The *Homo* habitat niche: using the avian fossil record to depict ecological characteristics of Palaeolithic Eurasian hominins

Clive Finlayson [a,b,*], José Carrión [c], Kimberly Brown [a], Geraldine Finlayson [a], Antonio Sánchez-Marco [d], Darren Fa [a], Joaquín Rodríguez-Vidal [e], Santiago Fernández [c], Elena Fierro [c], 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 at Scarborough, Canada
[c] Department of Plant Biology, University of Murcia, Spain
[d] Catalan Institut of Paleontology, Cerdanyola del Vallès, Spain
[e] Department of Geodynamics and Palaeontology, University of Huelva, Spain

ARTICLE INFO

ABSTRACT

Although hardly applied to human palaeoecology, bird fossils offer a unique opportunity for quantitative studies of the hominin habitat. Here we reconstruct the *Homo* habitat niche across a large area of the Palaearctic, based on a database of avian fauna for Pleistocene sites. Our results reveal a striking association between *Homo* and habitat mosaics. A mix of open savannah-type woodland, wetlands and rocky habitats emerges as the predominant combination occupied by *Homo* across a wide geographical area, from the earliest populations of the Lower Palaeolithic to the latest hunter-gatherer communities of the Upper Palaeolithic. This observation is in keeping with the view that such landscapes have had long standing selective value for hominins.

1. Introduction

Descriptions of habitat occupation by *Homo* in prehistory abound (Carrión et al., 2003; Finlayson, 2004; Ségalen et al., 2007; Zhu et al., 2008; Joordens et al., 2009). The importance of savannah grasslands across large areas of the Afrotropical and the Palaearctic regions has been highlighted as central to the early hominin dispersals (de Menocal and Bloemendal, 1995; Dennell, 2003; Jacobs, 2004; Dennell and Roebroeks, 2005; Finlayson, 2009). Most habitat descriptions available are qualitative, however, and are based on general interpretations using plant and mammal fossils as indicators. Birds have rarely been used in such studies even though, through the specific habitat requirements of many species, they are excellent for this purpose. Exceptions are quantitative reconstructions and models that have used birds as

indicators (Sánchez-Marco, 1999; Finlayson and Giles-Pacheco, 2000; Finlayson, 2006; Louchart et al., 2010). Sites of Pleistocene *Homo* occupation with associated bird fossils are relatively abundant and geographically and temporally widespread (Sánchez-Marco, 2004a, b; Louchart, 2008), offering an opportunity for a quantitative study of the *Homo* habitat niche across the Pleistocene over a wide geographical area. Here we quantitatively reconstruct the *Homo* habitat niche across a large area of the Palaearctic, based on a database of Pleistocene sites in order to test whether there is a common habitat pattern in *Homo* across a wide geographical area and a long time range.

2. Methods

A database of 79 Palaearctic *Homo* occupation Pleistocene sites with associated bird fossils was compiled (Supplementary Data). No judgment was made regarding the nature of the bird fossil accumulations in each site, in particular if they had been the product of human activity. Instead, the presence of a bird species in a site of

* Corresponding author. 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).

Table 1

Frequency of representation of major habitat categories in Palaeolithic sites. The figures represent the number of times in which taxa representative of each habitat category were represented in sites. Lower Palaeolithic (LP) sites $n = 15$; Middle Palaeolithic (MP) $n = 25$; Upper Palaeolithic (UP) $n = 44$. Wetland includes lakes, lagoons, marshes. Coastal includes the intertidal fringe and shallow coastal waters. Marine refers to pelagic. Rocky are cliffs and other vegetation-free habitats with a rock substrate. Terrestrial includes all terrestrial vegetated habitats including forests, shrublands, savannahs, grasslands, etc. Human habitat categories follow Finlayson (2006). The three lower rows indicate the mean ($\pm$2.standard deviations) number of bird species found in Palaeolithic sites by habitat category.

Period	Wetland	Wetland %	Coastal	Coastal %	Marine	Marine %	Rocky	Rocky %	Terrestrial	Terrestrial %
LP	15	100	6	40	2	13.3	14	93.3	14	93.3
MP	22	88	7	28	7	28	23	92	25	100
UP	37	84.1	16	36.4	8	18.2	44	100	44	100

Period N° species	Wetland	Coastal	Marine	Rocky	Terrestrial
LP	9.07 ± 4.11	1.6 ± 1.38	0.27 ± 0.34	6.53 ± 2.6	26.33 ± 10.46
MP	6.2 ± 2.53	2.72 ± 2.46	1.16 ± 0.98	10.52 ± 3.22	25.48 ± 12.95
UP	5.52 ± 2.07	2.41 ± 1.17	0.73 ± 0.55	6.66 ± 1.43	19.06 ± 3.27

Homo occupation was used to infer the presence of habitats typical of that bird species in the vicinity of the site. Where a number of species indicated a similar habitat, then confidence of the presence of that habitat close to the site increased. 467 bird species currently occurring in the Palaearctic (Cramp, 1977–1994) were therefore listed in the database. 213 (45.6%) of these were recorded in the 14 Lower Palaeolithic sites identified, 229 (49%) in 25 Middle Palaeolithic sites, and 250 (53.5%) in 40 Upper Palaeolithic sites. The mean number of bird species per site was 44 in the Lower Palaeolithic; 34 in the Middle Palaeolithic; and 27 in the Upper Palaeolithic. In all, 333 (71.3%) of the species currently regularly occurring in the western Palaearctic were represented. Each bird species was allocated into five broad habitat categories (Table 1). Where species were known to occupy more than one habitat category they were assigned to each. The difference in number of sites from Lower (14) to Upper (40) Palaeolithic is not considered large enough to distort the results. They reflect a taphonomic temporal preservation differential and possible sampling intensity.

The database compiled is a combination of many sites covered by excavations over a distended period. Our results, however, are based on positive data. Thus it is the presence of species which indicates particular conditions. The fact that some species may have been missed in older excavations does not negate our conclusions.

3. Overall trends in habitat occupation

An inspection of the frequency of representation of major habitat categories in Palaeolithic sites supports the view of a close association between human occupation sites and wetlands, including lakes, lagoons and marshes (Table 1). Wetlands are rich sources of a wide range of animal and plant resources (Finlayson and Moser, 1991) and fresh water. They appear to be central to the *Homo* habitat niche. Coastal sites (e.g. intertidal fringes and shallow coastal waters) are also of high significance (Table 1). The lower proportion of coastal species represented is a reflection, as expected, of the absence of coastal habitats in sites that are inland. Many are also now submerged (Bailey et al., 2008). The presence of marine species, being especially pronounced in the Middle and Upper Palaeolithic, may reflect a tendency towards the exploitation of the sea as a resource by humans. A number of the marine species recorded, however, breed in rocky habitats so that their presence

may simply be indicative of the existence of coastal breeding habitats. The high proportion of rocky habitat (Table 1) is not unexpected as many of the sites in the database are caves. Rocky habitats may therefore be over represented in the sample. The habitat categories used reflect the generalised preferences of birds. They are, however, not mutually exclusive. Thus, for example, the presence of a coastal bird which exploits the rocky shore would be scored as rocky and coastal.

Almost all sites record bird species that are indicators of terrestrial vegetated habitats, including forests, woodlands, savannahs, grasslands, etc. (Table 1). This indicates that the presence of other habitats should be seen in the context of mosaics or ecotones in proximity to terrestrial vegetation. This observation is confirmed when the number of habitats represented per site is examined (Table 2). The results clearly show that single habitat sites have been ignored by humans throughout the Palaeolithic. Very few two-habitat sites are recorded and the majority of sites are situated close to between three and five habitats (Table 2). Thus *Homo* throughout the Palaeolithic seems to have exploited habitat mosaics that have included a mix of terrestrial and aquatic habitats.

4. Shifting strategies in habitat occupation

In order to test whether the association of hominins with bird indicators of particular habitats was related to the natural presence of bird species, we compared the presence of birds in hominin sites against a database of 401 avian Pleistocene palaeontological sites that had no human occupation (Brown, 2009). As we were unable to attribute the sites to a specific time period, we compared the hominin sites from each cultural period directly with this database. In all three cases there was a positive relationship between the presence of bird species in the palaeontological and archaeological sites (Fig. 1). The strength of the relationship increased significantly, however, from the Lower through to the Upper Palaeolithic. This implies that the cultural sequence Lower–Middle–Upper Palaeolithic involved a reduction in the habitat specificity of humans. Thus, in the Upper Palaeolithic, the presence of bird species in hominin sites most closely resembled a random pattern of presence depending on natural availability. It was least so in the Lower Palaeolithic, suggesting greater habitat specificity then.

Table 2

Number of habitats represented in Palaeolithic sites referred to in Table 1 and Supplementary Data. LP = Lower Palaeolithic, MP = Middle Palaeolithic, UP = Upper Palaeolithic.

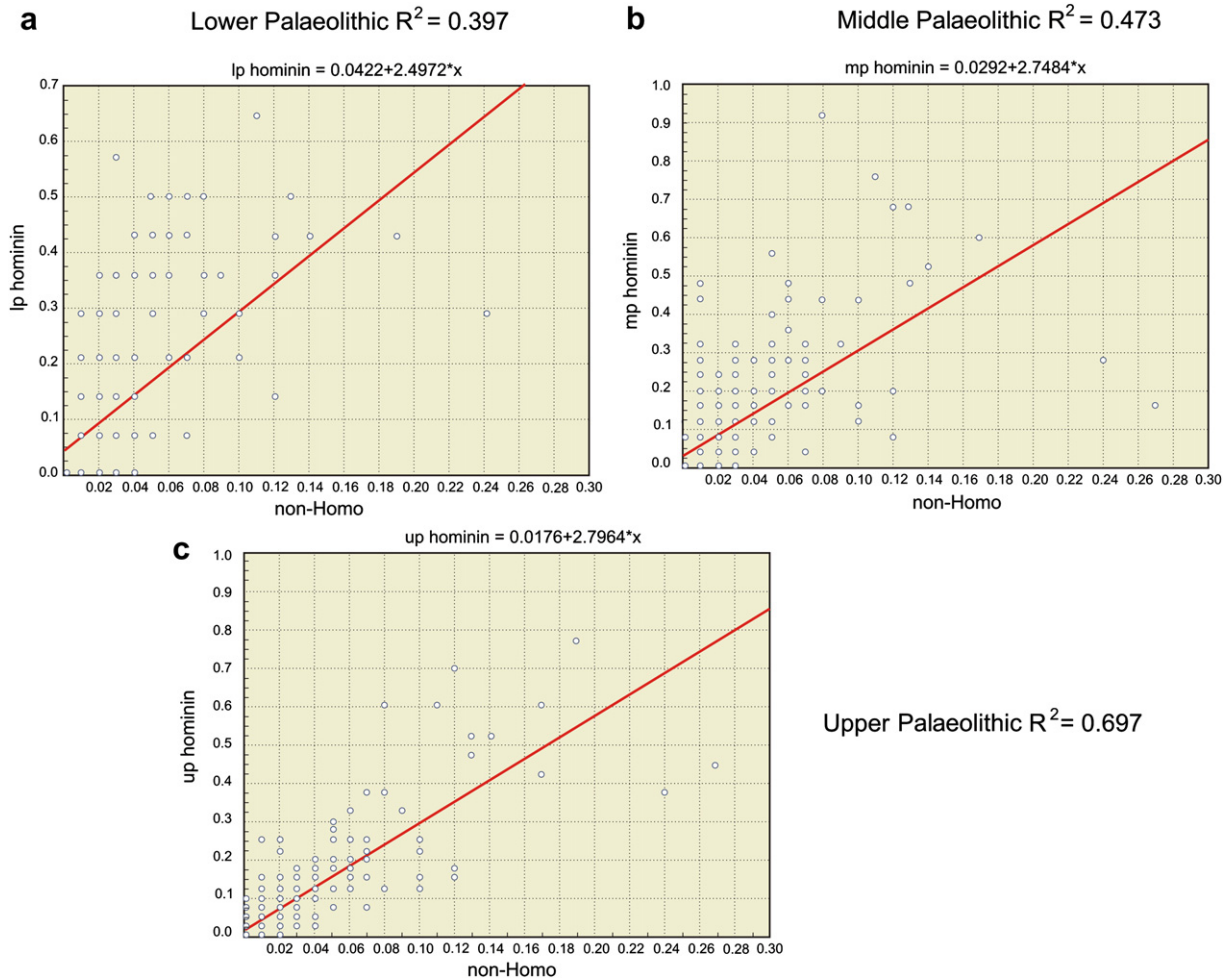| Period	1 habitat	% 1 habitat	2 habitats	% 2 habitats	3 habitats	% 3 habitats	4 habitats	% 4 habitats	5 habitats	% 5 habitats
LP	1	6.25	0	0	8	50	4	26.67	2	12.5
MP	0	0	4	16	14	56	1	4	6	24
UP	0	0	7	15.91	20	45.46	10	22.73	7	15.91

Fig. 1. Distribution (frequency of occurrence in sites) of birds in hominin sites and in palaeontological sites without hominins.

From the regression equations we estimated the deviation in the frequency of presence of each bird species in hominin sites from that predicted by each equation. We expressed the deviation as a percentage of the expected. Positive deviations suggested that the habitat associated with that particular species was found in hominin sites at a greater frequency than expected by random rate of encounter. In order to broaden the terrestrial fraction in Table 1, we separated terrestrial species into: (a) woodland (i.e. trees and shrubs present); (b) shrubland (shrubs, no trees); (c) savannah (trees, no shrubs); (d) open temperate (no trees nor shrubs, mostly

Table 3
Distribution of bird species occurring more frequently than expected in hominin sites by habitat indicated. One bird species may represent more than one habitat category. LP Lower Palaeolithic; MP Middle Palaeolithic; UP Upper Palaeolithic. Percentages refer to degree of deviation from expectation predicted by the regression equations in Fig. 1.

|	Pelagic	Coastal	Wetland	Tundra	Steppe-Grassland	Savannah	Shrubland	Woodland	Rocky
LP <1%	1	11	18	11	2	4	3	6	6
LP 1−10%	3	18	33	8	13	25	8	20	16
LP 11−25%		2	5	3	8	14	5	10	14
LP 26−50%			2		1	5	2	4	1
LP >50%									
LP total	4	31	58	22	24	48	18	40	37
MP <1%								2	
MP 1−10%	12	32	37	17	12	28	7	19	37
MP 11−25%		3	1	3	2	13	2	7	10
MP 26−50%					2	1	1		6
MP >50%									1
MP total	12	35	38	20	16	42	10	28	54
UP <1%	4	19	23	12	5	7	2	10	12
UP 1−10%	8	27	29	17	7	19	8	17	28
UP 11−25%			1		3	5	1	1	6
UP 26−50%					0	1			3
UP >50%									
UP total	12	46	53	29	15	32	11	28	49
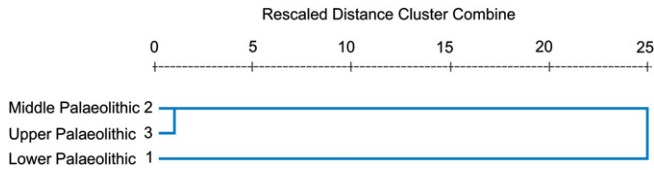
Fig. 2. Cluster Analysis of Lower, Middle and Upper Palaeolithic sites by species differentials from expected. The dendrogram is using average linkage (between groups).

grassland or steppe); (e) open cold (no trees, no shrubs, mostly tundra or montane). The intensity of the signal provided by each species was measured in accordance with the degree of deviation from the expected. Frequencies greater than 26% suggest a strong signal for the habitat, 11–25% a reduced signal, and so on. In this way we are able to assess habitat occupation by weighting the strength of the signal from each bird species. Our results suggest that hominins have reduced their main habitat range from the

Lower Palaeolithic (6 habitats with frequencies >26%), through the Middle Palaeolithic (4 habitats) to the Upper Palaeolithic (2 habitats) (Table 3). Savannah and rocky habitats remained main habitats throughout: savannah decreased in importance, and rocky increased, with time. One way of interpreting this strong signal is that it indicates habitats permanently occupied. The next order signal (11–25%) might suggest less frequently occupied, perhaps seasonal, habitats. In the Lower Palaeolithic coastal and tundra habitats fit in this category. In the Middle Palaeolithic they are joined by wetlands and woodland that were first order habitats in the Lower Palaeolithic. In the Upper Palaeolithic coastal and tundra habitats are reduced in rank, further supporting the idea of increased habitat specificity. The third order signal (1–10%) could be interpreted as indicating occupation of ephemeral habitats. If so, the marine habitat remains in this category throughout and coastal and tundra are added in the Upper Palaeolithic.

If our interpretation is correct and bearing in mind that the Upper Palaeolithic pattern is that which resembles most closely the
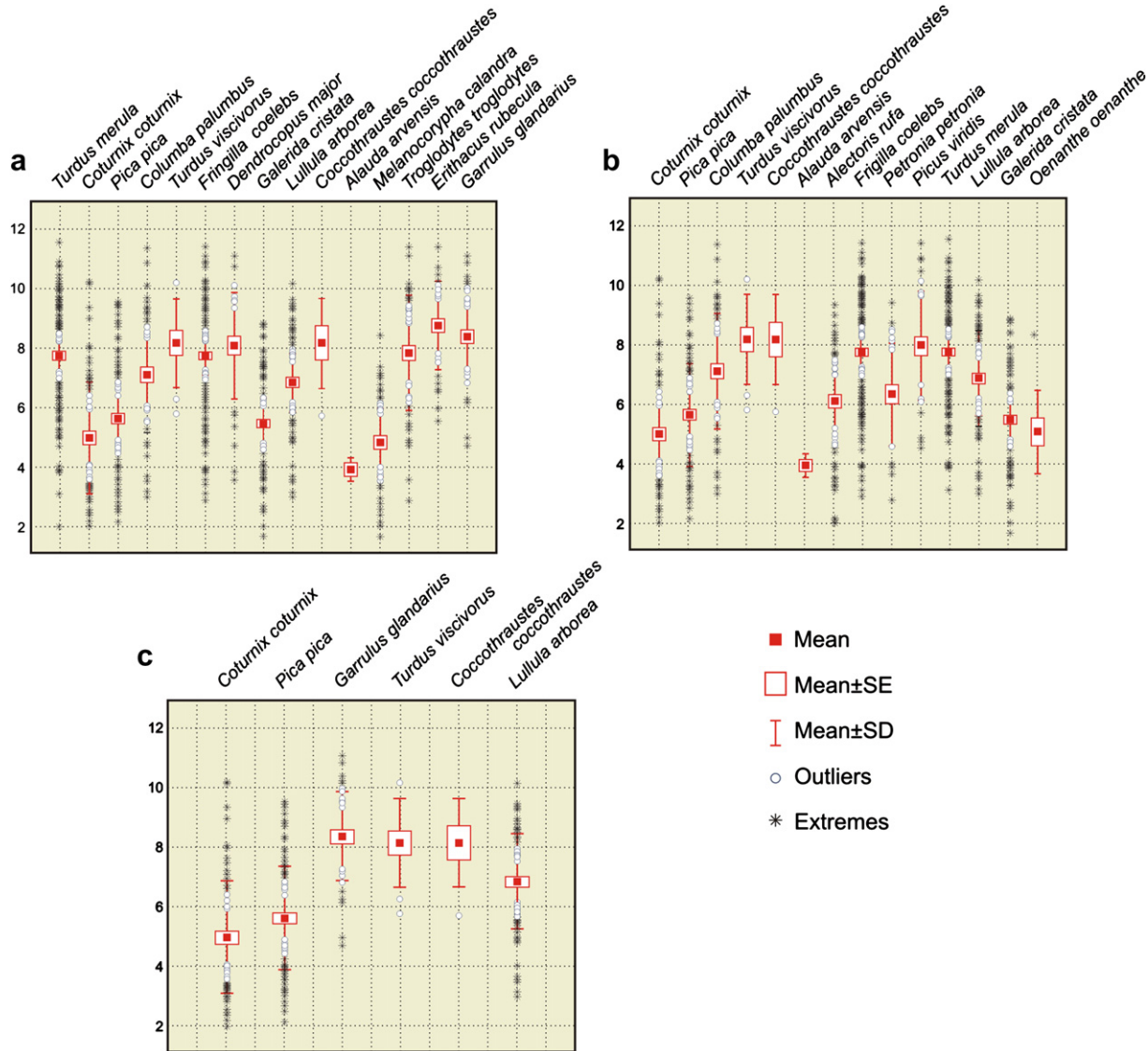

Fig. 3. Foliage Height Diversity (FHD) of 1-ha plots associated with terrestrial bird species found in frequencies of over 25% in Palaeolithic sites. Species are ranked from most frequent (left) to least frequent (right). (a) Lower Palaeolithic, (b) Middle Palaeolithic, (c) Upper Palaeolithic. The y-axis range indicates the total range of values sampled for all bird species. High FHDs are associated with dense, well vertically-structured, forests. Low FHDs are associated with unstructured uni-dimensional habitats, e.g. grasslands. Bird species names are along the top of (a)–(c).

pattern of habitat availability, our results indicate that there must have been significant reduction in woodland and shrubland habitats at this time. In effect the strongest signal of permanent habitat is rocky, which might be linked to an increased use of caves with climatic deterioration. The results also suggest a shifting strategy towards intense seasonal or sporadic habitat occupation such as tundra and the coast. This shift appears to have also involved wetlands, woodland and probably savannah from the Middle Palaeolithic onwards. Our results are in keeping with a progressive climatic deterioration and increased seasonality in the Palaearctic during the Pleistocene (Finlayson and Carrión, 2007). When all bird species are compared together, the Lower Palaeolithic stands out as the most distinctive period (Fig. 2).

5. Ecological structure of *Homo* landscapes

In order to further quantify the vegetation within the terrestrial fraction, we analysed a database of vegetation structure associated with breeding bird territories collected over a wide geographical area of the Iberian Peninsula (Finlayson, 1999; Finlayson, 2006). The database consisted of 860 1-ha plots within which all breeding

birds and a range of vegetation structural variables were recorded (Finlayson, 2006). We then applied the results for the terrestrial bird species in the fossil sites in order to model the associated vegetation structure. For the purpose of this study we focused on two measures of vegetation structure. The first is Foliage Height Diversity (FHD) (MacArthur and MacArthur, 1961). In each 1-ha plot sampled, percentage vegetation cover by structural layers − grass, shrub and tree layers − was measured. Each layer was subdivided into three subcategories according to height reached above the ground (Fig. 3). This resulted in nine vertical vegetation categories. Simpson's Index (Simpson, 1949) was used to calculate diversity for each 1-ha plot. A high diversity reflected woodland with a rich shrub and grass layer. At the other extreme, a low diversity reflected treeless and shrubless grassland. In Fig. 3, FHD is plotted for all sites in which bird species (for which data were available) found in the fossil record in frequencies greater than 25%. Only species fully associated with terrestrial vegetation have been included. Thus, for example, birds known to forage in terrestrial vegetation habitats but which nest or roost in rocky habitats were excluded as we could not separate their presence in fossil sites as being indicative of terrestrial vegetation or rocky habitats. It is clear
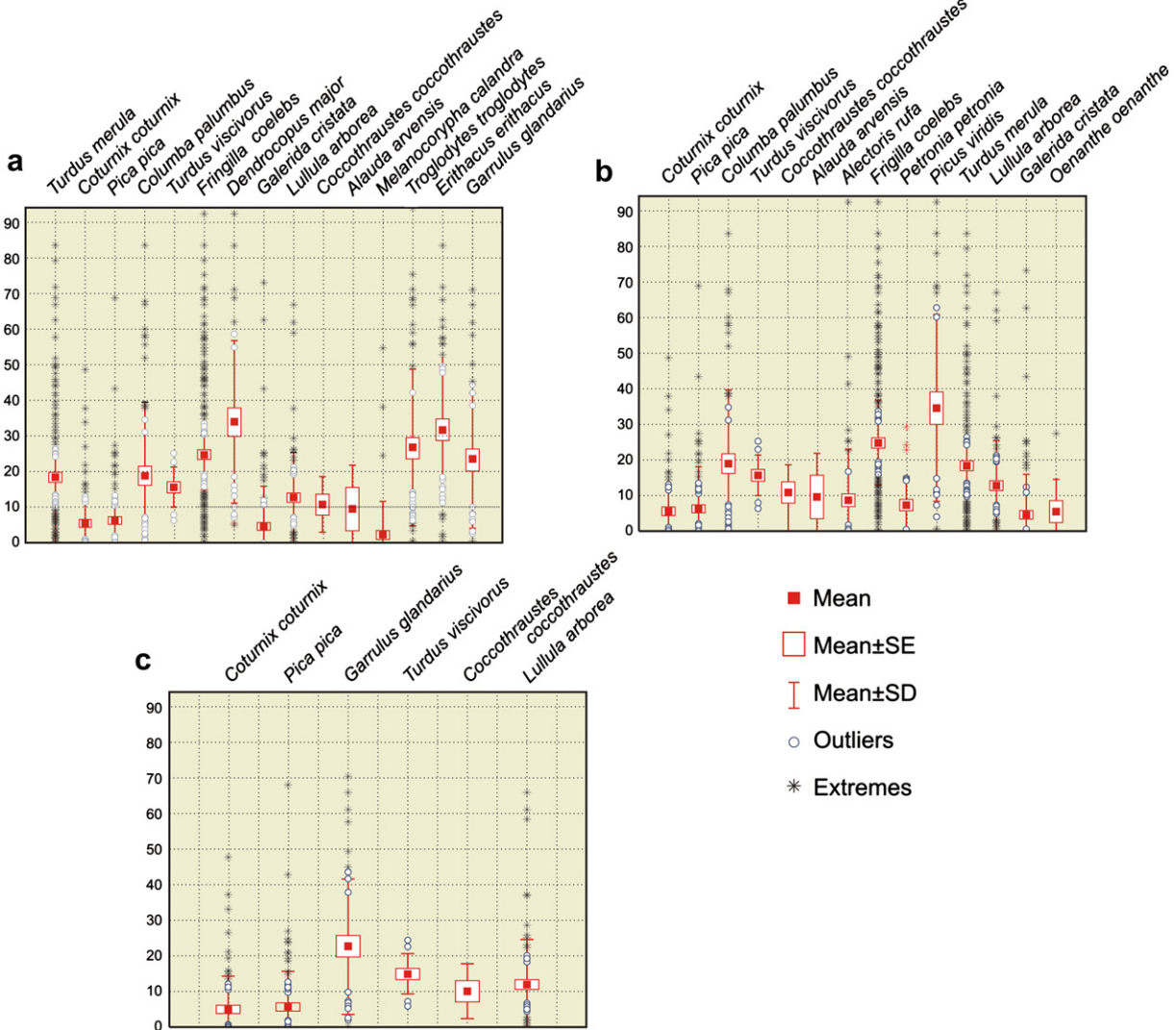

Fig. 4. Tree Density (trees/ha) of 1-ha plots associated with terrestrial bird species found in frequencies of over 25% in Palaeolithic sites. Species are ranked from most frequent (left) to least frequent (right). (d) Lower Palaeolithic; (e) Middle Palaeolithic; (f) Upper Palaeolithic. The *y*-axis range indicates the total range of values sampled for all bird species. Bird species names are along the top of (a)–(c).
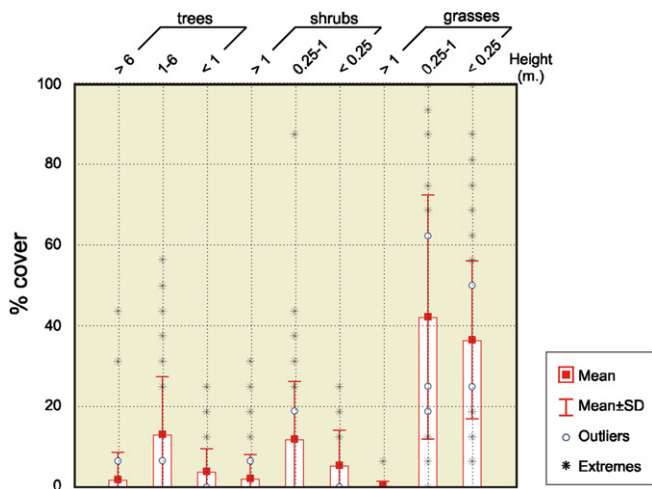
Fig. 5. Habitat Structure of 1-ha plots associated with Quail, *Coturnix coturnix*. Percentage cover is represented in relation with the height (m) of trees (categories: >6, 1–6, and <1), shrubs (categories: >1, 0.25–1, and <0.25) and grasses (categories >1, 0.25–1, and <0.25).

from this analysis that the birds associated with Palaeolithic human sites are species with FHD values that are intermediate between those of dense forest or fully open habitats. Fig. 3 indicates shrubland and savannah-type habitats and habitat mosaics that incorporate patches of woodland within open vegetation.

The second measure used was tree density, the number of trees per 1-ha plot (Fig. 4). The results support the vegetation cover data. All species found in Palaeolithic sites are characteristic of lightly wooded landscapes. Trees are usually present but generally at low densities, mean values typically ranging from under 10 trees/ha to approximately 35 trees/ha.

Put together these results confirm in a striking manner the close association that humans have had with terrestrial habitats that are structurally intermediate between dense forest and open plains and which we refer to in a broad sense as "wooded savannahs". These landscapes appear in the form of vegetation mosaics that are ecologically diverse. Furthermore, Palaeolithic sites regularly incorporate wetlands, coastal and rocky habitats which, together with the wooded savannahs would have formed ecologically rich ecotones or mosaics (Kerr and Packer, 1997).

The terrestrial bird species that occurred in highest frequency in Palaeolithic sites was the Quail *Coturnix coturnix*: 40% of Lower Palaeolithic sites; 76% Middle Palaeolithic; and 45% Upper Palaeolithic. Fig. 5 shows the habitat structure associated with this species. Quails occupy treeless and shrubless habitats, or habitats with low tree and shrub densities (mean < 20% cover). On the other hand, these habitats are associated with a high cover of grasses (Fig. 5). These results confirm the observations made so far about the Palaeolithic *Homo* habitat. Open habitats with a rich grass cover, that would have attracted herbivorous mammals, and the presence of scattered trees and shrubs, that would have provided cover for hunters, appear ideally suited for the *Homo* ambush hunting strategy (Finlayson, 2004, 2009; Finlayson and Carrión, 2007).

6. Concluding remarks and implications in human palaeogeography

The results described above strongly point towards a *Homo* habitat occupation pattern in the Palaearctic, which closely matches one which, in the Afrotropical region, would be associated with a mix of wooded savannah, wetland and rocky habitats. The consistency of the observed pattern across a wide geographical area and over the entire period of *Homo* occupation indicates a specific and clear association between *Homo* and, ecologically rich, semi-open savannah-type ecotonal and mosaic landscapes in which wetlands, coastal and rocky habitats were a regular and prominent feature.

Interestingly, this is a feature that appears to transcend species boundaries and is a property of the genus. It is a property with origins that could even predate the genus *Homo* itself. The degree of forest cover in the habitat occupied by early hominins has been the subject of recent controversy (White et al., 2009; WoldeGabriel et al., 2009). Most descriptions of the habitat of early hominins in Africa, however, support the idea of occupation of habitat mosaics put forward in this paper. Examples include *Sahelanthropus tchadensis* at 7–6 Ma (Brunet et al., 2002); *Ardipithecus ramidus* at 4.5–4.3 Ma (WoldeGabriel et al., 2001; Cerling et al., 2010); *Australopithecus anamensis* at 4.2–3.9 Ma (Leakey et al., 1995; White, 2003); *Australopithecus afarensis* at 3.6–2.9 Ma (Radosevich et al., 1992; Bonnefille et al., 2004; Haile-Selassie et al., 2010); *Australopithecus robustus* (de Ruiter et al., 2009), *Kenyanthropus platyops* at 3.5–3.2 Ma (Leakey et al., 2001); *Australopithecus bahrelghazali* at 3.5–3 Ma (Brunet et al., 1996); *Australopithecus garhi* at 2.7–2.3 Ma (De Heinzelin et al., 1999); and *Homo habilis* at 2.33 Ma (Wood and Strait, 2004).

It has been also suggested, supported by isotopic evidence from a number of African sites, that C_4 grassland expansion provided more complex and heterogeneous habitats with expanded opportunities for early hominins (Ségalen et al., 2007). Stable isotope analyses of pedogenic carbonates and ungulate enamel, as well as faunal data from 2 Ma archaeological occurrences in the Oldowan Kanjera site of southern Kenya, show that early *Homo* was active in a broad spectrum of environments, from open grassland to riparian forests (Plummer et al., 2009).

In this context, the close association found here of *Homo* with mosaic environments allows us to infer the probable mechanism of dispersals out-of-Africa through tracking habitats and habitat mosaics that approached those in the centre of origin. Descriptions of habitats associated with early *Homo* dispersing from tropical Africa are in keeping with the results reported here: Dmanisi, Georgia, at 1.8 Ma (Messager et al., 2011); Ain Hanech and El-Kherba, Algeria, at 1.95–1.77 Ma (Sahnouni et al., 2011); Ubeidiya, Israel, at 1.6–1.2 Ma (Bar-Yosef and Belmaker, 2011); the Solo Basin at Sangiran, Indonesia, at 1.60/1.02 Ma (Bettis et al., 2009); Zhokhoudian, China, at 780–680 ka (Ciochon, 2009); and Atapuerca, Spain, between 1.2 and 0.5 Ma (Rodríguez et al., 2011). The occurrence of such habitats and landscapes along coastal areas may explain the regular use of coastal corridors of dispersal by *Homo* (Lahr and Foley, 1994; Bailey et al., 2008; Carrión et al., 2008; Finlayson, 2008; Bailey and King, 2011). Routes inland are likely to have followed river networks and savannah-type corridors.

Within this generalised habitat preference, our results also show how climatic and ecological changes in the Palaearctic from the Lower to the Upper Palaeolithic shifted the habitat occupation pattern towards one of exploiting habitats by availability and of intense but punctual occupation of seasonal and ephemeral habitats. Thus, emphasis on particular habitats and the intensity with which they were occupied, embedded in a broad pattern of specific habitat occupation of savannahs, wetland and rocky mosaics, characterised the Palaeolithic of the Palaearctic region. Thus the selective advantages derived from occupation of such habitats in the Afrotropics (Orians, 1998) were carried into the Palaearctic as part of the human biological package.

The exploitation of the treeless plains of the Palaearctic and also the Nearctic, a feature of some populations of *Homo sapiens* in the Upper Palaeolithic (Finlayson and Carrión, 2007; Finlayson, 2009),

would only have been possible with the development of projectile technology, which would permit hunting away from cover, and portable tool kits that would allow long-range mobility. Such a development awaited a taxon that had been exploiting semi-open landscape mosaics, and using savannah corridors (Dennell and Roebroeks, 2005; Dennell, 2009), since the very origins of the genus and probably long before that.

Acknowledgements

Appendix. Supplementary material

Supplementary data associated with this article can be found in on-line version at doi:10.1016/j.quascirev.2011.01.010.

References

Bailey, G., King, G.C.P., 2011. Dynamic landscapes and human dispersal patterns: tectonics, coastlines, and the reconstruction of human habitats. Quaternary Science Reviews 30, 1533–1553.

Bailey, G., Carrión, J.S., Fa, D.A., Finlayson, C., Finlayson, G., Rodríguez-Vidal, J., 2008. The coastal shelf of the Mediterranean and beyond: corridor and refugium for human populations in the Pleistocene. Quaternary Science Reviews 27, 2095–2099.

Bar-Yosef, O., Belmaker, M., 2011. Early and middle Pleistocene faunal and hominins dispersals through Southwestern Asia. Quaternary Science Reviews 30, 1318–1337.

Bettis, E.A., Milius, A.K., Carpenter, S.J., Larick, R., Zaim, Y., Rizal, Y., Ciochon, R.L., Tassier-Surine, S.A., Murray, D., Suminto Bronto, S., 2009. Way out of Africa: early Pleistocene paleoenvironments inhabited by *Homo erectus* in Sangiran, Java. Journal of Human Evolution 56, 11–24.

Bonnefille, R., Potts, R., Chalié, F., Jolly, D., Peyron, O., 2004. High-resolution vegetation and climate change associated with Pliocene *Australopithecus afarensis*. Proceedings of the National Academy of Sciences, USA 101, 12125–12129.

Brown, K., 2009. The middle to Upper Palaeolithic transition in an Iberian refugium. PhD Thesis, University of Cambridge, Cambridge.

Brunet, M., Beauvilain, A., Coppens, Y., Heintz, E., Moutaye, A.H.E., Pilbeam, D., 1996. *Australopithecus bahrelghazali* une nouvelle espèce d'hominidé ancien de la région de Koro Toro (Tchad). Comptes Rendus Academie Sciences Paris 322, 907–913.

Brunet, M., Guy, F., Pilbeam, D., Mackaye, H.T., Likius, A., Ahounta, D., Beauvilain, A., Blondel, C., Bocherens, H., Boisserie, J.-R., De Bonis, L., Coppens, Y., Dejax, J., Denys, C., Duringer, Ph, Eisenmann, V., Fanone, G., Fronty, P., Geraads, D., Lehmann, T., Lihoreau, F., Louchart, A., Mahamat, A., Merceron, G., Mouchelin, G., Otero, O., Peláez Campomanes, P., Ponce de León, M.S., Rage, J.-C., Sapanet, M., Schuster, M., Sudre, J., Tassy, P., Valentin, X., Vignaud, P., Viriot, L., Zazzo, A., Zollikofer, C.P.E., 2002. A new hominid from the Upper Miocene of Chad, Central Africa. Nature 418, 145–151.

Carrión, J.S., Finlayson, C., Finlayson, G., Fernández, S., Allué, E., López-Sáez, A., López-García, P., Fuentes, N., Gil, G., González-Sampériz, P., 2008. A coastal reservoir of biodiversity for Upper Pleistocene human populations. Quaternary Science Reviews 27, 2118–2135.

Carrión, J.S., Yll, E.I., Walker, M.J., Legaz, A., Chaín, C., López, A., 2003. Glacial refugia of temperate, Mediterranean and Ibero North African flora in south-eastern Spain: new evidence from cave pollen at two Neanderthal man sites. Global Ecology and Biogeography 12, 119–129.

Cerling, T.E., Levin, N.E., Quade, J., Kingston, J.D., Klein, R.G., Brown, F.H., 2010. Comment on the paleoenvironment of *Ardipithecus ramidus*. Science 328, 1105D.

Ciochon, R., 2009. The mystery ape of Pleistocene Asia. Nature 459, 910–911.

Cramp, S. (Ed.), 1977–1994, Handbook of the Birds of Europe the Middle East and North Africa: The Birds of the Western Palaearctic, Vols. 1–9. Oxford University Press, Oxford.

De Heinzelin, J., Clark, J.D., White, T., Hart, W., Renne, P., WoldeGabriel, G., Beyene, Y., Vrba, E., 1999. Environment and behavior of 2.5-million-year-old Bouri hominids. Science 284, 625–629.

de Menocal, P.B., Bloemendal, J., 1995. Plio-Pleistocene Subtropical African Climate Variability and the Paleoenvironment of Hominid Evolution: a Combined Data-model Approach. In: Vrba, E., Denton, G., Burckle, L., Partridge, T. (Eds.), Paleoclimate and Evolution with Emphasis on Human Origins. Yale University Press, New Haven, pp. 262–288.

de Ruiter, D.J., Pickering, R., Steininger, C.M., Kramers, J.D., Hancox, P.J., Churchill, S.E., Berger, L.R., Backwell, L., 2009. New *Australopithecus robustus*

fossils and associated U–Pb dates from Cooper's cave (Gauteng, south Africa). Journal of Human Evolution 56, 497–513.

Dennell, R., 2003. Dispersal and colonisation, long and short chronologies: how continuous is the Early Pleistocene record for hominids outside East Africa? Journal of Human Evolution 45, 421–440.

Dennell, R., 2009. The Palaeolithic settlement of Asia. Cambridge World Archaeology, Cambridge University Press, Cambridge.

Dennell, R.W., Roebroeks, W., 2005. An Asian perspective on early human dispersal from Africa. Nature 438, 1099–1104.

Finlayson, C., 1999. Species abundances across spatial scales. Science 283, 1979.

Finlayson, C., 2004. Neanderthals and Modern Humans. Cambridge University Press, Cambridge.

Finlayson, G., 2006. Climate, vegetation and biodiversity. A multiscale study of the south of the Iberian Peninsula. PhD Thesis, Anglia Ruskin University, Cambridge.

Finlayson, C., 2008. The importance of coastal areas in the survival of Neanderthals populations during the Late Pleistocene. Quaternary Science Reviews 27, 2246–2252.

Finlayson, C., 2009. The Humans Who Went Extinct. Oxford University Press, New York.

Finlayson, C., Carrión, J.S., 2007. Rapid ecological turnover and its impact on Neanderthal and other human populations. Trends in Ecology and Evolution 22, 213–222.

Finlayson, C., Giles-Pacheco, F., 2000. The Southern Iberian Peninsula in the Late Pleistocene: geography, ecology and human occupation. In: Stringer, C.B., Barton, R.N.E., Finlayson, C. (Eds.), Neanderthals on the Edge. Oxbow Books, Oxford, pp. 139–154.

Finlayson, M., Moser, M., 1991. Wetlands. Facts on File. Oxford.

Haile-Selassie, Y., Latimer, B.M., Alene, M., Deino, A.L., Gibert, L., Melillo, S.M., Saylor, B.Z., Scott, G.R., Lovejoy, C.O., 2010. An early *Australopithecus afarensis* postcranium from Woranso-Mille, Ethiopia. Proceedings of the National Academy of Sciences, USA 107, 12121–12126.

Jacobs, B.F., 2004. Palaeobotanical studies from tropical Africa: relevance to the evolution of forest, woodland and savannah biomes. Philosophical Transactions of the Royal Society B: Biological Sciences 359, 1573–1583.

Joordens, J.C.A., Wesselingh, F.P., de Vos, J., Vonhof, H.B., Kroon, D., 2009. Relevance of aquatic environments for hominins: a case study from Trinil (Java, Indonesia). Journal of Human Evolution 57, 656–671.

Kerr, J.T., Packer, L., 1997. Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. Nature 385, 252–254.

Lahr, M.M., Foley, R.A., 1994. Multiple dispersals and modern human origins. Evolutionary Anthropology 3, 48–60.

Leakey, M.G., Feibel, C.S., McDougall, I., Walker, A., 1995. New four-million-year-old hominid species from Kanapoi and Allia Bay, Kenya. Nature 376, 565–571.

Leakey, M.G., Spoor, F., Brown, F.H., Gatogo, P.N., Kiarie, C., Leakey, L.N., McDougall, I., 2001. New hominin genus from eastern Africa shows diverse middle Pliocene lineages. Nature 410, 433–440.

Louchart, A., 2008. Fossil birds of the Kibish Formation. Journal of Human Evolution 55, 513–520.

Louchart, A., Wesselman, H., Blumenschine, R.J., Hlusko, L.J., Njau, J.K., Black, M.T., Asnake, M., White, T.D., 2010. Taphonomic, avian, and small-vertebrate indicators of *Ardipithecus ramidus* habitat. Science 326 66e1-66e4.

MacArthur, R.H., MacArthur, J.W., 1961. On bird species diversity. Ecology 42, 594–598.

Messager, E., Lebreton, V., Marquer, L., Russo-Ermolli, E., Orain, R., Renault-Miskovsky, J., Lordkipanidze, D., Despriée, J., Peretto, C., Arzarello, M., 2011. Palaeoenvironments of early hominins in temperate and Mediterranean Eurasia: new palaeobotanical data from Palaeolithic key-sites and synchronous natural sequences. Quaternary Science Reviews 30, 1439–1447.

Orians, G., 1998. Human behavioral ecology: 140 years without Darwin is too long. Bulletin of the Ecological Society of America 79, 15–28.

Plummer, T.W., Ditchfield, P.W., Bishop, L.C., Kingston, J.D., Ferraro, J.V., Braun, D.R., Hertel, F., Potts, R., 2009. Oldest evidence of toolmaking hominins in a grassland-dominated ecosystem. PLoS ONE 4, e7199. doi:10.1371/journal.pone.0007199.

Radosevich, S.C., Retallack, G.J., Taieb, M., 1992. Reassessment of the paleoenvironment and preservation of hominid fossils from Hadar, Ethiopia. American Journal of Physical Anthropology 87, 15–27.

Rodríguez, J., Burjachs, F., Cuenca-Bescós, G., García, N., Van der Made, J., Pérez González, A., Blain, H.-A., Expósito, I., López-García, J.M., García Antón, M., Allué, E., Cáceres, I., Huguet, R., Mosquera, M., Ollé, A., Rosell, J., Parés, J.M., Rodríguez, X.P., Díez, C., Rofes, J., Sala, R., Saladié, P., Vallverdú, J., Bennasar, M.L., Blasco, R., Bermúdez de Castro, J.M., Carbonell, E., 2011. One million years of cultural evolution in a stable environment at Atapuerca (Burgos, Spain). Quaternary Science Reviews 30, 1396–1412.

Sánchez-Marco, A., 2004a. Birds from layers III and IV of Gorham's cave (Gibraltar), in press.

Sánchez-Marco, A., 2004b. Avian zoogeographic patterns during the Quaternary in the Mediterranean region and paleoclimatic interpretation. Ardeola 51, 91–132.

Ségalen, L., Lee-Thorp, J.A., Cerling, Th, 2007. Timing of C$_4$ grass expansion across sub-Saharan Africa. Journal of Human Evolution 53, 549–559.

Sahnouni, M., Van der Made, J., Everett, M., 2011. Ecological background to Plio-Pleistocene hominin occupation in North Africa: the vertebrate faunas from Ain Boucherit, Ain Hanech and El-Kherba, and paleosol stable-carbon-isotope studies from El-Kherba, Algeria. Quaternary Science Reviews 30, 1303–1317.

Simpson, E.H., 1949. Measurement of diversity. Nature 163, 688.

White, T.D., 2003. Early hominids. Diversity or distortion? Science 299, 1994–1997.

White, T.D., Asfaw, B., Beyene, Y., Haile-Selassie, Y., Owen, Lovejoy C., Suwa, G., WoldeGabriel, G., 2009. *Ardipithecus ramidus* and the paleobiology of early hominids. Science 326, 75–86.

WoldeGabriel, G., Haile, S.Y., Renne, P.R., Hart, W.K., Ambrose, S.H., Asfaw, B., Heiken, G., White, T., 2001. Geology and palaeontology of the Late Miocene middle Awash valley, Afar rift, Ethiopia. Nature 412, 175–178.

WoldeGabriel, G., Ambrose, S.H., Barboni, D., Bonnefille, R., Bremond, L., Currie, B., DeGusta, D., Hart, W.K., Murray, A.M., Renne, P.R., Jolly-Saad, M.C., Stewart, K.M., White, T.D., 2009. The geological, isotopic, botanical, invertebrate, and lower vertebrate surroundings of *Ardipithecus ramidus*. Science 326 65e1-65e5.

Wood, B., Strait, D., 2004. Patterns of resource use in early *Homo* and *Paranthropus*. Journal of Human Evolution 46, 119–162.

Zhu, R.X., Potts, R., Pan, Y.X., Yao, H.T., Lü, L.Q., Zhao, X., Gao, X., Chen, L.W., Gao, F., Deng, C.L., 2008. Early evidence of the genus *Homo* in East Asia. Journal of Human Evolution 55, 1075–1085.