MIDDLE PLEISTOCENE MORTALITY PATTERN AND FERTILITY: THE CASE OF THE ATAPUERCA HOMINIDS (SIMA DE LOS HUESOS SITE, BURGOS, SPAIN)

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Bermúdez de Castro, J.M. and Díez, J.C. 1995. Middle Pleistocene mortality pattern and fertility: the case of the Atapuerca hominids (Sima de los Huesos site, Burgos, Spain). *Revista Española de Paleontología*, **10** (2), 259-272. ISSN 0213-6937.

ABSTRACT

The Sima de los Huesos cave site in the Sierra de Atapuerca, northern Spain, has yielded up to the 1994 season a large sample of more than one thousand human fossil remains belonging to at least 32 individuals, which represent a same European Middle Pleistocene biological population. The elaboration of the survivorship curve of this hominid group has emphasized a high mortality among adolescents and young adults, a low older adult mortality and a longevity probably non greater than 40 years. This pattern of mortality resembles to that of other European Middle and early Upper Pleistocene hominids, and is quite different from that observed in recent foraging human groups. Consideration of the main determinants of human fertility suggests that the average interval between successful births in Atapuerca, and probably in all European Middle Pleistocene populations, was shorter than that of living hunting and gathering peoples, and that the age at menarche and nubility was earlier than those of living girls. Implications of these findings for the yet unresolved question of body sexual dimorphism in the Middle Pleistocene populations are discussed as well.

Keywords: Middle Pleistocene, Atapuerca, paleodemography, fertility, sexual dimorphism.

RESUMEN

El yacimiento de la Sima de los Huesos de la Sierra de Atapuerca (Burgos) ha proporcionado hasta la campaña de 1994 una muestra de más de un millar de restos fósiles humanos pertenecientes a un mínimo de 32 individuos, que representan a una misma población biológica del Pleistoceno Medio. La elaboración de la curva de supervivencia de este grupo de homínidos ha puesto en evidencia una alta mortalidad entre los adolescentes y los adultos jóvenes, que disminuye considerablemente el grupo de adultos mayores de 25 años, y una longevidad probablemente no superior a 40 años. Este patrón de mortalidad es similar al de otros homínidos del Pleistoceno Medio y Superior de Europa, pero difiere del patrón que caracteriza a los grupos de cazadores-recolectores actuales. La estimación de la tasa total de fertilidad en una población con el patrón de mortalidad de Atapuerca indica que el mantenimiento de la estabilidad numérica de dicha población requiere un intervalo promedio de nacimientos inferior al observado en grupos de cazadores-recolectores actuales, así como una edad de menarquia y nubilidad inferiores a las de las poblaciones humanas modernas. Se discuten las implicaciones de los resultados para la debatida cuestión del dimorfismo sexual en el tamaño corporal de los homínidos del Pleistoceno Medio.

Palabras clave: Pleistoceno Medio, Atapuerca, paleodemografía, fertilidad, dimorfismo sexual.

INTRODUCTION

The paleodemographic studies of the pre-Holocene hominid populations run up against some difficulties, the main of which is related to the fact that the samples analyzed include fossil specimens belonging to individuals that lived in very different places and/or time periods. Furthermore, in these population samples some age groups may be under-represented due to differential preservation, while the methodological problems of obtaining an accurate age at death and sex determination are well known (Acsádi & Nemeskéri, 1970; Hassan,

https://doi.org/10.7203/sjp.24150

1981; Hillson, 1986). Thus, the construction of life tables for the Pliocene and Pleistocene hominid populations would be a very speculative exercise, or even virtually impossible. Therefore, it is hardly surprising that only a few paleoanthropologists focused their efforts in this field of research during the past decades (Weidenreich, 1943, 1951; Vallois, 1960; McKinley, 1971; Mann, 1975; Wolpoff, 1979). The analysis of the age at death of the Neandertals is particularly interesting, since it has shown a mortality pattern and a longevity different from those of the living foraging human groups (Trinkaus & Thompson, 1987; Trinkaus & Tompkins, 1990; Trinkaus, in press). This analysis has raised the scepticism of Aiello (in press) on the reliability of the age at death estimated by these authors and/or the representativeness of the fossil record concerning the survivorship of the Neandertal population. In order to shed some light to this controversy we present in this paper the new information supplied by the important hominid sample recovered from the Sima de los Huesos Middle Pleistocene cave site at Atapuerca (Arsuaga *et al.,* 1993). We will examine the pattern of mortality and longevity of this sample and we will try to relate these issues to some aspects of the biology of the Middle Pleistocene populations.

THE SIMA DE LOS HUESOS SITE

The karst of the Atapuerca Hill, near the city of Burgos (Spain) includes several filling fossiliferous deposits ranging from below the Matuyama/Bruhnes reversal up to the end of Middle Pleistocene (Aguirre *et al.*, 1990). One of these deposits fills the Sima de los Huesos (SH), and has yielded the most complete sample of Middle Pleistocene hominids yet found from one site. SH is located within the Cueva Mayor-Cueva del Silo karst system, and consists of a narrow sock-shaped crevice formed by a 13 m deep vertical duct which connects with a 10 m long inclined gallery, at the end of which there is a small blind chamber of about 17 m^2. The hominids found in SH are associated with bear bones belonging to *Ursus deningeri.* The identification of this species was based on the study of more than nine thousand fossils (Torres, 1978, 1988; Torres *et al.*, 1978). A bone breccia which includes only carnivore bones belonging to *Ursus deningeri, Panthera leo, Panthera* cf. *gombaszoegensis, Lynx pardina spelaea, Vulpes vulpes,* Canidae indet. and Mustelidae indet. (Cervera, 1992), overlays a part of the sediments which holds the human fossil assemblage. The first human remains were discovered in 1976 (Aguirre *et al.,* 1976; Aguirre & Lumley, 1977), and from 1984 to 1994 systematic excavations have yielded more than one thousand and three hundred cranial, dental and postcranial human remains. The human sample is remarkably homogeneous (Arsuaga *et al.*, 1990; Rosas, 1992; Bermúdez de Castro, 1993), thus suggesting that all the human remains could belong to individuals of a same population. A speleothem overlying the human fossils has been dated by James Bischoff of the U.S.A. Geological Survey to >300 Kyr (Arsuaga *et al.*, 1993), but during the last months an exhaustive research also conducted by J. Bischoff is being made to obtain a chronology as precise as possible of the SH hominids.

The SH bone sample is not comparable with that of other Middle Pleistocene sites. In fact, though more than eleven thousands fossil remains have been recovered up to the present from SH, there is no evidence of herbivores, thus indicating that this cavity was not a consumption site neither for carnivores nor for humans. Further, the absence of hearths, stone tools or cut-marks excludes the possibility that the human fossils derive from a camp site (Díez, 1992; Arsuaga *et al.*, 1993). The accumulation of ursids and hominid seems to be simultaneous, but its origin has been not resolved yet. The entry into SH of the human remains probably occurred by mud flows from some upper deposit (Gil *et al.*, 1987), and therefore, we hypothesize an allochtonous origin for the SH human remains. This section of the karstic system fundamentally was a hibernation site for bears, which kept other predators out the cavity. The hominids take the second place concerning the number of specimens and the number of individuals. The presence of such a big hominid sample close to an hibernation site can not be explained by the hunting activity of bears, and distinct causes have been suggested to interpret this anomalous accumulation: natural trap, catastrophic death into the cave, carnivore transport, and anthropic deposition (Aguirre, 1991/1992; Arsuaga *et al.*, 1990; and see also Aguirre, 1995).

THE ATAPUERCA HOMINID SAMPLE

Minimum number of individuals (MNI)

After finishing the 1994 excavation the SH hominid sample includes sixteen important mandibular specimens, most of which preserve teeth *in-situ*, as well as eleven smaller mandibular fragments. The sample also includes four upper maxillary fragments preserving the premolars and/or molars *in-situ.* One of these specimens (AT-405) belongs to Cranium 6, which was reconstructed from more than 40 cranial fragments (Arsuaga *et al.*, 1993). The more complete Cranium 5 also preserves some maxillary teeth *in-situ* (Arsuaga *et al.*, 1993). A total of 174 teeth were catalogued as isolated specimens: 88 mandibular teeth and 86 maxillary teeth. Only two deciduous teeth belong to this dental sample. The determination of the MNI was made from this material. Firstly, we fitted some isolated teeth into the sockets of the maxillary and mandibular remains. Next, we found some dental associations and some isolated teeth which were incompatible with each other and with the teeth of the other individuals. The criteria used for the association of specimens involved the fit of interproximal wear and continuity of occlusal wear, the similarity in size, morphology and degree of interproximal and occlusal wear, the stage of development (root maturity), the occlusal fit, and the appearance of unique features, such as the presence of severe hypoplasia scars surrounding the crown of some teeth. Using these criteria, we have estimated that at least thirty two individuals are represented in the SH hypodigm (Table 1).

Sex estimation

The estimation of the sex of the SH hominids starting from the mandibular features was made by Rosas (1992) for the specimens belonging to the individuals I, II, III, IV, VI, X, XII, XIX, XXII, XXIII and XXV (Table 1). The mandible AT-792 (individual XXVII), recovered during the 1993 excavation, and the mandible AT-950 (individual XXXI), found in 1994, shows unquestionable male and female traits respectively. The mandible AT-888, also recovered during the 1993 excavation, belongs to Cranium 5 (individual XXI) and exhibits some robustness. However, the assessment of the cranial traits allows to assign these remains to a female individual (J.L. Arsuaga, A. Gracia, and I. Martínez, personal communication). The sex of other individuals was estimated considering the pattern of size variability of the canines and postcanine teeth (Bermúdez de Castro *et al.*, 1993). The estimation of the sex from dental size coincides with that of the mandible for the individuals III, IV, VI, VII, X, XII, XIX, XXII, XXIII, XXV, and XXXI. The mandible AT-1 (individual I) is small, tough robust, and their teeth are of medium size. The mandible AT-2 (individual II) is also small, though it belongs to an adolescent who died about at the age of fourteen, and only preserves a small portion of the mandibular body. The teeth of this individual are also of medium size. The mandible AT-792 is very robust and have small premolars and intermediate molars, though the canine alveolus is large. The teeth of the mandible AT-888 are small. Therefore, in eleven of fifteen cases (73.3%), the size of the teeth corresponds to the size of the jaws, i.e. the small mandibles have also small teeth and the large mandibles have also large teeth. In three cases the estimation of the sex from the dental size could offer some difficulty, whereas in only one case the size of the mandible and the teeth are clearly uncorrelated. In short, the sex estimation from the dental size offers reasonable guarantees when the specimens are very small and large or very large. Following this criterion, we have estimated the sex of four more individuals: VIII, XIII and XX, who show large or very large teeth, and XI, who exhibit very small teeth. Thus, the sex has been estimated in a total of 19 individuals, ten of whom would be females and nine males (Table 1).

Age at death determination

In the Atapuerca hominid sample there is no suitable material to estimate the age at death of subadult individuals using the method and techniques based on dental histological observations (Bromage & Dean, 1985; Beynon, 1986; Bromage, 1987; Dean, 1987; Dean & Beynon, 1991). This and other methods (Smith, 1986; Conroy & Vannier, 1987, 1988, and see also Smith, 1991) have allowed the arising of diverse lines of evidence that converge on the conclusion that Plio-Pleistocene hominids had an ape-like dental development pattern and abbreviated growth periods relative to modern humans. In spite of the fact that some authors have questioned the reliability of these methods (Mann *et al.*, 1987, 1990a, 1990b; Mann, 1988; Simpson *et al.*, 1990; Lampl *et al.*, 1993), it is best to proceed cautiously when we investigate, for example, the age at death of the Middle Pleistocene hominids from the timing of tooth development and eruption. Interestingly, the study of the Neandertal child from Pech-de-l'Azé (Legoux, 1970), as well as Wolpoff (1979)'s observations in the Krapina hominid sample and the more recent reassessment of the age at death of the Gibraltar child from Devil's Tower by counting perikymata of the upper right central incisor (Dean *et al.*, 1986) suggest that Neandertals had slightly accelerated dental formation and eruption schedules in relation to modern humans. Furthermore, if we consider that the dental developmental events of the Middle Pleistocene populations had a certain and unknown variability, the accurate determination of the individual age at death is remarkably difficult. However, we can not give up trying to make this determination and, firstly, we ought to consider the exactness needed to obtain valid conclusions.

The traditional method of assessing dental developmental status based on modern human standards may be an approach to estimate the age at death of the Atapuerca young individuals. In order to make this estimation we have used the ranges of dental formation timing in modern humans of Scott & Symons (1974) and Gustafson & Koch (1974), as well as the mean ages of the more precise system for determining age from third molar formation obtained by Johanson (1971). When necessary, conventional radiographic observations of the Atapuerca specimens (AT-1, AT-2, AT-3, AT-75, AT-300, AT-505) were made. If Neandertals and their ancestors, the European Middle Pleistocene hominids, had dental formation and eruption schedules accelerated in relation to modern humans, then we would have obtained ages at death greater than the true ones.

In order to determine the age at death of the SH adult individuals we have employed the tooth wear based procedure developed by Miles (1963), which use as a baseline group those individuals with incompletely developed dentitions to establish criteria about rates of wear for particular teeth. The same methodology was used by Wolpoff (1979) to determine the age at death of the Krapina specimens. This author comments that a major source of inaccuracy would be the use of this procedure when the fossil samples are composed of individuals representing different populations. Fortunately, this seems to be not the case of the SH sample. The use of this method also implies the assumption that the pattern of wear is similar in all the individuals aged. However, a fairly high degree of consistency in wear pattern within populations has been

Individual	Inventory number	Tooth/Maxilla	*in-situ* Teeth	Estimated age at death	Estimated* sexe
IX	AT-90	right LdC		4 - 6	–
XXV	AT-947	left Ldm2		7 - 9	–
XVIII	AT-410	left LC		10-11	–
XXX	AT-949	right UP4		12	–
XX	AT-405 AT-820 AT-558 AT-955 AT-589 AT-809 AT-406 AT-587 AT-407 AT-821 AT-946	upper maxilla right UI2 right UC left UC right UP3 right LP3 left UM1 right UM1 left UM2 right UM2 left LM2	(P3-P4) left	13	M
XXIX	AT-41	right UP3		13	-
II	AT-2 AT-767 AT-27 AT-42 AT-162 AT-55 AT-597 AT-578 AT-603 AT-43 AT-142	mandible maxilla left UI1 right UI1 right LI1 right LI2 right LI2 left LC left LP4 left LM1 left LM2	(C-M1) right (M1-M3) left	14	M
XIV	AT-272 AT-286	right LM1 left LM1		14	–
XI	AT-148 AT-168	right LP3 right LP4		14	F
XXVIII	AT-808	left LC		15	–
XVI	AT-277	right LP4		15	–
XXIII	AT-607	mandible	(I2-M3) right (I2-P3, M1-M3) izq.	17	F
XV	AT-22 AT-101 AT-271	left LM1 right LM1 right LM2		17	–
X	AT-172 AT-141 AT-556	mandible right LM1 left LM1		17	F
III	AT-3 AT-104 AT-103 AT-67 AT-47 AT-28 AT-273	mandible left LI1 left LI2 left LC left LP3 right LP4 left LM2	left P4	18	F
XIX	AT-505 AT-604 AT-952 AT-576 AT-812 AT-815 AT-827 AT-816 AT-826	mandible mandible mandible left LM1 right UM1 right UM2 left UM2 right UM3 left UM3	(M2-M3) left right M3 right M2	18	F
XXVI	AT-30	right LM3		18	–
I	AT-1 AT-60 AT-276 AT-221 AT-580	mandible right LC left LC right LP4 left LP4	(M1-M3) right & left	18	F
XII	AT-300	mandible	(I2-M3) right	19	M
VI	AT-75	mandible	(M2-M3) left	21	F
XXIV	AT-509 AT-169	mandible left LM3		21	–
VIII	AT-15	left UM2		21	M
XXII	AT-605 AT-197 AT-282 AT-608	mandible right UI1 right LI2 left LI2	(M1-M3) right & left	22	M
XXVII	AT-772 AT-792	maxilla mandible	(P3-M2) right (P3-M2) right & (P3-M1) left	23	M
VII	AT-303a AT-23 AT-193 AT-16 AT-139 AT-46 AT-270 AT-140 AT-147 AT-21 AT-13	mandible right UP4 left UP4 left UM1 right UM1 right UM2 left UM2 left UM3 left LP4 left LM1 left LM3		24	M
XVII	AT-279 AT-823	left UP4 right UP3		25	M
XIII	AT-195 AT-145 AT-591 AT-64 AT-590 AT-9	left LI2 left LC right LC left LP3 right LP3 right LP4		26	M
XXXI	AT-950 AT-951	mandible left UM3	(M1-M3) right & left	26	F
IV	AT-250 AT-793 AT-102 AT-74 AT-14 AT-100 AT-810 AT-811	mandible mandible left LP3 left LP4 left LM1 left LM3 left UM2 right M3	left M2 right M2	27	F
XXI	AT-700 AT-888	maxilla (skull 5) mandible	(I1, M2 & M3) right (M1-M3) left (P3-M3) right & left	32	F
XXXII	AT-1130 AT-940 AT-948	maxilla right UP4 right UM3	(M1-M2) right	32	–
V	AT-11	M2 inf. izq.		35	–

* Based on dental (Bermúdez de Castro *et al.*, 1993) and mandibular evidence (Rosas, 1992)

Table 1. Estimated sexe and age at death of the individuals identified in the Atapuerca human hypodigm, with the inventory number of the dental and maxillary remains assigned to these individuals.

observed by Lavelle (1970) and Nowell (1978), whereas Trinkaus (1983) and Trinkaus & Thompson (1987) have noted that dental wear is reasonably well correlated with age in Neandertals. On the other hand, observations on high-resolution epoxy full-crown replicas of the Krapina deciduous and permanent teeth (originally collected and kindly provided by E. Trinkaus) indicates a close similarity between the Atapuerca and Krapina samples concerning the pattern and premolar and molar rates of occlusal wear. This fact evokes Trinkaus & Tompkins (1990)´s comments on Trinkaus and Wolpoff's personal observations that the patterns of permanent tooth wear appear to be surprisingly uniform across European and Near Eastern Neandertals.

For the moment there is no evidence in SH of individuals deceased during the infancy period, that is before the age of 2 (the classification of the stages in the life cycle is an adaptation from Timiras, 1972 made by Bogin, 1991, pag. 16). We have identified only one individual died during early chilhood (second to sixth year), and it is represented by the deciduous lower canine AT-90 (individual IX). This tooth had completed the

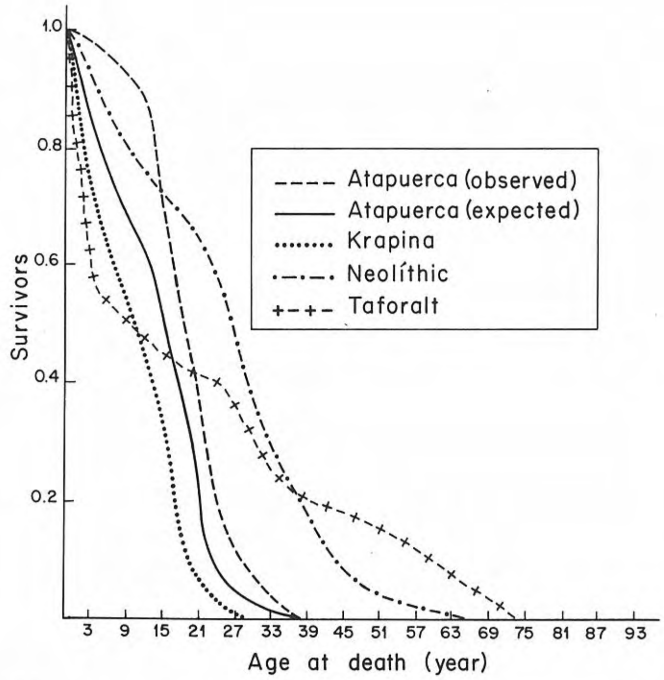

Figure 1. Survivorship curves of Atapuerca (Sima de los Huesos), Krapina, the Epipalaeolithic sample from Taforalt and a Neolithic sample from Catal Hüyük. The expected curve of Atapuerca assumes that 35% of the individuals died before age twelve. Data from Wolpoff (1979), Ferembach (1962: in Acsádi and Nemeskeri, 1970) and Angel (1971: in Hassan, 1981). The 0-3 age group at Krapina includes 27 individuals (25% of the sample): see text and note 2 for further details. The determination of the age at death of the Taforalt adult individuals was based on the closure of the cranial sutures, and on the dental wear.

growth of the root, which does not present signs or resorption, and exhibits a conspicuous wear on the distal part of the occlusal surface, where the dentine is exposed in a band about 1 mm wide. The age at death of the individual IX cannot be estimated accurately, but probably he/she died between the ages of 4 and 6 years. One individual died during middle childhood (ages 7 to 10), and it is represented by the deciduous lower second molar AT-947 (individual XXX). This tooth is severily worn and shows some signs of resorption at the apical one third of the roots. This individual probably died between the ages of 7 and 9 years. There is evidence that one individual (XVIII) deceased during later childhood (Table 1). The permanent lower canine AT-410, that did not erupt, represents this individual. The root of this tooth measures 9 mm on the buccal face and 10 mm on the lingual face. Tough there are clear evidences of breakage *post-mortem* at the distal margin of the developing root, this margin is thined down, thus indicating that the root did not grow beyond half of its definitive length, and an age at death of around 11 years for this individual. Therefore, we have determined that only a 9.4 per cent of the SH hominids deceased before reaching the age of twelve. This fact is illustrated by the survivorship curve showed in figure 1, and the frequency distribution of the age at death showed in figure 2.

The survivorship curve of the SH hominids falls sharply between the ages of 12 and 20 years, since about 50% of the SH individuals died during adolescence, before reaching the age of twenty (Fig. 1). The age at death of the individual XXX, who is represented by an upper fourth premolar (AT-949), has been reckoned at a twelve years because the apex of the root of this tooth remains still open. The upper second molars of the individual XX do not show interproximal distal wear facet, and the occlusal wear of these teeth does not affect the hypocone. The upper canine and the upper and lower premolars of this individual exhibit small areas of occlusal wear, and his/her age at death could be around 13 years. The same age at death may be estimated for the individual XXIX, whose upper third premolar shows an incipient occlusal wear similar to that of the upper third premolars of the individual XX. The age at death assigned to the individual II (14 years) is based on the development stage of the root of the upper third molar, which is about 2 mm long, and on the incipient occlusal wear of the lower canines and premolars, whose root had completed growth. The age at death of the individuals XIV and XI probably was also 14 years, because of the similarity of occlusal wear of their preserved teeth with that of the teeth of the individual II. The occlusal wear of the lower canine AT-808 (individual XXVIII) and the lower fourth premolar AT-277 (individual XVI) was slightly greater than that of the same teeth in the individual II, and we have estimated that the age at death of these individuals was around 15 years.

The third molars of the mandible AT-607 (individual XXIII) were start erupting (gingival eruption). The roots of this tooth are 10 mm long. This represents the 55-60% of the total length of the root, i.e. the third molars reached the stage E of the Johanson (1971) classification, and the age at death of this individual occurred when he/she was 17 years old. The occlusal wear of the lower molars of the individuals X and XV is similar to that of the molars of AT-607, and they probably died about 17 years as well. The eruption of the lower third molars of the individuals I, XXV, XII and XIX was completed. These teeth exhibit an incipient occlusal wear, and they were at the stage F of the Johanson classification, that is, the root of these teeth is practically fully developed, with only the apex still not closed (18-19 years). The lower second molar of the individual III shows an incipient interproximal distal wear facet, which indicates that the third molar was just erupted. The occlusal wear of the teeth of this individual is similar to that of the individual I, XXV and XIX, and slightly lesser than that of the individual XII. The third molar AT-30 (individual XXVI) lost the apical half of the roots, and it is not possible to know their stage of development. The occlusal wear of this tooth is similar to that of the individual I, and the age at death of the individual XXVI probably was also around 18 years.

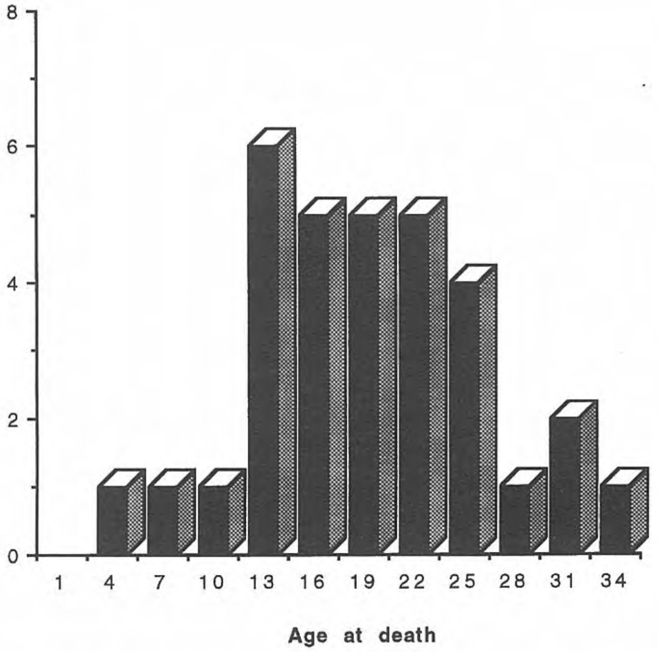

Figure 2. Frequency distribution of the age at death of the individuals identified in the Atapuerca (SH) fossil hominid sample. Three years intervals.

The age at death of the remaining individuals of the SH hypodigm was greater than 20 years, but only three of these individuals lived beyond 30 years. The oldest individual at SH is around 35, and it is very reasonable to consider that the maximum life span in the Atapuerca population was not greater than 40 years. This estimation is based on the high rate of wear observed in the anterior teeth. In fact, the evidence (Cranium 5, individual XXI) indicates that incisal wear may remove practically the whole of the incisor crowns by the early thirties. This could implicate important pathological consequences derived from exposure of the dental pulp, such as alveolar abscesses and premortem tooth loss, with the consequent decrease in the survival capacity of the individuals. Furthermore, the available European Middle Pleistocene hominid fossil record does not give any indication that people lived more than 40 years. Only two specimens from this period show an occlusal wear similar or slightly greater than that of individual V from SH: the Arago 2 mandible, and the specimen AT-76-T1H, a small mandibular fragment recovered from the TG complex, a Middle Pleistocene site also located in the Sierra de Atapuerca not far from SH (Bermúdez de Castro & Rosas, 1992). Lumley & Lumley (1973) comment that the mandible Arago 2 belonged to a 40 to 55 year old female. However, these authors do not explain the methods used to estimate the age at death of this individual. If the rate of occlusal wear in the postcanine teeth was similar in both the Arago and Atapuerca populations, then the individual to whom belonged the specimen Arago 2, as well as the individual to whom belonged the specimen AT-76-T1H, probably died before reaching age 40. The observed and expected age at death distributions at Krapina are significantly different from those of Atapuerca. Figure 1, in which the Krapina (expected) and Atapuerca (observed) survivorship curves are compared, illustrates graphically these differences.

In short, the Middle Pleistocene hominid sample from SH is characterized by a high adolescent and prime-age adult and low older adult mortality, as well as a maximum longevity of about 35 years. This pattern of mortality resembles to that observed by Trinkaus (in press) in a large sample of Neandertals, but it is quite different from that observed in living foraging human groups. If the main determinants of fertility of the Atapuerca population were similar to those of these human groups, we will demonstrate next that the Atapuerca hominids would have been not able of a high enough reproductive output to maintain constant population numbers over the generations.

Representativeness of the SH hominid sample

The first question which raises the SH hominid fossil record concern its representativeness, with regard to the actual death rate of the population throughout the time. Is there in this fossil record any significant bias of that death rate?. Obviously, the infantile individuals are clearly underrepresented in SH. One of the following three causes, or a combination of them, may explain this anomaly: 1) differential distribution, for instance due to differential transport; 2) differential accumulation, i.e. the adult individuals were certainly preferably accumulated in SH; 3) differential preservation. The first possibility can be refused because neither a concrete spatial distribution concerning the human postcranial elements nor a spatial distribution with regard to the age at death of bears have been recognized in SH (Arsuaga *et al.*, 1990; Díez, 1992). In relation to the second possibility, we do not know any taphonomic agent, except the hominids, which could select specific age classes among the adults. However, to invoke some cultural selection by hominids is very speculative. In contrast, the third possibility is supported by the age representation of ursids; the immature individuals, i.e. those which died before the age of two, are represented by a 30% less of postcranial elements than the adults in relation to their NMI (Díez, 1992). Furthermore, the percentage of neonates in SH is significantly lower than that observed in other sites (5.5% in SH vs. 19.1% in Odessa: Kurten, 1958, in Trinkaus, in press).

Wolpoff (1979) observed that no individuals represent the 0- to -3 year life span in the Krapina hypodigm. Nevertheless, the proportion of individuals who died before age 12 was 40.2% (Table 2). Wolpoff (1979) suggests that the infant mortality at Krapina could have been as high as that of the Libben Amerind aboriginal population studied by C.O. Lovejoy; that is, we have no evidence of at least 25% of the Krapina sample, who probably died from birth to the age of two or three. Therefore, if we consider, in accordance with Wolpoff, that the absence of individuals under three years of age at Krapina could be the result of destructive taphonomical

	KRAPINA		ATAPUERCA
Age at death interval	Observed number of individuals (frequencies)	Expected number of individuals[1] (frequencies)	Observed number of individuals (frequencies)[2]
0 - 2.9	0 (0.0)	27 (24.8)	0 (0.0)
3 - 5.9	10 (12.2)	10 (9.2)	1 (3.1)
6 - 8.9	13 (15.8)	13 (11.9)	1 (3.1)
9 - 11.9	10 (12.2)	10 (9.2)	1 (3.1)
12 - 14.9	10 (12.2)	10 (9.2)	6 (18.8)
15 - 17.9	20 (24.4)	20 (18.3)	5 (15.6)
18 - 20.9	9 (11.2)	9 (8.2)	5 (15.6)
21 - 23.9	6 (7.3)	6 (5.5)	5 (15.6)
24 - 26.9	3 (3.6)	3 (2.7)	4 (12.5)
27 - 29.9	1 (1.2)	1 (0.9)	1 (3.1)
30 - 32.9	0 (0.0)	0 (0.0)	2 (6.3)
33 - 36.0	0 (0.0)	0 (0.0)	1 (3.1)
Total	82	109	32

1. According to Wolpoff'assumptions, it is expected that about a 25 per cent of the Krapina population died before the age of three. Therefore, we increase this population sample with 27 more individuals to get an adequate representation (25%) of this life span. However, Wolpoff (1979) operates in a different way. He includes 21 individuals (the 0 - 3 age group) in the total population sample (82 individuals), to obtain a 25 per cent of individuals died before the age of three, thus reducing the true representation of the other age groups.

2. Considering seven-year intervals, the differences between the Krapina (observed frequencies) and Atapuerca distributions (X^2 test) are statistically significant (P<0.001).

Table 2. Age at death distributions for the Krapina and Atapuerca hominid population samples.

agents and excavation, we can increase the population sample with 27 more individuals (82 + 27= 109: see table 2) to get an adequate representation (25%) of this life span.

In a recent study Trinkaus (in press) compares the Neandertal mortality pattern with that of some living predominantly foraging human groups: Dobe !Kung (Howell, 1979), Hadza (Blurton Jones *et al.*, 1992) and Ache (Hill & Hurtado: in Trinkaus, in press). In these groups the percentage of individuals deceased before the age of 10 years ranges from 39.4% to 59.3%. In the Neandertal sample, which takes into account only the associated dentitions from Krapina (MNI=23), Trinkaus (in press) obtains observed and expected percentages of the individuals died before the age of 10 years within this range of variation. It seems reasonable to assume that childhood mortality during the Middle Pleistocene was as high as that of the Neandertals. This assumption can take advantage from the data of Zhoukoudian, where 68.2% of the individuals died before age 15 (Weidenreich, 1943), and from the observations of the hominid fossil record from the Caune de l´Arago, where the dental evidence indicates that about half of the individuals deceased during childhood (personal observations of the authors in 1986, by courtesy of H. and M.A. de Lumley). Furthermore, it is also reasonable to assume that infant mortality of the European Middle Pleistocene populations was high, probably very closely related to the premature death of the mothers, though non-parental care of the orphaned infantile or young individuals by members of the social group may have been the habitual behavior in Pleistocene populations (Wolpoff, 1980a; Bogin, 1991).

Since that there are no taphonomic arguments to support a differential preservation inside the adult age group, the SH hominid fossil record would be not representative of the actual mortality of the population throughout the time only on the assumption that: 1- the accumulation of hominid corpses were due to a catastrophic event, implicating the simultaneous death of a whole group, or 2- one or more determinated age class/classes was/were preferentially selected. Under the first assumption, the SH human fossil record would represent the age distribution of a same live human group. On considering this possibility, we ought to remember: 1- that we have estimated the MNI represented in the SH hypodigm, 2- that future excavations may increase the MNI, and 3-that this MNI does not include most of the offspring younger than 12 years, who would belong to that live human group. It seems difficult to accept the simultaneous death of a group formed by at least 50 people, and the absence of any archaeological material in SH is not compatible with that hypothesis either.

Specimen		Estimated age at death	Atapuerca-SH individuals
Montmaurin	mandible	18	I, XIX, XXVI
Montmaurin	C.G. 14B3S right UP3 & UP4 & C.G.10B3T right UC	15	XXVIII
Montmaurin	C.G.2F3 left UC	19	XII
Montmaurin	C.G.6B3 left UP4	15	XXVIII
Montmaurin	C.G.2D3 right LM3	18	I, XIX, XXVI
Petralona	maxilla	24-25	VII-XVII
La Chaise, A. Suard 36	right UP3	14	II
La Chaise, A. Suard 37	right UC	19	XII
Vergranne	left dC	4[2]- 6	
Mauer	mandible	22	XXII
Pinilla del Valle	right UM1 &UM3	22	XXII
Mollet I	right UM1	8-10	<XX
Pontnewydd	PN4 right UM1& Udm1	(8-9)[3]	
Pontnewydd	PN1 left UM2	24	VII
Lazaret I	right LC	21-2	XII-XIII
Lazaret II	left di1	2[4]	
Steinheim	maxilla	18-22	I-XXII
Arago II	mandible	35	V
Arago XIII	mandible	18	I
Arago XXI	maxilla	24	VII

[1] The information has been obtained from the following references: Billy, 1982: isolated teeth from Montmaurin (Coupe-Gorge); Bonis & Melentis, 1982: Petralona; Genet-Varcin, 1975, 1976: isolated teeth from La Chaise (Abri Suard); Vandermeersch & Tillier, 1983: Vergranne; Alférez, 1985: Pinilla del Valle; Cortada & Maroto, 1990: Mollet I; Stringer, 1984: Pontnewydd. Data from the Arago, Lazaret, Mauer and Montmaurin (mandible) specimens come from personal observations of the first author on the originals, and dental wear of the Steinheim specimen was observed in a cast.

[2] According to Vandermeersch & Tillier, 1983.

[3] According to Stringer, 1984.

[4] According to de Lumley, 1973.

Table 3. Equivalence between the occlusal tooth wear of some European Middle Pleistocene specimens [1] and that of the teeth of the Atapuerca-SH individuals.

Furthermore, all age classes, except the infants, are represented in the SH hypodigm. Therefore, there are no reasons to support hypotheses which implicate a selective accumulative agent, such as an internal or external natural trap. The completeness of the skeletons, and the absence of hienids and herbivores in association with the human remains do not support the transport of hominids by predators either. Tooth marks have been observed on less 1% of the bear bones, whereas we have not appreciated carnivore marks on the human bones. In accordance with Arsuaga *et al.* (1990), we consider that the deposition of the hominids by other hominids is the most feasible hypothesis to explain the presence of the human remains in SH.

As far as the mortality pattern of the European Middle Pleistocene hominids is concerned, table 3 shows a rough estimation of the age at death of some of these hominids based on the equivalence of their occlusal wear with that of the teeth of the Atapuerca-SH individuals. Most of the European Middle Pleistocene remains belonged to children, adolescents or young adults as well.

A LIFE HISTORY PATTERN FOR THE ATAPUERCA HOMINIDS

We are interested in estimating the so-called net fertility rate (NFR), i.e. the ability of the population to renew itself (Hassan, 1981):

$$\mathrm{NFR}= N_f \,.\, w \,.\, f \qquad (1)$$

where N_f is the number of females in one generation (or in the group), w is the proportion of women surviving to the mean age of childbearing, and f is the total fertility rate, i.e. the estimated average of the number of live births for each mature female. The fertility of the population depends mainly on two factors, namely:

1. The age at which a female can give birth for the first time (A). Concerning this factor, the mean age at menarche for modern human populations ranges from 12 to 18 years, according to the list of 116 population samples published by Eveleth and Tanner (1990). This

		B						
		3.5	3.0	2.5	2.0	1.5	f critical values	w
A	15	2.2	2.8	3.1	3.9	**5.0**	4.0	0.50
	14	2.5	2.9	3.2	**4.0**	**5.0**	3.6	0.55
	13	2.6	2.9	**3.4**	**4.3**	**5.5**	3.3	0.60
	12	2.7	**3.3**	**3.7**	**4.6**	**5.9**	3.1	0.65

Table 4. Estimated averages of the total fertility rate (f) in the Atapuerca hominid sample for different values of the average period between successful births (B), and the age at which a female can give birth for the first time (A). w=percentage of women surviving to the mean age of childbearing (see text for further details).

considerable interpopulation variation depends basically, according to these authors, on socioeconomic, climatic and genetic factors, but the mean age at menarche in most populations is around age thirteen. The statistical parameters of the mean values for the age at menarche given in table 10 of Eveleth & Tanner (1990) are: X=13.3, S.D.=0.97, mode=13.1). A 82.7 per cent of the populations listed in this table have mean ages at menarche between 12 and 13.8. Therefore, the null hypothesis is that the age at menarche in the Atapuerca population was around 13 as well. However, menarche is an indicator of sexual maturity, but it is not a marker of fertility (Bogin, 1991). In fact, it is well known that a period of adolescent sterility (anovulatory menstrual cycles) which ranges from one to three years in both chimpanzees (Goodall, 1983) and humans (Lancaster & Lancaster, 1983) follows the first ovulation, previous to the age of initiation of the capacity for conception (nubility). This period of sterility allows females to reach almost 100% of their physical growth before confronting their first pregnancy. Therefore, we assume (the null hypothesis) that the females of the Atapuerca population gave birth for the first time at an average age of 15 years.

2. The average period between successful births (B) is the most important determinant of the biological potential for reproduction (Hassan, 1981). Some authors have estimated, through different means, an average between 27 to 29 months (2.33 years) for the birth interval of modern populations (Perrin & Sheps, 1964; Hassan, 1975; Barret, 1972: quoted in Hassan, 1981). There is evidence, however, that lactation inhibits ovulation (Frisch, 1977), and a prolonged nursing period has been reported in some hunting-gathering groups (Krzywicki, 1934; Lee 1972; Hayden, 1972). It probably has much to do with this fact that successful births in modern hunting and gathering populations are spaced three to four and even five years apart (Lee, 1972; Howell, 1979, and see also Bogin, 1991). Mckinley (1971) also concluded that *Australopithecus* birth intervals were similar to those for living, hunting and gathering groups, i.e. three to four years. Therefore, our first approach to this question may be to assume that birth intervals in the Atapuerca population were spaced out like in living hunting and gathering peoples. Thus, the null hypothesis is that in Atapuerca B=3.5 years.

We may consider, initially, that at least 50% of the individuals died before reaching the reproductive age. This percentage is more conservative than Wolpoff´s estimation for Krapina, and than Weidenreich´s observations for Zhoukoudian, where about 64% and 68.2% of the individuals respectively died before age 15. If w=0.5, the theoretical f value is equal to 4. We assume a 1:1 sex ratio in the Atapuerca population and the same mortality schedules for both sexes. We also assume that the present age composition of the SH sample represents the actual male or female mortality in the Atapuerca population; therefore, let us calculate the value of f for the SH hominid sample, considering that all the individuals are females. Thus, we will estimate the maximum number of offspring for each female aged 15 or older (A=15), for B= 3.5, 3, 2.5, 2 and 1.5. Then we will obtain, according to the above definition of f, the average of the number of live births for each mature female (Table 4). When B=3.5 the f value is equal to 2.2, and the population almost decreases to N/2 during the first generation, and even when B=2.5 the obtained f value is lower than 4.

Now, let us consider that the average age at menarche in the Atapuerca population was 10 years, and that, therefore, A=12. In table 2, column 2 we can note that about 55% of the Krapina individuals died before age 12. A more conservative alternative is to consider that in the Atapuerca population only 35% of the individuals deceased before age 12. Thus, if w=0.65 the theoretical f value is equal to 3.1. Table 4 shows the obtained f values for A=12 and B=3.5, 3, 2.5, 2 and 1.5. Only when B=3 the theoretical f value is accomplished, i.e. in order to maintain a stable population size it would be necessary to accept an average age at initiation of the capacity for conception previous to the age of twelve, and an average birth interval shorter than those for living hunting and gathering peoples. It should also be remembered that these results have been obtained by assuming Atapuerca rates of infant mortality less than those observed for Pleistocene and living foraging populations.

The ages at death presented in table 1 are estimations which can admit a certain error. In fact, the present analysis does not claim to be a precise mathematical model, but an exercise of interest to know more about the reproductive biology of the Middle Pleistocene populations. However, let us to assume, for example, that we have sistematically underaged all individuals, and the error is two years. If A=15 and B=3.5 we obtain in this case a figure of f=2.6, which is still far from the critical value of f=4, when the prereproductive mortality percentage is of 50%.

It may be also contended that the prereproductive mortality was lower than that observed in living foraging groups. Using the expression (1), it is easy to check that only when the percentage of prereproductive mortality is 10% we obtain a figure of f=2.2, thus matching the f observed value for A=15 and B=3.5 (Table 4). A 10% of prereproductive mortality for the Middle Pleistocene populations is an extremely low figure, but there are no reasons to reject values lower than those observed in living hunting and gathering human groups either.

In spite of that, for the moment, we have estimated a 1:1 sex ratio in the SH human sample, we can also consider the possibility that the Middle Pleistocene groups were composed of a greater number of females, thus increasing the total fertility rate. This implies a high male mortality rate due, for instance, to the more dangereous male daily activities. If we assume, for example, a prereproductive mortality of 50% and a 0.6F:0.4M sex ratio, the f critical value for A=15 and B=3.5 decreases to 3.3. Unfortunately, it is very difficult to verify this hypothesis, that would require the fossil evidence of the simultaneous death of a whole group, as well as an accurate sexual determination.

On the other hand, we consider unrealistic to accept that the average period between successful births in the Middle Pleistocene populations were lower than 3 years. However, when A=15 and the prereproductive mortality is 50%, a value of B=3 or even greater is insufficient to have maintained constant population numbers. We also consider difficult to accept that the age at menarche in the Middle Pleistocene populations were 10 years, since this figure is similar to that observed for female chimpanzees in the wild (Goodall, 1983).

However, it is important to bear in mind the variability of the trait in this species, since captive chimpanzees reach menarche at a mean age of 8.9 years (Goodall, 1983). In the same way, the average age at menarche in living human populations varies between 12 and 18 years (Eveleth & Tanner, 1990), thus indicating the plasticity of this trait under the influence of a great number of circumstances. Furthermore, there is a remarkable variability of the age at menarche within each living population, so that an appreciable percentage of women begin to menstruate between ages 8 to 10 (Hernández & García-Moro, 1985, 1987; Bock, 1986, Shangold *et al.*, 1989). It is obvious, given the high mortality among the young adults, that we can not accept either a mean age at menarche for the Middle Pleistocene populations similar to that of the living foragers, that is about the ages of 15 or 16 years. But it is admissible that in the Middle Pleistocene populations this average were slightly lower than that of modern humans. In fact, some studies relating life history traits with the brain weight and the body size in primates (Sacher, 1975; Harvey & Clutton-Brock, 1985, and see also Smith, 1991) provide arguments to support that the growth and development periods of the Middle Pleistocene hominids were slightly lower than those of modern humans. Furthermore, there is some evidence to suggest that Neandertals, and therefore their ancestors the European Middle Pleistocene hominids, had growth and development rates slightly accelerated with regard to modern humans (Dean *et al.*, 1986). Thus, a mean age at menarche ranging from 11 to 12 years for the Middle Pleistocene hominids would imply that the first childbirths could have occurred about the age of 13 or 14 years.

We have examined some of the possible variables which define the life history pattern of the Atapuerca hominids. However, we wish to emphasize that an early age at menarche is the most convincing explanation, though not the only one, to increase the total fertility rate of the Middle Pleistocene populations, and this allow us to reexamine the issue of sexual dimorphism in this period.

IMPLICATIONS FOR SEXUAL DIMORPHISM IN THE MIDDLE PLEISTOCENE

Concerning the Middle Pleistocene human fossil record, the differences in size between the skull from Petralona (Greece), on the one hand, and the skulls from Swanscombe (Britain) and Steinheim (Germany), on the other, as well as the differences in robustness between the mandibles Arago 13 and Arago 2 (France), have been repeatedly pointed out by some authors (Wolpoff, 1980 a, b). Furthermore, there is also growing evidence to suggest that the Atapuerca hominids had a remarkable sexual dimorphism in cranial (Arsuaga *et al.*, 1991; Arsuaga *et al.*, 1993), mandibular (Rosas, 1992), postcranial (Arsuaga *et al.*, 1991; Carretero, 1994), and dental (Bermúdez de Castro *et al.*, 1993) dimensions. To some scholars, the evidence offered by the Arago, Petralona, Steinheim, and Swanscombe specimens is enough to consider that the Middle Pleistocene hominids had a sexual dimorphism in body size greater than that of living populations (Wolpoff, 1980b; Frayer, 1980). The most popular hypothesis to explain the degree in sexual dimorphism in this period holds that the division of labor (hunting and gathering activities) favor larger body size in males than in females (Wolpoff, 1976, Brace & Ryan, 1980; Frayer, 1980).

It could be argued, however, that the Petralona, Steinheim, and Swanscombe fossil specimens belong to individuals that lived in very different places and/or time periods, and that they represent diverse and not

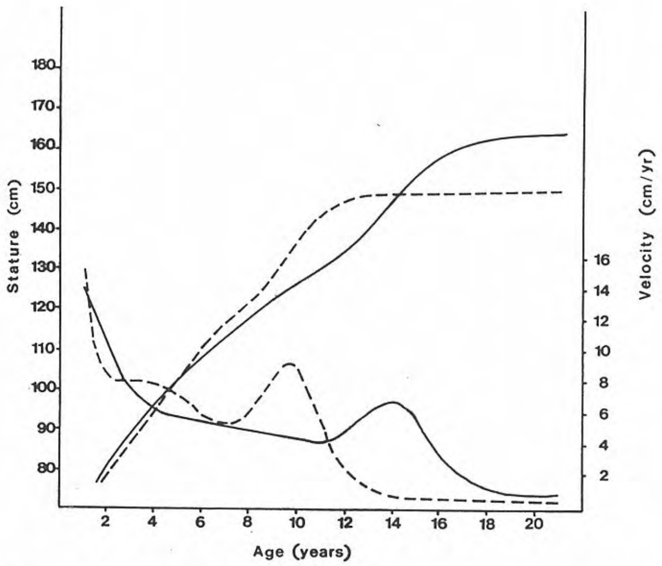

Figure 3. Growth velocity in height and growth curves of the latest maturing girl (solid lines) and shortest girl (dashed lines) of the Fels sample (after Bock 1986).

necessarily dimorphic populations. Furthermore, the considerable differences in robustness between Arago 2 and Arago 13, for instance, could give a deceptive illusion of a remarkable sexual dimorphism. In fact, the variability of many cranial, mandibular, dental and postcranial quantitative traits is also sizeable in living populations. However, there is a considerable overlapping between the male and female distributions in these populations, and the mean values are generally close to each other. Therefore, if we wish to test the hypothesis that sexual dimorphism in the Middle Pleistocene was greater than that of modern humans, we ought to prove that the degree of overlapping between the male and female distributions for any relevant metrical trait in the Middle Pleistocene population was significantly less than that of living populations (Bermúdez de Castro *et al.*, 1993). For the moment, there is no measurable evidence to support this hypothesis that, however, arise as a prediction of the model of reproduction presented in this paper.

At present, in most human populations the stature of women averages between 91 and 94 percent of the stature of men (data obtained from Eveleth & Tanner, 1990). Two main factors account for these differences: the onset of boys´s adolescent growth spurt is delayed about two years in relation to the onset of this growth period in the girls, and the size of the spurt is greater in boys than in girls, the former having an average peak height velocity between one and two cm/yr higher than that of the girls (Tanner *et al.*, 1976; Largo *et al.*, 1978; Bogin, 1991). Therefore, the differences between the averages of the stature for men and women or, what amounts to the same thing, the sexual differences in body size, may become absolutely greater either through a greater separation between the onset of the adolescent growth spurt, or by a greater sexual difference of the intensity of the growth spurt, or both.

From the reasons here exposed, we suggest that during the Middle Pleistocene natural selection might work intensively by favouring an earlier and less variable age at maturity (and consequently an earlier and less variable adolescent growth spurt) of the girls in relation to that observed in living populations, thus lengthening the female reproductive life span. That an early age at menarche may imply a shorter stature is supported by Bock (1986)´s studies on the variability in the inheritance of patterns of growth in the sample of Ohio children of the Fels Growth Study. The observation of the unusual Fels cases indicated that an early maturation is related to a shorter stature in both boys and girls (Fig. 3). Shangold *et al.* (1989) also found that menarcheal age is significantly and positively correlated with adult height in a sample of 425 overwhelmingly white American women. On the other hand, some authors have suggested that the control of fire and the appearance of home bases were especially relevant in producing important changes in the social organization of the Middle Pleistocene populations (Singer & Wymer, 1982; James, 1989). These facts probably allowed an increase in the number of births and the life expectancy of the children. Therefore, a Middle Pleistocene female very probably was engaged from her first pregnancy to her death in the reproductive process, and hence the fact that many of her energy requirements would be chanelled into the high costs of pregnancy and lactation (Stini, 1985). Thus, a reduction of the bodyweight may be an advantageous strategy to overcome the extra metabolic load of pregnancy and lactation experienced by Middle Pleistocene females during the greater part of their adult lifetimes (Pickford, 1986; Bogin, 1991). In contrast, the problems derived from the reproduction did not affect the Middle Pleistocene boys, that thus were free to undergo a delay in the onset of the adolescent growth spurt in relation to early hominids; in consequence, the possibility of a sexual dimorphism probably significantly greater than that of modern humans clearly emerges.

CONCLUSIONS

The analysis of the age at death of the Middle Pleistocene hominid sample from Atapuerca reveals a high mortality among the adolescents and young adults, a low older adult mortality, as well as a longevity probably non greater than 40 years. This new evidence of the fossil record confirms previous observations about the mortality pattern of the European Middle and early Upper Pleistocene human populations. There are no taphonomic arguments which allow to claim the existence of a significant representational bias of the young and older adults in the European Middle and early Upper Pleistocene fossil record. Consequently, there is a contradiction between this mortality pattern and the demographic viability of these populations, if we accept that the mortality of the prereproductive individuals and the main determinants which control the fertility rate were similar to those of the living foraging human groups. Thus, a methodological approach, which deals with some solutions, has been elaborated to circumvent this problem. This methodological approach lead us to made an exercise of reflection on the different possibilities which allow to harmonize the observed mortality pattern with the demographic viability of the European Middle and early Upper Pleistocene populations. None of these possibilities can solve the problem by itself, and we ought to accept that, apart from the obvious limitations of the fossil record, the demography of the Middle Pleistocene hominids was determined by a mortality pattern and a combination of life history traits different from those of the living foraging human groups. The present fossil evidence, therefore, offer new outlooks to improve our still limited knowledge of the reproductive biology of these hominids.

ACKNOWLEDGEMENTS

We wish to thank Juan Luis Arsuaga, Ignacio Martínez, Marina Mosquera, Elena Nicolás, and Jesús Rodriguez for their suggestions concerning this work. We also thank Erik Trinkaus, and the three referees who examine the manuscript for their useful and constructive criticisms. This research was supported by the Dirección General de Investigación Científica y Técnica of the Spanish M.E.C., Project N° PB93-0066-C03-03. Funding for the field work came from the Consejería de Cultura y Bienestar Social of the Junta de Castilla y León. The excavation at SH is conducted by Juan Luis Arsuaga. The help in the field of the Grupo Espeleológico Edelweiss of Burgos is much appreciated. The radiographs were made by Bernabé Roldán. The English usage was revised by Erik Kiefer.

BIBLIOGRAPHY

Acsádi, G.Y. and Nemeskeri, J. 1970. *History of Human Life Span and Mortality*. Akadémiai Kiadó, Budapest, 346 pags.

Aguirre, E. 1991/92. Atapuerca: land change, caves and humans over Middle Pleistocene. *Journal of Human Ecology*, **2/3**, 227-270.

Aguirre, E. 1995. Atapuerca (Burgos, España): su contribución a las Ciencias del Cuaternario. *Revista Española de Paleontología,* **10**, 58-82.

Aguirre, E. and Lumley, M.A. de. 1977. Fossil men from Atapuerca, Spain: Their bearing on human evolution in the Middle Pleistocene. *Journal of Human Evolution*, **6**, 681-688.

Aguirre, E., Basabe, J.M. y Torres, T. 1976. Los fósiles humanos de Atapuerca (Burgos): Nota preliminar. *Zephyrus*, **26-27,** 489-511.

Aguirre, E., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., Ceballos, M., Díez, J.C., Enamorado, J., Fernández-Jalvo, Y., Gil, E., Gracia, A., Martín-Nájera, A., Martínez, I., Morales, J., Ortega, A.I., Rosas, A., Sánchez, A., Sánchez, B., Sesé, C., Soto, E. and Torres, T.J. 1990. The Atapuerca sites and the Ibeas hominids. *Human Evolution*, **5**, 55-73.

Aiello, L.C. in press. Neandertal longevity and reproduction. *L´Anthropologie* .

Alférez, F. 1985. Dos molares humanos procedentes del yacimiento del Pleistoceno Medio de Pinilla del Valle (Madrid). *Trabajos de Antropología,* **19**, 303.

Arsuaga, J.L., Carretero, J.M., Gracia, A. and Martínez, I. 1990. Taphonomical analysis of the human sample from the Sima de los Huesos Middle Pleistocene site (Atapuerca/Ibeas, Spain). *Human Evolution*, **39**, 179-185.

Arsuaga, J.L., Carretero, J.M., Martínez, I. and Gracia, A. 1991. Cranial remains and long bones from Atapuerca/Ibeas (Spain). *Journal of Human Evolution,* **20**, 191-230.

Arsuaga, J.L., Martínez, I., Gracia, A., Carretero, J.M. and Carbonell, E. 1993. Three new human skulls from the Sima de los Huesos Middle Pleistocene site (Atapuerca, Spain). *Nature,* **362**, 534-537.

Bermúdez de Castro, J.M. 1993. The Atapuerca dental remains. New evidence (1987-1991 excavations) and interpretations. *Journal of Human Evolution*, **24**, 339-371.

Bermúdez de Castro, J.M. and Rosas, A. 1992. A human mandibular fragment from the Atapuerca Trench (Burgos, Spain). *Journal of Human Evolution*, **22**, 41-46.

Bermúdez de Castro, J.M., Durand, A. and Ipiña S.L. 1993. Sexual dimorphism in the human dental sample from the SH site (Sierra de Atapuerca, Spain). A statistical approach. *Journal of Human Evolution*, **24**, 43-56.

Beynon, A.D. 1986. Tooth growth structure in living and fossil hominoids. In: *Teeth and Anthropology* (Eds. E. Cruwys & R.A. Foley). Oxford: B.A.R. Int. Series, 23-30.

Billy, G. 1982. Les dents humaines de la Grotte du Coupe-Gorge a Montmaurin. *Bulletin et Mémoires de la Societé d´Anthropologie de Paris,* **9**, 211-225.

Blurton Jones, N.G., Smith, L.C., O´Conell, J.F., Hawkws, K. and Kamazora, C.L. 1992. Demography of the Hadza, an increasing and high density population of savanna foragers. *American Journal of Physical Anthropology*, **89,** 159-181.

Bock, R.D. 1986. Unusual growth patterns in the Fels data. In: *Human Growth. A Multidisciplinary Approach* (Ed. A. Demirjian). London: Taylor and Francis, 69-84.

Bogin, B. 1991. *Patterns of Human Growth* . Cambridge: Cambridge University Press, 267 pags.

Bonis, L. de et Melentis, J. 1982. L´Homme de Petralona: Comparaisons avec l´Homme de Tautavel. In: *L´Homo erectus et la place de l´Homme de Tautavel parmi les hominidés fossiles*. Colloque International du C.N.R.S., Nice, Tome 2, 847-874.

Brace, C.L. and Ryan, A.S. 1980. Sexual dimorphism and human tooth size differences. *Journal of Human Evolution*, **9,** 417-435.

Bromage, T.G. 1987. The biological and chronological maturation of early hominids. *Journal of Human Evolution*, **16,** 257-272.

Bromage ,T.G. and Dean, M.C. 1985. Re-evaluation of the age at death of immature fossil hominids. *Nature*, **317,** 525-527.

Carretero, J.M. 1994. *Estudio del esqueleto de las dos cinturas y el miembro superior de los homínidos de la Sima de los Huesos*. Tesis Doctoral, Universidad Complutense, Madrid, 546 págs.

Cervera, J. 1992. Nuevos hallazgos de carnívoros en el complejo de yacimientos meso-pleistocenos de la Sierra de Atapuerca, Burgos. *Revista Española de Paleontología*, **nº extraordinario,** 21-28.

Conroy, G.C. and Vannier, M.W. 1987. Dental development of the Taung skull from computerized tomography. *Nature*, **329,** 625-627.

Conroy, G.C. and Vannier, M.W. 1988. The nature of Taung dental maturation continued. *Nature* , **333,** 808.

Cortada, T. i Maroto, J. 1990. La dent humana paleolítica de la Cova de Mollet I (Serinyà). *Quaderns d´Estudis Comarcals de Banyoles,* **1988-1989**, 135-148.

Dean, M.C. 1987. Growth layers and incremental markings in hard tissues; a review of the literature and some preliminary observations about enamel structure in *Paranthropus boisei. Journal of Human Evolution*, **16**, 157-172.

Dean, M.C. and Beynon, A.D. 1991. Histological reconstruction of crown formation times and initial root formation times in a modern human child. *American Journal of Physical Anthropology*, **86,** 215-228.

Dean, M.C., Stringer, C.B. and Bromage, T.G. 1986. Age at death of the Neanderthal child from Devil´s Tower, Gibraltar and the implications for studies of general growth and development in Neanderthals. *American Journal of Physical Anthropology*, **70**, 301- 309.

Díez, J.C. 1992. *Zooarqueología de Atapuerca (Burgos) e implicaciones paleoeconómicas del estudio tafonómico de yaciminetos del Pleistoceno medio*. Madrid: Publ. Universidad Complutense de Madrid, 365 págs.

Eveleth, P.B. and Tanner, J.M. 1990. *Worldwide Variation in Human Growth* . Cambridge: Cambridge University Press, 397 pags.

Frayer, D.W. 1980. Sexual dimorphism and cultural evolution in the Late Pleistocene and Holocene in Europe. *Journal of Human Evolution* , **9**, 399-415.

Frisch, R.E. 1977. Population, food intake, and fertility. *Science* , **199,** 22-30.

Genet-Varcin, E. 1975. Etude de dents humaines isolées provenant de la Chaise de Vouthon (Charente). *Bulletin et Mémoires de la Societé d´Anthropologie de Paris,* **2**, 277-286.

Genet-Varcin, E. 1976. Etude de dents humaines isolées provenant de la Chaise de Vouthon (Charente). *Bulletin et Mémoires de la Societé d´Anthropologie de Paris,* **3**, 243-259.

Gil, E., Aguirre, E. y Hoyos, M. 1987. Contexto estratigráfico. In: *El Hombre fósil de Ibeas y el Pleistoceno de la Sierra de Atapuerca I* (Eds. E. Aguirre, E. Carbonell y J.M. Bermúdez de Castro). Soria, Junta de Castilla y León, 47-54.

Goodall, J. 1983. Population dinamycs during a 15-year period in one community of free-living chimpanzees in the Gombe National Park, Tanzania. *Zietschrift für Tierpsychologie*, **61,** 1-60.

Gustafson, G. and Koch, G. 1974. Age estimation up to 16 years of age based on dental development. *Odontologisk Revy*, **3**, 1-10.

Harvey, P.H. and Clutton-Brock, T.H. 1985. Life history variation in primates. *Evolution,* **39**, 559-581.

Hassan, F.A. 1975. Determinants of the size, density and growth rates of hunting- gathering populations. In: *Human Ecology and Evolution* (Ed. S. Polgar). Mouton: The Hague, 27-52.

Hassan, F.A. 1981. *Demographic Archaeology*. New York: Academic Press Inc, 298 pags.

Hayden, B. 1972. Population control among hunter/gatherers. *World Archaeology*, **4,** 205-221.

Hernandez, M. y García-Moro, C. 1985. Aspectos de la estacionalidad de la menarquia en la población de Barcelona. *Actas del IV Congreso Español de Antropología Biológica, Barcelona*, 213-222.

Hernandez, M. y García-Moro, C. 1987. Avance del estudio de la evolución de la edad de menarquia en una muestra de mujeres andaluzas. *Actas del V Congreso Español de Antropología Biológica, León*, 219-228.

Hillson, S. 1986. *Teeth*. Cambridge: Cambridge University Press, 376 pags.

Howell, N. 1979. *Demography of the Dobe !Kung*. New York: Academic Press, 254 pags.

James, S.R. 1989. Hominid use of fire in the Lower and Middle Pleistocene. *Current Anthropology*, **30**, 1-26.

Johanson, S.J. 1971. Age determinations from human teeth. *Odontologisk Revy*, **22**, Supplement, 1-62.

Krzywicki, L. 1934. *Primitive society and its vital statistics*. London: Macmillan, 178 pags.

Lampl, M., Monge, J.M. and Mann, A.E. 1993. Further observations on a method for estimating hominoid dental developmental patterns. *American Journal of Physical Anthropology,* **90**, 113-127.

Lancaster, J.B. and Lancaster, C.S. 1983. Parental investment: The hominid adaptation. In: *How Human Adapts* (Ed. D.J. Ortner). Washington DC: Smithsonian Institution Press, 33-65

Largo, R.H., Gasser, T.H., Prader, A., Stutzle, W. and Huber, P.J. 1978. Analysis of the adolescent growth spurt using smoothing spline functions. *Annals of Human Biology*, **5,** 421-434.

Lavelle, C.L.B. 1970. Analysis of attrition in adult human molars. *Journal of Dental Research*, **49**, 822- 828.

Lee, R.B. 1972.!Kung spatial organization: An ecological and historical perspective. *Human Ecology*, **1**, 125-147.

Legoux, P. 1970. Etude odontologique de l´enfant Néanadertalien du Pech-de-l´Azé. *Archives de l´Institut de Paléontologie Humaine*, **33**, 53-87.

Lumley, M.A. de. 1973. Anténéandertaliens et Néandertalliens du bassin méditterranéen occidental européen. *Etudes Quaternaires,* **2**, 626 pp.

Lumley, H. de and Lumley, M.A. de. 1973. Pre-Neanderthal human remains from Arago Cave in Southeastern France. *Yearbook of Physical Anthropology*, **17,** 162-168.

Mann, A.E. 1975. Some paleodemographic aspects of the South African australopithecines. *Univ. of Pennsylvania Publications in Anthropology*, **1,** 215 pp.

Mann, A.E. 1988. The nature of Taung dental maturation. *Nature*, **333**, 123.

Mann, A.E., Lampl, M. and Monge, J.M. 1987. Maturational patterns in early hominids. *Nature*, **328**, 673-674.

Mann, A., Monge, J.M. Lampl, M. 1990 a. Dental caution. *Nature*, **348**, 202.

Mann, A.E., Lampl, M. and Monge, J.M. 1990 b. Patterns of ontogeny in human evolution: evidence from dental development. *Yearbook of Physical Anthropology*, **33**, 111-150.

McKinley, K. 1971. Survivorship in gracile and robust australopithecines: A demographic comparison and a proposed birth model. *American Journal of Physical Anthropology*, **34**, 417-426.

Miles, A.E.W. 1963. The dentition in the assessment of individual age in skeletal material. In: *Dental Anthropology* (Ed. D.R. Brothwell). Oxford: Pergamon Press, 191-209.

Nowell, G.W. 1978. An evaluation of the Miles method of ageing using the Tepe Hissar dental sample. *American Journal of Physical Anthropology*, **49**, 271-276.

Perrin, E.P. and Sheps, M.C. 1964. Human reproduction: A stocastic process. *Biometrics*, **20**, 28-45.

Pickford, M. 1986. On the origins of body size dimorphism in primates. *Human Evolution*, **1**, 77-90.

Rosas, A. 1992. *Ontogenia y filogenia de la mandíbula en la evolución de los homínidos. Aplicación de un modelo de morfogenésis a las mandíbulas fósiles de Atapuerca*. Tesis Doctoral, Universidad Complutense, Madrid, 551 págs.

Sacher, G.A. 1975. Maturation and longevity in relation to cranial capacity in hominid evolution. In: *Primate Functional Morphology and Evolution* (Ed. R.H. Tuttle). Mouton: The Hague, 417-441.

Scott, J.H. and Symons, N.B.B. 1974. *Introduction to Dental Anatomy*. Edinburg: Churchill Livingstone, 324 pp.

Shangold, M.M., Kelly, M., Berkeley, A.S., Freedman, K.S. and Groshen, S. 1989. Relationship between menarcheal age and adult height. *South Medical Journal*, **82**, 443-445.

Simpson, S.W., Lovejoy, C.O. and Meindl, R.S. 1990. Hominoid dental maturation. *Journal of Human Evolution*, **19**, 285-297.

Singer, R. and Wymer, J. 1982. *The middle Stone Age at Klasies River Mouth in South Africa*. Chicago: Univ. Chicago Press, 289 pp.

Smith, B.H. 1986. Dental development in *Australopithecus* and early *Homo*. *Nature*, **323**, 27-330.

Smith, B.H. 1991. Dental development and the evolution of life history in Hominidae. *American Journal of Physical Anthropology*, **86**, 157-174.

Stini, W. 1985. Growth rates and sexual dimorphism in evolutionary perspective. In: *The Analysis of Prehistoric Diets*. (Eds. R.I. Gilbert Jr and J.H. Mielke). London: Academic Press, 191-226.

Stringer, C.B. 1984. The hominid finds. In: *Pontnewydd Cave. A Lower Palaeolithic Hominid Site in Wales. The First Report*. (Ed. H.S. Green). National Museum of Wales Quternary Studies, Monographs, **1**, 227 pp.

Tanner, J.M., Whitehouse, R.H., Marubiri, E. and Resele, F. 1976. The adolescent growth spurt of boys and girls of the Harpenden Growth Study. *Annals of Human Biology*, **3**, 109-126.

Torres, T. 1978. Los osos fósiles de la Sierra de Atapuerca (Burgos-España). *Boletín Geológico y Minero*, **89**, 123-132.

Torres, T. 1988. Osos (Mammalia, Carnivora, Ursidae) del Pleistoceno de la península Ibérica. *Publicaciones Especiales del Boletín Geológico y Minero*, 316 pp.

Torres, T., Quintero, I., Gómez, E., Mansilla, H. y Martínez, C. 1978. Estudio comparativo de las mandíbulas de *Ursus spelaeus* , Rosemmüller-Heinroth - *Ursus deningeri*,Von Reichenau y *Ursus arctos*, Linneo. *Boletín Geológico y Minero*, **89**, 203- 222.

Trinkaus, E. 1983. *The Shanidar Neandertals*. New York: Academic Press, 320 pags.

Trinkaus, E. in press. Neandertal mortality patterns. *Journal of Archeological Science*.

Trinkaus, E. and Thompson, D.D. 1987. Femoral diaphyseal histomorphometric age determinations for the Shanidar 3, 4, 5 and 6 Neandertals and Neandertal longevity. *American Journal of Physical Anthropolology*, **72**, 123-129.

Trinkaus, E. and Tompkins, R.L. 1990. The Neandertal life cycle : the possibility, probability, and perceptibility of contrasts with recent humans. In: *Primate Life History and Evolution* (Ed. C.J. DeRousseau). New York: Wiley-Liss, Inc., 153-180.

Vallois, H.V. 1960 Vital statistics in prehistoric populations as determined from archaeological data. Quantitative methods. *Viking Fundation Publications in Anthopology*, **28**,186-222.

Vandermeersch, B. et Tillier, M.M. 1983. La dent humaine de Vergranne. *Annales Scientifiques de l'Université de Franche-Besançon. Géologie*, **5**, 27-29.

Weidenreich, F. 1943. The skull of *Sinanthropus pekinensis*, a comparative study on a primitive hominid skull. *Paleontologia Sinica* New Series, **10**, Peiping, 245 pags.

Weidenreich, F. 1951. Morphology of Solo Man. *American Museum Natural History Anthropological Papers*, **43**, 205-290.

Wolpoff, M.H. 1976. Some aspects of the evolution of early hominid sexual dimorphism. *Current Anthropology*, **17**, 579-606.

Wolpoff, M.H. 1979. The Krapina dental remains. *American Journal of Physical Anthropology*, **50**, 67-114.

Wolpoff, M.H. 1980a. *Paleoanthropology*. Alfred A. Knopf: New York, 379 pags.

Wolpoff, M.H. 1980b. Cranial remains of the middle Pleistocene European hominids. *American Journal of Physical Anthropology*, **9**, 339-358.

Manuscrito recibido: 23 de septiembre, 1994
Manuscrito aceptado: 7 de abril, 1995