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KLISSOURA CAVE 1 AND THE UPPER PALEOLITHIC OF SOUTHERN GREECE IN CULTURAL AND ECOLOGICAL CONTEXT

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Abstract

Klissoura Cave 1 preserves a long series of Middle Paleolithic, Upper Paleolithic and Mesolithic cultural layers, interrupted by at least three significant erosional hiatuses. The sedimentary features, artifacts and animal remains of the Upper Paleolithic though Mesolithic layers testify a wide range of on-site activities, with complex cycles of feature construction and abandonment. The industry of Layer V closely resembles Uluzzian assemblages from southern Italy. Its age remains uncertain but almost certainly exceeds 39 kyrs BP. The most intense use of the site occurred during the formation of Aurignacian layers IV and IIIe-g, distinguished by many superimposed plain and clay-lined hearths, and in Layer IV, the remnants of a small structure enveloping a dense concentration of perforated shell beads. Fireplaces were fed mainly with dicotyledonous wood and bark-producing plants, whereas grass remains are concentrated in other parts of the occupied area. Post-dating the Aurignacian are two non-Aurignacian layers, followed by an ephemeral Epipaleolithic occupation and substantial Mesolithic occupations. The botanical, faunal and geological data identify a gradual trend toward climatic cooling through the Upper Paleolithic sequence. Warmer, wetter conditions returned only well after MIS 2, during the Mesolithic. Faunal data indicate opportunistic hunting of a variety of ungulate species, but mainly fallow deer, one or a few animals at a time. The patterns of small game exploitation reveal a trend of increasing dietary breadth that began in the early Upper Paleolithic and involved progressively greater use of animals such as hares and/or birds with time. Land snail exploitation became important in the later Upper Paleolithic phases and peaked in the Mesolithic. Perforated shell ornaments are present in the Uluzzian layer (V) and in all subsequent layers. The ornaments consist almost exclusively of finished products, worn from use and lacking evidence of production debris.

Key words: Mesolithic, phytoliths, anthracology, zooarchaeology, lithic industries, osseous technology, paleoecology.

INTRODUCTION

Klissoura Cave 1 preserves a regionally unique sequence of Middle Paleolithic and Upper Paleolithic though Mesolithic cultural layers dating to the Late Pleistocene (Koumouzelis *et al.*, 1996, 2001; Kozłowski, 1999; Pawlikowski *et al.*, 2000; Tomek and Bocheński, 2002; Karkanas *et al.*, 2004; Sitlivy *et al.*, 2007). Klissoura 1 is one of several archaeological cave sites in the Klissoura Gorge (Koumouzelis *et al.*, 1996, 2004; Runnels, 1996), and it contains the deepest and earliest Paleolithic sequence for the area. Here we report only the material from the final sedimentary cycle in Klissoura 1, that representing the Upper Paleolithic through Mesolithic occupations. The Upper Paleolithic is clearly distinguished from the Middle Paleolithic on the basis of lithic and other artifactual contents. The Upper Paleolithic layers contain ornament assemblages and osseous tools, whereas the Middle Paleolithic layers do not, except where minor post-depositional mixing at the MP-UP layer contact is indicated.

The formation of the Upper Paleolithic through Mesolithic stratigraphic sequence was dominated by anthropogenic processes. Constructed hearths of diverse forms, ash dumps, raked-out ash features, and trampled ash remains are very common (Karkanas, this issue). The earliest Upper Paleolithic layer (V) truncates the top of the Middle Paleolithic sedimentary series. As of this writing, Layer V represents the only Uluzzian occupation documented in Greece (though unpublished finds from Kephalari Cave may also be Uluzzian), and its industry resembles essentially contemporary industries in Italy. The Aurignacian layers have a generally discrete appearance, and the earliest Aurignacian layer (IV) truncates the underlying deposits.

The Aurignacian components in Klissoura 1 are distinguished from all other cultural layers by the remarkable complexity of in situ hearths, which range from simple small basin or stacked forms to clay-lined types (Karkanas *et al.*, 2004). Remnants of a small structure are demarcated in the earliest Aurignacian layer (IV) by a roughly oval scatter of large stones, a discrete organic stained area within, and an exceptionally dense concentration of perforated shell beads.

Following the upper Aurignacian layers are two enigmatic cultural horizons. The definition of these horizons suffers in part from the lack of information for the region and period, but also from ambiguities concerning the behavioral causes of variation in the lithic industries. Hypotheses for explaining this variation include ethnic differences and distinct traditions of tool manufacture and, alternatively, differences in the circumstances of occupation by essentially similar groups by season. We offer some preferred explanations below but acknowledge that resolution of these questions ultimately requires more information from as yet undiscovered Upper Paleolithic sites in the Peloponnese.

Moderately rich faunal and lithic assemblages were obtained from the Epigravettian and Mesolithic layers. These cultural layers experienced frequent truncations and considerable disturbance, mainly from human activity, and diffuse interfaces characterize the contacts between them. The second major hiatus in the stratigraphic series corresponds to the LGM, after which appears the typical middle (or early-middle) Epigravettian with conspicuous links to south-central Italy. The third hiatus separates the Epigravettian (layers IIa-d) from the Mesolithic (layer 5a). Here, however, cultural continuity can be seen despite the presence of depositional hiatus. The occurrence of the Terminal Paleolithic marked by a Epigravettian tradition in neighboring caves of the Klissoura Gorge indicates that Epigravettian groups did not abandon the region at this time, but rather occupied different caves and shelters in the area.

The rich and varied archaeological record of Klissoura Cave 1 provides an unprecedented and for the moment unique body of information about the Upper Paleolithic of southern Greece. Coherent lithic, bone, shell and osseous tool assemblages and many features and spatial data were recorded and studied in this collaborative research project. This detailed record of Upper Paleolithic activities yields several of surprises and insights on Upper Paleolithic behavior and cultural diversity in Eurasia, including the great age of the earliest Upper Paleolithic occupation and the contexts of on-site activities throughout the Upper Paleolithic.

CULTURAL SEQUENCE BASED ON LITHIC ASSEMBLAGES

The sequence of cultural horizons and lithic assemblages does not document an uninterrupted local evolution of Paleolithic cultures (Kaczanowska *et al.*, this issue). Instead, it is characterized by cultural and occupational discontinuities. The Upper Paleolithic begins with the Uluzzian (layer V), replaced by the Aurignacian as represented by layer IV and layers IIIg-a. Layer III'' contains a non-Aurignacian Upper Paleolithic industry. The Gravettoid component in layer III' contains what we have described as a "Mediterranean backed bladelet/blade industry." The technological character and stylistically distinct nature of the Gravettoid assemblage rules out a local evolution, suggesting instead origins from different regions of the mid-northern Mediterranean region. Layers 6, 6a, and 6/7 in fact represent the mixed filling of what may be an anthropogenic ditch and will not be discussed further.

The artifactual record in Klissoura Cave 1 affords important insights on the process of cultural evolution and differentiation in the region. Above the Uluzzian layer V is a series of Aurignacian layers (IV, IIIa-g) overlain by layer III" that could represent the final phase of the Uluzzian. Higher in the stratigraphic column, layer III' contains a "Mediterranean backed bladelet/blade" industry, which, after sedimentological/erosional hiatus, is overlain by the Epigravettian (layer II). These observations from the lithic assemblages (Kaczanowska *et al.*, this issue) suggest that the various culture units identified in Klissoura 1 correspond not so much to the adaptation of the same foragers to specific raw materials and ecological conditions, but rather represent different cultural traditions corresponding to distinct groups who periodically coexisted within the larger region.

Culturally diagnostic artifact forms in Klissoura 1 include the following: arched backed blades and convex truncations for the Uluzzian; carenate cores/endscrapers and micro-retouched bladelets for the Aurignacian; backed blades and bladelets for the "Mediterranean Early Gravettoid"; component various backed blades (also with ventral retouch), para-geometric forms and shouldered points for the Epigravettian; and geometric microliths for the Mesolithic.

Technological diversity is quite narrow from the Upper Paleolithic through the Mesolithic assemblages and contrasts with the cultural taxonomy based on the indicative artifact classes. The limited technological variability in these assemblages is probably due to the fact that a fairly homogenous group of primarily local raw materials (radiolarites and flints) were exploited throughout the sequence (Koumouzelis *et al.*, 1996). The proportion of radiolarites remains fairly stable (60–70%) through time, whereas the proportion of flint is more variable; the lowest frequency of flint is found in the Aurignacian layers (20–29%), and the highest in layer III' (42%) and the Mesolithic (33–37%). Extra-local raw materials are rare throughout the layers, with some of the red radiolarites in layer V being of the highest quality. Unquestionably exotic materials from the later cultural layers include Melian obsidian from Mesolithic layer 5a. The relatively uniform composition of the raw material across assemblages, and the dominance of local raw materials overall, suggest a fairly limited range of mobility of all of the groups while inhabiting this cave. Local raw materials were determined from field survey of raw material outcrops over a radius of 3–4 km around the site. The nearest known sources of higher quality stone are Mesozoic outcrops located in the northeastern Peloponnese. Several sites on the Argolid, particularly those of the Early Neolithic, contain these high quality raw materials, but Klissoura Cave 1 does not.

The structure of the major technological categories also is similar across most of the lithic assemblages. The large quantities of lithic shatter/chunks in all levels are clearly attributable to the low quality of the local raw materials. Tabular fragments of both radiolarite and flint from the study area contain many internal fractures and flaws as a rule. The high frequency of chips and small flakes is also partly explained by the use of poor quality raw materials, but it simultaneously attests to the intensive use of these materials, including the frequent rejuvenation of retouched tools.

Shatter/chunks, chips and small flakes constitute more than half of the lithic artifacts. This property of the stone tool assemblages reduces the indices of other technological categories – cores, blades, and retouched tools. Indices for the latter categories nonetheless are consistent with values for other sites at which the full cycle of blank and tool production and diverse activities took place. The high indices of backed pieces used as inserts in the Uluzzian and Gravettoid industries indicate the use of hafts, apparently made from perishable materials. In the Aurignacian levels, on the other hand, the bladelet index is low, and carenate cores/endscrapers from which the bladelets were detached, occur in large quantities. This pattern suggests that some bladelets were taken away from the site during the Aurignacian occupations, hafted as exchangeable parts of weapons, tools or both of these. Macroscopic impact fractures and microscopic marginal scars indicate that both Aurignacian micro-retouched (or unretouched) bladelets and Gravettoid backed bladelets were used for projectile hunting weapons and as inserts for cutting or scraping tools.

The contrast between the Aurignacian and other industries is most evident in the tools/cores typological group. In the Aurignacian levels, endscrapers/cores (mainly carenate forms) are very common, with an index of about 60 for the industries of layers IV and IIIe-g. By contrast, the scraper/core index is between 16 and 36 in the Uluzzian, and about 30 in levels III' and II. Such high tool to core indices in the Aurignacian are due to the dual roles of carenate pieces, which functioned both as cores for bladelets and as endscrapers. In other levels, bladelets were detached from other, specialized core types, while endscrapers functioned primarily as tools for activities such as hide processing.

The indices of blades and bladelets do not fluctuate very much through the Upper Paleolithic sequence, oscillating between the values of 4 and 6. It is only in the Late Mesolithic (layer 3) that the blade index is significantly higher (9.5). More significant differences can be seen among the cultural layers in the frequency of flake tools (i.e. denticulated, notched and retouched flakes). An especially high index of these tools (20) is found in layer III" and in some of the Aurignacian layers.

DATING

The dates for the Gravettoid–Aurignacian sequence (layers III', IIIe-g and IV) are relatively well constrained. They show a generally monotonic trend of increasing age, from ca. 27–29 ^{14}C kyrs BP to ca. 32–33 ^{14}C kyrs BP. These ages are consistent with other classic or late Aurignacian sites in southern Europe (Kuhn *et al.*, this issue).

The Uluzzian industry in layer V clearly predates the Aurignacian stratigraphically, but the radiocarbon results for layer V are ambiguous. Based on one date on a sample reported to be from layer V (source location is unclear, see Kuhn *et al.*, this issue), and two dates from layer VI (which is stratgraphically mixed), it is possible to suggest an age of >40,000 years for layer V. Other radiocarbon data are significantly younger and may or may not truly originate from layer V, the limits of which are locally difficult to distinguish from layer IV.

Fortunately, microtephra analysis conducted as part of the RESET project has identified one major peak concentration of tephra shards at the interface of layers IV and V, tailing upwardly to layer III', along with a minor peak at the interface of layers VI and VII. Attempts currently are underway to correlate the tephra(s) with specific eruptions of known age (Dustin White, personal communication, 2010). In nearby Franchthi Cave, a wind-blown Y-5 tephra (Campanian Ignimbrite) was found in stratum Q. Originating from the Naples area of Italy, this tephra is dated to 39.28± 0.11 kyrs by ^{40}Ar/^{39}Ar (De Vivo *et al.*, 2001). There is a strong possibility that Klissoura 1 may also contain this tephra.

Importantly, the tephra seals layer V in Klissoura 1. The radiocarbon results suggest that the industry of layer V is about 6000 years older than most currently reported ages for similar lithic assemblages from Europe.

Karkanas (this issue) concludes that the temporal gap between layers VII and V is considerably greater than the gap between layers V and IV. Published ages from Uluzzian sites in Italy tend to be significantly younger than 39,000 years BP (reviewed by Kuhn *et al.*, this issue). However, almost all published dates for the Uluzzianin southern Europe should be considered minimum estimates, and current efforts at re-dating the sites are likely to push age estimates backward in time.

The ABOX pre-treatment technique was used successfully used to obtain finite dates of >60,000 years on wood charcoal from the Middle Paleolithic layers. Although these should be also taken as minimum ages, they illustrate the technique's potential for pushing back the maximum limits of radiocarbon dating. ABOX proved less useful when applied to more recent Upper Paleolithic samples for reasons that may include greater water circulation or other sources of contamination.

The two important depositional/occupational hiatuses in the later part of the Klissoura 1 sequence correspond to major paleoclimatic events. One of these occurs within sequence B between the Mediterranean Backed Bladelet layer III' and the Epigravettian (layer II). Because layer III' is dated at about 30–28 Kyr and the Epigravettian cannot be older than 16–15 Kyrs BP, this hiatus should include the Last Glacial Maximum (LGM) within Marine Oxygen Isotope Stage (MIS) 2. Sites dated to the LGM are absent in the gorge as well as in other parts of Argolid. The only cultural entities that are chronologically close to LGM are lithic phase II in Franchthi Cave (22.3–21.4 kyrs BP; see Perlès, 1987) and probably layer D3 in

Kephalari Cave, which unfortunately lacks radiocarbon dates. It is possible that the inland areas were depopulated during the LGM.

The last major hiatus in Klissoura 1 occurs between the geological sequences B and A, or between the Epigravettian (layer II) and the lower Mesolithic (layer 5a). Given that the Epigravettian occupation almost all certainly spans the time interval from 16 to 14 kyrs BP, and the Mesolithic is synchronous with the Early Holocene, the second hiatus must cover the end of the Late Glacial, spanning at least 12 to 10 kyrs BP. This most recent hiatus in Klissoura Cave 1 may be unique to the site, since there are numerous Late/Final Paleolithic sites in the area, including the dated layers from Klissoura Caves 4 and 7 (Koumouzelis *et al.*, 2004), sites in the Voidomatis Gorge, and in other parts of Argolid such as at Kephalari Cave (layer C) and Franchthi Cave (Perlès, 1987).

PALEOENVIRONMENTS AND PALEOCOMMUNITIES OF THE ARGOLID

The results from the botanical, faunal and geological analyses suggest a gradual trend toward climatic cooling through the Upper Paleolithic sequence in Klissoura Cave 1. Warmer, wetter conditions returned only well after MIS 2, or during the Mesolithic. These general conclusions can be qualified by indications about the broader environment and the sedimentary environment inside the cave.

Grass phytoliths are the most important elements in the phytolith assemblages from Klissoura 1 (Albert, this issue). Most of the identified specimens correspond to the C3 festucoid subfamily, which is very common in the Mediterranean basin. The grass phytolith assemblages of layers IIIe-g and IV indicate only a moderately humid environment. Pytoliths representing C4 grasses and probably also reeds (*Arundo donax*) are present in the Epipaleolithic (II) layers, and reed phytoliths occur in the uppermost portion of the III sequence (III-III'). Although reeds require very wet conditions, their presence may simply indicate small pockets of wet land somewhere in the area and possibly localized changes in water tables caused by sea level changes, tectonic events or other non-climatic factors. The presence of C4 grasses, on the other hand, suggests a significantly drier and more open environment during the Epipaleolithic.

Wood charcoal remains from the Upper Paleolithic layers reflect a mosaic of perennial vegetation types (Ntinou, this issue). It is likely that dry parkland vegetation covered the rocky hills, giving way to open woodland with mesophilous and thermophilous trees in the foothills and valley floors. Burned wood remnants of oak (*Quercus* sp., deciduous type) and elm (*Ulmus*), genera that prefer somewhat moister conditions such as might occur in gullies and small canyons, are most common in layers V though IIIe-g. Elm all but disappears from the charcoal assemblages thereafter. The wood-charcoal record of the early part of the Upper Paleolithic sequence indicates interstadial conditions during mid-MIS 3 (40–30 kyrs BP) and gradual cooling and drying towards the end of the MIS 3 (after 30 kyrs BP).

The scope of variation in moisture that would have been available to plants near Klissoura Cave 1 warrants some discussion. Even the earliest Aurignacian phases, in which some moisture-dependent tree species are represented, coincided with generally dry conditions. A marginal balance of moisture availability and water uptake by plants was enough during this interval to support the development of some mesophilous and thermophilous vegetation. While this situation helped to suppress erosion in the area during the formation of layer IV (and possibly layer V), conditions were still sufficiently dry to prevent ash in the site from becoming cemented by dripping water. During the later occupations, the environment became very dry and, based on higher rates of clastic sediment accumulation, more prone to erosion during infrequent storms. The main explanation for increased erosion in the area is a decline in perennial vegetation. Precipitation seems to have increased again only with the Mesolithic, but erosion was considerable until forest development caught up with water availability.

The composition of the mammal and avian faunas in Klissoura 1 suggests corresponding changes in animal community structure during the Upper Paleolithic through Mesolithic (Bocheński and Tomek, this issue; Starkovich and Stiner, this issue). The ungulate assemblages from layers

IIIe-g, IV and V are relatively diverse for their sizes. Hares (and tortoises in V) dominate the small game fractions. The assemblages from the middle and upper Aurignacian layers (IIId-a) are less rich in ungulates, and they are dominated by one ungulate species in particular, European fallow deer (*Dama dama*). Hunting of large and medium-sized ground birds (bustard and partridges, respectively) also became important in the interval represented by layers IIId-a. The dominance of fallow deer together with the high incidence of partridges and bustards in the later Aurignacian layers suggests an expansion of open grassy areas. Ungulate diversity expands again in the Mesolithic (and possibly in the Epipaleolithic, but this is a small sample), and hares once again dominate the small game fraction.

It is unlikely that the variations in ungulate species diversity stem mainly from human hunting preferences. Changes in temperature and sea level forced qualitative shifts in the structure of terrestrial animal communities on the Argolid. A more heterogeneous environment would support a broader range and more even proportions of ungulate species, because greater macro-structural variation in available habitats makes it more difficult for one species to outcompete others. Relatively heterogeneous habitats are indicated by the faunal and botanical results for the earliest Upper Paleolithic. Subsequently, drier or cooler conditions prevailed and vegetation became more uniform, allowing *Dama* populations to dominate locally.

The small animal component of the dietary spectrum poses the main contradiction strictly climate-driven patterns in prey choice. The overall contribution of small animals to the meat diet increased dramatically in layer III' and above. This is clearly apparent within the vertebrate assemblages, but also from the rising economic importance of large land snails. Expansions in dietary breadth are generally thought to represent either temporary or long-term responses by consumers to the decline in the most profitable resources (Stephens and Krebs, 1986) – large game in the case of the Paleolithic. Such trends may represent cultural preferences only in the sense of their becoming permanent solutions with time, supported by significant technological investments made in spite of other important demands on foragers' time. It is likely, therefore, that the relentless expansion in dietary breadth evidenced in Klissoura Cave 1 reflects a growing human ecological footprint in the region and probably also mild increases in human population densities. That the trend is evidenced principally within the small game fraction of the faunas is not surprising, as these resources were the main means for filling gaps in the availability of large game animals (Kelly, 1995; Kuhn and Stiner, 2006).

The cultural sequence of Franchthi Cave on the southern Argolid partly overlaps with the most recent part of the Klissoura 1 chronology (Perlès, 1987; Farrand, 2000). The Aurignacian fauna from Franchthi is small and as yet under-documented, but the large Gravettoid assemblage dated to ca. 21–22 kyrs appears to follow in time the III layer series of Klissoura 1. Although the southern Argolid experienced sea changes much more directly than the Klissoura Gorge area, the Franchthi data are of comparative interest.[1] Five of the ungulate species found in the Klissoura 1 faunas also occur in the upper Aurignacian, "Gravettoid," Epipaleolithic, and Mesolithic layers of Franchthi Cave (Stiner and Munro, n.d.; Payne, 1975, 1982). Both red deer and European wild ass were important prey in the early part of the Franchthi sequence, but red deer was the only significant large prey item in the later part. Other ungulates are represented in low frequencies, namely aurochs, wild pig and ibex. Interestingly, no fallow deer remains were found in Franchthi,[2] despite the singular importance of this species in Klissoura 1. The contrast in dominant deer species in Klissoura 1 and Franchthi are one of several lines of evidence that climate-driven environmental conditions were strongly influenced by local factors on the Peloponnese.

Another contrast in ungulate representation between the two sites concerns the European wild ass. In Franchthi, wild ass remains dominate during the "Gravettoid" occupations (Stiner and Munro, n.d.). Deer dominate the entire Upper Paleolithic–Mesolithic sequence in Klissoura 1 where wild asses were always rare. The importance of wild ass at Franchthi Cave during the Gravettoid occupations must relate to more open conditions on the southern end of the peninsula going into the LGM. European equids of the Late Pleistocene are thought to have preferred open and steppic conditions, particularly *E. hydruntinus*. Modern fallow deer feed mainly in open grassy areas but must have some tree cover for protection from the elements and predators. The optimal habitat for fallow deer therefore is deciduous and mixed woodlands on gently rolling terrain. Red deer, the dominant deer species in Franchthi, are grazers by preference but can also feed on dwarf shrubs such as heather and other low quality browse, provided that conditions are relatively moist. They are also more tolerant of wet winds and cool, exposed conditions than are fallow deer.

The findings on the shell ornaments from Klissoura Cave 1 also speak to questions about the degree of environmental heterogeneity in southern Greece during the Late Pleistocene (Stiner, this issue). Although Klissoura 1 was never situated on the Aegaen shore during the Paleolithic or Mesolithic, the inhabitants visited the sea and other aquatic habitats, and they brought many small ornamental shells back to the site. These shells fall within a narrow range of sizes and shapes. However, the species collected during the earliest Upper Paleolithic phases are quite varied, whereas few species were utilized for ornamental purposes in the later occupations (above layers IIIg-e). The great variety of ornamental mollusk species in the assemblages from layers IV and V reflect a mosaic of aquatic habitats, more complex than exists in the Peloponnese today. The taxonomic diversity of the early Upper Paleolithic ornament assemblages from Klissoura 1 also greatly exceeds that of every post-Aurignacian ornament assemblage from Franchthi Cave (Shackleton, 1988; C. Perlès, personal communication, 2010). The more recent shell assemblages from Klissoura 1 and Franchthi invariably are dominated by just a few brackish water and lagunal mollusk species (*Columbella rustica* and *Cyclope* spp.). Reduction in taxonomic diversity in the marine shell types was almost certainly linked to changes in sea level.

Based on the dating and environmental data, the early Upper Paleolithic part of the Klissoura 1 cultural sequence correlates with an interstadial and the last minor high sea stand (ca. 35 kyrs calibrated BP), before the big drop in sea level that began about 30 kyrs (calibrated BP) and culminated in the LGM (Chappel, 2002; Wright *et al.*, 2009). The high sea stand in the early Upper Paleolithic helps to explain the great diversity of coastal and inland habitats, since elevated water tables would result in the formation of marshes, lagoons and sand bars. According to van Andel *et al.* (1990), for example, the northern part of the Argolis Gulf is an extended flat shallow area less than 50 m deep. During the last high sea stand of MIS 3a this area would have been only partly submerged and thus would have supported a wider range of aquatic habitats. The decline in sea levels thereafter probably also explains the abrupt decline in ornament shell diversity in the layers above IIIe-g in Klissoura 1.

HUNTING PATTERNS

Klissoura Cave 1 lies at the interface of rugged hills and a large plain, thereby providing access to a varied food supply. The site is located strategically where the gorge opens onto the upper Argos plain. There is no indication of mass hunting of ungulates at this site. Rather the data suggest opportunistic hunting of a variety of species, one or a few at a time (Starkovich and Stiner, this issue). As the local animal community changed with climate and vegetation, hunters responded opportunistically and pursued whatever ungulate species were available. There is the question of where the Upper Paleolithic inhabitants of Klissoura 1 obtained the ibex and chamois (layer IV only), since the area does not include true alpine habitats. In fact ibex may inhabit a much wider variety of elevations, provided that the terrain is rugged (Phoca-Cosmetatou, 2004). The low but persistent presence of ibex in the ungulate faunas may simply reflect the extent to which hunters chose to search craggy uplands nearby. Today chamois tend to occupy rocky or alpine areas, but they along with wild goats may descend to much lower, forested pastures in winter (Forsyth, 2000; Baumann *et al.*, 2005).

Small game exploitation at Klissoura 1 exhibit a pattern of increasing dietary breadth. Generally similar trends have been documented in other regions of the Mediterranean Basin (Tchernov, 1992; Hockett and Bicho, 2000; Stiner *et al.*, 2000; Stiner, 2001; Munro, 2004; Manne and Bicho, 2009). Specifically, there is a decrease through time in the proportion of small, slow-moving game species and an increasing reliance of more productive quick small animals such as hares and/or birds. At Klissoura 1, this trend begins around the time of the Middle to Upper Paleolithic transition (Starkovich, 2010), though occasional hare exploitation occurred before this time, in the late Middle Paleolithic. The relative contribution of small animals to the meat diet increased further in the most recent layers (3-5a, II), where the NISP counts for quick small game actually surpass those for medium-sized ungulates (Bocheński and Tomek, this issue; Starkovich and Stiner, this issue).

The shells of the large edible land snail, *Helix figulina*, also are prevalent in the late Upper Paleolithic through Mesolithic strata of Klissoura 1. Most of these were modified by humans rather than small predators, although none is burned by fire (Koumouzelis *et al.*, 2001; Starkovich and Stiner, this issue). The relative quantity of land snails in the archaeofaunas increases exponentially with time, and shell sizes become larger and more uniform. Specifically, land snails are rare in layers IV or V and show no clear evidence of human modification, whereas human-modified snail shells are moderately abundant in layer IIIc and increase greatly through layers III" and III, and snail abundance peaks in Mesolithic layers 3-5a. Epigravettian layer IIa-b represents a striking exception in that snails are uncommon and a wide range of tiny to large species are represented, similar to the natural snail assemblages that litter the ground in the site vicinity today. Snails are not difficult to find or collect after heavy rains, but cooking and extraction is relatively labor intensive.

Other findings on Upper Paleolithic subsistence at Klissoura 1 relate to large game hunting, specifically the patterns of prey age selection and food transport. Minor biases were found for body part representation in this site. These biases are not explained by *in situ* attrition and therefore must reflect human transport decisions. The parts of ungulate skeletons are fairly evenly represented, except for the scarcity of axial elements below the neck. Nearly all meaty parts of carcasses were brought to the site for processing, and axial parts were often left at or near the kill sites. In fact the dressed weight for most of the prey animals would not have exceeded what a few hunters could carry back to camp within a day. The mortality patterns of the ungulates indicate fairly even representation of young, prime adult and old adult individuals in all layers except the early Aurignacian (IV), where old adults are less well represented. The lack of strong age biases in the ungulate faunas suggests a consistently emphasis on encounter hunting, without focusing on sex-sorted herds.

Small quantities of fetal or neonate remains are present in the ungulate assemblages throughout the sequence, and most of these represent unborn animals. Hunting of pregnant female fallow deer must have taken place before or during the spring birthing season (late May–June). Other seasons of occupation are not necessarily excluded by these findings, however, since the phytolith evidence from layers IIIg, and to a lesser degree in IIIe, indicates the presence of grass flowers. In modern Greece, grasses may begin blooming in March, but most inflorescenses develop from April to June, and at much lower frequencies from July to September (Albert, this issue). Hearths and large volumes of wood ash are also a major component of the Klissoura 1 record, and some of the occupations must have included cool months of the year.

Deer antler is proportionately common in the Mesolithic (3-5a), though this is a small sample, and in layers III", IIIe-g, IV, and V (also a small sample). Worked antler and (rarely) bone artifacts occur in all of the layers, but most of these are from Aurignacian layers IIIe-g and IV. The layers that contain the most antler fragments of any sort generally also contain the most worked antler artifacts, with the exception of the Mesolithic (Starkovich and Stiner, this issue). Microscopic analysis of the antler fragments revealed few unequivocal examples of trimming debris from antler working, but the lack of such evidence in this site may be explained by the extensive breakage of the antler by the humans and post-depositional microsurface alterations (Christidou, personal communication, 2010).

Male fallow deer possess antlers from roughly July to April (Chapman and Chapman, 1975), and the antlers harden in time for the autumn rut. Some of the male fallow deer in the Upper Paleolithic Klissoura assemblages therefore must have died in the colder months of the year (autumn through early spring). It is possible, however, that antler was collected and curated over long periods in anticipation of tool-making. Thus the presence of antler in direct connection with osseous tool-making may not provide a reliable indication of the season of occupation.

PALEOLITHIC ORNAMENTS

Shell ornaments occur throughout the Upper Paleolithic, Epipaleolithic and Mesolithic layers (Stiner, this issue). As is generally true of the Upper Paleolithic in Europe, the ornament assemblages from Klissoura Cave 1 are well developed in character. The earliest Upper Paleolithic ornaments occur in layer V in association with an Uluzzian industry. The largest assemblage of ornaments comes from the earliest Aurignacian or layer IV. There are a few ornaments in layers VI–VII, but most of these were found immediately below the area of the man-made shelter in layer IV. Layer V does not extend to this area of the excavation, and taphonomic evidence and direct dating of some of the shells (K. Douka, personal communication, February 2010) indicate that the shells in VI–VII represent very localized downward intrusions from layer IV.

The Klissoura 1 ornament assemblages differ from those typical of coastal sites in that the Klissoura 1 assemblages consist almost exclusively of finished products. There is considerable evidence of "high-grading" or human selection of the assemblages for harmony in shell color, form and quality, and there are few, if any, examples of manufacturing errors. The prevalence of cord-wear suggests that many of the ornaments arrived already attached to organic materials or human bodies. What breakage occurred to the shells resulted primarily from long-term use. Faded or worn shells of species that would have originally been red in color (*Clanculus* spp.) were renewed with red ochre.

The ornament assemblages from the earliest Upper Paleolithic layers are particularly rich in species. The high frequency of *Dentalium* (tusk) shells nonetheless sets the small Uluzzian ornament assemblage apart from the Aurignacian and later bead assemblages in the site. *Dentalium* shells are also prominent in the Uluzzian horizons of Grotta del Cavallo in southern Italy (Palma di Cesnola, 1966), though sample size variation may be a complicating factor.

The ornament is considerable variation in abundance through the Upper Paleolithic and Mesolithic layers in Klissoura 1 is not explained by differences in the thickness of the excavated layers. As noted above, the assemblage from the earliest Aurignacian layer IV is exceptionally large, and most of the ornaments from this layer occur within the inferred perimeter of the man-made shelter, ringed by large stones. This feature is surrounded by hearths but none occurs within the inferred area of the shelter where the ornaments are concentrated.

SITE FUNCTION AND OCCUPATION INTENSITY

The variety of features, artifacts and faunal remains in the early Upper Paleolithic layers of Klissoura 1 indicate that the site served as some kind of residential base during most or all of these occupations. The intensity or duration of the occupations probably varied greatly, however, with the most intense use of the site occurring during the formation of Aurignacian layers IV and IIIe-g. In addition to many clay-lined and unlined hearths, these layers contain a diverse assortment of lenses, pits and other features. Antler points and probable manufacturing debris, mainly on antler, are particularly abundant in layer IV. Unlike the situation in the layers above, where osseous artifacts are widely scattered among horizontal units, worked antler speciments are spatially concentrated within and around the immediate area of the shelter feature in layer IV (Christidou, personal communication, 2010).

The indications of human activities are only somewhat less varied in the later part of the Upper Paleolithic-Epipaleolithic sequence. Unfortunately, the upper layers suffered from greater amounts of erosion or disturbance, possibly reducing the diversity of visible activity areas. For example, the material in layers 6, 6a and 6/7, which includes a mixture of Aurignacian and other artifacts, represents material that was dumped episodically into a large pit. Its sediment is homogenous, generally loose and porous, and the matrix is almost pure ash and contains more than the usual proportion of fragmented lithic debitage. Normally such concentrated refuse would associate with an intensive occupation, but we find no horizontal layer associated with the pit. A significant erosional hiatus is apparent in this part of the stratigraphic column (Karkanas, this issue), however, and some sediment may have been lost during the LGM.

Plant phytoliths are abundant in most of the Upper Paleolithic sediment samples, but they generally are not found in the hearths. The contrast in phytolith distributions between hearths and open areas testifies to the horizontal integrity of features in the Upper Paleolithic layers, consistent with the geological observations. The input of plant matter into fireplaces was selective – mainly dicotyledonous wood and bark-producing plants. It is the grasses that show the greatest spatial separation from the hearths. The abundant grass inflorescences in Layer IIIe-g may point to their use as food, or the harvesting of mature stems for fiber working or bedding. Small amounts of sedge phytoliths in layer IV, and reed phytoliths in layers II and III-III' could also relate to fiber working on site. There is considerable evidence of osseous technology use and production on site (Christidou, personal communication, 2010), particularly in layers III'' IIIe-g and IV. Plant fiber working and hunting may rank among the many potential uses of these tools. Clearly, a wide range of activities took place in the cave, a situation typical of base camps.

The record of fire use in the Upper Paleolithic layers of Klissoura 1 is unusually complex (Karkanas *et al.*, 2004; Karkanas, this issue). Hearths are often superimposed in Klissoura 1, with repeated building and maintenance of fires in certain areas of the site. The function of the clay-lined hearths in the Aurignacian layers is difficult to interpret from the sparse wood charcoal remains alone. However, the scarcity of charcoal in these layers might be the result of intentional production of hot embers for use in the clay hearths. Embers – the incandescent stage of a fire – allow one to exploit the properties of conduction and convection to heat a small, semi-enclosed space. Complete combustion from continuous stoking of embers would destroy most of the wood charcoal produced in these fires. Embers may also be used to cook food indirectly with radiant heat, for drying and curing of food and other materials, and possibly heating sweat lodges (saunas). Ember transfer and multiple uses of hearths likely occurred during the formation of the Upper Paleolithic layers, particularly in layers where clay-lined hearths co-occur with unlined hearths.

CONCLUSION

The Paleolithic deposits in Klissoura Cave 1 preserve a well-ordered stratigraphy that covers a large portion of the Late Pleistocene Middle Paleolithic and Upper Paleolithic, along with Epipaleolithic and Mesolithic components. The Upper Paleolithic record is especially well preserved and complex due to a dense assortment of intact features and artifacts. These cultural components provide a rich and only partly overlapping complement to the Paleolithic record of Franchthi Cave on the southern Argolid.

Among the important findings of this research on the Upper Paleolithic through Mesolithic in Klissoura Cave 1 are the identification of an early Uluzzian occupation in layer V that may be more than 39,000 years old, the first Upper Paleolithic occupation in the stratigraphic series, followed by a long and relatively well-dated Aurignacian sequence. Ornament assemblages appear suddenly with the onset of the early Upper Paleolithic (Uluzzian) in this site, and all intact (unmixed) Middle Paleolithic layers that underlie the Upper Paleolithic lack ornaments entirely. Some inter-stratification of Aurignacian, later Uluzzian-like (III'') and Gravettoid (III') components is suggested on the basis of formal artifact types. The lithic industries in some layers of Klissoura 1 show demonstrable, periodic links to Paleolithic populations in ltaly, particularly the Uluzzian of layer V.

Zooarchaeological findings indicate early increases in dietary breath during the Upper Paleolithic, consistent with trends observed in other Mediterranean areas where this phenomenon has been studied intensively. Diets expanded further during the later Paleolithic and Mesolithic occupations. The small game trends in Klissoura 1 and other Mediterranean faunal sequences are not explained by climate driven environmental changes, since they persist through MIS 3 and generally intensify in MIS 2 (Stiner, 2001).[3]

Paleoenvironmental data from the studies of intact charcoal fragments, plant phytoliths, sedimentary characteristics, and animal species representation indicate moderate changes in moisture availability over the Upper Paleolithic through Mesolithic sequence. Overall, dry conditions prevailed in the area throughout the Upper Paleolithic, but moisture availability was somewhat greater during the formation of layers V and IV. Local environments became drier and cooler during the formation of the middle and upper Aurignacian layers and more so through the Epipaleolithic. Moisture availability increased again only in the Mesolithic.

Important hiatuses marked by erosion events separate the Middle and Upper Paleolithic sedimentary groups. There is no seamless transition between the two cultural entities in this site. Depositional hiatuses also separate the Uluzzian from the earliest Aurigancian, and the Upper Paleolithic layer series from the Epipaleolithic. There is no record of human occupation at Klissoura 1 during the Last Glacial Maximum nor, apparently, at the nearby site of Franchthi Cave (Farrand, 2000).

Klissoura Cave 1 provides considerable detail about the daily existence of Upper Paleolithic foragers at one site. The sedimentary features, artifacts and animal remains testify a wide range of on-site activities that is typical of residential bases. Anthropogenic processes greatly shaped the character of the Upper Paleolithic through Mesolithic sediments, particularly the many cycles of hearth building, cleaning, renovation and trampling. Humans were also the main sources of disturbance in the cave deposits, as the result of creating and cleaning hearth basins, clearing activity surfaces, and digging small pits. The remarkable clay hearths of Klissoura 1 Aurignacian are unique as of this writing, and may have been used as satellite fire installations to which hot coals were moved for the purposes of cooking or heating activity areas. The intensity of the occupations seems to have varied over time, with those of layer IV being particularly intense. Greater post-depositional disturbances to the later layers may have undermined the visibility of features, and thus the relative intensity of the later occupations is more difficult to judge, but site use does seem to have been lighter during the Epipaleolithic and Mesolithic.

The cultural sequences identified at Klissoura Cave 1 and at other important sites in southern Greece (see Perlès, 1987, 1999 on Franchthi Cave; Panagopoulou *et al.*, 2002–2004 on Lakonis) testify to significant regional differences the classic chronologies of western and central Europe beyond the Balkans (e.g., Kozłowski, 1999). As might be expected for a part of the world defined by distinctive ecosystems and a uniquely broken and diverse topography, there is much evidence for regional or "endemic" patterns of cultural evolution. While processes that promote cultural divergence are to be expected for peninsular conditions, as the Peloponnese certainly represents, there were also significant intervals of increased contact westwardly across the upper Adriatic seabed, such as during the Uluzzian.

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Notes

1. The ages of the cultural layers differ; the early UP in Klissoura 1 is older, and there is a major gap in cultural material between 27–16 kyrs BP at Klissoura 1; Franchthi is particularly rich in deposits containing "Gravettoid", Final Paleo- lithic and Mesolithic industries (Perlès, 1987; Farrand, 2000).
2. Payne mentions having found a few fallow deer bones in Franchthi Cave, but this diagnosis remains unclear.
3. Data on a variety of higher latitude archaeo- faunas in continental Europe (e.g., Berke, 1984; Jochim, 1988) indicate related but significantly later shifts in dietary breadth.