



Ecological transitions – But for whom? A perspective from the Pleistocene

Clive Finlayson^{a,b,*}, Antonio Monclova^c, José S. Carrión^d, Darren A. Fa^a, Geraldine Finlayson^a, Joaquín Rodríguez-Vidal^e, Elena Fierro^d, Santiago Fernández^d, Marco Bernal-Gómez^a, Francisco Giles-Pacheco^a

^a The Gibraltar Museum, 18-20 Bomb House Lane, Gibraltar

^b Department of Social Sciences, University of Toronto, Canada

^c Area de Prehistoria, Universidad de Cádiz, Spain

^d Departamento de Biología Vegetal, Facultad de Biología, 30100, Campus de Espinardo, Universidad de Murcia, Spain

^e Departamento de Geodinámica y Paleontología, Universidad de Huelva, Campus del Carmen, 21071 Huelva, Spain

ARTICLE INFO

Article history:

Received 22 December 2010

Received in revised form 5 April 2011

Accepted 7 April 2011

Available online 14 April 2011

Keywords:

Extinction

Faunal turnovers

Palaeobiogeography

Palaeoecology

Quaternary

Pleistocene

Europe

Palaeartic

ABSTRACT

This paper deals with the so-called Middle Pleistocene revolution, that is, the transition between the Early and Middle Pleistocene between 1.2 and 0.5 million years ago. Our knowledge about biotic changes during this transition has been so far largely based on studies of large mammals. Here we address the issue whether all faunal groups were equally affected. Three datasets have been used: (a) European large mammals present in the Middle and Late Pleistocene, (b) European fossil bird species recorded from the Early, Middle and Late Pleistocene of Europe, and (c) present-day birds currently classified in subfamilies that contain at least one Palaeartic representative species. Each species was allocated to all those geographical areas, climates, habitats in which it is present today; migratory status was also recorded. These datasets serve to undertake a biochronological analysis of mammal and bird groups, thus establishing patterns and processes of extinction and survival at the genus and species levels. The end of the Middle Pleistocene appears to have been a significant boundary in respect of herbivorous mammals, which suffered considerable depletion. In contrast, most genera and species of European birds in the Middle Pleistocene survived into the Late Pleistocene, even to the present day. Furthermore, at least 58% of the Middle–Pleistocene bird species were already present in the Early Pleistocene record. The most successful survivors in the Palaeartic Pleistocene were species from genera that had been the most climatically-tolerant during the late Cenozoic, usually from speciose and widely-distributed genera. We conclude that major transitions in Earth history have leant largely on biochronology and the perceived turnovers of faunas. Boundaries have usually depended heavily on changes to specific taxa of organisms. In this paper we show that what may appear as epic boundaries are largely scale- and taxon-dependent. Their usefulness must therefore be open to question. Here we advocate an individualistic and taxon specific approach in understanding the major ecological changes that have marked the history of organisms.

© 2011 Elsevier B.V. All rights reserved.

1. Introduction

The transition between the Early and Middle Pleistocene between 1.2 and 0.5 million years ago (Ma), sometimes known as the Middle–Pleistocene revolution, is recognised as a major event in Earth history. High amplitude 100 thousand year (ka) climate cycles replaced low-amplitude 41 ka cycles and there was a significant build-up of global ice volume after 940 ka (Head and Gibbard, 2005). Such drastic changes appear to have been accompanied by significant restructuring of the Palaeartic and other mammalian faunas (van den Bergh et al., 2001; Markova, 2005, 2007; O'Regan et al., 2005; Kahlke et al., 2007; Palombo,

2007; Arribas et al., 2009). During the Pleistocene the emergence of new species and the disappearance of others occurred at a similar rate although there has been the generalised view that there was an overall decline in species diversity through the Middle and Late Pleistocene (Stuart, 1991). Thus the Middle Pleistocene appears to be a long period of transition in the Palaeartic, between the relatively warm old world of the Pliocene and Early Pleistocene and the new ice world of the Late Pleistocene (Finlayson, 2009).

The Middle Pleistocene world clearly did not come to an abrupt end with the onset of the Late Pleistocene. New steppe-tundra mammals were replacing the established warm savannah ones during the Middle Pleistocene but the process continued into the Late Pleistocene up to MIS 3 (Stewart, 2005) and even later (Stuart et al., 2004). What does appear to have changed is the almost total halt of appearance of new species to replace the old ones (Stuart, 1991). Long evolutionary trajectories, such

* Corresponding author at: The Gibraltar Museum, 18-20 Bomb House Lane, Gibraltar. Tel.: +350 200 74289; fax: +350 200 79158.

E-mail address: jcfinlay@gibraltar.gi (C. Finlayson).

- Mayr, G., 2000. Tiny hoopoe-like birds from the Middle Eocene of Messel (Germany). *The Auk* 117, 964–970.
- Mayr, G., 2005. The Palaeogene fossil record of birds in Europe. *Biological Reviews* 80, 515–542.
- Mayr, G., 2006. First fossil skull of a Palaeogene representative of the Pici (woodpeckers and allies) and its evolutionary implications. *Ibis* 148, 824–827.
- Mlikovsky, J., 2002. Cenozoic Birds of the World. Part 1: Europe. Ninox Press, Prague.
- Moigne, A.M., Heriech-Briki, D., Quiles, J., Lacombat, F., Rivals, F., Testu, A., 2004. Fauna of the Mediterranean Middle Pleistocene site of La Caune de L'Arago (Tautavel, Pyrénées-Orientales, France). 18th International Senckenberg Conference 2004. Weimar, Deutschland.
- O'Regan, H.J., Bishop, L.C., Lamb, A., Elton, S., Turner, A., 2005. Large mammal turnover in Africa and the Levant between 1.0 and 0.5 Ma. *Geological Society of London, Special Publications* 247, 231–249.
- Orlando, L., Leonard, J.A., Thenot, A., Vincent Laudet, V., Guerin, C., Hänni, C., 2003. Ancient DNA analysis reveals woolly rhino evolutionary relationships. *Molecular Phylogenetics and Evolution* 28, 485–499.
- Palombo, M.R., 2007. The Early to Middle Pleistocene "faunal revolution". *Quaternary international* 167–168 (Suppl.), 314.
- Pasitschniak-Arts, M., Larivière, S., 1995. *Gulo gulo*. *Mammalian Species* 499, 1–10.
- Pérez, T., Albornoz, J., Domínguez, A., 2002. Phylogeography of chamois (*Rupicapra spp.*) inferred from microsatellites. *Molecular Phylogenetics and Evolution* 25, 524–534.
- Petronio, C., 1995. Note on the taxonomy of Pleistocene Hippopotamuses. *Ibex J.M.E.* 3, 53–55.
- Pidancier, N., Jordan, S., Luikart, G., Taberlet, P., 2006. Evolutionary history of the genus *Capra* (Mammalia, Artiodactyla): discordance between mitochondrial DNA and Y-chromosome phylogenies. *Molecular Phylogenetics and Evolution* 40, 739–749.
- Pushkina, D., 2007. The Pleistocene easternmost distribution in Eurasia of the species associated with the Eemian *Palaeoloxodon antiquus* assemblage. *Mammal Review* 37, 224–245.
- Rivals, F., 2006. Découverte de *Capra caucasica* et d'*Hemitragus cedrensis* (Mammalia, Bovidae) dans les niveaux du Pléistocène supérieur de la Caune de l'Arago (Tautavel, France): implication biochronologique dans le contexte du Bassin Méditerranéen. *Geobios* 39, 85–102.
- Rivals, F., Schulz, E., Kaiser, T.M., 2009. Late and middle Pleistocene ungulates dietary diversity in Western Europe indicate variations of Neanderthal paleoenvironments through time and space. *Quaternary Science Reviews* 28, 3388–3400.
- Schreve, D.C., 2001a. Mammalian evidence from Middle Pleistocene fluvial sequences for complex environmental change at oxygen isotope substage level. *Quaternary International* 79, 65–74.
- Schreve, D.C., 2001b. Differentiation of the British late Middle Pleistocene interglacials: the evidence from mammalian biostratigraphy. *Quaternary Science Reviews* 20, 1693–1705.
- Sempere, A.J., Sokolov, V.E., Danilkin, A.A., 1996. *Capreolus capreolus*. *Mammalian Species* 538, 1–9.
- Sommer, R.S., Fahlke, J.M., Schmölcke, U., Benecke, N., Zachos, F.E., 2009. Quaternary history of the European roe deer *Capreolus capreolus*. *Mammal Reviews* 39, 1–16.
- Sotnikova, M., Nikolskiy, P., 2006. Systematic position of the cave lion *Panthera spelaea* (Goldfuss) based on cranial and dental characters. *Quaternary International* 142–143, 218–228.
- Stewart, J.R., 2005. The ecology and adaptation of Neanderthals during the non-analogue environment of oxygen isotope stage 3. *Quaternary International* 137, 35–46.
- Stuart, A.J., 1991. Mammalian extinctions in the Late Pleistocene of Northern Eurasia and North America. *Biological Reviews* 66, 453–562.
- Stuart, A.J., Lister, A.M., 2001. The mammalian faunas of Pakefield/ Kessingland and Corton, Suffolk, UK: evidence for a new temperate episode in the British early Middle Pleistocene. *Quaternary Science Reviews* 20, 1677–1692.
- Stuart, A.J., Lister, A.M., 2007. Patterns of Late Quaternary megafaunal extinctions in Europe and northern Asia. *Courier Forschungsinstitut Senckenberg* 259, 287–297.
- Stuart, A.J., Kosintsev, P.A., Higham, T.F.G., Lister, A.M., 2004. Pleistocene to Holocene extinction dynamics in giant deer and woolly mammoth. *Nature* 431, 684–689.
- Turner, A., 2009. The evolution of the guild of large Carnivora of the British Isles during the Middle and Late Pleistocene. *Journal of Quaternary Science* 24, 991–1005.
- Tyrberg, T., 1998. Pleistocene Birds of the Palearctic: A Catalogue. Publications Nuttall Ornithol. Club 27. Cambridge, Massachusetts.
- Tyrberg, T., 2008. <http://web.telia.com/~u11502098/pleistocene.html>.
- Valli, M.F., 2010. Dispersion of the genus *Procapreolus* and the relationships between *Procapreolus cusanus* and the roe deer (*Capreolus*). *Quaternary International* 212, 80–85.
- van den Bergh, G.D., de Vos, J., Sondaar, P.Y., 2001. The Late Quaternary palaeogeography of mammal evolution in the Indonesian Archipelago. *Palaeogeography, Palaeoclimatology, Palaeoecology* 17, 384–408.
- van der Made, J., Tong, H.W., 2008. Phylogeny of the giant deer with palmate brow tines *Megaloceros* from west and *Sinomegaceros* from east Eurasia. *Quaternary International* 179, 135–162.
- Vrba, E.S., 1993. Turnover-pulses, the Red Queen, and related topics. *American Journal of Science* 293-A, 418–452.