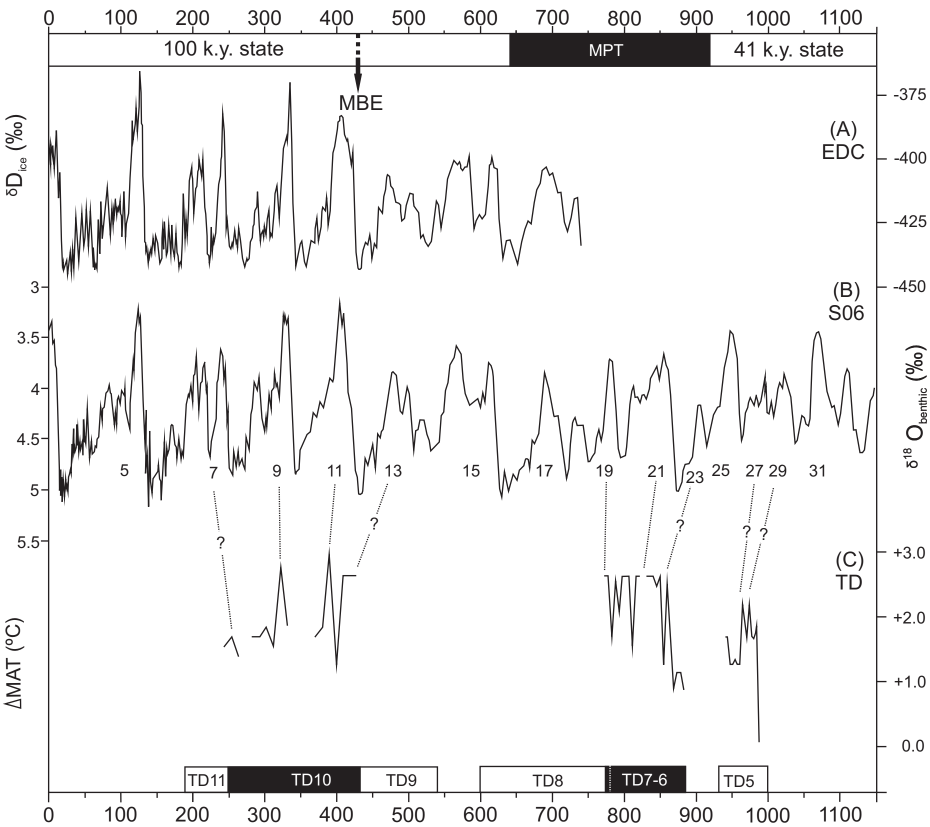

Figure 2. Correlation and comparison between ice, sea-surface, and Gran Dolina temperature records. MBE—Mid-Brunhes Event; MPT—Mid-Pleistocene transition; TD—Trinchera Dolina. A: EPICA (European Project for Ice Coring in Antarctica; EPICA community members, 2004) Dome C (EDC) deuterium (δD) record. B: S06 $\delta^{18}O_{benthic}$ composite record from sites in equatorial east Pacific (Tzedakis et al., 2006). C: Trinchera Dolina (TD) herpetofauna-based mean annual temperature (ΔMAT) plotted on numeric date time scale. Position of MBE is indicated, as are interglacial marine isotopic stages (numbers).

within level TD6 (T33, T35–T37, T40, T41, T43–T45, T48, and T50), numerically attributed to the late-early Pleistocene (from 0.80 to 0.88 Ma; Moreno García, 2011), may correspond to MIS 21 and MIS 23. Because the highest MAT reaches the same value for this period, a single layer (T43) is used to characterize MIS 21. T50 is cautiously correlated with MIS 23. Within level TD5 (ranging between 0.94 and 1.00 Ma; Moreno García, 2011), two small peaks appear at T65 and T68, and are tentatively correlated with MIS 27 and MIS 29.

Because the ΔMAT curve (Fig. 2) does not represent absolute values, but rather relative values regarding the deviation from today's values, our results first suggest that all post-MBE and pre-MBE interglacials were warmer than present-day temperatures. Together with the relatively high percentages (30%–40%) in taxa with plant cover requirements ("% wood" in Appendix DR2) and the fact that no typical large glacial mammals have been recovered (Rodríguez et al., 2011), this may suggest that only warm periods (i.e., interglacials) have been documented in the Gran Dolina sequence. Independent of their absolute values, the ΔMAT curve (Fig. 2) shows interesting trends. When compared (Fig. 3), post-MBE interglacials (at least MIS 11 and MIS 9) reach higher temperatures than pre-MBE interglacials (MIS 13, MIS 19, MIS 21, MIS 23, MIS 27, and MIS 29) in accordance with ice (SPECMAP and EPICA) and marine sea-surface temperature records (EPICA community members, 2004; Jouzel et al., 2007, Lisiecki and Raymo, 2005; Becquey and Gersonde, 2002). This may suggest that a MBE climatic transition occurred in the terrestrial environments of northern Spain.

The fact that pre-MBE interglacials are estimated to have been warmer than present day (i.e., Holocene) contradicts the MBE, because all ice and marine records show lower than present values in pre-MBE interglacial temperatures. However, other terrestrial sequences spanning the MBE have also suggested that pre-MBE interglacials were warmer than present day. This phenomenon has been well documented in the terrestrial record of Britain (Candy et al., 2010) and in the long pollen record of Tenaghi Philippon (Greece), where the amplitude of interglacials, as reflected in variations in the Arborean pollen (AP) curve, does not appear to significantly affect the extent of the tree population expansions of the various forest stages. With particular reference to the terrestrial equivalents of MIS 13 and MIS 15, not only the AP maxima, but also their vegetational character (mainly dominated by *Quercus* and *Carpinus*), are similar to post-MBE interglacials (Tzedakis et al., 2006).

According to our estimation, in northern Spain, MIS 11 was the warmest interglacial, followed by MIS 9 and MIS 7. MIS 5 is unfortunately not represented in the Gran Dolina sequence; moreover, to date no clear MIS 5.5 paleontological site has been studied on the Iberian Peninsula. Global simulations by Yin and Berger (2010) suggest that MIS 9.3 is probably the warmest post-MBE interglacial, followed by MIS 5.5, MIS 11.3, MIS 1, and MIS 7.5 is the coolest. In addition, paleontological evidence from Britain strongly suggests that the MIS 9 temperate stage was warmer than the temperate stages of MIS 11 and MIS 7 or the Holocene, and approached the temperatures typical of the Eemian-Ipswichian (MIS 5.5) in terms of warmth (Green et al., 2006). However, based on evidence derived from the EPICA ice record, Masson-Delmotte et al. (2010) suggested that MIS 5.5 and MIS 11 were the warmest interglacial maxima.

The seasonal variation of temperature simulated by Yin and Berger (2010) for post-MBE interglacials shows that the higher MAT is mainly due to warming during boreal winter: over the Northern Hemisphere, the linear response to astronomical forcing leads to a slightly warmer Northern Hemisphere in winter and a cooler Northern Hemisphere in summer. Our results (except for MIS 11) disagree with these simulations, in that MTW increases are higher than MTC for all pre-MBE and post-MBE interglacials. Only for MIS 11 is the MTC increase much higher than the MTW (Fig. 3).

MAP drops by ~100 mm after the MBE transition, but the minima do not coincide with interglacial peaks. Seasonal variations suggest more precipitation in summer (ΔJJA) compared to today's levels and, except for MIS 7, less precipitation during winter (ΔDJF). According to these results, middle Pleistocene interglacials were characterized in this region by a more homogeneous rainfall distribution throughout the year. Because the summer drought period is the main feature that characterizes the Mediterranean climate, increased summer rainfall suggests a reduced Mediterranean character for these interglacial climates. A higher moisture level than within current climatic conditions in northern Spain is in accordance with the development of woodland areas and wet meadows supporting grazer and browser type of large mammals represented in the paleontological record of Gran Dolina. The decrease in MAP after the MBE is in accordance with the increase in the representation of open dry environment–preferring small-mammal taxa in level TD10 (Cuenca-Bescós et al., 2005; "% OD+R" in Appendix DR2) as well as with the changes documented in the large mammal communities toward herbivores better adapted to arid conditions in level TD10, like the large bisons (*Bison priscus*), aurochs (*Bos primigenius*), caballoid horses (*Equus germanicus* and *E. mosbachensis*), and stronger rhinos (*Stephanorhinus hemitoechus*) (Cuenca-Bescós and García, 2007).

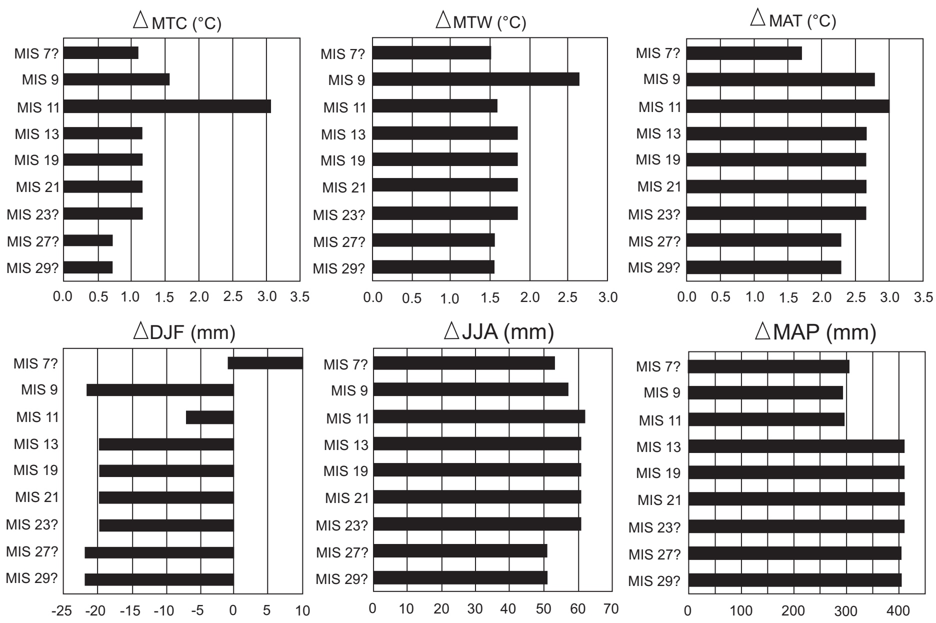

Figure 3. Comparison between interglacials identified in Trinchera Dolina sequence. Abbreviations: ΔMTC—difference between mean temperature of coldest month and present day; ΔMTW—difference between mean temperature of warmest month and present day; ΔMAT—difference between mean annual temperature and present day; ΔDJF—difference between winter precipitation and present day (DJF is December, January, February); ΔJJA—difference between summer precipitation and present day (JJA is June, July, August); ΔMAP—difference between mean annual precipitation and present day; MIS—marine oxygen isotope stage.

CONCLUSIONS

The analysis of the differences between the successive interglacial peaks reveals the following.

1. Post-MBE interglacials were warmer than pre-MBE interglacials in accordance with the MBE climate transition as documented by ice (EPICA and SPECMAP) and sea-surface temperature records.

2. Pre-MBE interglacials were warmer than present day.

3. The reconstructed MIS 11 mean annual temperature is slightly warmer than MIS 9, and much warmer than MIS 7 in northern Spain. MIS 5 is not represented in the Gran Dolina sequence.

4. Post-MBE interglacials had lower rainfalls than pre-MBE interglacials, resulting in the increasing development of open dry environments on the Iberian Peninsula. This is in accordance with the increase in the presence of dry-terrain small mammals in the Gran Dolina sequence after the MBE, as well as with the turnover documented in large mammal communities toward herbivores better adapted to arid conditions.

ACKNOWLEDGMENTS

We thank Ellen Thomas (Yale University) and three anonymous reviewers for comments that improved the manuscript. The Atapuerca excavation team helped with the extraction, sieving, and washing of sediments each year. The excavation campaigns and the sorting of material were supported by the Junta de Castilla y León, the Fundación Atapuerca, the INAEM Instituto Aragonés de Empleo), MICINN (Ministerio de Ciencia e Innovación) projects CGL2006-13532-C03-02 and CGL2009-12703-C03-01/02/03, and the University of Zaragoza. López-García has been supported by a postdoctoral grant from the Juan de la Cierva Subprogram (JCI-2009-04026), with the financial sponsorship of the former Spanish Ministry of Science and Innovation. This paper is also part of CGL2009-7896/BTE, SGR2009-188, and SGR2009-324.

REFERENCES CITED

Becquey, S., and Gersonde, R., 2002, Past hydrographic and climatic changes in the Subantarctic Zone of the South Atlantic—The Pleistocene record from ODP Site 1090: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 182, p. 221–239, doi:10.1016/S0031-0182(01)00497-7.

Bennàsar Serra, M.L., 2010, Estudio tafonómico de los micromamíferos de los yacimientos del Pleistoceno Inferior de los yacimientos de Gran Dolina y Sima del Elefante. (Atapuerca, Burgos, Spain) [Ph.D. thesis]: Tarragona, Universitat Rovira i Virgili, 602 p.

Berger, G.W., Pérez-González, A., Carbonell, E., Arsuaga, J.L., Bermúdez de Castro, J.-M., and Ku, T.-L., 2008, Luminescence chronology of cave sediments at the Atapuerca paleoanthropological site, Spain: Journal of Human Evolution, v. 55, p. 300–311, doi:10.1016/j.jhevol.2008.02.012.

Blain, H.-A., 2005, Contribution de la Paléoherpétofaune (Amphibia et Squamata) à la connaissance de l'évolution du climat et du paysage du Pliocène supérieur au Pléistocène moyen d'Espagne [Ph.D. thesis]: Paris, Muséum National d'Histoire Naturelle, 402 p.

Blain, H.-A., Bailon, S., and Cuenca-Bescós, G., 2008, The early-middle Pleistocene palaeoenvironmental change based on the squamate reptile and amphibian proxies at the Gran Dolina site, Atapuerca, Spain: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 261, p. 177–192, doi:10.1016/j.palaeo.2008.01.015.

Blain, H.-A., Bailon, S., Cuenca-Bescos, G., Arsuaga, J.L., Bermúdez de Castro, J.M., and Carbonell, E., 2009, Long-term climate record inferred from early-middle Pleistocene amphibian and squamate reptile assemblages at the Gran Dolina Cave, Atapuerca, Spain: Journal of Human Evolution, v. 56, p. 55–65, doi:10.1016/j.jhevol.2008.08.020.

Candy, I., Coope, G.R., Lee, J.R., Parfitt, S.A., Preece, R.C., Rose, J., and Schreve, D.C., 2010, Pronounced warmth during early middle Pleistocene interglacials: Investigating the Mid-Brunhes Event in the British terrestrial sequence: Earth-Science Reviews, v. 103, p. 183–196, doi:10.1016/j.earscirev.2010.09.007.

Cuenca-Bescós, G., and García, N., 2007, Biostratigraphic succession of the early and middle Pleistocene mammal faunas of the Atapuerca cave sites (Burgos, Spain): Courier Forschunginstitut Senckenberg, v. 259, p. 99–110.

Cuenca-Bescós, G., Rofes, J., and García-Pimienta, J., 2005, Environmental change across the Early-Middle Pleistocene transition: Small mammalian evidence from the Trinchera Dolina cave, Atapuerca, Spain, *in* Head, M.J., and Gibbard, P.L., eds., Early-Middle Pleistocene transitions: The land-ocean evidence: Geological Society of London Special Publication 247, p. 277–286, doi:10.1144/GSL.SP.2005.247.01.16.

Cuenca-Bescós, G., Rofes, J., López-García, J.M., Blain, H.-A., De Marfá, R.J., Galindo-Pellicena, M.A., Bennàsar-Serra, M.L., Melero-Rubio, M., Arsuaga, J.L., Bermúdez de Castro, J.M., and Carbonell, E., 2010, Biochronology of Spanish Quaternary small vertebrate faunas: Quaternary International, v. 212, p. 109–119, doi:10.1016/j.quaint.2009.06.007.

Cuenca-Bescós, G., Melero-Rubio, M., Rofes, J., Arsuaga, J.L., Martínez, I., Blain, H.-A., López-García, J.M., Carbonell, E., and Bermúdez de Castro, J.M., 2011, The Early-Middle Pleistocene environmental and climatic change and the human expansion in Western Europe: A case study with small vertebrates (Gran Dolina, Atapuerca, Spain): Journal of Human Evolution, v. 60, p. 481–491, doi:10.1016/j.jhevol.2010.04.002.

EPICA community members, 2004, Eight glacial cycles from an Antarctic ice core: Nature, v. 429, p. 623–628, doi:10.1038/nature02599.

Falguères, C., Bahain, J.-J., Yokoyama, Y., Bischoff, J.L., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., and Dolo, J.M., 2001, Datations par RPE et U-Th des sites pléistocènes d'Atapuerca: Sima de los Huesos, Trinchera Dolina et Trinchera Galería. Bilan géochronologique: L'Anthropologie, v. 105, p. 71–81, doi:10.1016/S0003-5521(01)80006-6.

Font Tullot, I., 1983, Atlas Climatico de España: Madrid, Spain, Ministerio de Transportes, Turismo y Communicaciones, Instituto Nacional de Meteorologia, 43 plates.

Font Tullot, I., 2000, Climatología de España y Portugal: Salamanca, Spain, Ediciones Universidad de Salamanca, 422 p.

Green, C.P., Branch, N.P., Coope, G.R., Field, M.H., Keen, D.H., Wells, J.M., Schwenninger, J.L., Preece, R.C., Schreve, D.C., Canti, M.G., and Gleed-Owen, C.P., 2006, Marine Isotope Stage 9 environments of fluvial deposits at Hackney, north London, UK: Quaternary Science Reviews, v. 25, p. 89–113, doi:10.1016/j.quascirev.2004.10.011.

Jouzel, J., and 31 others, 2007, Orbital and millennial Antarctic climate variability over the past 800,000 years: Science, v. 317, p. 793–796, doi:10.1126/science.1141038.

Lisiecki, L.E., and Raymo, M.E., 2005, A Pliocene–Pleistocene stack of 57 globally-distributed benthic $\delta^{18}O$ records: Paleoceanography, v. 20, PA1003, doi:10.1029/2004PA001071.

Masson-Delmotte, V., and 17 others, 2010, EPICA Dome C record of glacial and interglacial intensities: Quaternary Science Reviews, v. 29, p. 113–128, doi:10.1016/j.quascirev.2009.09.030.

Moreno García, D., 2011, Datation par ESR de quartz optiquement blanchis (ESR-OB) de la région de Atapuerca (Burgos, Espagne). Application au site préhistorique de Gran Dolina (contexte karstique) et aux systèmes fluviatiles quaternaires de l'Arlanzón et l'Arlanza [Ph.D. thesis]: Tarragona, Universitat Rovira i Virgili and Paris, Muséum National d'Histoire Naturelle, 304 p.

Pleguezuelos, J.M., Márquez, M., and Lizana, M., eds., 2004, Atlas y libro rojo de los anfibios y reptiles de España: Madrid, Spain, Asociación Herpetologica Española, Dirección General de Conservación de la Naturaleza, 584 p.

Rodríguez, J., and 26 others, 2011, One million years of cultural evolution in a stable environment at Atapuerca (Burgos, Spain): Quaternary Science Reviews, v. 30, p. 1396–1412, doi:10.1016/j.quascirev.2010.02.021.

Sanderson, M.G., Hemming, D.L., and Betts, R.A., 2011, Regional temperature and precipitation changes under high-end (≥4°C) global warming: Royal Society of London Philosophical Transactions, ser. A, v. 369, p. 85–98, doi:10.1098/rsta.2010.0283.

Tzedakis, P.C., Hooghiemstra, H., and Pälike, H., 2006, The last 1.35 million years at Tenaghi Philippon: Revised chronostratigraphy and long-term vegetation trends: Quaternary Science Reviews, v. 25, p. 3416–3430, doi:10.1016/j.quascirev.2006.09.002.

Tzedakis, P.C., Raynouad, D., McManus, J.F., Berger, A., Brovkin, V., and Kiefer, T., 2009, Interglacial diversity: Nature Geoscience, v. 2, p. 751–755, doi:10.1038/ngeo660.

Winograd, I.J., Landwehr, J.M., Ludwig, K.R., Coplen, T.B., and Riggs, A.C., 1997, Duration and structure of the past four interglaciations: Quaternary Research, v. 48, p. 141–154, doi:10.1006/qres.1997.1918.

Yin, Q.Z., and Berger, A., 2010, Insolation and CO_2 contribution to the interglacial climate before and after the Mid-Brunhes Event: Nature Geoscience, v. 3, p. 243–246, doi:10.1038/ngeo771.

Manuscript received 19 March 2012
Revised manuscript received 12 May 2012
Manuscript accepted 16 May 2012

Printed in USA