

Transitions in human evolution and faunal changes during the Pleistocene in Latium (Central Italy)

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SUMMARY: The analysis of human evolution should not leave aside the evaluation of faunal and paleoenvironmental changes. As far as the evolution of the genus *Homo* is concerned, it seems at present that at least three major evolutionary transitions occurred in Europe during the time span between the late Early Pleistocene and Late Pleistocene. Looking at the Italian peninsula, Latium is a region of utmost interest to test hypotheses about these transitions. It includes in fact many bearing-hominid sites, from some among the earliest evidence of human settlements in Europe until the evolution of the Neandertals and the advent of early modern humans. Consolidate knowledge about the fossil evidence dealing with micro and macro vertebrates, bio-chronological mammal faunas sequences, and major faunal changes in Latium appears from the present analysis rather consistent with predictions about human evolution. Particularly, one of the most important faunal renewals took place in correspondence of the Early/Middle Pleistocene boundary, in the same time range when a transition from the human morph represented by the archaic cranium from Ceprano (ca. 800 ka) and Middle Pleistocene Europeans, presently referred to the species *Homo heidelbergensis*, is observed. By contrast, the transition in the Late Pleistocene between Neandertals and modern humans is not paralleled by any sharp faunal change. This occurrence supports scenarios where the emergence (in Africa) and subsequent world-wide diffusion of modern humans is seen as an exceptional event in the natural history of our species; it probably conditioned the faunal composition instead of being conditioned by large mammals paleobiogeographic trajectories.

1. INTRODUCTION

Latium is a region along the Tyrrhenian coast of central Italy of utmost interest to test hypotheses concerning human evolution during the Pleistocene and, particularly, in correspondence to crucial stages of transition between different species (and/or subspecies) of the genus *Homo*. As a matter of fact, our present knowledge about human evolution in the entire

Italian peninsula find in Latium great part of the pertinent fossil record (Fig. 1). At the same time, the biochronological setting recently proposed for the Italian Middle Pleistocene large mammal faunas is based on faunal units (FU) that are represented in Latium by many key-sites (Gliozzi *et al.* 1997; Sardella *et al.* 1998).

The scenario of human evolution in Europe overcome the chronological limit posed by the advocates of the so-called "short chronology

(Roebroek & van Kolfschoten 1995) and suggest that hominids were present on the continent from about 1 million years or more (e.g., Peretto 2001; but compare Villa 2001). Hominids associated with archaic Paleolithic (Mode 1) are only represented so far in two sites, respectively in Italy (Ascenzi *et al.* 1996; Manzi *et al.* 2001) and Spain (Carbonell *et al.* 1999), both referred to about 800 ka (thousand years BP). A more abundant fossil record parallels the diffusion in Europe of Mode 2, or Acheulean, assemblages, largely represented after about 600 ka. It is commonly shared the conclusion that these human populations, referred to as *Homo heidelbergensis*, are the direct ancestors of the Neandertals, whose morphology clearly emerge only at the end of

the Middle Pleistocene. Würmian Neandertals, included in the species *Homo neanderthalensis*, are recognised in several sites across Europe and the Near East. These late archaic humans – with the associated Mode 3, or Mousterian, artifacts – are the best known non-modern representatives of the genus *Homo* (cf. e.g. Trinkaus & Shipman 1993) and probably became extinct with the arrival in Europe of anatomically modern populations bringing Mode 4 cultures. It is presently largely recognised that these early modern Europeans, in turn, ultimately spread from Africa after 200-150 ka according to a model of “recent African origin” of *Homo sapiens* (e.g., Stringer & Andrews 1988; Aiello 1993; Krings *et al.* 1997).

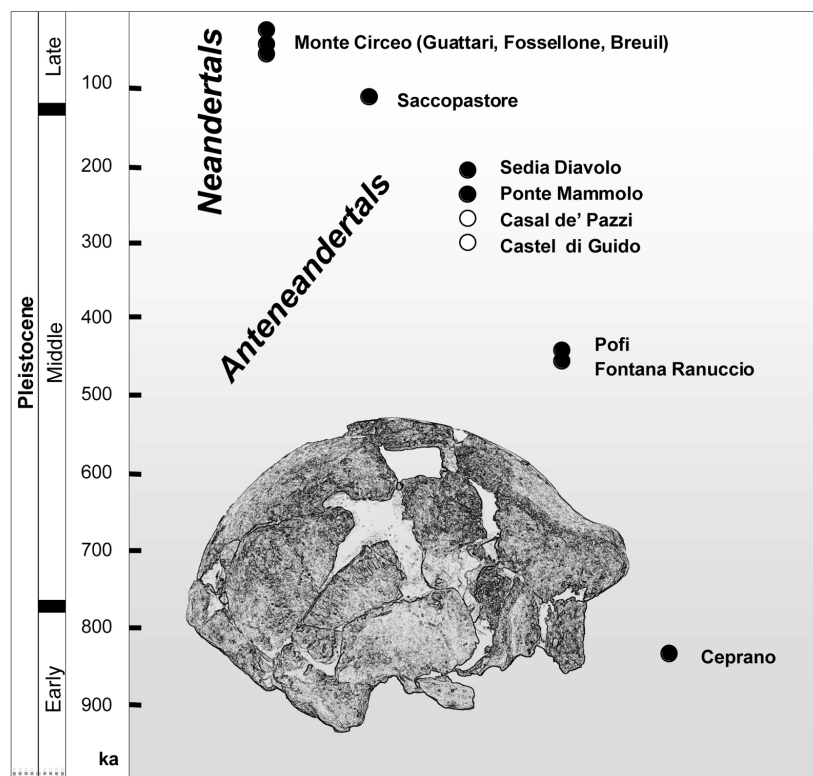


Fig.1 - Chronological inventory of sites in Latium with fossil human remains before the emergence of *Homo sapiens*; filled circles indicate discoveries due to the activity of the Italian Institute of Human Paleontology; "ka" is for thousands years before present. A drawing in right lateral view of the archaic cranium from Ceprano is also reported.

2. LATEST EARLY - EARLY MIDDLE PLEISTOCENE

The most ancient human remain found so far in Italy is the calvaria from Ceprano, in Southern Latium, a specimen that probably antedates the Early/Middle Pleistocene boundary, according to geo-chronological correlations at a regional scale supported by a series of K/Ar datings (Ascenzi *et al.* 1996, 2000; Ascenzi & Segre 2000). According to the phylogenetic interpretation recently given by Manzi *et al.* (2001), Ceprano may be considered as a good candidate to represent the last common ancestor of European and African Middle Pleistocene humans, ultimately between *Homo neanderthalensis* and (anatomically modern) *Homo sapiens*. The most relevant features of this important fossil specimen include the “erectus-like” general shape of the cranial vault, as well as a series of more localised traits that exhibit a very peculiar pattern and confer to the hominid from Ceprano the role of morphological link between more archaic (*Homo ergaster/erectus*) and more derived (*Homo heidelbergensis/rhodesiensis*) phenotypes.

In Latium, mammal faunas in close relationship with this important human remain are not clearly documented at present. However, the Redicicoli local fauna (Rome), including some Villafranchian species side by side with more advanced taxa – as *Stephanorhinus hundsheimensis*, megacerini and a bison closely related to *Bison schoetensacki* – seems to be older, while the faunal complex of Ponte Galeria FU (*sensu* Petronio & Sardella 1998) is younger. The latter is characterised by the arrival of immigrant species from Asia or central Europe (*Hyaena prisca*, *Mammuthus trogontherii*, “*Megaloceros*” *savini*, *Cervus elaphus acoronatus*, *Bos galerianus*), by the local evolution of pre-existing typical Villafranchian taxa (*Pseudodama* sp.), and by long-lasting latest Villafranchian-Galerian taxa (*Stephanorhinus hundsheimensis*, *Equus altidens*, *Hippopotamus* ex gr. *H. antiquus*, “*Megaceroides*” *verticornis*). Among elephants, the persistence of *Mammuthus meridionalis* cannot be ruled out, whereas the occurrence of *Elephas antiquus*

has still to be proved. Scanty remains coming from the uppermost levels of Ponte Galeria Formation (*Hyaena prisca*, *Equus caballus*, *Bos primigenius*) possibly belong to the Isernia FU.

Therefore, the first occurrence of the genus *Homo* in Latium – and at present also in Europe, as far as skeletal remains are concerned and in association with the fossil samples found at Atapuerca TD6, Spain, referred to the new species *Homo antecessor* (Bermúdez de Castro *et al.* 1997) – seems to predate the transition from early to middle Galerian Mammal Ages (MAs), that took place after the post-Jaramillo strong climate worsening (OIS 24 and 22) and is referable to the early Middle Pleistocene (Gliozzi *et al.* 1997). Latium middle Galerian faunas, in fact, can be referred to three FUs – namely Ponte Galeria, Isernia, and Fontana Ranuccio – that have a fairly good stratigraphic and chronological control, ages around 750 ka (Milli 1998), 600 ka (Coltorti *et al.* 2000) and 450 ka (Biddittu *et al.* 1979) being respectively hypothesised. In the Fontana Ranuccio assemblage – the most representative of the homonymous FU – some typical Galerian taxa last occurred, while *Hippopotamus* ex gr. *H. amphibius* firstly appeared and the red deer is represented by the more advanced subspecies *C. e. eastephanoceros*. Thus, the faunal change that marks the transition to the following Aurelian MA has get under way.

Probably as younger as 300 Ka (or more) than the Ceprano hominid, there are sites with human remains in Italy which are referable to the core of the Middle Pleistocene (e.g., Manzi 2000, and references therein). Fontana Ranuccio (with four teeth, K/Ar dated to 458 ka) and possibly Pofi (with a fragment of cranial vault and two post-cranial elements), are in southern Latium, along the valley of the river Sacco. According to the analyses published so far about the human remains recovered in these two sites (Passarello & Palmieri 1968; Ascenzi & Segre 1996), few or no Neandertal affinities have been encountered in the skeletal and dental elements, while features recalling those of *Homo erectus* have been reported for the central incisor found at Fontana Ranuccio.

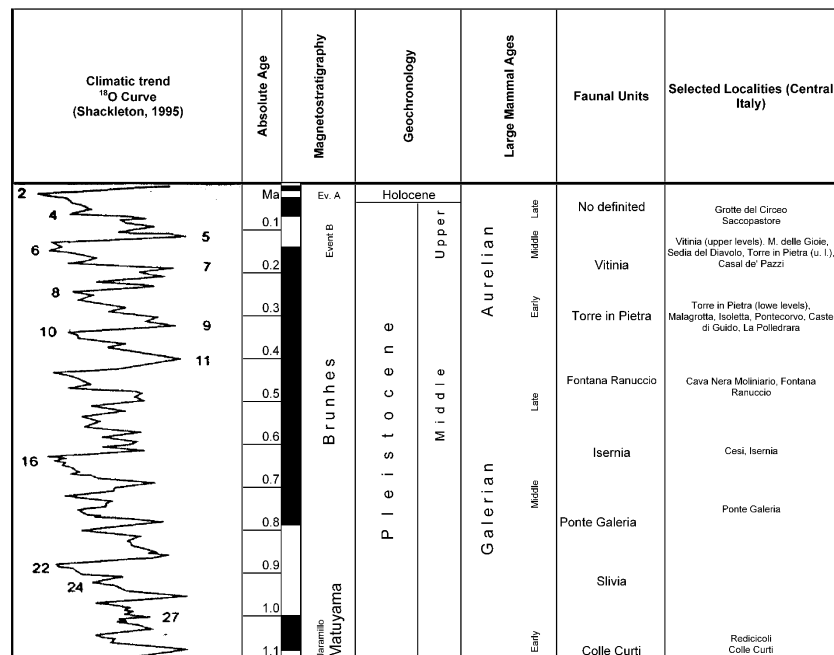


Fig.2 - Biochronological framework of Galerian and Aurelian mammal faunas of central Italy.

3. LATE MIDDLE PLEISTOCENE

During the late Middle Pleistocene, and particularly in the chronological range between approximately 350 and 150 ka, there are sites in Latium with fossil hominids commonly referred to as Anteneandertals, or *Homo heidelbergensis*. Among these sites, the most informative one is certainly Castel di Guido, near Rome, where fragmentary evidence of cranial and postcranial elements dated to about 300 ka was recovered (Mallegni *et al.* 1983; Mallegni & Radmilli 1988). Virtually all of the anatomical portions found at Castel di Guido are indicative of the trend which characterises human evolution in Europe during the Middle Pleistocene, that is the progressive appearance of Neandertal features. Such a “transitional” morphology toward more typical Neandertal phenotypes is represented by other specimens in Latium, actually in sites concentrated in the North-East outskirts of Rome (lower valley of the river Aniene). These are the Casal de’ Pazzi archaic parietal (Manzi *et al.* 1990), which is referable to about 250-200 ka, as well as the penecontemporaneous femur and metatarsal

from Sedia del Diavolo (Mallegni, 1986), and the femoral shaft from Ponte Mammolo (Biddittu *et al.* 1987).

Apparently, the morphological continuum observed in the evolution of human populations during the late Middle Pleistocene in Latium overlaps the transition in faunal assemblages, from previous FUs such as that from Fontana Ranuccio to the following Aurelian MA (Gliozzi *et al.* 1997). This took place around the climatic improvement which characterised the Mediterranean area starting from OIS 11 and followed until the beginning of the Late Pleistocene, given that latest Middle Pleistocene faunas are rather similar to OIS 5 complexes (early late Aurelian, *sensu* Gliozzi *et al.* 1997).

Two faunal complexes can be detected, namely Torre in Pietra and Vitinia FUs. In the Campagna Romana these faunas belong to two distinct sedimentary cycles: the “Aurelia Formation”, related to OIS 9, and the “Vitinia Formation”, related to OIS 7 (Conato *et al.* 1980; Caloi *et al.* 1998a). This late Middle Pleistocene mammal fauna (Torre in Pietra and Vitinia FUs), taken as a whole, shows relative-

ly modern characters on account of the disappearance of the persistent Galerian taxa present in the Fontana Ranuccio FU (e.g. *Ursus deningeri*, stenoroid horses, megacerini) and the occurrences of *Ursus spelaeus*, *Canis lupus*, *Stephanorhinus hemitoechus*, a large horse with advanced morphology, *Megaloceros giganteus*, a red deer with a complete crown, and later (in the Vitinia FU) of *Dama dama tiberina*. At the beginning of climate worsening that will characterised the OIS 6, also *Equus hydruntinus* and a primitive *Mammuthus primigenius* appear in Latium. Mammal associations of this time range are modern in character and, generally, characterised by the abundance of *Elephas antiquus*, *Bos primigenius* and cervids. This should be consistent with the improvement of warm-temperate, quite wet climate during the positive oscillations and with the major extension of thermophilous forests and/or the absence of arid grasslands.

4. LATE PLEISTOCENE

Fossil human remains dated to the Late Pleistocene are scattered along the entire peninsula. As briefly recalled above, these include specimens referred to two distinct species, namely *Homo neanderthalensis* and *Homo sapiens*; the former being the result of the regional evolutionary continuum well documented by the European fossil record since – at least – 350 ka, whereas the latter probably derives from an allopatric event of speciation occurred in Africa at about 200-150 ka.

About Neandertals, the Italian fossil sample is mainly composed by fragmentary or largely incomplete specimens that, in general, are referable to a more stable characterisation than the previous late Middle Pleistocene fossil evidence. Until now, the sites where the most informative Neandertals can be found are, once more, in Latium and come from the well known sites of Saccopastore (Rome) and Grotta Guattari (Monte Circeo). The two Saccopastore crania (e.g. Sergi 1944, 1948) exhibit a clear Neandertal phenotype, including most of the derived traits which characterise this human

group, although a number of plesiomorphic features are still present. From this perspective, their morphology is definitely consistent with their chronology, intermediate between those of the Anteneandertals of the Middle Pleistocene and the so-called "classic" Würmian Neandertals. According to the geochronology of the site proposed by Segre (1983), the two human specimens should be both referred to the OIS 5e; however, faunal remains from the same levels, compared with the Torre in Pietra sequence, better fit with the OIS 5c, suggesting a date around 100 ka (Caloi *et al.* 1998b).

Typically Neandertals are, some 50 thousand years later, the cranium and the two mandibles from Grotta Guattari. The detailed study carried out by Sergi (cf. Sergi 1974) and more recent reappraisals (e.g., various papers in Piperno & Scichilone 1991) agree in regarding the morphology of these specimens as a paradigmatic example of the pattern shared by all the European Neandertals of the OIS 4 and 3; with their long and broad braincase, the mid-facial prognathism, the suite of more localised derived features (double-arched brow ridge, peculiar conformation of the occipital region, features of the petro-mastoid region, and so on). Monte Circeo is also a place where the late Neandertals can be found, and their possible bio-cultural relationships with modern human immigrants can be investigated ("acculturation"? see, e.g., Mellars 1992). Grotta Breuil, furnished in fact few specimens of Neandertal morphology associated to a Mousterian archaeological record at the young age of about 35 ka (various papers in Bietti & Manzi 1991; Manzi & Passarello 1995). After 30 ka or so, Neandertals can be considered extinct and modern humans are largely represented in Italy – in Latium, unfortunately, by very few and fragmentary specimens (recorded in sites such as Fossellone and, possibly, Farnesina) – by larger samples and sometimes by spectacular collections of entire skeletons, as those coming from the Gravettian and Epigravettian horizons in the chain of caves along the western coast of Liguria (e.g. Formicola 1991).

In the Late Pleistocene, particularly after the OIS 5, the renewal of faunas is almost completed. During late Aurelian, climatic events became more and more important; microclimatic and environmental conditions influenced the composition of mammal assemblages, which may be also strongly affected by anthropic influence. Among the large mammals, all extant species characterising the western Mediterranean area were present, while the Middle Pleistocene survivals – as large carnivores, pachyderms, and some cervids – progressively disappeared during latest Glacial stages (from OIS 4 to OIS 2), in association with the new occurrence of some species, more adapted to temperate/cold climatic conditions. However, according to the relatively temperate climate of the peninsula during the major glacial worsening, typical “cold” taxa are only sporadically recorded.

5. A TENTATIVE CONCLUSION

From this brief overview, it is apparent that in Latium – according also to the general pattern observed in Europe – at least three major transitions are documented by the human fossil record included between the late Early Pleistocene and the Late Pleistocene. Approximately, these transitional phases took place respectively at the beginning of the Middle Pleistocene, during the late Middle Pleistocene, and in a limited period (probably no longer than 10 thousand years) of the Late Pleistocene, close to the boundary between OIS 3 and 2.

We have seen in a certain detail how the consolidate knowledge on major mammal faunal changes can help in testing these predictions about human evolution. Particularly, the important paleoclimatic and paleoenvironmental variations characterising the transition from the Early Pleistocene to the early Middle Pleistocene (from early Galerian to middle Galerian MAs), favoured a considerable faunal renewal in the same time span in which we observe the transition between hominids represented by Ceprano (ca. 800 ka) and Middle Pleistocene human populations referred to as

Homo heidelbergensis (after about 600 ka), in possible association with the arrival in Europe of Acheulean immigrants (i.e., allochthonous populations bringing into Europe the Acheulean complexes).

Conversely, the passage from Galerian to Aurelian MAs does not seem to correspond to any sharp event in human evolution, but it has to be observed that while humans express features that will be subsequently fixed in the Neandertal variability, changes among large mammal assemblages appears similarly gradual, paralleling the increase of warm-temperate and relatively wet climates. Eventually, in the Late Pleistocene, the replacement by *Homo sapiens* of the latest archaic humans (the Neandertals) does not seem related to any particular change in the associated mammal faunas, but for the moderate increase of species adapted to colder conditions. This occurrence supports scenarios where the emergence (in Africa) and subsequent world-wide diffusion of modern humans is seen as an exceptional event in the natural history of our species, and that it probably conditioned the faunal composition instead of being conditioned by large mammals paleobiogeographic trajectories.

6. REFERENCES

- Aiello, L.C. 1993. The fossil evidence for modern human origins in Africa: a revised view. *Am. Anthropol.* 95: 73-96.
- Ascenzi, A. & Segre, A.G. 1996. Artefacts and human teeth at the Fontana Ranuccio Middle Pleistocene site (central Italy). *Anthropologie* XXXIV/1-2: 39-46.
- Ascenzi, A. & Segre, A.G. 2000. The fossil calvaria of *Homo erectus* from Ceprano (central Italy): a new reconstruction. M. Aloisi, B. Battaglia, E. Carafoli & G.A. Danieli (eds.), In *The Origin of Humankind*: 25-33. Amsterdam: IOS.
- Ascenzi, A., Biddittu, I., Cassoli, P.F., Segre, A.G. & Segre Naldini, E. 1996. A calvarium of late *Homo erectus* from Ceprano, Italy. *J. Human Evol.* 31: 409-423.
- Ascenzi, A., Mallegni, F., Manzi, G., Segre, A.G. & Segre-Naldini, E. 2000. A re-

- appraisal of Ceprano calvaria affinities with *Homo erectus*, after the new reconstruction. *J. Human Evol.* 39: 443-450.
- Bermúdez de Castro, J.M., Arsuaga, J.L., Carbonell, E., Rosas, A., Martínez, I. & Mosquera, M. 1997. A hominid from the Lower Pleistocene of Atapuerca, Spain: possible ancestor to Neandertals and modern humans. *Science*, 276: 1392-1395.
- Bietti, A. & Manzi, G. (eds) 1991. The Fossil Man of Monte Circeo. Fifty years of studies on the Neandertals in Latium. *Quaternaria Nova* I (1990-91): 9-678.
- Biddittu, I., Cassoli, P.F., Radicati di Brozolo, F., Segre, A.G., Segre-Naldini, E. & Villa, I. 1979. Anagni a K/Ar dated Lower Middle Pleistocene site, Central Italy: preliminary report. *Quaternaria* 21: 53-71.
- Biddittu, I., Mallegni, F. & Segre, A.G. 1987. Riss age human remain recovered from Pleistocene deposits in Ponte Mammolo (Rome, Italy). *Z. Morphol. Anthropol.* 77: 181-191.
- Caloi, L., Palombo, M.R., Zarlenga, F. 1998a. Late Middle Pleistocene mammal faunas of Latium (Central Italy): Stratigraphy and Environment. *Quaternary International* 47-48: 77-86.
- Caloi, L., Manzi, G. & Palombo, M.R. 1998b. Saccopastore, a stage-5-site within the city of Rome. In *SEQS Symposium (INQUA-SEQS'98), "The Eemian – Local sequences, global perspectives" (Kerkrade, The Netherlands, September 1998), abstracts.*
- Carbonell, E., Bermúdez de Castro, J. & Arsuaga, J.L. (eds.) 1999. Gran Dolina Site: TD6 Aurora Stratum (Burgos, Spain). *J. Human Evol.*, 37: 309-700.
- Coltorti, M., Ton-That, T., Marzoli, A., Arzarello, M., Buoso, N., Corrado, S., Di Buscchi, D., Minelli, A., Naso, G., Peretto, C., Thun Hohenstein, U., Villa, I. 2000. New Chronostratigraphic and Paleoclimatic Data from the "Isernia La Pineta" site, Molise, Italy. In *SubCommission on European Quaternary Stratigraphy (SEQS), 2000 Meeting The Plio-Pleistocene Boundary and the Lower/Middle Pleistocene transition. Type Areas and Sections: Abstracts.*
- Conato, V., Esu, D., Malatesta, A. & Zarlenga, F. 1980. New data on the Pleistocene of Rome. *Quaternaria* 22: 131-176.
- Formicola, F. 1991. Le sepolture paleolitiche dei Balzi Rossi. *Le Scienze* 280: 76-85.
- Gliozzi, E., Abbazzi, L., Aambrosetti, P., Argenti, P., Azzaroli, A., Caloi, L., Capasso Barbato, L., Di Stefano, G., Esu, D., Ficarelli, G., Girotti, O., Kotsakis, T., Masini, F., Mazza, P., Mezzabotta, C., Palombo, M.R., Petronio, C., Rook, L., Sala, B., Sardella, R., Zanalda, E. & Torre D. 1997. Biochronology of selected Mammals, Molluscs, Ostracods from the Middle Pliocene to the Late Pleistocene in Italy. The state of the art. *Riv. It. Paleont. Stratigr.*, 103 (3): 369-388.
- Krings, M., Stone, A., Schmitz, R.W., Krainitzki, H., Stoneking, M. & Pääbo, S. 1997. Neandertal DNA sequences and the origin of modern humans. *Cell*, 90: 19-30.
- Mallegni, F. 1986. Les restes humaines du gisement de Sedia del Diavolo (Rome) remontant au Riss final. *L'Anthropologie* 90: 539-553.
- Mallegni, F. & Radmilli, A.M. 1988. Human temporal bone from the lower Paleolithic site of Castel di Guido near Rome. *Am. J. Phys. Anthropol.* 76: 175-182.
- Mallegni, F., Marani-Costantini, R., Fornaciari, G., Longo, E.T., Giacobini, G. & Radmilli, A.M. 1983. New European fossil hominid material from an Acheulean site near Rome (Castel di Guido). *Am. J. Phys. Anthropol.* 62: 263-274.
- Manzi, G. 2000. Fossil Italians. What we know and what we could learn about human evolution from the Italian fossil record. In M. Aloisi, B. Battaglia, E. Carafoli & G.A. Danieli (eds.), *The Origin of Humankind*: 51-67. Amsterdam: IOS (IVSLA Series).
- Manzi, G. & Passarello, P. 1995. At the archaic/modern boundary of the genus *Homo*: the Neandertals from Grotta Breuil. *Current Anthropol.*, 36: 355-366.
- Manzi, G., Salvadei, L. & Passarello, P. 1990. The Casal de' Pazzi archaic parietal: comparative analysis of a new fossil evidence

- from the late Middle Pleistocene of Rome. *J. Human Evol.* 19: 751-759.
- Manzi, G., Mallegni, F. & Ascenzi, A. 2001. A cranium for the earliest Europeans. Phylogenetic position of the hominid from Ceprano, Italy. *Proc. Natl. Acad. Sci. USA* (in press).
- Mellars, P.A. 1992. Archaeology and the population-dispersal hypothesis of modern human origins in Europe. *Philos. Trans. R. Soc.* 337(1280): 225-234.
- Milli, S. 1998. Depositional setting and high-frequency sequence stratigraphy of the middle-upper Pleistocene to Holocene deposits of Roman Basin. *Geologica Romana* 33 (1977): 99-136
- Palombo, M.R., in press, Herbivore guils from the Middle Pliocene to the Middle Pleistocene in Italy. *Le Quaternaire*.
- Passarello, P. & Palmieri, A. 1968. Studio sui resti umani di tibia e di ulna provenienti da strati pleistocenici della cava Pompei di Pofi (Frosinone). *Riv. di Antropol.* LV: 139-162.
- Peretto, C. 2001. The oldest human population in Europe: 'long' and 'short' chronologies. In P.V. Tobias, M.A. Raath, J. Moggi-Cecchi & G.A. Doyle (eds.), *Humanity from African Naissance to Coming Millennia: 175-180*. Firenze-Johannesburg: Firenze University Press-Witwatersrand University Press.
- Piperno, M. & Scichilone, G. (eds) 1991. *The Circeo I Neandertal Skull. Studies and Documentation*. Roma: Istituto Poligrafico e Zecca dello Stato.
- Roebroek, W. & Van Kolfschoten, T. 1995. The earliest occupation of Europe: a reappraisal of artefactual and chronological evidence. *Analecta Praehist. Leidensia* 27: 297-315.
- Segre, A.G. 1983. Geologia quaternaria e Paleolitico nella bassa valle dell'Aniene. In *L'Uomo di Saccopastore e il suo Ambiente - I Neandertaliani nel Lazio. Riv. di Antropol.*, suppl. vol. LXII: 87-98.
- Sergi, S. 1944. Craniometria e craniografia del primo paleantropo di Saccopastore. *Ricerche di Morfologia* 20-21: 733-791.
- Sergi, S. 1948. Il cranio del secondo Paleantropo di Saccopastore. *Palaeontographia Italica* XLII (1942-46): 25-164.
- Sergi, S., 1974, *Il cranio neandertaliano del Monte Circeo (Circeo I)*. Roma: Accademia Nazionale dei Lincei.
- Stringer, C.B. & Andrews, P. 1988. Genetic and fossil evidence for the origin of modern humans. *Science* 239: 1263-1268.
- Trinkaus, E. & Shipman, P. 1993. *The Neandertals. Changing the Image of Mankind*. New York: A.A. Knopf.
- Villa, P. 2001. Early Italy and the colonization of Western Europe. *Quaternary International* 75: 113-130.