ARTICLES

The Paleoanthropology of Greece

KATERINA HARVATI, ELENI PANAGOPOULOU, AND CURTIS RUNNELS

European paleoanthropology and paleolithic archeology were already well-established by the early twentieth century. The human fossil record from this continent is the longest known and perhaps most intensively studied. Nonetheless, important gaps remain to this day in the map of Pleistocene Europe; perhaps the most glaring of these is located in the southeastern corner of the continent. This region's record is critical for addressing questions about the course of human evolution in Europe because its geographic position lends it a dual role: on one hand, it encompasses a frequently hypothesized dispersal corridor from Africa into Europe for both archaic and early modern humans; on the other, as one of the three Mediterranean peninsulas, it acted as a refugium for plant, animal, and, most likely, human populations during glacial conditions. This article is a review of the paleoanthopological record of Greece, one of the least known in Europe.

Greece occupies the southern part of the Balkan peninsula. This region includes a likely route by which both archaic and modern humans entered Europe from Africa or vice versa.[1–7] During glacial periods, it also preserved important refugial areas for faunal and floral communities,[8–11] and possibly for human populations. The Balkan Peninsula might therefore have played a dual role as both migration corridor and cul-de-sac at different times in the glacial cycles.[2] It is a reasonable expectation that both situations would have left their traces in the paleoanthropological and archeological records.[6]

Even though its geographic importance has long been recognized, systematic paleoanthropological research in Greece began only relatively recently. As a result, the region's human fossil and archeological records are relatively little known. Nonetheless, recent work has resulted in a wealth of new information, from which a picture of the region in the Pleistocene slowly begins to emerge.

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Key words: Balkans; Apidima; Petralona; Lakonis; Theopetra

DOI 10.1002/evan.20219
Published online in Wiley InterScience (www.interscience.wiley.com).

THE PALEOLITHIC RECORD OF GREECE

The Paleolithic in Greece is discontinuous in space and time. The patchy record is in part the result of natural processes and in part the result of academic priorities that favored Bronze Age and Classical research.[12] Lower Paleolithic (LP) sites are poorly represented (Table 1, Fig. 1A), probably because of the active geology of this region, where frequent disturbance by uplift, subsidence, erosion, and deposition combined to obscure the record.[4] Recent field work has succeeded in demonstrating that some sites, so far only open-air sites, have survived. In Epirus, research at Kokkinopilos and Alonaki produced assemblages dominated by core-choppers and flake tools made on local flint, along with small numbers of bifaces (handaxes) (Fig. 2). These sites are found in karstic formations called poljes, which filled with sediments rich in clay and formed intermittent, probably seasonal, lakes.[13] The sites were on the margins of these lakes. In time, deposition in the poljes ceased and they were capped by paleosols that have been dated by a combination of their degree of pedogenic maturity and optically stimulated luminescence (OSL), providing a minimal age (ca. 80–90 ka) for the LP assemblages that lie below, which are estimated to be ca. 250–350 ka. The open-air site at Rodia in Thessaly also produced a core-chopper assemblage, this time made on massive quartz, and apparently without bifaces.[14] The site is stratified in the high terrace of the Peneios River. Its minimum age, based on associated animal fossils and thermoluminescence (TL) dating of the terrace deposits, is ca. 200–400 ka, although the actual age may be greater.[15]

A predominance of core-chopper assemblages and a lack of handaxes in the region have been noted. Handaxes appear to be absent in the eastern part of Greece and the Balkan peninsula in general, while present, albeit rare, in the west. Several explanations have been proposed

TABLE 1. Important Paleolithic Sites in Greece: Geological Age, Lithic Industries, and Hominins

Site	Age (ka)	Method	Industry	Hominins	Classification
Megalopolis (Peloponnese)[39]	Middle Pleistocene	Faunal		Isolated upper M3	*Homo sp.*
Petralona Cave (Macedonia)[45–48]	>240	ESR/U/Th, Faunal		Petralona cranium	*H. heidelbergensis*
Kokkinopilos (Epirus)[13]	250–350	OSL	LP to UP		
Alonaki (Epirus)[13]			Core-chopper		
Rodia (Thessaly)[14–15]	350–400	U/Th	Core-chopper		
Apidima Cave A (Mani)[59]	Middle-Late Pleistocene			Two partial crania LAO 1/S1 and LAO 1/S2	*H. heidelbergensis* – *H. neanderthalensis*
Lakonis Site 1 (Mani)[24,33]	40–100	OSL/U/Th/^{14}C	Mousterian/IUP	Isolated lower M3 LKH1	*H. neanderthalensis*
Kalamakia Cave (Mani)[69–70]	>40	^{14}C	Mousterian	Isolated teeth, cranial and postcranial fragments	*H. neanderthalensis?*
Asprochaliko Cave (Epirus)[25–26]	26–>90	TL/^{14}C	Mousterian, UP		
Klisoura Cave 1 (Argolid)[29,35]	14–>40	^{14}C	MP/EUP/ Aurignacian/ Epigravettian		
Elaea (Mani)[4]			Mousterian		
Triadon Bay (Melos)[21]			Mousterian		
Peneios River (Thessaly)[14]	28–50	^{14}C	Mousterian		
Alonnisos (Sporades)[20]			Mousterian		
Theopetra Cave (Thessaly) [23]	11–>130	TL/^{14}C	Mousterian/ Epigravettian/ Mesolithic/Neolithic	Two partial skeletons	*H. sapiens*
Apidima Cave Γ (Mani)[59,79]	Late Pleistocene		Possibly Aurignacian	Partial skeleton LAO 1/S3	*H. sapiens*
Spilaion (Epirus)[37]	Late Pleistocene		Aurignacian		
Elaiochori (Achaia)[4]	Late Pleistocene		Aurignacian?		
Franchthi Cave (Argolid)[84]	13–35	^{14}C	Aurignacian/ Epigravettian		*H. sapiens*
Kastritsa Cave (Epirus)[92]	13–24	^{14}C	Gravettian/ Epigravettian		
Klithi Cave (Epirus)[93]	13–16	^{14}C	Epigravettian		
Boila Cave (Epirus)[94]	14–10	^{14}C	Epigravettian/Mesolithic		
Megalakkos Cave (Epirus)[93]	15–10	^{14}C	Epigravettian		
Grava Cave (Corfu)[38]			Gravettian?/ Epigravettian		

to account for this biased distribution, including insufficient research and functional, environmental, and cultural arguments.[16]

The Middle Paleolithic (MP) record is richer. It includes a small number of cave sites and a rather larger number of open-air surface sites and find-spots (approximately 200), few of which have been excavated (Table 1, Fig. 1B). Although open-air sites are commonly found in lowland areas near the coast, recent research has demonstrated that inland areas, like the Thessalian plain,[17] Epirus, and even the highland zone of the Pindus mountain chain in western Macedonia,[18] were visited during the Late Pleistocene. Known sites are most numerous in the northwestern, central, and southern provinces of Greece, but there are reports of sites from almost every part of the country, from Thrace in the north to the southernmost peninsula of Mani. In recent years, growing numbers of sites and find-spots with undated but

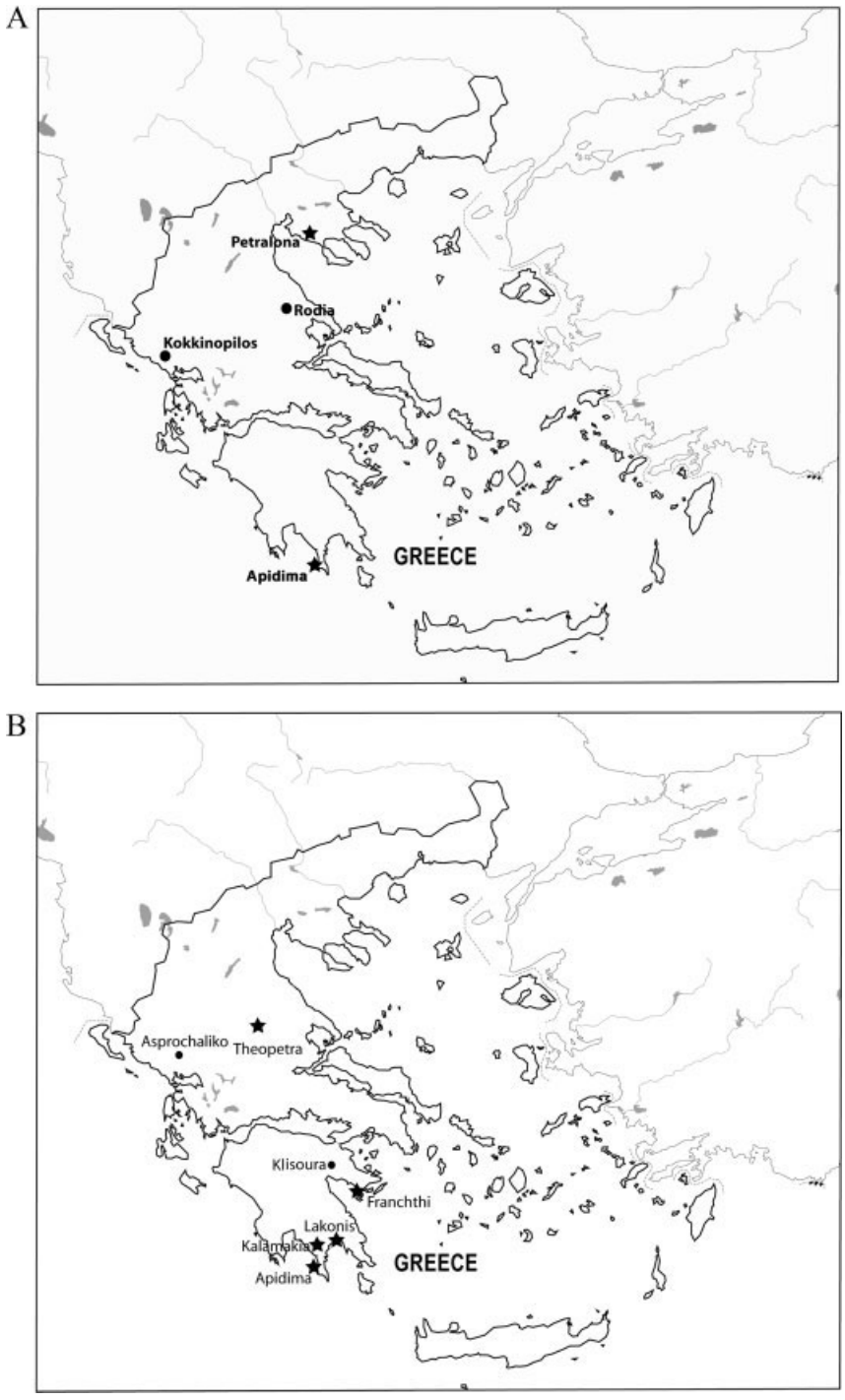

Figure 1. Map of important Pleistocene sites in Greece. Sites indicated by stars preserve human remains. A. Middle Pleistocene/Lower Paleolithic sites. B. Late Pleistocene/Middle and Upper Paleolithic sites.

typologically MP material have been identified on islands that were unconnected to the mainland during the Pleistocene in the Ionian (reviewed by Bailey and colleagues)[19] and the Aegean seas.[4,20] There are, for example, the recently identified sites at Triadon Bay in Melos[21] and Alonissos.[20] These island sites point to the possibility that at least some short-distance (a few km) sea crossings were made in the Pleistocene, perhaps even by Neanderthals (see survey in Broodbank[22]). The available radiometric dates from stratified MP cave sequences are still few. The earliest ones date to Oxygen Isotope Stage (OIS) 6 (ca. 135 ka or more)[23] and the latest to ca. 40 ka.[24]

Although there have been no systematic excavations of open-air surface sites, five MP cave sites have been excavated. Asprochaliko Cave in northwestern Greece[25,26] was excavated in the 1960s but is poorly dated. The basal Mousterian industry is associated with a single TL date to ca. 90 ka and is characterized by the use of the laminar Levallois method. The younger, final Mousterian, tentatively dated by conventional ^{14}C to ca. 40 ka, is represented by the "Asprochaliko industry," a prepared core reduction sequence devoted to the production of pseudo-Levallois points. At Theopetra Cave in western Thessaly, the MP sequence was originally dated by conventional ^{14}C to ca 46–34 ka.[17,27,28] This set of dates is now considered unreliable in light of recent TL dates.[23] Redating of the sediments and the considerable degree of bioturbation at the site call for reexamination of the cultural and contextual evidence. On the basis of the data currently available, the lower part of the MP occupation at Theopetra appears to predate the Last Interglacial (ca 130 ka).

The excavations of the Middle-Upper Paleolithic site of Klisoura Cave 1 in the northern Argolid[29] yielded a 6.5-m deep, as yet undated, MP sequence.[30] Significant technological variability is observed throughout the sequence. Blade and bladelet production is found in the lowest layers together with flake technologies, while discoidal, centripetal, and Levallois methods are prominent in the overlying younger layers. The presence of blade and bladelet technology, however, has been documented in several European and Near Eastern MP assemblages and does not necessarily indicate a precursor of the Upper Palaeolithic. The tool inventory is dominated by a Mousterian toolkit with a few bifacial pieces in the lower deposits, while an Upper-Paleolithic-like component is present in the uppermost MP layers.

Figure 2. Handaxe from Kokkinopilos, Epirus. Reproduced from the Journal of Field Archaeology with the permission of the Trustees of Boston University. All rights reserved.

Most of the excavated MP sites are on the southernmost edge of the Greek mainland, in the peninsula of Mani, where a significant MP occupation has been documented in recent years. The cave complex of Lakonis consists of five karstic formations that preserve an extensive record of hominin use from ca. 100–20 ka. The sequence of Cave I is assigned to the MP and the Initial Upper Paleolithic (IUP) and almost exclusively contains anthropogenic deposits with rich cultural remains and overlapping hearths.[24] The lowermost deposits probably date to the earliest part of the last glaciation. Six radiometric dates from the upper part of the sequence, dated by accelerator mass spectrometry (AMS) ^{14}C on charcoal, indicate that the Middle-Upper Paleolithic interface is chronologically bracketed between 44 and 38 ka. The lithic assemblages are heavily Levallois (mainly laminar, but also centripetal and convergent), while discoidal and Quina technological elements are present in small percentages, the latter in the lowermost layers. The tool inventory includes the full range of Mousterian morphological variability. Bifacial tools are present in small percentages throughout the sequence. The cave of Kalamakia, at a distance of 22 km from Lakonis, has yielded a 7-m-deep sequence with temporally dispersed occupational episodes dated in its upper part by a single ^{14}C determination to >40 ka.[31,32] The lithic assemblages are similar to that at Lakonis in the types of raw materials, as well as the use of the Levallois and, to lesser extent, discoidal reduction sequences, although detailed information on the technology is not yet available. In addition to Lakonis and Kalamakia, the area of Mani includes a cave (Apidima, and an open-air surface site, Elaea).

Despite the wealth of recent evidence, understanding of the chronological, regional, and cultural variability of the Greek MP record is currently limited due to the small number of excavated and fully published sequences, and the paucity of reliable dates. At the moment it appears that, despite considerable technological variation, the Levallois reduction strategy is a constant characteristic of most assemblages from caves and open-air sites, exhibiting similarities with the Levantine Mousterian. In terms of tool morphology, the presence of bifacial tools and intense retouch indicates, among other things, resemblances with the Balkan and Zagros Mousterian.[24,72] The explanation for these resemblances remains elusive for the time being. In the absence of a finer chronological resolution, cultural affinities are impossible to prove or contradict. The high levels of technological and morphological variation in the lithic industries, however, probably reflect the country's great environmental diversity which includes, for example, the temperate climate in the south and the moister, colder climates of the north of Greece.[24]

The large number of MP sites in some regions has enabled the study of their spatial distribution. In Epirus, it has been suggested that Neanderthals, the presumed makers of the Mousterian, pursued a foraging strategy based on residential mobility, with some logistical field camps and stations.[13] The residential bases are associated with karstic features that provided seasonally dependable water sources in an arid landscape. It has been argued that this logistical land-use pattern shows that Neanderthal foraging behavior was essentially the same as that among anatomically modern humans in the same region at the end of the Pleistocene. In eastern Thessaly, Mousterian assemblages from open-air sites on the lower terrace of the Peneios River South of Rodia have been dated by conventional ^{14}C from ca. 44 to 28 ka (uncalibrated).[14] These in-situ assemblages combine features of the traditional Mousterian along with new types such as end scrapers and carinated burins more characteristic of the Upper Paleolithic. The possible persistence of the Mousterian in eastern Thessaly until ca. 28 ka, and the fact that this region appears to have been uninhabited in the early Upper Paleolithic, suggests that Neanderthals may have survived there later than in most parts of Europe.

The Upper Paleolithic (hereafter UP) in Greece is represented by stratified sequences, chiefly in caves and rockshelters, and also from the survey of open-air sites (Table 1, Fig. 1B). The evidence now includes sites in almost every district of Greece.[4] Some regions, however, are poorly represented by sites in this period. Surveys in Macedonia and eastern Thessaly, for instance, have found few UP sites. Detailed surveys in places such as Nemea in the northern Argolid and Messenia in the south west Peloponnese have also failed to detect evidence of UP occupation.

The earliest phase of the UP is represented at two caves in the Peloponnese, Lakonis I and Klisoura I. At Lakonis I, the long MP sequence is overlain by hearth deposits with an IUP assemblage characterized by increasing reliance on UP prismatic core technology (Figs. 3 and 4). The industry retains a considerable MP technological and morphological component.[24,33] The assemblage, which is directly associated with a Neanderthal tooth,[34] is dated by ^{14}C (AMS, charcoal) to between 44 and 38 ka (uncalibrated). At the Klisoura Cave 1, an arched backed blade industry described as Ulluzian is dated by a single AMS ^{14}C measurement to ca. 40 ka (uncali-

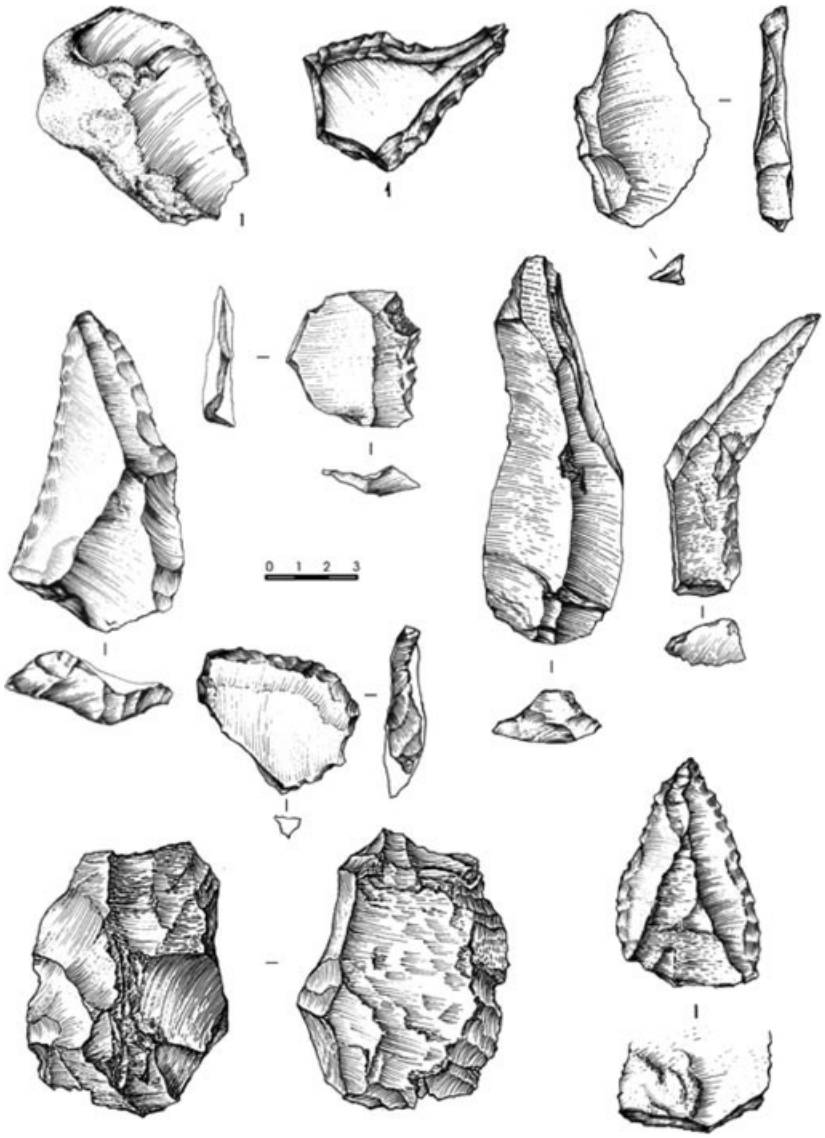

Figure 3. Lakonis I: MP lithic artifacts.[24] Reproduced from the Journal of Field Archaeology with the permission of the Trustees of Boston University. All rights reserved.

brated).[35] An attempt to clarify and refine the chronology of the described Ulluzian layer is currently under way. The Aurignacian is represented by a small assemblage in the deepest layers of the Franchthi Cave in the southern Argolid, dated by an old conventional ^{14}C determination to ca. 35 ka,[36] the undated open-air sites of Spilaion in Epirus and Elaiochori in Achaia,[4,37] and the long Aurignacian sequence of Klisoura Cave I.[29] The deeper layers of the latter sequence date to ca 32–34 ka, while published dates for the upper Aurignacian layers are not considered conclusive as yet. The Aurignacian is unconformably overlain by Epigravettian assemblages dated to after 14 ka without an intervening Gravettian occupation.[29] Open-air sites of the UP are rare. The sites that are known, such as Elaiochori or Spilaion, do not occupy the locations favored by the Mousterian inhabitants.[4,37]

By the beginning of OIS 2, ca. 30 ka, humans appear to have shifted the core of their settlement from open-air locations to caves and rockshelters as part of a complex logistical collecting strategy.[19] However, few sites provide sequences corresponding to the Gravettian technocomplex, which is widespread in Europe between 30 and 20 ka. These are the cave sites of Kastritsa and possibly Grava in northwestwern Greece.[38] It is hypothesized that this part of the country yielded the fullest record of the period, probably because environmental conditions and diverse resources provided refuge to human populations during this period of deteriorating climatic conditions. After this period, the archeological record testifies to the exploitation of various regions like Epirus (Klithi, Boila, Megalakkos in the Voidomatis gorge), Thessaly (Theopetra), and the Peloponnese (Franchthi and Klisoura). These sites have all yielded rich cultural assemblages of Epigravettian character dated to between 17 and 11 ka BP.

Altogether, only a few sites have yielded human remains. Most hominin fossils have been recovered in the Mani peninsula (southern Peloponnese), although the best known of these, the Petralona cranium, was found in northern Greece. Unfortunately, the most important fossils recovered to date lack secure archeological, faunal, and chronological context.

HUMAN FOSSIL RECORD

Middle Pleistocene

Despite the region's crucial position on one of the likely proposed migration routes of early humans from Africa into Europe, no human remains dated to the early Middle Pleistocene have been recovered. One possible exception is an isolated upper third molar from the site of Megalopolis, in the Peloponnese (southern Greece). This tooth, found in the early 1960s during an excavation in the Megalopolis lignite mines, was associated with fauna attributed to the Biharian, the mammal age spanning the Early to mid-Middle Pleistocene (up to as late as 400 ka).[39] The initial description did not reach a conclusive taxonomic assessment[40] and no further investigation has been undertaken since. Work is currently in progress to confirm and refine the specimen's chronology and to better assess its affinities.[41] In contrast, the later part of the Middle Pleistocene is relatively well represented, although the relevant sites of Petralona and Apidima are not securely dated and are only tentatively placed within this time period (Table 1, Fig. 1A).

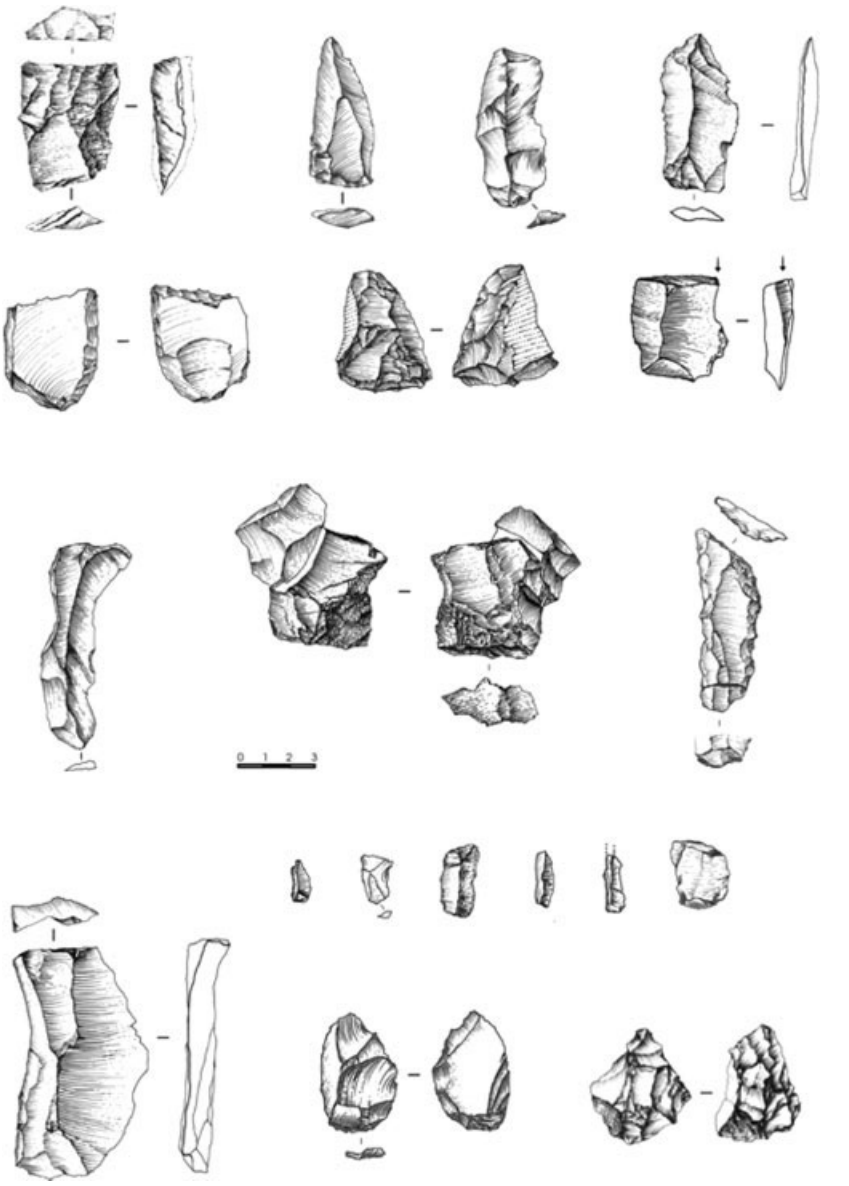

Figure 4. Lakonis I: IUP lithic artifacts.[24] Reproduced from the Journal of Field Archeology with the permission of the Trustees of Boston University. All rights reserved.

Petralona

Discovered in 1960 by a group of local villagers in the Petralona cave, Chalkidiki (northern Greece),[42,43] the Petralona cranium (Fig. 5A) is one of the most complete in the European fossil record. It is virtually intact and undistorted, lacking only its incisors. Since its discovery, the specimen has been surrounded by controversy regarding its classification and especially its age.

The Petralona cave was excavated by Poulianos during 1968 and 1974–1975,[43] several years after the specimen's accidental discovery. The cave yielded abundant faunal remains, both from the excavated areas and the surface. These included many carnivores, such as cave bear, wolf, and hyaena, as well as large herbivores and microfauna.[43] Several contradictory and widely ranging ages have been proposed for this faunal assemblage,[44] with an estimate of about 700 ka put forth by Kurtén and Poulianos.[45] However, the association of the fauna with the human cranium, a surface find, is questionable, making any faunal age estimate of dubious relevance. The use of absolute dating has also proven controversial, with electron spin resonance (ESR) and uranium-series (U-series) dates on the stalagmitic sediments and travertines associated with the cranium yielding widely ranging ages between 670 ka[46] and 240-160 ka.[47] This discrepancy was, to a large extent, due to the lack of certainty about the exact original position of the cranium relative to the sediments analyzed. A recent revision of these dates concluded that an approximate age of 250 ka is most likely.[48]

No clear cultural remains were found in the Petralona cave. Some stone and bone "tools" have been listed as having been recovered during excavation,[43] but these seem to be of dubious artifact status. Finally, claims for the existence of postcranial remains associated with the cranium and damaged during initial excavation[43] have not been substantiated.

Early views on the cranium's classification adopted contradictory taxonomic assignments.[42–43,49–52] Stringer[53,54] found it to be similar to other Middle and Late Pleistocene fossils from Europe and Africa, often placed in the past in the loosely defined evolutionary grade "archaic *H. sapiens*." Current consensus includes Petralona in *H. heidelbergensis*.[55,56] Together with other European representatives of this taxon, Petralona is generally believed to represent one of the earliest members of the Neanderthal lineage in Europe. It has been described as showing incipient Neanderthal facial characteristics,[57] though it still retains strong overall similarities to its African contemporaries.[58]

Apidima caves, Mani peninsula

This site comprises four caves (A-Δ) formed in the Middle Triassic–Late Eocene limestone on the coast of the inner Mani in the southernmost Peloponnese. The caves are very near the current sea level, cave A being the lowermost at 4 m above sea level. (Caves B-Δ are at 11, 19, and 24 m asl, respectively), and are accessible only by boat. They were partially excavated between 1978 and 1985 by a team from the University of Athens.[59–62] In 1978, two partial crania were discovered in cave A. The speci-

Figure 5. The two most complete hominins from Greece: A. Petralona, frontal and lateral views; B. Apidima 2 on block of matrix (cast), frontal and superior views. Photos courtesy of and copyright Eric Delson.

mens were encased in a block of breccia found wedged between the cave walls deep in the cave,[60] from which they have been mechanically cleaned. Both the site and the human skeletal remains are known only from preliminary descriptions, short communications, and a few published photographs.

Currently, no date is available for the Apidima crania, although a Middle Pleistocene age is usually assumed based on their rather archaic morphology. In addition to the human specimens, the breccia block contained a tortoise carapace, but no other fauna or lithic remains. Further faunal and lithic material reported from the site were recovered from other sediments and is not directly associated with the hominins.[60] Lithic remains from test trenches, though not from the breccia block containing the hominins, have been reported in all four caves,[62] but no detailed publication describing them exists to date (with the exception of the lithics recovered in cave Γ).

Apidima 2 (LAO 1/S2, Fig. 5B) is relatively complete although lacking the occipital bone and parts of the temporal bones, as well as all teeth and part of the palate. The cranium is somewhat distorted and shows multiple cracks. The second cranium (Apidima 1, LAO 1/S1) is less complete, preserving the posterior part of the neurocranium and base. It was partially eroded before collection, and has only recently been cleaned. Apidima 2 exhibits a low vault, a pronounced supra-orbital torus, a wide interorbital breadth, large rounded orbits, and a large nasal aperture. Despite its primitive features, Apidima 2 is quite gracile, especially when compared to Petralona, and may represent a female.[60,61,63,64]

To help elucidate the taxonomic position of Apidima 2, we made a first attempt at comparative analysis of this specimen using multivariate statistical analysis of five published facial measurements for Apidima[64] and a sample of relevant fossil humans. The latter included four Middle Pleistocene European and African specimens (*H. heidelbergensis s.l.*), five Neanderthals, and four early modern humans. After correcting the measurements for size by subtracting the log geometric mean of the five measurements for each individual from each log-transformed measurement, we performed a principal components analysis (Fig. 6). The first two principal components, accounting for nearly 80% of the total variance, separate Neanderthals and *H. heidelbergensis* (*s.l.*) from *H. sapiens*, although there is some degree of overlap along both axes. Neither axis separates Neanderthals from *H. heidelbergensis* (*s.l.*). Apidima 2 falls on the negative end of both PC 1 and PC 2 and near the Neanderthal and the *H. heidelbergensis* ranges. Its PC 1 score is most similar to that of Petralona; on PC 2 it falls nearest Kabwe, Arago 21 and Guattari. These results are suggestive, though not conclusive as to the precise affinities of the specimen, and illustrate the need for further analysis of the Apidima material.

Like Petralona and other European *H. heidelbergensis* specimens, Apidima 2 has facial features that have been described as "incipient" Neanderthal traits, such as posteriorly sloping zygomatics and a somewhat inflated maxilla. The posterior vault of the less complete individual, Apidima 1, does not show a chignon or other Neanderthal-like morphology. In this respect, it appears that the Apidima crania might fit into the early part of the temporal trend observed in the European Neanderthal lineage according to the accretion hypothesis of Neanderthal evolution, which postulates that Neanderthal-like facial features appeared earlier in the European lineage than did occipital ones.[57]

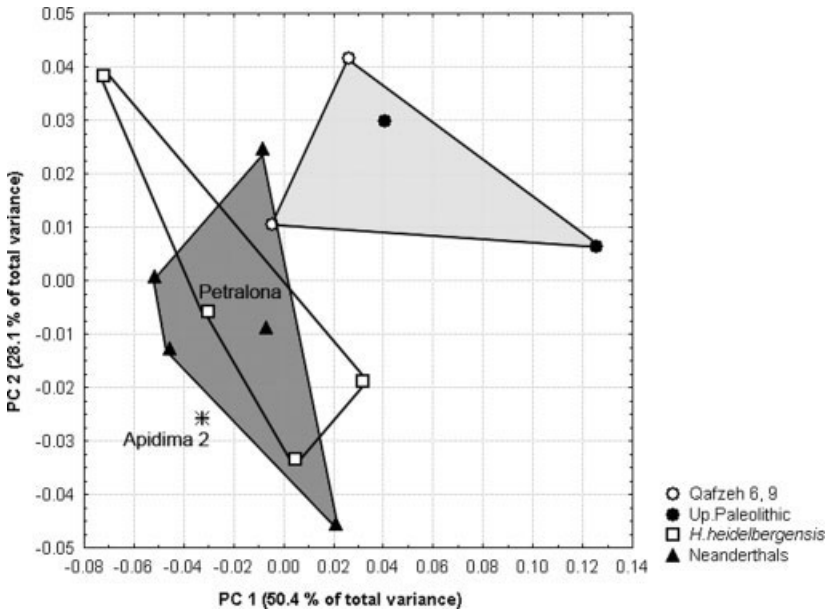

Figure 6. Principal components analysis of five facial measurements (bizygomatic breadth, nasion-prosthion height, nasal height, nasal breadth, and orbital breadth) in Apidima and other Middle/Late Pleistocene specimens. Apidima 2 (star); *H. heidelbergensis*: Petralona, Arago, Cranium 5, Kabwe (open squares); *H. neanderthalensis*: La Ferrassie 1, La Chapelle-aux-Saints, Guattari, Shanidar 1, Shanidar 5 (black triangles); *H. sapiens*: Qafzeh 6, Qafzeh 9 (open diamonds), Cro Magnon 1, Abri Pataud 1 (black diamonds). Neanderthal (dark grey), early modern human (light grey) and *H. heidelbergensis* (open) convex hulls shown. Data from the literature[64,93–97] and supplemented by Stinger C (personal communication).

Late Pleistocene-Middle Paleolithic

Only a few MP sites in Greece have yielded human remains, despite the relatively good representation of this period in the archeological record (Table 1, Fig. 1B).

Lakonis, Mani peninsula

This site is located on the eastern coast of the Mani peninsula, in the southern Peloponnese. It consists of a cave and several collapsed karstic formations in a limestone bedrock. Of these, Site I preserves the richest deposits and has been the object of systematic excavations by an international and interdisciplinary team from the Ephoreia of Paleoanthropology and Speleology (Greek Ministry of Culture) and other institutions since 1999.[24,34]

Lakonis I is a collapsed cave with a floor area of approximately 250 m^2. It shows a steep, partially submerged, wave-eroded sequence of brecciated sediments more than 7 m in height, the lowermost part of which is at current sea level. The sediments are strongly lithified due to postdepositional circulation of water, which, however, has not affected stratigraphic integrity.[24,65] The lowermost unit is a coastal conglomerate, indicating a coastal environment and sea level similar to those of present time. This fossilized beach suggests that the accumulation of sediments in Lakonis I probably began after OIS 5. The top levels are dated to between approximately 38–44 radiocarbon ka by AMS carbon dating on charcoal.[24,33,34] The sedimentary sequence is divided into five broad stratigraphic units, with many sublayers each, of which Units IV to Ib have yielded extremely rich MP lithic assemblages (Fig. 3).[24] Unit Ia has yielded an Initial Upper Paleolithic industry (Fig. 4).[24,33] The faunal material is also rich, but relatively poorly preserved. The majority of the remains are extremely fragmented and burned. Preliminary analysis shows a predominance of cervids, fallow deer in particular, and an almost complete lack of carnivore remains.[24] Relatively low numbers of seashells (*Pecten jacobaeus, Pina nobilis*)[66] have also been recovered in the deposits. The faunal composition, the high density of both faunal and lithic assemblages, and the presence of hearths all point to a highly anthropogenic and intensive occupation at Lakonis I.

In 2002, a well-preserved human left lower third molar (Fig. 7) was found *in situ* during excavation in Unit Ia and has been dated to between approximately 38 and 44 radiocarbon ka.[33,34] This well-preserved tooth, which exhibits characteristic Neanderthal morphology, including slight taurodontism, an accessory rootlet, a well-defined anterior fovea, and a mid-trigonid crest, as well as Neanderthal-like growth patterns as determined from enamel histology, has been assigned to *Homo neanderthalensis*.[34,67] The specimen was found in an undisturbed context, as shown by lithic refits, faunal remains found in anatomical position, and sediment micromorphology, in association with the Initial UP assemblage.[24,33,34] Lakonis is one of only three known sites preserving diagnostic human remains associated with "transitional" and Initial UP industries in Europe, the other two being Châtelperronian sites in France.[68] Although the Initial UP industry at Lakonis is not analogous to the Châtelperronian, the instance of Neanderthals associated with assemblages showing UP affinities is intriguing. Because no early modern human remains are currently known from this region and time period, the possibility of direct cultural exchange with modern humans seems slim, unless such

Lakonis is one of only three known sites preserving diagnostic human remains associated with "transitional" and Initial UP industries in Europe

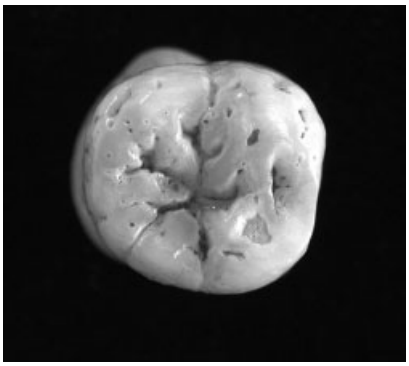

Figure 7. The Neanderthal molar from Lakonis (LKH 1). Occlusal view.

exchange occurred relatively far away (for example, in the Northern Balkans) and arrived in Southern Greece via stimulus diffusion. An alternative hypothesis is that this industry was developed independently by the local Neanderthal population.

Kalamakia, Mani peninsula

The Kalamakia site is located on the western coast of the Mani peninsula in the vicinity of Apidima and Lakonis. Like them, Kalamakia is a karstic cave formed in the limestone cliffside. Excavations, run jointly by the Ephoreia of Paleoanthropology and Speleology (Greek Ministry of Culture) and the Musée National d'Histoire Naturelle (Paris), began in 1993 and were concluded in 2006.[31,69,70]

Like Apidima and Lakonis, the Kalamakia cave is located directly on the coast, some 10 m from the current sea line at 2.5 m asl, directly above what is interpreted as the Tyrrhenean terrace formed during the last interglacial.[69] Seven broad stratigraphic units are recognized. The lower two of these comprise marine sediments most probably dating from OIS 5a or 5c,[69,70] thus putting a lowermost limit on the dating of the human occupation. The upper units comprise sandy and clay terrestrial sediments that preserve fauna, lithic remains, and hearths, and are topped by a stalagmitic layer. The uppermost archeological level has been dated to $>$ 40 radiocarbon ka with a single ^{14}C AMS dating on charcoal. The site is thought to have been occupied intermittently by humans, with several episodes of animal occupation.[69,70]

The lithics from Kalamakia have been described as Mousterian.[70] The faunal remains are dominated by wild goat and fallow deer, but several carnivores are also present (*Panthera pardus, Lynx lynx, Felis sylvestris, Canis lupus, Vulpes vulpes, Mustela* sp.). The bones of many small vertebrates, including frogs, snakes, tortoises, lizards, bats, rodents, and birds have also been found, some of which may represent the remains of the meals of birds of prey. Perhaps one of the most interesting findings at the site was the discovery of several seashells (*Callista chione* and fewer *Spondylus geaderopus*) in two of the archeological layers. Most shells of the former species have been retouched and appear to have been used as scrapers. Darlas and de Lumley[70] suggested that their small number is evidence that the items were not consumed, though the possibility remains that they were part of the human diet.

Kalamakia has yielded several human specimens, most of them isolated teeth, both permanent and deciduous, from various levels. Because of their association with Mousterian lithics, it has been assumed that they represent Neanderthals. Only one of these, a worn upper third molar, has been referred to in the literature.[31] A detailed description of the Neanderthal affinities of the human assemblage is currently in preparation.

Late Pleistocene–Upper Paleolithic

Upper Paleolithic human remains from Greece are very rare (Table 1, Fig. 1B).

Apidima caves, Mani peninsula

In addition to the Apidima 1 and 2 crania, the Apidima site preserves what has been interpreted as a UP female burial. The skeleton (LAO 1/S 3), excavated in cave Γ of the Apidima cave complex, is represented by most of the postcranium, a mandibular fragment preserving the left molar series, and some isolated teeth.[59,76,77] Its assignment as a female was based on the morphology of the pelvis.[59] Dental wear on the teeth indicates a young adult age.[59,77]

The skeleton was reportedly associated with stone and bone tools, animal bones, and charcoal pieces,[59,77] as well as about forty small perforated shells of *Nassa neritea*, possibly beads.[77] In a preliminary analysis of the lithic material, Darlas[78] concluded that the sixty-two artifacts found in association with LAO 1/S 3 can be tentatively attributed to an Aurignacian industry, but stressed the need for additional study. A reported date of 30 ka[59,62] seems largely conjectural, being based on stratigraphic observations and the preliminary taxonomic assignment of the lithic assemblage.[78] An attempt to obtain ESR dates from the Apidima cave G deposits produced ages of 20–30 ka and 25–15 ka for two travertine samples.[79] However, the large variability of the dates, as well as the uncertainty surrounding the stratigraphic position of the dating samples relative to the burial, limit the usefulness of this dating attempt.

Theopetra cave, Thessaly

This site preserves a long series of deposits from the MP up to the Neolithic and fragmentary human remains attributed to the UP, Mesolithic, and Neolithic periods.[27,71]A calvarium, recovered as several cranial vault fragments, and fragmentary postcranial remains (Theopetra 1) were found in a disturbed UP layer at this site.[80,81] The remains were tentatively interpreted as a UP burial, based on sedimentary observations and their association with two UP artifacts; no other artifacts or grave goods were recovered with the skeleton.[80,81] A ^{14}C date obtained from a long bone fragment has indicated an age of 13,723 $\pm$ 60 radiocarbon ka.[82] Nonetheless, the age of the remains, the association between the calvarium and the long bones, as well as the association of the skeletal remains with the UP artifacts, are uncertain due to the disturbed nature of the sediments. A recent attempt to date the calvarium directly was unsuccessful due to

Box 1. Theopetra Cave, Thessaly

This site, located in central Greece, consists of a large cave in a limestone formation 300 asl on the Thessalian plain. Excavations undertaken by the Ephoreia of Paleoanthropology and Speleology (Greek Ministry of Culture) from 1987 to 1998 uncovered a long series of deposits dating from the MP to the Neolithic.[27,71] Although no human remains are known from the MP context, this site is notable for the preservation of human footprints from the Mousterian levels (Fig. 1).

The Middle Paleolithic layers at Theopetra have been dated to between > 130 ->60 ka based on recent thermoluminescence dates.[23] They have yielded lithic assemblages characterized by the use of both Levallois and non-Levallois reduction techniques, high variability in the tool inventory, and low artifact density.[28,72] The site also preserves plant remains from the MP context, including mostly burned seeds of various wild legumes and fruits.[73]

Human footprints were found in the lower levels of the Theopetra sedimentary sequence and are associated with MP tools.[74] Two of these are complete and are most comparable in length to footprints of modern children of 2–3 years of age (approximately 15 and 13.8 cm, respectively). One complete and one partial footprint may have been made by a covered or shod foot.[74] If this interpretation is correct, these Theopetra footprints are the oldest archeological evidence of footwear, and much older than the previously known evidence would suggest.[75] Although footprint morphology does not allow for taxonomic assessment, these prints are thought, because of the age of the deposits and their association with Mousterian lithics, to have been left by Neanderthal children. Although footwear use by Neanderthals may have been rare, the Theopetra finding suggests that it might have occurred at least in some instances.

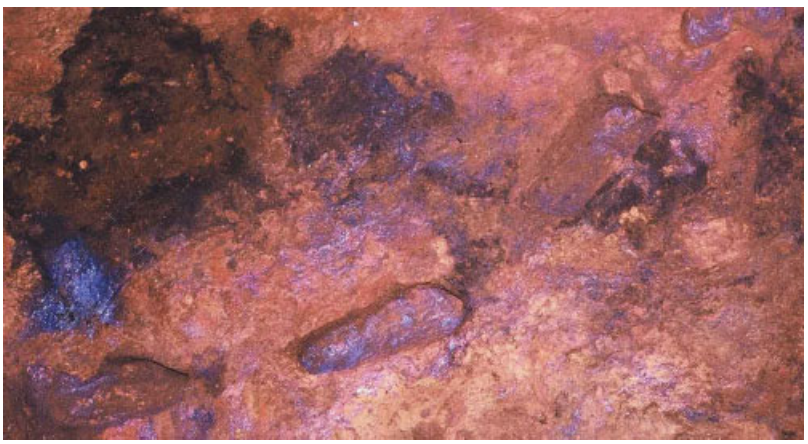

Figure 1. Three of the Theopetra footprints. Photographs courtesy of Nina Kyparissi, copyright Ephoreia of Paleoanthropology and Speleology, Greek Ministry of Culture. (Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.)

poor preservation of bone collagen (Richards personal communication).

The Theopetra 1 calvarium preserves the frontal and parietal bones almost in their entirety, as well as the upper scale of the occipital bone. Its morphology is clearly modern. Though relatively gracile, it has been tentatively assigned as a male.[80,81] Ancient DNA analysis on the specimen produced an HLA_DR 311, DQ 27 type, a type globally distributed and common in Greece.[83] Evison and coworkers[83] interpreted this result as consistent with a Paleolithic origin of the observed current south east–north west genetic gradient in Europe. However, given the contamination problems of ancient DNA analysis in modern human remains, as well as problems with the stratigraphic placement and chronology of the specimen, this result must be treated with caution.

Franchthi

Some fragmentary human remains, attributed to the final Paleolithic, were recovered during excavations in Franchthi cave, located in the southern Argolid, Peloponnese. The site consists of a very large karstic cave (more than 150 m deep, with an opening 30 m in width), situated near the current coastline at 12.5 m asl.[36,84,85] The cave, excavated from 1967 to 1976 by Indiana University under the auspices of the American School of Classical Studies at Athens and the Greek Ministry of Culture, preserves sediments from the UP, to the final Neolithic,[36,84,85] including an Aurignacian level radiocarbon date of >22 ka.

Franchthi appears to have been only sparsely inhabited until the end of the Pleistocene (approximately 10–13 radiocarbon ka),[85] when an intensification of occupation occurred. This period at Franchthi exhibits Epigravettian lithic industries, characterized by backed bladelets, end scrapers, and geometric microliths, like triangles or trapezes.[36] The faunal remains are dominated by equids and cervids; fish and marine mollusks as food refuse are also present, though rare.[86,87] Plant remains from these layers, including pistachios, almonds, pears, several legumes, wild oats, and barley, indicate an open woodland habitat.[88] No bone tools or objects of art were found, although marine shell and animal tooth beads are known from the Paleolithic deposits at the cave.[36,86] The human remains from these layers include a mandibular fragment, an adult molar fragment, two shed deciduous teeth, and two

postcranial fragments, all modern (Papathanassiou personal communication). A detailed description is pending.

CONCLUSION

This short overview makes clear the richness of the known paleoanthropological record from Greece, as well as the potential of this region for further discoveries. The current picture of Pleistocene Greece that emerges is one of contradictions. While the human fossil record is rich for the Middle Pleistocene, showing human presence both in the north and possibly also in the mostly southern part of the mainland, cultural remains from that period are very rare. Furthermore, even though the number of known MP sites with well-documented Mousterian industries has recently grown, human remains from this period are scarce. This phenomenon, which has also been observed in Italy and other Eastern Mediterranean regions, might reflect a widespread taphonomic bias or a lack of burials as a Neanderthal mortuary practice. The southernmost tip of mainland Greece seems to have been particularly important for human habitation at this time, with several rich fossil-bearing sites located in the Mani peninsula. Furthermore, a late date for an open-air Mousterian assemblage in central Greece suggests that some regions of the country may have acted as refugia for late Neanderthal populations. On the other hand, UP human and cultural remains are rare and unevenly distributed, suggesting an absence of human populations at least in some regions during this period.

Although future field work will no doubt bring forth new finds, and perhaps also help resolve the poor chronology of the majority of the region's fossil record, several issues remain to be investigated. These include the potential geological biases in preservation of Pleistocene sites, including the possibility that human activity might have been focused in coastal areas that are now submerged. Another potentially useful area of investigation is the influence of climatic cycles, topography, and geological events, such as the Campanian Ignimbrite eruption,[89] on human occupation and dispersal patterns. It would also be useful to know how these regional patterns might fit with continent-wide and eastern-Mediterranean-wide evolutionary processes, including gene flow and isolation among Pleistocene human populations, ecological adaptation, biogeography, and cultural and technological developments. What is clear is that the recent years of intensified interest in paleoanthropological research in Greece have already started bearing fruit. Continuation of that progress will help highlight the importance of the southeastern European record in elucidating human evolution in the continent.

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ACKNOWLEDGMENTS

We thank John Fleagle for the invitation to write this article and five anonymous reviewers for their helpful comments and suggestions. We are grateful to the Ephoreia of Paleoanthropology and Speleology of the Greek Ministry of Culture and, in particular, to Andreas Darlas, Anastasia Papathanassiou, and Panagiotis Karkanas. Constantin Doukas provided helpful input, Eric Delson kindly provided the photographs used in Figure 2, and Nina Kyparissi provided the photograph in Figure 5. The maps in Figure 1 were created by Sabine Giesser. We also thank the Greek Ministry of Culture, the American School of Classical Studies at Athens, the L. S. B. Leakey Foundation, the Wenner-Gren Foundation, the National Geographic Society, the Institute for Aegean Prehistory, and the Stavros Niarchos Foundation and the max Planck Society for their generous support of our research in Greece.

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