ARTICLE IN PRESS

Quaternary International xxx (2017) 1–18

Contents lists available at ScienceDirect

Quaternary International

journal homepage: www.elsevier.com/locate/quaint

The Palaeolithic record of Greece: A synthesis of the evidence and a research agenda for the future

Vangelis Tourloukis [a, b, *], Katerina Harvati [a, b]

[a] *Palaeoanthropology, Senckenberg Centre for Human Evolution and Palaeoenvironment, Eberhard Karls Universität Tübingen, Rümelinstrasse 23, 72070, Tübingen, Germany*

[b] *DFG Centre for Advanced Studies 'Words, Bones, Genes, Tools: Tracking Linguistic, Cultural and Biological Trajectories of the Human Past', Eberhard Karls Universität Tübingen, Rümelinstrasse 23, 72070, Tübingen, Germany*

ARTICLE INFO

Article history:
Received 12 August 2016
Received in revised form
9 February 2017
Accepted 24 April 2017
Available online xxx

ABSTRACT

The Palaeolithic record of Greece remains highly fragmented and discontinuous in both space and time. Nevertheless, new surveys and excavations, along with the revisiting of known sites or old collections, and the conduction of lithic and faunal laboratory analyses, have altogether enriched the Greek Palaeolithic dataset with important new evidence and novel interpretations. The goal of this paper is threefold: 1) to critically review the most important aspects of the Greek Pleistocene archaeological record, from the Lower to the Upper Palaeolithic; 2) to provide a synthesis of current knowledge about the Palaeolithic of Greece and in the framework of broader discussions in human evolution research; and 3) to put in prospect the Greek record by addressing a research agenda for the future. The review of the evidence shows that Palaeolithic research in Greece has expanded its focus not only geographically but also temporally: it now includes investigations at previously under-studied areas, such as the insular settings of the Aegean and Ionian Seas, as well as formerly overlooked targets, such as Lower Palaeolithic open-air sites. The synthesis and discussion which follows offers a state-of-the-art perspective on how the primary Palaeolithic data can be assessed within local or regional geomorphic, paleoenvironmental and chronological contexts; here, our focus is on spatio-temporal discontinuities, trends in subsistence strategies and lithic technology, as well as potentially emerging biogeographical patterns. Finally, we highlight the complex topography and mosaic landscapes of the Greek peninsula in order to address two major themes for a future research agenda: the potential role of Greece as a glacial refugium, and how the Greek record could contribute to our knowledge of early hominin mobility patterns.

1. Introduction

The Palaeolithic period is generally understudied in Greece, because research has traditionally focused on the later parts of prehistory (Neolithic, Bronze Age) and the Classical times. Nevertheless, significant advances have been achieved during the last years and the record has been enriched with new material, collected mostly in the framework of regional surveys but also through systematic or rescue excavations. Not only new caves and rockshelters (Darlas and Psathi, 2016), but also recently discovered and important open-air sites are now being excavated (Panagopoulou et al., 2015; Galanidou et al., 2016). A seemingly growing interest on the latter type of sites may be signalling the onset of a long-awaited paradigm shift in Greek Palaeolithic research, which will help remedy the imbalance towards Middle and Upper Palaeolithic sheltered contexts. It is noteworthy that the excavation works currently being conducted at two Lower Palaeolithic open-air sites, Marathousa 1 and Rodafnidia, are the first ones in Greece to target open-air sites of this period. The Palaeolithic record of Greece has been expanded also geographically and includes now areas that would have been largely ignored a few decades ago, such as the highlands of the Pindus Mountain Range (Efstratiou et al., 2006), or the insular settings of the Aegean Sea (e.g. Carter et al., 2014; Runnels, 2014; Runnels et al., 2014b). Furthermore, alongside critical reviews (e.g. Papoulia, in press), a number of new specialized and/or interdisciplinary studies have

* Corresponding author. Palaeoanthropology, Senckenberg Center for Human Evolution and Palaeoenvironment, Eberhard Karls Universität Tübingen, Rümelinstrasse 23, 72070, Tübingen, Germany.

E-mail addresses: vangelis.tourloukis@ifu.uni-tuebingen.de (V. Tourloukis), katerina.harvati@ifu.uni-tuebingen.de (K. Harvati).

http://dx.doi.org/10.1016/j.quaint.2017.04.020
1040-6182/

appeared, which either examine lithic or faunal assemblages (e.g. Ligkovanlis, 2011; Papoulia, 2011; Starkovich, 2014) or integrate the archaeological signatures within local or regional paleoenvironmental, climatic, geological and chronological frameworks (e.g. Karkanas, 2002; Ntinou, 2010; Kuhn et al., 2010; Athanassas et al., 2012; Tsartsidou et al., 2015; Karkanas et al., 2015).

Our aim here is not to provide a detailed account of the substantial body of evidence that has accumulated in recent times. Rather, the goal is to distill from it a synthesis of the Palaeolithic of Greece, which has been missing from the literature for over twenty years, since the publications of Darlas (1994), Kourtessi-Philippakis (1995) and Runnels (1995); with regard to the relevant paleoanthropological material, we refer the reader to the reviews by Harvati et al. (2009) and Harvati 2016). In this study, we first assess the most important sites per period, including new data from our own on-going field work. Then, we contextualize this corpus of both older and more recent material, by focusing on the spatio-temporal distribution of sites and related gaps in the record, the emerging biogeographical patterns, and the knowledge gained about subsistence strategies and hominin adaptations in the mosaic landscapes of the Greek peninsula. Finally, in suggesting an agenda for the future, we briefly address research questions and hypotheses that we consider worthwhile to be further investigated and tested against the empirical record.

2. The Lower Palaeolithic record

Lower Palaeolithic sites and findspots are extremely few, ill-dated and scattered on disparate locations across the mainland and the Aegean islands. A critical assessment of the Greek Lower Palaeolithic record has been detailed elsewhere (Tourloukis, 2010) and demonstrated the lack of archaeological material that can be securely attributed to the Early Pleistocene. If we exclude finds and sites with questionable stratigraphic associations and/or lacking good chronological control, there are currently only four sites that can be assigned to this period on chronostratigraphic grounds: Marathousa 1 in Megalopolis (Peloponnese), Rodafnidia (Lesvos), Kokkinopilos (Epirus) and some of the Plakias localities (Crete) (Fig. 1). Besides Marathousa 1, which dates to around 500–400 ka BP (see below), the rest of the sites have yielded minimum ages that place them at the latest parts of the Middle Pleistocene.

The important cranium from the Petralona Cave has been dated to ca. 150–250/350 ka BP (Grün, 1996). The original stratigraphic position of the specimen is unknown and it cannot be associated with any of the rich faunal assemblages. Some lithic material that is claimed to derive from inside the cave lacks any provenience data, it has not been published properly and its artificial character is questionable, especially because the purported ‘industry’ is made on quartz and includes basically amorphous ‘cores’ and ‘tools’ made on debris (Darlas, 1995; Harvati et al., 2009).

Marathousa 1 (MAR-1) is an open-air site located in one of the lignite mines of the Megalopolis basin, which has long been known for its rich Pleistocene paleontological localities (e.g. Melentis, 1961). A hominin tooth that was collected in the 1960's as a surface find (Sickenberg, 1975), as well as a report on possible Middle Palaeolithic finds (Darlas, 2003) indicated the potential of the area for yielding paleoanthropological finds. Nevertheless, the first systematic archaeological investigations in the basin began only recently by a collaboration between the Ephoreia of Paleoanthropology and Speleology (Greek Ministry of Culture) and the University of Tübingen in the framework of the PaGE Project (Harvati and Tourloukis, 2013; Panagopoulou et al., 2015). MAR-1 was discovered in 2013 during survey, when lithic artifacts and elephant skeletal remains were observed eroding out of a profile. Thus far, systematic excavations during two field seasons (2014, 2015) have revealed the presence of lithic artifacts in stratigraphic association with elephant and other faunal remains, such as carnivores, bovids, cervids, micromammals, turtles and birds. An elephant cranium and several postcranial elements were found in close anatomical association and most likely belong to a single individual, which has been attributed to *Elephas (Palaeoloxodon) antiquus* on the basis of the cranio-dental morphological characteristics (Fig. 2). Some of the elephant bones, as well as remains from middle-sized mammals, bear striations that have been preliminary interpreted as anthropogenic cut-marks (Harvati et al., 2016). A detailed taphonomic analysis of those specimens is underway. The lithic assemblage is composed of small-sized flakes and flake fragments, cores, retouched tools and chunks/shattered pieces (Fig. 3; Panagopoulou et al., 2015; Harvati et al., 2016). Platforms are mainly plain, cortical or dihedral, and indicate hard hammer percussion. Flake scar patterns, core reduction modes and other technological traits suggest relatively simple operational sequences, which aimed mostly at the production of flake blanks. Possible traces of use wear have been macroscopically identified in a number of retouched tools, but also on plain flakes, suggesting that the latter could have been used directly for tasks such as cutting, without further modification. Overall, a key aspect of the industry refers to its 'microlithic' character: in their majority, debitage products are ca. 2 cm-long or less. So far, there are no indications of bifacial debitage and Large Cutting Tools are absent; this is all the more interesting, considering that the very first report on Palaeolithic finds from Greece referred to a handaxe from Megalopolis, which was reportedly found in association with elephant bones (Lenormant, 1867). Nevertheless, the lithic industry recovered up to now from MAR-1 fits well in a group of important sites with flake-based, small-tool, non-handaxe assemblages, such as Ficoncella, Isernia and La Polledrara (Italy), Schöningen and Bilzingsleben (Germany), Vértesszőlős (Hungary), Caune de L'Arago (France), and Revadim (Levant), many of which, like MAR-1, also preserve evidence for elephant or other mega-fauna exploitation by early humans (see e.g. Rocca et al. in press; Aureli et al., 2016 and references therein). Preliminary observations suggest that the small size of the specimens is related to raw material attributes, namely the original (small) size of radiolarite and flint pebbles, as well as the mediocre quality of the raw materials, which bear a lot of cleavage plains and impurities. The find-bearing layers occur between two lignite seams and are composed of silty sands. The context of the site likely represents a low-energy depositional environment, such as a shallow-water swamp close to the shore of a lake. Fast burial in a very fine-grained matrix ensured extraordinary preservation conditions for the faunal and lithic material, but also for paleobotanical micro- and macro-remains (Panagopoulou et al., 2015; Harvati et al., 2016). The find-bearing strata of MAR-1 belong to the Marathousa Member of the Choremi Formation and are part of the detrital interval that occurs between Lignite seams II and III (Löhnert and Nowak, 1965; Vinken, 1965). According to the chronostratigraphic model of van Vugt et al. (2000) those deposits between Lignite II and III correlate to marine isotope stage (MIS) 16, while according to Okuda et al. (2002) they date to MIS 14. ESR dating of a mollusk sample from a unit overlying the find-bearing layers provided a minimum age for this unit at 414 $\pm$ 42 ka, while five subsamples of a cervid tooth excavated from the find horizon gave an age of 484 $\pm$ 13 ka (Blackwell et al., 2016). Consequently, first results from radiometric dating place the site at ca. 500–400 ka, making it currently the oldest dated open-air site in Greece and South East Europe.

The site of Rodafnidia, in Lesvos, was discovered by chance by Charisis and colleagues, who reported in 2000 on the wealth of Middle and Lower Palaeolithic finds that they observed lying on the surface of an olive grove. The site is located 2 km South-West from

Fig. 1. Map of Greece showing key Lower Palaeolithic and/or Middle Pleistocene archaeological and paleoanthropological sites, as well as key sites with pollen records mentioned in text. M = Megalopolis, P = Petralona Cave, A = Apidima Cave; I = Ioannina pollen record, T = Tenaghi Philippon pollen record. 1: Marathousa-1; 2: Rodafnidia; 3: Kokkinopilos; 4: Plakias sites.

the Kalloni Gulf, a shallow basin with Plio-Pleistocene fluvio-lacustrine deposits. At the eastern part of the island, the Mytilene Strait that now separates Lesvos from Turkey, is only 50 m deep, hence a 50 m-drop of the sea-level during glacials would have exposed the Strait, enabling terrestrial migrations of animals and humans —a fact that is confirmed by the 'continental' character of the Pleistocene fauna of Lesvos (Charisis et al., 2000). The authors identified characteristic Levallois products (Levallois 'tortoise' cores, points and flakes), as well as other typical Middle Palaeolithic tools (scrapers with Quina retouch, dejeté scrapers, denticulates, limaces, couteau à dos naturel, perçoirs, burins), which co-occurred with bifaces of Acheulean morphology. On the basis of the co-occurrence of Levallois and Acheulean specimens, they postulated an age at the end of the Lower Palaeolithic ("ca. 200 ka BP"). Survey investigations were initiated in 2010 and were followed by systematic excavations starting in 2013, confirming the main conclusions of the earlier report: Rodafnidia is a spatially extensive open-air site with abundant Middle and Lower Palaeolithic surface lithic finds (Galanidou et al., 2013). The excavations have shown that lithic artifacts occur inside a deposit of river conglomerates that belong to a channel fill (Unit 1). Artifacts that have been assigned to a 'Prepared Core Technology (PCT) techno-group', e.g. classic Levallois products, are being found together with Acheulean 'Large Cutting Tools' (LCT's). The authors therefore note that "the presence of Levallois may signal an Acheulean with PCT or the presence of a Middle Palaeolithic assemblage" (Galanidou et al., 2016). Noteworthy is also the presence of a flake cleaver deriving from the excavation, as well as a surface find that is possibly a cleaver, too. Overall, the lithic assemblage of Rodafnidia is said to have a distinct "African flavour" and to "demonstrate the presence

Fig. 2. Marathousa 1, Excavation Area A: elephant skeletal remains exposed during the 2014 field season; the white plaster-jacket covers the cranium. Reproduced from Panagopoulou et al., 2015.

Fig. 3. Artifacts from the Lower Palaeolithic site of Marathousa 1, Megalopolis. Reproduced from Panagopoulou et al., 2015.

of Early Stone Age Acheulean hunters in this locality and possibly Middle Stone Age hominins associated with PCT (Levallois) technology" (Galanidou et al., 2013). Moreover, the excavators consider the artifacts from Rodafnidia to resemble those from the sites of Kaletepe Deresi (Turkey), Gesher Benot Ya'aqov (Israel) and sites in the Olduvai Gorge (Africa) (Galanidou et al., 2016). Notwithstanding possible typological affinities with material from the above-mentioned sites, which date to ca. 800 ka BP (Gesher Benot Ya'aqov) or even older (Kaletepe Deresi, Olduvai sites), luminescence dating for the Rodafnidia find-bearing streambed deposit (Unit 1, directly underlying the topsoil) produced ages of 164 $\pm$ 33 ka and 258 $\pm$ 48 ka BP, placing the site at the end of the Middle Pleistocene (Galanidou et al., 2016).

In Epirus, the site of Kokkinopilos lies in a small fault-bounded basin, which used to host a shallow lake that would periodically dry out and become a marsh. Kokkinopilos exemplifies a very particular type of open-air sites, which consist of red deposits (*terra rossa)* and are known as 'red-bed sites'. Since the 1960's (Dakaris et al., 1964; Higgs and Vita-Finzi, 1966), it has been established that these red-beds are almost always associated with Palaeolithic artifacts —in fact, some of them are littered with tens of thousands of stone-tools, most of which are attributed to the Middle Palaeolithic. The interpretation of this association has been the subject of a long and intense discussion (see Tourloukis, 2010 and references therein). The red-beds have until recently been regarded as a fortuitous admixture of archaeological remains from different periods: sites with reworked deposits that essentially provide no context for the artifacts, cannot be dated and are of low archaeological value. Consequently, none of these sites has yet been excavated. A latest study, however, has rejected the aforementioned view, showing that red-bed sites *can* be excavated and dated (Tourloukis et al., 2015). The latter work focused at Kokkinopilos and demonstrated the presence of archaeological evidence that is geologically *in situ*: pedo-stratigraphic criteria can be used to distinguish artifact occurrences and define lithic assemblages. The red-bed sites represent small paleo-lakes (Macleod and Vita-Finzi, 1982; van Andel, 1998). While the lakes were only seasonal at some localities, other sites would retain perennial water bodies. Paleosol horizons represent intervals of dry conditions with subaerially exposed surfaces (Runnels and van Andel, 2003). Artifacts stratified inside paleosols point to the presence of hominins when the lakes were dry, while artifacts found in sediments that were deposited underwater indicate exploitation of the sites when the lakes were active (van Andel and Runnels, 2005; Tourloukis et al., 2015). The fine-grained sediments and the fresh condition of the artifacts suggest very low energy processes and indicate minimum transport of the lithics from their original places of discard. There are artifact assemblages of homogeneous nature in terms of raw material type, degree of patination and typo-technological traits. These occur either as archaeological horizons visible in profiles and sealed within palaeosols (Fig. 4); or as clustered, surface occurrences that have undergone minimum, if any, dislocations. In both cases, Tourloukis et al. (2015) were able to securely assess that, instead of being later intrusions post-dating the geological sequence, the finds are *in situ* and belong to the same time-span represented by the deposits/palaeosols in which they occur (Runnels and van Andel, 1993a, 2003a; Tourloukis, 2010). At Kokkinopilos, radiometric dating indicated that a lithic component, which includes bifacially-shaped specimens, is older than ca. 170–200 ka; however, due to the absence of proper technological analysis based on an adequate sample of implements from excavated contexts, it is not yet possible to ascertain whether this component should be attributed to a late Lower or to an early Middle Palaeolithic techno-complex (Tourloukis et al., 2015). That said, we tentatively propose that, in addition to Upper and Middle Palaeolithic material, Kokkinopilos likely preserves also a Lower Palaeolithic component. We argue this on the basis of two observations: 1) Kokkinopilos Unit B, which has yielded a stratified Micoquian-type handaxe (Runnels and van Andel, 1993a) returned a minimum age of >200 ka; and 2) on current evidence, the earliest-dated appearance of the Middle Palaeolithic in Greece dates to ca. 130 ka and therefore significantly postdates it (Theopetra Cave; Karkanas et al., 2015; see also discussion below). Nevertheless, this hypothesis remains to be tested with subsurface investigations.

A similar question (Lower or -early- Middle Palaeolithic?) surrounds the lithic assemblage from the area of Plakias, Crete, where Palaeolithic artifacts, some of which are attributed to the Acheulian tradition, were found at eight open-air localities during a survey that originally targeted —and eventually discovered— Mesolithic sites (Strasser et al., 2010). While most of the artifacts were collected as surface finds, a number of specimens derived from undisturbed geological contexts (paleosols formed on alluvial deposits, and marine terraces), which have yielded *minimum ages* of ca. 114–130 ka on the basis of marine terrace uplift rates and pedogenic maturity stages of paleosols anchored on ^{14}C and OSL radiometric dates (Strasser et al., 2010, 2011; Runnels, 2014; Runnels et al., 2014a). The researchers carefully remark that the artifacts “may belong to more than one Palaeolithic industry, including in traditional terms the Lower and Middle Palaeolithic” (Strasser et al., 2010). The Acheulian component of the assemblage numbers 211 artifacts made mostly on quartz but also quartzite, chert and igneous greenstone, and consists of LCT's (handaxes, cleavers and trihedral pics), scrapers, denticulates, notches and large cores (Runnels et al., 2014a). In light of ample paleontological, paleogeographic and biogeographic evidence demonstrating that Crete remained disconnected from the mainland throughout the Pleistocene (see Runnels, 2014 and references therein), the Cretan finds have stirred up the discussion about water crossings by early hominins in the Mediterranean (e.g., see articles and debate in the *Journal of Mediterranean Archaeology*, issue 27.2; Howitt-Marshall and Runnels, 2016). As regards the Plakias finds, there are four key questions relevant to this discussion: 1) are these true artifacts; if so, 2) are they Palaeolithic; if yes, 3) how old are they; and 4) what are the implications in terms of early human sea-crossing capabilities (and, by extension, cognitive abilities and maritime

Fig. 4. Kokkinopilos: paleosol horizon with artifacts exposed *in situ*; inset: closer view of an artifact half-buried *in situ*. The artifacts are white because they are heavily patinated.

Please cite this article in press as: Tourloukis, V., Harvati, K., The Palaeolithic record of Greece: A synthesis of the evidence and a research agenda for the future, Quaternary International (2017), http://dx.doi.org/10.1016/j.quaint.2017.04.020

adaptations)? Our interpretation of the evidence is that these specimens are, for the most part, not geofacts. Secondly, convincing argumentation and illustrations have been published, demonstrating that this lithic material is distinguishable from the Mesolithic finds in techno-typological terms. Furthermore, it is also generally not found in the same places as the Mesolithic. We consider this component Palaeolithic and, based on the published accounts, we see no reason to ascribe it to the Upper Palaeolithic (UP): it can be described as Lower or Middle Palaeolithic, *or*, as an assemblage with time-transgressive characteristics that occur during both of the latter periods. Thirdly, although the dating can be improved, it is supported by radiometric ages and it is not simply typological, i.e. based on the cultural ascription of the finds; as such, the dates can be at present considered as supporting an attribution of the material to a period preceding the UP. Yet, anything beyond such a cautious conclusion clearly enters the realm of speculation, and we feel that equations among hominin species and artifact taxonomies (e.g. see comments to Runnels' article in *JMA* issue mentioned above) are unwarranted at this stage of the research. The most parsimonious hypothesis about access to Crete, at least during periods of lowered sea-levels, entails two alternative routes: from the west, by way of emerged terrestrial platforms that would have connected the SE end of Peloponnesus with Kithira and Antikithira; and from the east, by 'island hoping' through Rhodes and the adjoined islands of Karpathos-Kassos (Tourloukis, 2010: 171). In contrast to a direct crossing of the Libyan Sea from N. Africa, those routes would have required relatively short sea-crossings; in this sense, while *seagoing* to Crete can be credibly proposed, adept *seafaring* needs not be invoked until further refinement of the local paleogeography demonstrates that significantly longer sea-crossings were necessary, or until other lines of evidence provide clues for direct links with the coastal areas of Africa or the Near East. All the same, evidence from other Aegean and Ionian islands, which might have been separated from the mainland during certain time-spans in the Pleistocene, such as Naxos (Carter et al., 2014), Alonnisos (Panagopoulou et al., 2001), Gavdos (Kopaka and Matzanas, 2009), Kefalonia and Zakynthos (Kourtessi-Philippakis, 1999), altogether indicate that, some (as yet unknown) hominin species was/were able to engage in modest maritime crossings at latest by the Middle Palaeolithic. On the other hand, since large parts of the Aegean Sea (perhaps half of it) may have been subaerially exposed during most of the early-middle Pleistocene (Mountrakis, 1985; Lykousis, 2009), a 'terrestrial-wetland Aegean' could have played a central role in hominin dispersals, both as a biogeographical land-bridge and as a biologically highly productive landscape, favorable for hominin occupation (Tourloukis and Karkanas, 2012).

3. The Middle Palaeolithic

With a total of ca. 240 sites, the Middle Palaeolithic (MP) of Greece is the best represented of all three periods; most sites are located in Epirus and the adjacent Ionian islands (ca. 100 sites), followed by the Mani, Argolid and Elis regions in the Peloponnese (Fig. 5; Elefanti and Marshall, 2015). Over 90% of the MP sites are open-air, but only a handful of MP open-air sites have been systematically excavated. Those were essentially rescue excavations of sites that are very broadly chronologically bracketed on the basis of the typo-technological characteristics of the lithic assemblages (e.g. Palli and Papadea, 2004). As a result, the backbone of the Greek Middle Palaeolithic is essentially restricted to five cave sites, which offer relatively thick sequences and archaeological material that has been dated with chronometric methods: Asprochaliko in Epirus, Theopetra in Thessaly, Kalamakia and Lakonis in Mani, and Klissoura in the Argolid (Fig. 5). To these can be added the recently excavated cave site "Mavri Spilia", located on the Western coast of the Mani peninsula (Tourloukis et al., 2016).

The Asprochaliko rockshelter was for some time considered a reference site for describing Mousterian variability in Greece. Its basal MP levels produced abundant laminar Levallois specimens and were dated by thermoluminescence (TL) to ca. 100 ka BP (Huxtable et al., 1992). The upper Mousterian industry is characterized by the absence of Levallois and the presence of small-sized pseudo-Levallois points on flakes shaped by use of an original method for the production of triangular blanks (Papakonstantinou and Vassilopoulou, 1997), and is imprecisely ^{14}C-dated to >39.9 ka BP (Bailey et al., 1983). In central Greece, recent re-dating of the MP levels at the cave of Theopetra pushed back the earliest use of the cave at the transition from MIS 6 to MIS 5 (Valladas et al., 2007; Karkanas et al., 2015). Three technological phases have been identified in the MP industry, from bottom to top: a Quina Mousterian, a Levallois Mousterian, and a phase transitional to the Upper Palaeolithic (Panagopoulou, 2000); however, the identification of the Quina Mousterian and the phase 'transitional-to-UP' have been questioned (Darlas, 2007). In light of the new chronology, the original interpretation of the typo-technological changes observed in the MP layers (Panagopoulou, 1999), will have to be re-evaluated (Harvati et al., 2009; Karkanas et al., 2015). Further south, in the Peloponnese, the earliest of the six MP layers of the Klissoura Cave 1 were most likely deposited during sub-stages of MIS 5, and the later MP layers were formed during MIS 4 and 3 (Starkovich, 2014), while there is a date of ca. 53 ka BP for the youngest level (see Kuhn et al., 2010 for a detailed discussion of the Klissoura radiocarbon dates). Throughout the MP sequence there is a high degree of homogeneity in artifact types and assemblage composition, with a gradual replacement of Mousterian forms by Upper Palaeolithic tool types (Sitlivy et al., 2007). All levels present a low Levallois index and the most common reduction techniques were the (mostly non-Levallois) unidirectional or discoidal and centripetal methods, with small, heavily reduced cores and small-sized tools and blanks. Perhaps counterintuitively, the 'Upper Palaeolithic' method of prepared volumetric blade/bladelet production is more pronounced in the lowermost layers, where there is a higher tendency for bigger blanks together with the parallel use of flake reduction strategies, including Levallois; in the rest of the layers, blade production appears only occasionally (Sitlivy et al., 2007).

In the Mani area, the caves of Kalamakia, Lakonis and Apidima have yielded human remains as well as lithic assemblages; they belong to an extended, littoral karstic system with numerous caves and rockshelters formed in the limestone bedrock,. At Kalamakia Cave, successive occupational episodes are recorded in two units and the archaeological deposits have been chronologically bracketed between <100 ka BP (U/Th age from the basal, archaeologically sterile beach rock) and >39 ka BP (^{14}C date from the uppermost archaeological level; Darlas and de Lumley, 2004). Fourteen human skeletal elements, mostly isolated teeth, were excavated from several layers, representing a minimum of eight individuals, including two subadults, and identified as Neanderthals on the basis of diagnostic features (Harvati et al., 2013). In contrast to the Klissoura assemblages, the Levallois technique is well-represented here and discoidal cores are rare. Similarly to Klissoura, the main typo-technological traits remain unchanged throughout the sequence. Again, as in the Klissoura industry, key aspects at Kalamakia include the presence of small-sized blanks, exhaustively used cores, and off-site testing and decortication of raw materials. The reduction strategies and artifact characteristics were largely dictated by the raw material properties: while local flints are of poor quality and small size, a type of green andesite (*Lapis lacedaemonius*), which crops out ca. 30 km away from the site and is suitable for producing larger blanks, was used particularly for

Fig. 5. Map of Greece showing key Middle Palaeolithic sites. 1: Theopetra; 2: Asprochaliko; 3: Kokkinopilos; 4: Klissoura; 5: Lakonis; 6: Kalamakia.

obtaining Levallois blanks (Darlas and de Lumley, 1999) —a pattern well-known from many Eurasian MP sites, where the Levallois technique is often related with raw materials curated over longer distances (e.g. Pettitt, 2003). The aforementioned andesitic lava is the dominant raw material in the MP assemblages from the cave of Lakonis, which lies ca. 30 km to the west of Kalamakia and closer to the andesitic outcrops. Laminar, centripetal and convergent Levallois are the prominent methods at Lakonis, and the production of Levallois blanks was the focus of lithic reduction at the site, with materials carried to the cave in the form of already prepared (decorticated) blocks (Panagopoulou et al. 2002–2004). Kalamakia and Lakonis are very similar in terms of their chronologies (the Lakonis MP being bracketed also broadly between ca. 100 and 40 ka BP), as well as regarding the lithic raw materials, the composition of the faunal remains and some basic aspects of the reduction sequences (Darlas, 2007; Panagopoulou et al. 2002–2004). Lakonis has also yielded an isolated human lower left third molar, identified as Neanderthal on the basis of both external and internal characteristics (Harvati et al., 2003; Smith et al., 2009). However, so far their archaeological remains have not been comparatively assessed and the human remains from the two sites cannot be directly compared, as they do not preserve the same elements. To the north of Kalamakia, the cave of Mavri Spilia is another recently excavated but as yet undated site, with MP artifacts similar to those of Lakonis and Kalamakia, which occur together with burned and/or cut-marked bones inside or next to combustion features and hearth remains (Tourloukis et al., 2016). Discoidal and Levallois flaking techniques (laminar, centripetal, bipolar recurrent and preferential) have been identified on blanks that indicate the use of small flint pebbles (Fig. 6). Here, artifacts made on the green andesitic lava were carried to the site in finished form (Fig. 6: 4, 13) and suggest possible links among the different sub-regions of the Mani (Mavri Spilia, sites in the Kardamyli area, Kalamakia, Lakonis), through lithic raw material transfers and provisioning strategies, which are,

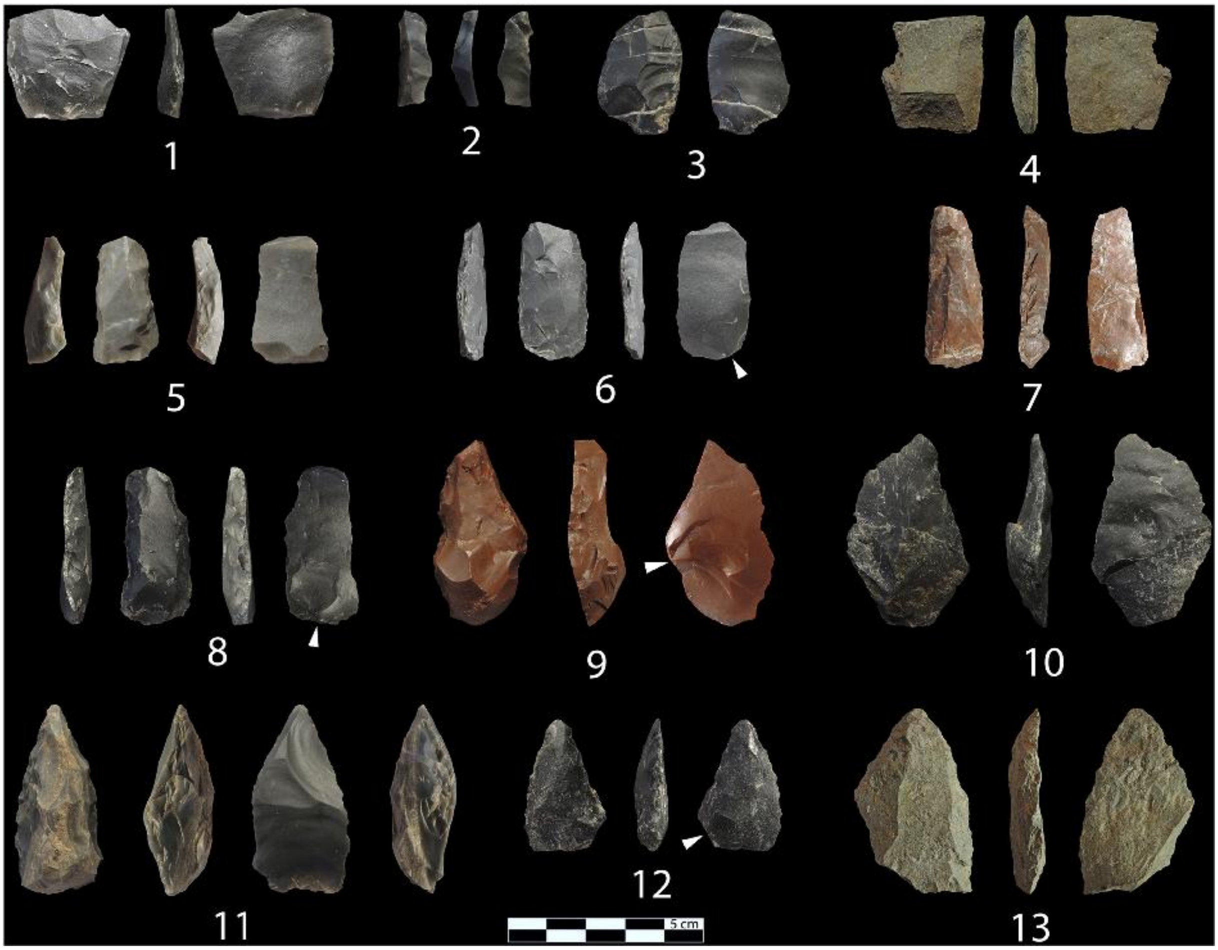

Fig. 6. Middle Palaeolithic artifacts from the excavations of the cave Mavri Spilia, Mani. Modified after Tourloukis et al., 2016: Fig. 7.

in turn, related to mobility patterns. As latest research has nearly doubled the number of MP sites from Mani, confirming that the peninsula has the strongest 'Neanderthal signal' identified to date in Greece, those caves and rockshelters are well-suited for investigating Neanderthal mobility and subsistence strategies in one of the southernmost regions of Europe (Tourloukis et al., 2016).

4. The Upper Palaeolithic

Most of the known Upper Palaeolithic (UP) sites are located in the Peloponnese (Mani, Argolid, Elis) and Epirus, whereas evidence from this period is conspicuously scarce in Macedonia and Thessaly (North and Central Greece, respectively; Fig. 7). Two cave sites in the Peloponnese, Klissoura and Lakonis, have yielded lithic assemblages with typo-technological features that are deemed as 'transitional' between the MP and the UP. A third cave, Kephalari, may also contain a transitional industry, but the material is not fully published (Reisch, 1980). At Klissoura, the occurrence of arched backed blades and microliths in layer V associate the assemblage with the 'middle' or 'evolved' Uluzzian of Italy (Kaczanowska et al., 2010). Besides an erosional contact and hiatus (Karkanas, 2010), there is a typological and technological discontinuity between the last MP layer and the Uluzzian layer (Kaczanowska et al., 2010), both of which produced problematic radiocarbon dates (Kuhn et al., 2010). Nevertheless, the Uluzzian layer V is capped by the Campanian Ignimbrite (CI) tephra, and recent radiocarbon dates on marine shells confirmed that it dates close to the CI-datum at ca. 35–34 ka BP, an age which places Klissoura layer V among the youngest of all known Uluzzian layers (Lowe et al., 2012; Douka et al., 2014; all dates are cited in radiocarbon years). The CI tephra has been identified also in the nearby Franchthi Cave, but there it caps a stratum with a poor and undiagnostic lithic assemblage (Douka et al., 2011). At the cave of Lakonis, the lithic industry from Unit Ia has been described as 'transitional', it is ascribed to the Initial Upper Palaeolithic (Panagopoulou et al. 2002–2004), and is associated with a Neanderthal tooth (Harvati et al., 2003). The prismatic (laminar volumetric) and the Levallois are the most prominent methods of blank production; Levallois points are thought to be similar to those from other sites with transitional industries, such as Üçağizli (Turkey) and Umm el Tlel (Syria), and bifacial implements resemble those from the Bohunician (Elefanti et al., 2008). Unfortunately, the ^{14}C dates from the IUP unit (AMS, charcoal, no ABOx treatment: ca. 44 to 38 ka BP) are statistically identical to those from the overlying unit Ib, which marks the end of the Middle Palaeolithic (Elefanti et al., 2008). The terminal MP-unit is separated by the overlying IUP unit by 15 cm of mixed burnt remains from raked-out hearths and the time gap between the two units could not be defined (Panagopoulou et al. 2002–2004); however, since both layers yielded indistinguishable dates, a large hiatus seems unlikely. At the western part of the Mani peninsula, the lowermost layers of the newly discovered cave of Kolominitsa have yielded lithic and faunal material that has been

Fig. 7. Map of Greece showing key Upper Palaeolithic sites. 1: Klithi, Boila, Megalakkos; 2: Kastritsa; 3: Theopetra; 4: Grava; 5: Asprochaliko; 6: Spilaion; 7: Eleochori; 8: Klissoura; 9: Kephalari; 10: Franchthi; 11: Lakonis.

provisionally ascribed to the MP-UP transition; radiocarbon (AMS) dating of a burnt bone and two charcoals produced ages that range from 42,800–42020 to 40,040–38730 years BP (Darlas and Psathi, 2016; Kolominitsa is part of the ‘Oitilo sites’, shown in Figs. 7 and 8). Finally, in Thessaly there are sites along the Peneios River where Middle and Upper Palaeolithic morphotypes (including small leaf points) were found together inside undisturbed river deposits, which have been U/Th- and ^{14}C-dated to ca. 45–30 ka BP; these have been compared to other ‘transitional’ industries, such as the Szeletian (Runnels, 1988; Runnels and van Andel, 1993b).

Besides two undated open-air sites (Eleochori in Achaia, Darlas, 1999; and Spilaion in Epirus, Runnels et al., 2003), the Aurignacian is best-known and dated at three cave sites. At Franchthi, an Early Aurignacian assemblage is embedded in the CI-tephra layer (Douka et al., 2011), hence it is relatively synchronous to the earliest Aurignacian of Klissoura, which starts directly at the base of the CI tephra that seals the Uluzzian layer (Lowe et al., 2012). The Aurignacian inventory from Klissoura, ^{14}C –dated to ca. 33–31 ka BP (Kuhn et al., 2010), shows similarities with the European Early Aurignacian and especially the Italian Aurignacian (Kaczanowska et al., 2010). Perhaps the most spectacular feature of the Klissoura Aurignacian layers is the presence of several clay-lined hearth structures, which provide evidence for the earliest intentional use of heated clay for construction purposes (Karkanas et al., 2004). At the Kolominitsa cave, a small assemblage with lithics that point to an early Aurignacian phase has been radiocarbon-dated to 33,870 ± 550 years BP (Darlas and Psathi, 2016). Interestingly, the green andesite that was extensively utilized as a raw material in Mani during the Middle Palaeolithic (e.g. at Kalamakia, Lakonis; see above), is missing from the Upper Palaeolithic levels of Kolominitsa, even though the locally available raw materials that were eventually used (jasper and local flint variants) were not of particularly

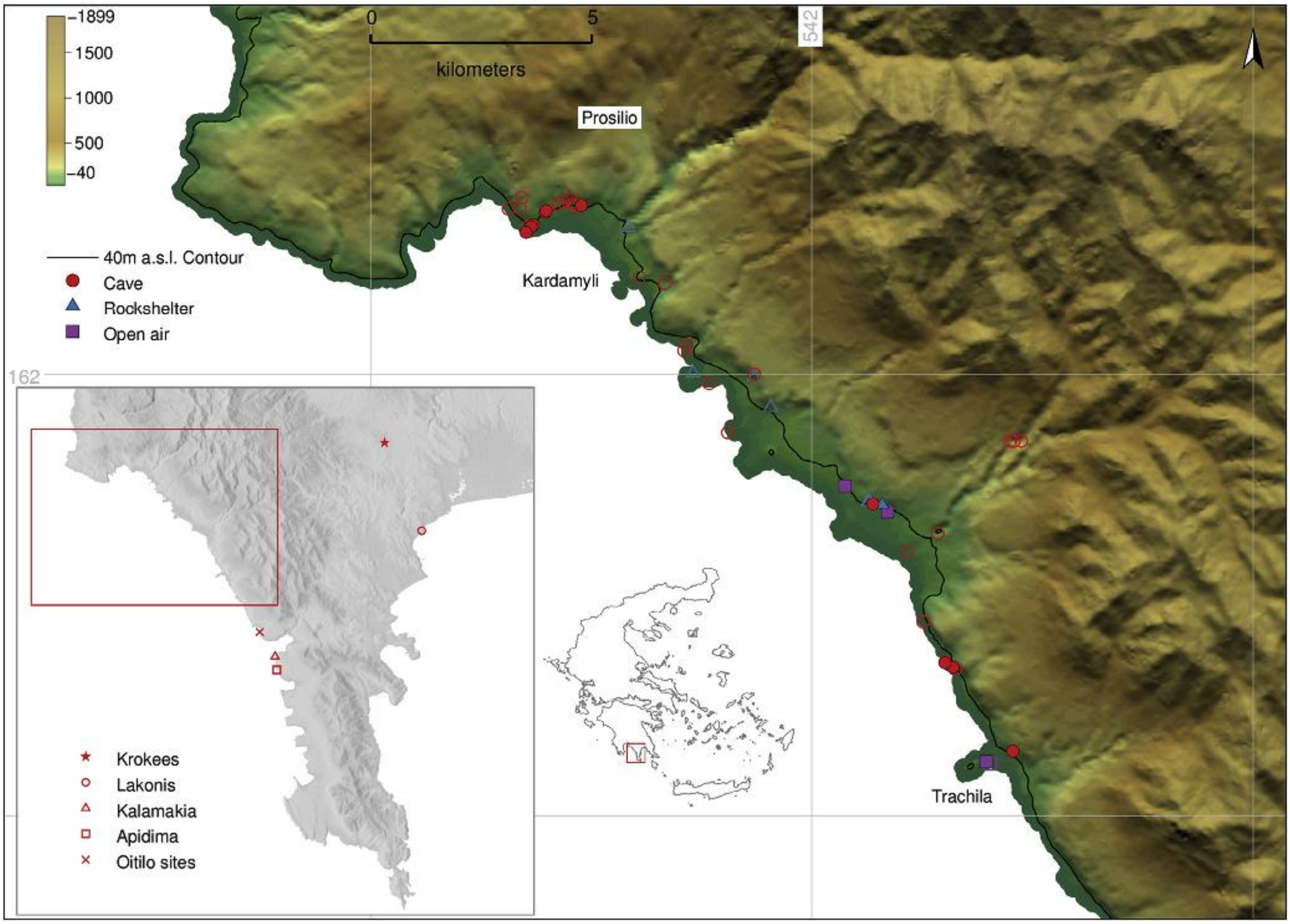

Fig. 8. Distribution of sites in the area of Kardamyli, Mani; sites and findspots are indicated with filled symbols. Insets: map of Mani showing key Palaeolithic sites, and map of Greece. Modified after Tourloukis et al., 2016: Fig. 1.

good quality and they occur in small sizes (Darlas and Psathi, 2008).

The rest of the UP record involves sites with Gravettian (or, "Mediterranean Gravettian", or "Gravettoid"), Epigravettian and Final UP assemblages; the best-studied and/or dated sites are again caves and rockshelters, and there is hardly any open-air site with Gravettian or later evidence: Asprochaliko, Kastritsa, Klithi, Megalakkos and Boila in Epirus (Bailey et al., 1983; Adam, 1989; Bailey, 1997; Kotjabopoulou et al., 1999), Grava in Corfu (Adam, 2007); Theopetra in Thessaly (Adam, 1999); Klissoura, Kephalari and Franchthi in the Argolid (Kaczanowska et al., 2010; Reisch, 1980; Perlès, 1999a); and the caves close to the Oitilo Bay in Mani: Melitzia, Kastanis, Skoini 3 and 4, and Tripsana (Darlas and Psathi, 2016). With a few exceptions, such as Klissoura, Kolominitsa and perhaps also Kephalari, all of the aforementioned sites were either occupied for the first time during the Gravettian/Epigravettian (Klithi, Kastritsa, Megalakkos, Boila and the Oitilo Bay sites), or their late UP levels are separated by hiatuses from the underlying Aurignacian (Franchthi) or MP levels (Asprochaliko; likely also Theopetra and Kephalari). Almost all of the localities appear to have served as specialized sites, such as hunting stations, which record short-term or seasonal and discontinuous occupation events. In some cases, such as Franchthi, Kastritsa and Asprochaliko, the density of the excavated material is sharply contrasted before and after ca. 20 ka; together with the relative scarcity of sites during the period between ca. 30–20 ka BP, this is thought to indicate an overall occupational decline or even depopulation during (and probably due to) the harsh climatic conditions that peaked during the last glacial maximum (Perlès, 1999b). While lithic assemblages are dominated by backed bladelets and backed points, there is a conspicuous lack of bone tools as well as mobile art or ornaments in this period (ca. 30–20 ka BP; Perlès, 1999b).

5. Synthesis and discussion: spatial/temporal site distributions, emerging biogeographical patterns, and the evidence for hominin subsistence strategies

5.1. Lower Palaeolithic

The oldest-dated evidence of human presence in Greece associated with a secure, stratified context is attested at Marathousa 1 (Megalopolis) at around 500–400 ka (Panagopoulou et al., 2015; Blackwell et al., 2016; Harvati et al., 2016). As the earliest sites in the Mediterranean date to around 1.4 Ma (e.g. 'Ubeidiya in Israel, the Orce sites in Spain, Pirro Nord in Italy), there is an apparent ca. 1.0 Myr-long gap in the Greek record until we find the first traces of hominin activity at the Megalopolis basin. Considering that Greece occupies a key biogeographical position and has contributed significant paleontological and paleoanthropological evidence from the Miocene (e.g. Koufos and de Bonis, 2004) up to the Holocene (Runnels, 1995), it is difficult to explain this Early Pleistocene-early Middle Pleistocene gap in terms of unfavorable paleogeographic or ecological conditions. While insufficient research is certainly part of the reason, it has recently been shown that this picture can be also interpreted as the outcome of geomorphological processes and taphonomic circumstances related to a dynamic landscape evolution, which significantly constrained the preservation and archaeological visibility of sites from this period (Tourloukis, 2010), particularly those in basin settings (Tourloukis, 2016). The taphonomic argument is relevant here with regard to not only the total lack of sites from the Early Pleistocene and the low number of sites in the Middle Pleistocene, but also to the 'quality' of the archaeological context: at the moment, Marathousa 1 is *the only open-air site in Greece with a primary context, preserving lithics, fauna and paleobotanical remains in stratigraphic association*. Bearing in mind the discontinuous nature of the LP record in most of Eurasia before about 500 ka BP (e.g. Dennell, 2003), it would not be unexpected if future research demonstrates that Greece, too, was a thinly-inhabited region before MIS 14–12. Especially during periods with prolonged suppression of plant and animal resources, for example MIS 16, which is recorded as the most extensive glacial of the last 1.35 Ma in the pollen record of Tenaghi Philippon (Tzedakis et al., 2006), highly mobile and unspecialized hunter-gatherers with a relatively narrow dietary spectrum and expanded operational radii would have left thin traces, almost invisible in the archaeological record –particularly if they are widely scattered over long distances. In the pollen diagrams from Tenaghi Philippon, MIS 8 displays the least extreme arboreal pollen minima of the last 450 ka BP (Tzedakis et al., 2003). The subdued glacial conditions of MIS 8 and both the preceding and the following interglacial complexes of MIS 9 and 7, altogether likely provided an environmental window of opportunity for a successful expansion of hominin home ranges into the wider Aegean region and/or a regional demographic growth. Meager as the evidence is, the radiometrically dated sites (Rodafnidia, Kokkinopilos, Plakias sites in Crete, Petralona) as well as those that are chronologically bracketed by 'relative dating' (e.g. Rodia in Thessaly, perhaps Alonaki in Epirus and possibly Apidima in Mani; Tourloukis, 2010 and references therein; Harvati et al., 2011) suggest that between ca. 350–150 ka BP the archaeological signal becomes more substantial. Interestingly, from around MIS 12, i.e. close to the chronology of Marathousa 1 (but possibly from even much earlier) and up to MIS 6, extensive coastal plains would have emerged in most of the Aegean and Ionian Seas (Lykousis, 2009), serving as biogeographical land-bridges and dispersal pathways, which connected Asia Minor to the Po basin (Italy) by way of low-relief drainage catchments and littoral belts (Tourloukis and Karkanas, 2012: Fig. 8).

In the absence of adequate samples from excavated contexts, it is difficult to discern trends in lithic variability for this earliest phase of hominin occupation. The Marathousa 1 industry fits well with a Eurasian group of sites with small tools, some of which are associated with megafauna exploitation (e.g. Aureli et al., 2015), while the material from Rodafnidia shows that Acheulian handaxe manufacture was certainly practiced in Greece in the Middle Pleistocene. Sample biases aside, it is interesting to note that all bifacial (flake-) cleavers that have been found thus far in Greece come from sites located at insular settings: Crete (Runnels et al., 2014a), Lesvos (Galanidou et al., 2016) and Naxos (Stelida; Runnels, pers. comm.). At some sites in Epirus (most notably at Kokkinopilos) as well as at some of the Plakias sites in Crete, there is a lithic component with bifacial specimens that, on current chronostratigraphic and typo-technological grounds, is likely not associated with Mousterian technologies; however, we have stressed here the *lack of excavated assemblages* from these localities and the *need for more stratified material* to confidently ascribe these components to a (late) Lower or a MP facies (see also Papoulia, in press). On current evidence, the earliest occurrence of a MP technology in Greece is attested by Levallois specimens in the cave of Theopetra and dates to the transition from MIS 6 to 5 (Karkanas et al., 2015). This timing fits with the emergence of the Levallois technique in neighboring Croatia (Krapina) and Italy (with the exception of San Bernardino cave; Picin et al., 2013). At Rodafnidia (Lesvos), artifacts indicative of prepared-core technologies, including Levallois products, occur in the same units as Acheulian LCT's (Galanidou et al., 2016). Yet, these have been recovered from coarse-grained riverbed deposits, which may contain a mixture of materials from different periods, a common phenomenon that occurs when channels cut into older alluvium. Therefore, the 'Levallois together with Acheulian' co-existence or interstratification at Rodafnidia could be the result of fluvial reworking and should be viewed with caution. In contrast, the lower-energy, semi-lacustrine depositional environments of the Epirus' red-beds render these sites promising targets for investigating the transition from the Lower to the Middle Palaeolithic and the introduction of prepared-core technologies in the Greek peninsula.

5.2. Middle Palaeolithic

Taking at face value all available evidence, namely both surface and excavated sites, we can conclude that large parts of Greece were inhabited by the times of and shortly after the last interglacial. For the period between ca. 100 and 40 ka BP, which comprises the main corpus of the MP record, there is hardly any dating control to allow us to identify synchronic and diachronic changes in lithic technology or subsistence strategies within or among sites. The Epirus MP assemblages are considered to "show little in common with the Peloponnese sites either in technological or typological terms" (Papakonstantinou and Vassilopoulou, 1997: 477), but such assessments have yet to be elaborated and explained. At Kalamakia and Klissoura, even though there are certain differences between the successive Mousterian levels (or, 'occupation floors'), e.g. in terms of tool-kit composition or the use of raw materials, the main technological choices and reduction strategies remain largely unchanged throughout the sequence. We can assume that, at least in those two cases, MP hominins either did not change their technological strategies (e.g. the food processing tool-kit) in response to a changing environment (e.g. with the onset of the MIS 4 cooler conditions), or any possibly new or altered adaptive solutions involved behavioral aspects other than those manifested in lithic technology. Nevertheless, our understanding of MP adaptations in Greece is heavily biased by the fact that all of the high-resolution information comes from sheltered sites, whereas the few excavated open-air MP sites have not yielded any faunal remains. Caves and rockshelters provide data on resource procurement strategies (e.g. the transport of specific anatomical parts of animals), local faunal and floral species diversity and special-activity areas associated with food consumption or tool production (aspects which are generally under-studied in Greece); but they lack the information offered from open-air localities (such as kill- and butchering-sites) about, for instance, the use of specific hunting equipment or on-the-spot tactics (cf. White et al., 2016). A relevant example is offered by some of the red-bed sites of Epirus (Kokkinopilos, Mikro and Megalo Karvounari, Morphi): these have yielded relatively large numbers of MP points, including specimens with indications of hafting (bulbar thinning, proximal retouch) or use-wear (impact fractures); the high occurrence of hunting tools and the strategic position of those sites in the landscape indicate that recurring hunting episodes took place at those locales (Papoulia, 2011). In Argolid, hare remains are occasionally present in the faunal assemblages from some of the MP levels of Klissoura Cave and, even if they never comprised a significant part of the diet (Starkovich, 2014), their mere presence suggests that, under specific ecological circumstances, MP hominins at Klissoura could

Please cite this article in press as: Tourloukis, V., Harvati, K., The Palaeolithic record of Greece: A synthesis of the evidence and a research agenda for the future, Quaternary International (2017), http://dx.doi.org/10.1016/j.quaint.2017.04.020

'afford' and/or were willing to invest in capturing game with high handling costs, a task that probably involved also an associated investment in more complex and 'fixed' technology, such as snares and traps.

The locations of the Greek MP sites cover a wide range of ecological and topographic settings, largely reflecting the overall environmental and physiographic heterogeneity of the peninsula. Nevertheless, most are located at low elevations (usually <200 m above sea-level), and are associated with drainage catchments and coastal plains. The Levallois artifacts found at altitudes >1000 m in the Grevena district (Efstratiou et al., 2006), the only exception in an otherwise 'MP world of lowlands', provide evidence for seasonal/ephemeral exploitation of upland habitats. Another strong trend throughout the temporal and spatial scope of the Greek Mousterian is the patterned association of sites with water bodies and/or well-watered areas (Runnels, 1995; van Andel and Runnels, 2005). Most of the sites are situated in the western part of the Greek peninsula, to the west of the Pindus mountain range, the areas with the highest precipitation values in the country (>800 mm of annual rainfall). Although temperature is an important parameter, especially for upland and northern regions, precipitation is the critical climatic factor controlling shifts in vegetation composition and reforestation during glacial-interglacial transitions (Bottema, 1979; Woodward et al., 1995; Tzedakis, 2007). As higher annual precipitation results in denser vegetation cover and hence higher vegetation biomass, this site distribution likely reflects a hominin preference for areas maintaining vegetation resources during glacial periods. Recent research indicates that vegetation resources were an important part of the diet of MP hominins: for instance, tooth microwear of Neanderthals from temperate (wooded) Mediterranean sites, including Greek sites, show evidence for increased dietary variability compared to those from open areas, reflecting the consumption of a diversity of plants, seeds and nuts (Harvati et al., 2013; El Zaatari et al., 2013, 2016), while analysis of Neanderthal dental calculus has revealed the importance of plant resources even at higher latitudes (Henry et al., 2010, 2014; Fiorenza et al., 2015). Plant remains from MP contexts of several Mediterranean sites, includingTheopetra Cave (Thessaly), conform to this pattern and suggest a broad diet that included herbs, fruits, wild grasses and sedges (Lev et al., 2005; Madella et al., 2002; Tsartsidou et al., 2015). Consequently, we suggest that the clustering of MP sites at the western parts of the country follows a biogeographical pattern that emerges at either sides of the Pindus Mountains —the orographic backbone of the Greek Peninsula: the eastern lowlands with more arid, continental climate would experience significant vegetation crashes during glacials and stadials, while the mid-altitude sites of western Greece acquired a refugial character for the survival of residual floral populations and subsequent recolonization during interstadials and interglacials (cf. Tzedakis et al., 2002). The survival of trees and plant communities would have controlled the distribution and availability of herbivore populations, hence the proposed link between precipitation values, vegetation biomass and subsistence does not relate only to vegetation consumption *per se*, but also to game abundance and hunting opportunities. Moreover, the importance of plant resources has to be appreciated also with regard to their potential consumption for medicinal purposes (cf. Hardy et al., 2012), or their usage as fuel: Ntinou (2010) has shown that the open woodland with mesophilous taxa, at the foothills and valley floor near Klissoura Cave, was an important source for firewood provisioning during the UP, and we could reasonably accept this conclusion for the MP occupation of the cave, too.

Topographic configuration is another important parameter: high topographic variability in Epirus provided trees with shelter from cold air masses, opportunities for altitudinal migrations, as well as a range of microhabitats suitable for survival (Tzedakis, 2005). Particularly for the Epirus sites, the role of tectonics, topographic barriers/corridors and associated vegetation districts have already been emphasized (King and Bailey, 1985; Bailey et al., 1993), while Runnels and van Andel (2003a; van Andel and Runnels, 2005) have stressed the importance of the red-bed wetlands, such as Kokkinopilos, as fixed locations in the landscape, where hominins could find essential and predictable resources such as water, plants, game and flint. At Asprochaliko, close to Kokkinopilos, the same species, *Cervus*, *Dama* and *Ibex* remain the dominant ungulate prey in the faunal assemblages throughout the Middle Palaeolithic levels (Bailey et al., 1983). This likely points to ecological stability in terms of species availability and abundance, but also to hominin economic decisions that focused on game procurement from local resources.

The Mani peninsula in southern Greece is, next to Epirus, an area with a high number of MP sites. Both Epirus and Mani are characterized by karst landscapes, but Mani has a more arid climate, a scant vegetation cover, fewer outcrops of good-quality raw materials, and a high relief that would have increased the energetic costs of foraging activities. The high number of sites is partly an artifact of preservation factors related to the sheltered nature of the investigated localities. Most sites are caves and rockshelters located on the western part of the peninsula and site distributions arguably reflect a hominin preference for coastal locations (Darlas, 2012; Tourloukis et al., 2016, Fig. 8). With the drop of the sea-level during the last glacial, most of the known sites would have been situated at the fringes of emerged coastal plains. In addition to the presence of freshwater-bearing karstic features such as dolines and springs, the attractiveness of these locations can be credited to the ecotone-like character of the Mani coastal habitats: over short distances, hominins would have had direct access to both marine and terrestrial resources, the latter being fairly closely spaced and variable if we consider that the foothills of the Taygetos Mountain lie less than a couple of kilometers inland from the coast, while upland resource patches (>600 m) are to be found <5 km onshore. Overall, resource diversity is evident in the zooarchaeological material from Kalamakia Cave: the assemblage is dominated by fallow deer, followed by ibex and wild boar, but includes also a high number of turtle bones and a few megafaunal elements such as elephant and rhino remains. Fallow deer (which are also the most abundant taxa in the fauna of Klissoura) usually prefer habitats with a combination of different vegetation types, while ibex prefer rugged terrain and their availability is strongly seasonal (Grzimek, 1990). Moreover, Kalamakia has also yielded a molluscan fauna, which points to the exploitation of the nearby littoral zone and includes several retouched valves of *C. chione* (Darlas, 2007), a species that was selectively chosen by MP hominins for the making of scrapers, as documented in a number of Italian sites (Douka and Spinapolice, 2012). Apart from a possibly worked bone from Klissoura (Starkovich, 2011) and a retouched bone fragment from Mavri Spilia in Mani (Tourloukis et al., 2016), there are no published accounts on MP bone-tools from Greece; in this light, the retouched shells from Kalamakia represent, in the Greek record, a rare example of MP tools made on raw materials other than stone.

Whatever foraging opportunities would have been available in the Mani peninsula as a whole, there is a strong concentration of sites on the western part, even though we cannot rule out that this is an artifact of preservation factors or research focus. Nevertheless, accessibility to water seems to have been a crucial parameter: in contrast to the eastern part, it is the western portion that enjoys most of the drainage and groundwater flow, while karstic springs also occur mainly along the western shoreline (Marinos et al., 1985). During cold periods with lowered sea-levels (i.e. most of the last glacial), new and numerous freshwater springs would appear on the emerged continental shelf, and groundwater flow at the coast would have increased (cf. Faure et al., 2002).

5.3. Upper Palaeolithic

The transition from the Middle to the Upper Palaeolithic in Greece is still poorly known. On one hand, the evidence from Klissoura Cave points to a stratigraphic hiatus and cultural discontinuity between the last MP layers and the Uluzzian technocomplex, which at Grotta del Cavallo (southern Italy) is associated with modern human remains (Benazzi et al., 2011). On the other hand, the Lakonis IUP industry is associated with a Neanderthal tooth and shows technological continuity with the underlying MP industries (for a discussion about comparisons with other 'transitional' industries see Panagopoulou et al. 2002–2004: 344–345). On current evidence, it seems that there was no overlap between the last Neanderthals at Lakonis (44–38 ka BP) and the first appearance date of modern humans (ca. 35–34 ka BP), if we assume the latter to be the makers of the Uluzzian and/or the Aurignacian. Assemblages with mixed MP and UP artifact types from open-air sites, such as those from Thessaly (see Runnels, 1988 for a discussion of more examples), as well as their associated dates, should be dealt with caution, since they come from non-excavated contexts.

The small number of Aurignacian sites does not allow us to discern shifts in settlement patterns between the late MP and the early UP. Coarse-grained trends can be discussed only if we lump all UP sites as a single chrono-cultural entity and consider that sample and preservation biases are negligible, which is not true, as already pointed out with regard to the over-representation of sheltered localities or the submergence of coastal sites. In this light, an increase in cave use during the UP (Elephanti and Marshall, 2015) currently cannot be either confirmed or rejected, yet might be a reasonable expectation, considering the advantages of sheltered dwellings, and the broader framework of the UP behavioral and socio-cultural developments. In certain areas that have been adequately surveyed, such as Thessaly, Elis (western Peloponnese) and S/SE Peloponnese, the overall absence of UP evidence (regardless of site-type) may reflect evidence of real absence (Runnels and van Andel, 1993b; Perlès, 1999b). The presence of Aurignacian assemblages in the dry landscapes of Mani (Kolominitsa) and Argolid (Klissoura, Franchthi, possibly Kephalari) seems to indicate that at those areas, certain environmental attributes outweighed the disadvantages of low precipitation, as suggested above also for the MP record of Mani. Indeed, at Kephalari, the location of the site at the intersection of mountainous, valley-floor and coastal plain biomes; the co-existence of woodland and open parkland vegetation taxa; as well as the composition of the fauna with animals that live in a range of different vegetation types and topographic settings, altogether explain the higher levels of faunal species diversity than those at Klissoura, which is situated at a more homogenous setting (Starkovich and Ntinou, in press). In the Mani, our own investigations have yielded only a small number of UP artifact types and failed to identify well-defined open-air sites similar to Eleochori in Achaia or Spilaion in Epirus. Even though marine transgressions have flushed many of the Mani coastal caves, wiping out possible MP anthropogenic deposits, it is noteworthy that, besides Kolominitsa, all of the published sites were occupied *either* during the MP (e.g. Lakonis, Kalamakia) *or* the UP (e.g. Oitilo sites). In contrast, there is a number of open-air sites in Epirus, particularly the red-bed sites, which apparently continued to serve as preferred locations for hominin activities from the MP through the UP and possibly also later (e.g. Runnels and van Andel, 2003a; Ligkovanlis, 2011; Papoulia, 2011). These sites, however, have not been excavated and we do not know whether there are cultural or stratigraphic hiatuses separating the MP and UP occupational phases. While Aurignacian and, generally, 'early UP' sites in Greece are very scarce, there is an equally conspicuous scarcity of sites for the period between ca. 30 to 20 ka BP, a near depopulation which, according to Perlès (1999b), cannot be linked directly to major environmental changes, even though climatic deterioration and increased aridity must have played a crucial role. For instance, during the LGM at Franchthi, Kephalari and Klissoura, a decline in precipitation caused a significant decrease of open deciduous woodland and reduced vegetation diversity (Starkovich and Ntinou, in press). Nevertheless, Perlès also notes that "Greece never seems to have been completely deserted" and recalls the assumption put forth by Runnels and Bailey that "the now-submerged coastal sites would have been the foci of activities during the Upper Palaeolithic" (1999b: 389).

As far as shifts in subsistence strategies are concerned, Klissoura Cave 1 offers some valuable insights. While MP hominins focused on high-ranked large game, the UP occupants of the site broadened their diet to include lower-ranked small and fast-moving animals, such as hare, great bastard and rock partridge (Starkovich, 2014); the same trend might be present in the Kephalari Cave, but here the MP assemblage is small and still under study, while the entire cultural sequence has not been fully published (Starkovich and Ntinou, in press). Overall, large-scale shifts in prey use and the observed long-term trend in resource depression at Klissoura seem to have occurred irrespective of environmental changes, and they could be linked to an increase in occupation intensity from the Aurignacian onwards, and/or to over-exploitation of high-ranked ungulate faunas (Starkovich, 2014; Starkovich and Ntinou, in press). Notably, the lack of a diachronic trend in transport decisions at Klissoura and the general presence of lower-utility body parts suggest the local procurement of game throughout the occupation. This may, in turn, indicate that local resources were never depleted enough to necessitate an increase in foraging distances. On the other hand, a greater environmental productivity, as inferred from the degree of species evenness, correlates with high processing (inferred from opened terminal phalanges); this could reflect an increase in the intensity of site use and/or population growth (Starkovich, 2014). In Epirus, the differences between the last MP and the first UP faunas at Asprochaliko do not hint at major shifts in prey choice or species availability (Bailey et al., 1983), even though the changes in climatic conditions were probably significant (see e.g. Tzedakis, 1994; Hughes et al., 2006).

6. Addressing a research agenda for the future

The Greek peninsula is tectonically one of the most active regions in Eurasia and is characterized by the most complex topography and heterogeneous ecosystems in the entire Mediterranean (Woodward, 2009). Intense tectonic activity set the background for a highly 'broken-up' topography with a basin-and-range arrangement (Collier et al., 1995; Jolivet and Brun, 2010), which in turn prevented the development of extensive ecological zonation (Allen, 2001). This geographical configuration, coupled with a seasonal climate, resulted in the prevalence of mosaic environments with a striking biological diversity and a variety of ecological resources distributed over short distances. Climatic fluctuations, active tectonics and topographic variability would have increased the environmental heterogeneity of Pleistocene Greece to levels possibly even higher than those at present (cf. Tourloukis, 2010: 127–195). Therefore, Greece is a natural laboratory for testing models of hominin habitat preferences and mobility, by examining the role of topography and climate as controlling agents in subsistence strategies and behavioral adaptations. In this light, we propose the following hypothesis: hunter-gatherer groups operating in the well-watered habitats of western Greece likely followed a pattern of mobility that entailed frequent moves of residential sites per year but over relatively short distances (cf. Binford, 1982). Assuming some degree of optimization in foraging decisions, and accepting that foraging patterns would have been conditioned by the eco-environmental fabric (Gamble, 1995) and the associated nutritional landscape (*sensu* Brown et al., 2013), we expect hominins in western Greece to have exploited one main advantage offered by the region's geoclimatic mosaicism: the distribution of diverse resources over short distances in space and throughout fairly predictable units in time; this combination provides different subsistence alternatives for minimizing risks during periods of resource depletion, or in habitats with high inter- or intra-specific competition. Our hypothesis is based on previous studies of hunter-gatherer behavioral ecology (Binford, 1982; Kelly, 1995), and on recent models, which identify habitat quality as the best predictor of the foraging radius as well as of the distances moved by hunter-gatherers between camps (Grove, 2009). In order to test such models against the archaeological evidence, a number of other (co-)varying parameters need to be taken into account (e.g. average occupation duration; group size; relative contribution of hunting to the diet), and the Greek record is still too fragmentary and coarse-grained to provide the necessary resolution. Notwithstanding these constraints and the fact that more field work is necessary, the time has come to start contextualizing the Palaeolithic of Greece and make use of models with potentially high explanatory power, such as that explored by Grove (2009). For instance, a model-bound approach to assess the aforementioned hypothesis could juxtapose data from the regional records of Epirus and Mani, which are the areas with a comparatively high number of well-studied Middle and Upper Palaeolithic sites. Subsequently, and at a higher-order level of inquiry, we can evaluate site distributions and behavioral variability across a bio-climatic transect, considering that precipitation decreases from West to East and temperature increases from North to South; mean annual rainfall and effective temperature are the two main indices of habitat quality.

The potential role of Greece as a glacial refugium for Neanderthals and their predecessors, as well as for modern humans, is another research venue to be explored (Harvati et al., 2003, 2009). Neanderthals retreated southwards as climate cooled in MIS 3 and Neanderthal refugia have been identified in Southern Iberia (e.g. Zafarraya, Gorham's Cave), Iraq and the Levant (Kebara, Amud), whereas a number of other MIS 3 sites in the Balkans and the Near East with modern human remains may be reflecting the expansion of *H. sapiens* geographic ranges into southern refugia (Stewart and Stringer, 2012). Neandertal mtDNA sequences provide support for a late bottleneck in their population (Pearson, 2013: 228) and Neanderthals eventually became extinct shortly after the dispersal of modern humans in Europe. Whether their final population crashes were due to competition with modern humans or due to climatic factors (or both), the very last groups of Neanderthals may have survived in southern refugia in Iberia, the Balkans and possibly also the Levant (Stewart and Stringer, 2012). Consequently, Neanderthal extinction may have taken place "in their respective refugial areas, as this is the direction toward which the last populations will have contracted in geographical range and numbers"; and this is likely to have happened also in the case of other archaic humans (ibid: 335). The region of Mani has yielded a rich sample of coastal Neanderthal sites and lies in one of the southernmost extremes of Europe. The Neanderthal remains from the site of Lakonis (44–38 ka BP) provide the youngest direct evidence for a late Neanderthal presence in the area. The MP record of Mani is overall well-suited for testing the hypothesis that this part of Greece may have served as a refugium for Neanderthal groups and it potentially witnessed the final demise of this species in the region.

Within each of the southern European peninsulas, particularly in Iberia and the Balkans, multiple refugial areas have been identified, prompting researchers to speak of 'refugia within refugia', as opposed to the notion of a continuous and homogeneous refugial region (Feliner, 2011). Rather than a single refugial entity, southern Iberia comprised a range of refugial environments during the Pleistocene, owing to the diversity in terrain morphology and precipitation (Jennings et al., 2011). In turn, the identification of two Neanderthal refugia is thought to indicate the possible existence of two Neanderthal populations in southern Iberia, "one occupying a lowland setting and exploiting coastal resources; the second living in upland environments and exploiting lacustrine areas" (ibid: 1833). Alternatively, Neanderthals could have been exploiting both coastal and upland environments at different times of the year. Both of these scenarios can be tested on the Greek record. For instance, new data on the palaeoenvironmental settings of the Klissoura and Kephalari caves suggest the existence of a mosaic type of vegetation and the persistence of thermophilous plants in local refugia (Starkovich and Ntinou, in press). Consequently, it was not only Epirus (Tzedakis et al., 2002), but also parts of the Peloponnese or areas in Central Greece (Karaiskou et al., 2014) that likely acted as localized refugia within the broader refugium of the Greek Peninsula.

What sort of biological and cultural processes took place during periods of confinement to refugia and what were the consequences of these processes on hominin phenotypic structure? Key hominin specimens from Greece show similarities with both African taxa (Petralona; Harvati, 2009) and European/Eurasian fossils (Apidima; Harvati et al., 2011). Considering its likely refugial status and geographic variability, Greece can be expected to have acted as an area promoting genetic isolation, allopatric speciation, and perhaps endemism for new species. With an adequate sample, Neanderthal remains from Greece should be in the future compared to those from Spain, Italy and the Near East, to assess hypotheses of geographic differentiation among Neanderthal populations (e.g. Condemi, 2001; Fabre et al., 2009).

7. Conclusions

We point out three kinds of inter-related and difficult to distinguish 'gaps' in the Palaeolithic record of Greece:

1) Research gaps.

Some parts of Greece have not been intensively explored and/or have not been investigated by research teams that explicitly target the Palaeolithic; this latter point is significant, as Palaeolithic sites can easily be missed by teams conducting the traditional field walking on —usually Holocene— land surfaces. Such under-explored areas include parts of Central Greece, Macedonia, Thrace and the Aegean islands. In terms of cultural periods, the Lower Palaeolithic is arguably the most overlooked part of the Greek prehistory and a lot more needs to be done in order to reverse this picture. Other research-related shortcomings relate to the fact that important lithic, faunal and paleoanthropological remains have yet to be fully published: examples include the Apidima crania and associated fauna and lithics; the faunal material from Lakonis, Asprochaliko and Kastritsa; and the entire archaeological collection from Kephalari.

2) Geological/geomorphological gaps.

The lack of solid evidence for a hominin presence in Greece in the early Lower Palaeolithic, i.e. from the Early to the early Middle Pleistocene, largely reflects preservation conditions and the fragmentary nature of the geological archive. In spatial terms, high-relief mountainous areas, such as the Pindos Mountain Range, occupy in total ca. 65% of the country, and these terrains are less promising for preserving open-air sites. Moreover, interglacial marine transgressions have resulted in the submergence of potentially site-bearing coastal plains. This type of preservation bias is relevant to sites of all periods in the Aegean and Ionian Seas, as well as to specific areas for particular time-spans, for instance the potentially early Middle Palaeolithic sites in Mani, which were submerged during the last interglacial.

3) Real occupational gaps.

“Last appearance dates” and the “last probable absence” of hominins (Dennell and Roebroeks, 2005) are extremely difficult to identify, as we first need to exclude research biases and geological gaps, admittedly a difficult task for regions such as Greece, where the geological archive is so fragmented and Palaeolithic research has been traditionally under-represented. That said, the scarcity or total lack of finds from certain relatively well-surveyed regions with a comparatively well-preserved geological record indicates a couple of real discontinuities in human presence. Such is the case of the mid-to high-altitude areas in the hinterland of north Greece, where a thin human presence is first evidenced during the Middle Palaeolithic and becomes more substantial in the Upper Palaeolithic. Similarly, areas with colder, drier and generally more continental climates of northern and eastern Greece seem to have been avoided during most of the Pleistocene. The period just before and during the last glacial maximum appears to signal an overall depopulation and/or contraction to habitats with a refugial status.

‘Gaps’ will always exist in the Palaeolithic record and it will always be difficult to disentangle them, in order to ascertain their true nature. Nevertheless, recent regional and site-focused field work has started filling up some of these discontinuities in the geographic extension and temporal coverage of Greek Palaeolithic investigations. Recent discoveries, the revisiting of known sites, as well as the analysis and publication of excavated lithic or faunal collections, have altogether contributed in introducing the Palaeolithic of Greece as an important agent in key debates of human evolution research. For instance, the antiquity of the Lower Palaeolithic site of Marathousa-1 (Megalopolis) and the remarkable conditions of preservation render this site unique and most of its finds unprecedented for this time-period and at this part of Europe. The finding of ‘African-style’ LCT's at Rodafnidia (Lesvos) is expected to offer valuable insights into the Acheulian, its duration, origins, geographical and temporal distribution, typological subdivisions or evolutionary implications. To the other side of the temporal spectrum, the Uluzzian assemblage from Klissoura Cave has contributed important evidence to the discussion about the timing and geographical span of this enigmatic technocomplex and its presumed association with the spread of modern humans, raising the standards for the on-going excavations of Upper Palaeolithic caves in the area of Mani, Southern Greece. On the other hand, it is the Middle Palaeolithic dataset which comes to remind us that cultural/stylistic, functional or technological properties of the material culture are relational concepts that need to be understood within the ecological and social context of hominin groups and individual agents. We are far from resolving the social landscape of Palaeolithic Greece, but we are better-equipped to explore how the observed variability in lithic reduction systems or subsistence strategies, and the related morphological diversity in tool inventories may or may not be related to an equally diverse geoclimatic and ecological setting. Mosaic landscapes and a complex topography seem to have been important factors in conditioning hominin lifeways in the Greek peninsula, and, in this regard, we have proposed two main venues for future research: the role of refugia and the mobility patterns of early humans. The Palaeolithic of Greece is still under-studied, but it is coming of age and will soon be able to address this sort of important research subjects.

Acknowledgements

Views and perspectives presented in this study have been shaped in the course of many years of field investigations and laboratory work in Greece. We are grateful to all of our colleagues and collaborators for their continuous help and encouragement to conduct research, as well as for the valuable discussions and exchange of ideas. We are particularly thankful to our collaborators in the Greek Archaeological Service (Ministry of Culture), the Universities of Athens, Thessaloniki and Ioannina, and the American School of Classical Studies at Athens. We also thank two anonymous reviewers for their comments and corrections that helped us improve the manuscript. This research was supported by the European Research Council (ERC STG no. 283503 awarded to KH).

References

Adam, E., 1989. A technological and typological analysis of Upper Palaeolitihic stone industries of Epirus, north-western Greece. Oxford. BAR Int. Ser. 512.
Adam, E., 1999. Preliminary presentation of the upper Palaeolithic and Mesolithic stone industries of Theopetra cave, western Thessaly. In: Bailey, G.N., Adam, E., Panagopoulou, E., Perlès, C., Zachos, K. (Eds.), The Palaeolithic Archaeology of Greece and Adjacent Areas: Proceedings of the ICOPAG Conference, Ioannina, September 1994. British School at Athens Studies 3, London, pp. 266–270.
Adam, E., 2007. Looking out for the Gravettian in Greece. Paleo 19, 145–158.
Allen, H.D., 2001. Mediterranean Ecogeography. Pierson Education Limited, Harlow.
Athanassas, C., Bassiakos, Y., Wagner, G.A., Timpson, M.E., 2012. Exploring paleogeographic conditions at two Paleolithic sites in Navarino, southwest Greece, dated by optically stimulated luminescence. Geoarchaeology 27, 237–258.
Aureli, D., Contardi, A., Giaccio, B., Jicha, B., Lemorini, C., Madonna, S., Magri, D., Marano, F., Milli, S., Modesti, V., Palombo, M.R., Rocca, R., 2015. Palaeoloxodon and human interaction: depositional setting, chronology and archaeology at the Middle Pleistocene Ficoncella site (Tarquinia, Italy). PLoS One 10 (4), e0124498. http://dx.doi.org/10.1371/journal.pone.0124498.
Aureli, D., Rocca, R., Lemorini, C., Modesti, V., Scaramucci, S., Milli, S., Giaccio, B., Marano, F., Palombo, M.R., Contardi, A., 2016. Mode 1 or mode 2? “Small tools” in the technical variability of the European lower Palaeolithic: the site of Ficoncella (Tarquinia, Lazio, central Italy). Quat. Int. 393, 169–184.
Bailey, G.N. (Ed.), 1997. Klithi: Palaeolithic Settlement and Quaternary Landscapes in Northwest Greece, vol. 2. McDonald Institute for Archaeological Research, Cambridge.
Bailey, G.N., Carter, P.L., Gamble, C.S., Higgs, H.P., 1983. Asprochaliko and Kastritsa: further investigations of Palaeolithic settlement and economy in Epirus (northwest Greece). Proc. Prehist. Soc. 49, 15–42.
Bailey, G., King, G., Sturdy, D., 1993. Active tectonics and land-use strategies: a Palaeolithic example from northwest Greece. Antiquity 67, 292–312.
Benazzi, S., Douka, K., Formai, C., Bauer, C., Kullmer, O., Svoboda, J., Pap, I., Mallegni, F., Bayle, P., Coquerelle, M., Condemi, S., Ronchitelli, A., Harvati, K., Weber, G., 2011. Early dispersal of modern humans in Europe and implications for Neanderthal behaviour. Nature 479, 525–529.
Binford, L.R., 1982. The archaeology of place. J. Anthropol. Archaeol. 1, 5–31.
Blackwell, A.B., Singh, I., Gopalkrishna, K.K., Chen, K.K., Sakhrani, N., Tourloukis, V., Karkanas, P., Florentin, J.A., Blickstein, J.I.B., Panagopoulou, E., Harvati, K., Skinner, A.R., 2016. ESR dating the fossil-bearing layers at the Marathousa 1 site, Megalopolis, Greece. In: Oral Contribution, Palaeoanthropology Society Meeting, Atlanta, Georgia.
Bottema, S., 1979. Pollen analytical investigations in Thessaly (Greece). Palaeohistoria XXI, 19–40.
Brown, A.G., Basell, L.S., Robinson, S., Burdge, G.C., 2013. Site distribution at the edge of the Palaeolithic World: a nutritional niche approach. PLoS One 8 (12), e81476.
Carter, T., Contreras, D., Doyle, S., Mihailovi, c, D., Moutsiou, T., Skarpelis, N., 2014. The Stelida Naxos archaeological project: new data on the Middle Palaeolithic and Mesolithic cyclades. Antiq. Proj. Gallery 341.
Charisis, H.B., Durand, P., Axiotis, M., Charisis, T.B., 2000. Traces of Palaeolithic settlement on Lesvos. Archaeol. Arts 76, 83–87 (in Greek, with English abstract).
Collier, R.E.L., Leeder, M.R., Jackson, J.A., 1995. Quaternary drainage development, sediment fluxes and extensional tectonics in Greece. In: Lewin, J., Macklin, M.G., Woodward, J.C. (Eds.), Mediterranean Quaternary River Environments, Rotterdam: Balkema, pp. 31–44.
Condemi, S., 2001. Les Néanderthaliens de La Chaise. Paris, Editions du Comitè des Travaux Historiques et Scientifiques CTHS. Doc. Préhist. 15.
Dakaris, S.I., Higgs, E.S., Hey, R.W., 1964. The climate, environment and industries of

stone age Greece: Part I. Proc. Prehist. Soc. 30, 199–244.
Darlas, A., 1994. Le Paléolithique inférieur et moyen de Grèce. L'Anthropologie 98, 305–328.
Darlas, A., 1995. The earliest occupation of Europe: the Balkans. In: Roebroeks, W., van Kolfschoten, T. (Eds.), The Earliest Occupation of Europe. Proceedings of the European Science Foundation Workshop at Tautavel (France), November 1993. Leiden University Press, Leiden, pp. 51–59.
Darlas, A., 1999. Palaeolithic research in western Achaia. In: Bailey, G.N., Adam, E., Panagopoulou, E., Perlès, C., Zachos, K. (Eds.), The Palaeolithic Archaeology of Greece and Adjacent Areas: Proceedings of the ICOPAG Conference, Ioannina, September 1994. British School at Athens Studies 3, London, pp. 303–310.
Darlas, A., 2003. Palaeolithic finds from the Megalopolis basin: their relation to the fossils of the same area. In: Vlachopoulos, A., Birtacha, K. (Eds.), ARGONAUTIS: Timetikos tomos yia ton Kathegete Christo G. Douma apo tous mathetes tou sto Panepistimio Athenon (1980-2000), pp. 27–37. Athens: Kathimerini (in Greek).
Darlas, A., 2007. The Mousterian of Greece under the light of recent research. L'Anthropologie 111, 346–366.
Darlas, A., 2012. Geomorphological evolution and occupation of the caves of the western coast of Mani during the late Pleistocene and Holocene. In: Zacharias, N., Georgakopoulou, M., Polykreti, K., Fakorellis, G., Vakoulis, Th (Eds.), Proceedings of the 5th Symposium of the Greek Archaeometry Society, Athens: Papazisi, pp. 237–253 (in Greek).
Darlas, A., de Lumley, H., 1999. Palaeolithic research in Kalamakia cave, Areopolis, Peloponnese. In: Bailey, G.N., Adam, E., Panagopoulou, E., Perlès, C., Zachos, K. (Eds.), The Palaeolithic Archaeology of Greece and Adjacent Areas Proceedings of the ICOPAG Conference, Ioannina, September 1994. British School at Athens Studies 3, London, pp. 293–302.
Darlas, A., De Lumley, H., 2004. La Grotte de Kalamakia (Aréopolis, Grèce). Sa contribution à la connaissance du Paléolithique Moyen de Grèce. In: Sessions Generales et Posters, Actes de la 5e Section: Le Paléolithique moyen, XIV e Congres UISPP, Liege, 2-8 Septembre 2001. British Archaeological Reports. International Series 1239. Archaeopress, Oxford, pp. 225–233.
Darlas, A., Psathi, E., 2008. Le Paleolithique superieur dans la peninsula du Mani (Peloponnese, Grece). In: Darlas, A., Mihailovic, D. (Eds.), The Paleolithic of the Balkans. Archaeopress, pp. 51–59.
Darlas, A., Psathi, E., 2016. The middle and upper Paleolithic on the western coast of the Mani peninsula (southern Greece). In: Harvati, K., Roksandic, M. (Eds.), Paleoanthropology of the Balkans and Anatolia: Human Evolution and its Context. Springer, Dordrecht, pp. 95–118.
Dennell, R., 2003. Dispersal and colonization, long and short chronologies: how continuous is the Early Pleistocene record for hominids outside East Africa? J. Hum. Evol. 45, 421–440.
Dennell, R., Roebroeks, W., 2005. An Asian perspective on early human dispersal from Africa. Nature 438, 1099–1104.
Douka, K., Higham, T.F.G., Wood, R., Boscato, P., Gambassini, P., Karkanas, P., Peresani, M., Ronchitelli, A.M., 2014. On the chronology of the Uluzzian. J. Hum. Evol. 68, 1–13.
Douka, K., Perlès, C., Valladas, H., Vanhaeren, M., Hedges, R.E.M., 2011. Franchthi cave revisited: the age of the Aurignacian in South-west Europe. Antiquity 85, 1131–1150.
Douka, K., Spinapolice, E., 2012. Neanderthal shell tool production: evidence from Middle Palaeolithic Italy and Greece. J. World Prehist. 25, 45–79.
Efstratiou, N., Biagi, P., Elefanti, P., Karkanas, P., Ntinou, M., 2006. Prehistoric exploitation of Grevena highland zones: hunters and herders along the Pindus chain of western Macedonia (Greece). World Archaeol. 38 (3), 415–435.
Elefanti, P., Marshall, G., 2015. Late Pleistocene hominin adaptations in Greece. In: Coward, F., Hosfield, R., Pope, M., Wenban-Smith, F. (Eds.), Settlement, society and Cognition in Human Evolution. Cambridge University Press, Cambridge.
Elefanti, P., Panagopoulou, E., Karkanas, P., 2008. The transition from the middle to the upper Palaeolithic in the southern Balkans: the evidence from Lakonis I cave, Greece. Eurasian Prehist. 5, 85–96.
El Zaatari, S., Grine, F.E., Ungar, P.S., Hublin, J.J., 2016. Neandertal versus modern human dietary responses to climatic fluctuations. PLoS One 11 (4), e0153277.
El Zaatari, S., Harvati, K., Panagopoulou, E., 2013. Occlusal molar microwear texture analysis: the method and its application for the dietary reconstruction of the Lakonis Neandertal. In: Voutsaki, S., Valamoti, M.S- (Eds.), Subsistence, Economy and Society in the Greek World. Peeters Publishers, Louvain, pp. 55–63.
Fabre, V., Condemi, S., Degioannu, A., 2009. Genetic evidence of geographical groups among Neanderthals. PLoS One 4 (4), e5151. http://dx.doi.org/10.1371/journal.pone.0005151.
Faure, H., Walter, R.C., Grant, D.R., 2002. The coastal oasis: ice age springs on emerged continental shelves. Glob. Planet. Change 33, 47–56.
Feliner, G.N., 2011. Southern European glacial refugia: a tale of tales. Taxon 60, 365–372.
Fiorenza, L., Benazzi, S., Henry, A., Salazar-Garcia, D.C., Blasco, R., Picin, A., Wroe, S., Kulmer, O., 2015. To meat or not to meat? New perspectives on Neanderthal ecology. Yearb. Phys. Anthropol. 156, 43–71.
Galanidou, N., Athanassas, C., Cole, J., Iliopoulos, G., Katerinopoulos, A., Magganas, A., McNabb, J., 2016. The Acheulean site at Rodafnidia, Lisvori on Lesbos, Greece. In: Harvati, K., Roksandic, M. (Eds.), Paleoanthropology of the Balkans and Anatolia: Human Evolution and its Context. Springer, Dordrecht, pp. 119–138.
Galanidou, N., Cole, J., Iliopoulos, G., McNabb, J., 2013. East meets west: the middle Pleistocene site of Rodafnidia on Lesvos, Greece. Antiq. Proj. Gallery 87, 336.
Gamble, C., 1995. The earliest occupation of Europe: the environmental background. In: Roebroeks, W., van Kolfschoten, T. (Eds.), The Earliest Occupation of Europe: Proceedings of the European Science Foundation Workshop at Tautavel (France), 1993. University of Leiden, Leiden, pp. 279–295.
Grove, M., 2009. Hunter-gatherer movement patterns: causes and constraints. J. Anthropol. Archaeol. 28, 222–233.
Grün, R., 1996. A re-analysis of electron spin resonance dating results associated with the Petralona hominid. J. Hum. Evol. 30, 227–241.
Grzimek, B., 1990. Grzimek's Animal Life Encyclopedia. Van Nostrand Renhold Co, New York.
Hardy, K., Buckley, S., Collins, M.J., Estalrrich, A., Brothwell, D., Copeland, L., et al., 2012. Neanderthal medics? Evidence for food, cooking, and medicinal plants entrapped in dental calculus. Naturwissenschaften 99, 617–626.
Harvati, K., 2016. Paleoanthropology in Greece: recent findings and interpretations. In: Harvati, K., Roksandic, M. (Eds.), Paleoanthropology of the Balkans and Anatolia: Human Evolution and its Context. Springer, Dordrecht, pp. 3–14.
Harvati, K., 2009. Petralona: link between Africa and Europe? In: Schepartz, L., Fox, S., Bourbou, C. (Eds.), New Directions in the skeletal Biology of Greece. Occasional Wiener Laboratory Series, ASCSA, Athens, pp. 31–48.
Harvati, K., Darlas, A., Bailey, S.E., Rein, T.R., El Zaatari, S., Fiorenza, L., Kullmer, O., Psathi, E., 2013. New Neanderthal remains from Mani peninsula, S. Greece: the Kalamakia middle Palaeolithic cave site. J. Hum. Evol. 64, 486–499.
Harvati, K., Panagopoulou, E., Karkanas, P., 2003. First Neanderthal remains from Greece: the evidence from Lakonis. J. Hum. Evol. 45, 465–473.
Harvati, K., Panagopoulou, E., Runnels, C., 2009. The paleoanthropology of Greece. Evol. Anthropol. 18, 131–143.
Harvati, K., Panagopoulou, E., Tourloukis, V., Thompson, N., Karkanas, P., Athanassiou, A., Konidaris, G., Tsartsidou, G., Giusti, D., 2016. New Middle Pleistocene elephant butchering site from Greece. In: Oral Contribution, Palaeoanthropology Society Meeting, Atlanta, Georgia.
Harvati, K., Stringer, C., Karkanas, P., 2011. Multivariate analysis and classification of the Apidima 2 cranium from Mani, southern Greece. J. Hum. Evol. 60, 246–250.
Harvati, K., Tourloukis, V., 2013. Human evolution in the southern Balkans. Evol. Anthropol. 22, 43–45.
Henry, A., Brooks, A.S., Piperno, D.R., 2010. Microfossils in calculus demonstrate consumption of plants and cooked foods in Neanderthal diets (Shanidar III, Iraq; Spy I and II, Belgium). Proc. Natl. Acad. Sci. (USA) 108, 486–491.
Henry, A., Brooks, A.S., Piperno, D.R., 2014. Plant foods and the dietary ecology of Neanderthals and early modern humans. J. Hum. Evol. 69, 44–54.
Higgs, E.S., Vita-Finzi, C., 1966. The climate, environment and industries of Stone Age Greece. Part II. Proc. Prehist. Soc. 32, 1–29.
Howitt-Marshall, D., Runnels, C., 2016. Middle Pleistocene sea-crossings in the eastern Mediterreanean? J. Anthropol. Archaeol. 42, 140–153.
Hughes, P.D., Woodward, J.C., Gibbard, P.L., Macklin, M.G., Gilmour, M.A., Smith, G.R., 2006. The glacial history of the Pindus mountains, Greece. J. Geol. 114, 413–434.
Huxtable, J., Gowlett, J.A.J., Bailey, G.N., Carter, P.L., Papakonstantinou, V., 1992. Thermoluminescence dates and a new analysis of the early Mousterian from Asprochaliko. Curr. Anthropol. 33 (1), 109–113.
Jennings, R., Finlayson, c., Fa, D., Finlayson, G., 2011. Southern Iberia as a refuge for the last Neanderthal populations. J. Biogeogr. 38, 1873–1885.
Jolivet, L., Brun, J.-P., 2010. Cenozoic geodynamic evolution of the Aegean. Int. J. Earth Sci. Geol. Rundschau 99, 109–138.
Kaczanowska, M., Kozłowski, J.K., Sobczyk, K., 2010. Upper Palaeolithic human occupations and material culture at Klissoura Cave 1. Eurasian Prehist. 7, 133–285.
Karaiskou, N., Tsakogiannis, A., Gkagkavouzis, K., Papika, S., Latsoudis, P., Kavakiotis, I., Pantis, J., Abatzopoulos, T., Triantaphyllidis, C., Triantafyllidis, A., 2014. Greece: a Balkan sub-refuge for a remnant red deer (*Cervus Elaphus*) population. J. Hered. 105, 334–344.
Karkanas, P., 2002. Micromorphological studies in Greek prehistoric sites: new insight in the interpretation of the archaeological record. Geoarchaeology 17, 237–259.
Karkanas, P., 2010. Geology, stratigraphy, and site formation processes of the Upper Palaeolithic and later sequence in Klissoura Cave 1. Eurasian Prehist. 7 (2), 15–36.
Karkanas, P., Koumouzelis, M., Kozlowski, J.K., Sitlivy, V., Sobczyk, K., Berna, F., Weiner, S., 2004. The earliest evidence for clay hearths: Aurignacian features in Klisoura Cave 1, southern Greece. Antiquity 78, 513–525.
Karkanas, P., White, D., Lane, C.S., Stringer, C., Davies, W., Cullen, V.L., Smith, V.C., Ntinou, M., Tsartsidou, G., Kyparissi-Apostolika, N., 2015. Tephra correlations and climatic events between the MIS 6/5 transition and the beginning of MIS3 in Theopetra Cave, central Greece. Quat. Sci. Rev. 118, 170–181.
Kelly, R.L., 1995. The Foraging Spectrum: Diversity in Hunter–Gatherer Lifeways. Smithsonian Institution Press, Washington.
King, G., Bailey, G., 1985. The palaeoenvironment of some archaeological sites in Greece: the influence of accumulated uplift in a seismically active region. Proc. Prehist. Soc. 51, 273–282.
Kopaka, K., Matzanas, C., 2009. Palaeolithic industries from the island of Gavdos, near neighbour to Crete in Greece. Antiquity 83 (321) (Project Gallery).
Kotjabopoulou, E., Panagopoulou, E., Adam, E., 1999. The Boila rockshelter: further evidence of human activity in the Voidomatis Gorge. In: Bailey, G.N., Adam, E., Panagopoulou, E., Perlès, C., Zachos, K. (Eds.), The Palaeolithic Archaeology of Greece and Adjacent Areas: Proceedings of the ICOPAG Conference, Ioannina. British School at Athens Studies 3, London, pp. 197–210.
Koufos, G.D., de Bonis, L., 2004. The deciduous lower dentition of *Ouranopithecus macedoniensis* (Primates, Hominoidea) from the late Miocene deposits of Macedonia, Greece. J. Hum. Evol. 46, 699–718.

Kourtessi-Philippakis, G., 1995. Le Paléolithique de la Grèce continentale. Etat de la question et perspectives de recherche. Publications de la Sorbonne, Paris.
Kourtessi-Philippakis, G., 1999. The lower and middle Palaeolithic in the Ionian islands: new finds. In: Bailey, G.N., Adam, E., Panagopoulou, E., Perlès, C., Zachos, K. (Eds.), The Palaeolithic Archaeology of Greece and Adjacent Areas: Proceedings of the ICOPAG Conference, Ioannina. British School at Athens Studies 3, London, pp. 282–287.
Kuhn, S., Pigati, J., Karkanas, P., Koumouzelis, M., Kozłowski, J.K., Ntinou, M., Stiner, M., 2010. Radiocarbon dating results for the early upper Palaeolithic of Klissoura cave 1. Eurasia Prehist. 7 (2), 37–46.
Lenormant, F., 1867. L'Âge de Pierre en Grèce. Rev. Archèol. Nouv. Sèrie 15, 16–19.
Lev, E., Kislev, M.E., Bar-Yosef, O., 2005. Mousterial vegetal food in Kebara cave, Mt. Carmel. J. Archaeol. Sci. 32, 475–484.
Ligkovanlis, S., 2011. Megalo Karvounari revisited. In: Forsén, B., Tikkala, E. (Eds.), Thesprotia Expedition II, Environment and Settlement Patterns, vol. XVI. Papers and Monographs of the Finnish Institute at Athens, Helsinki, pp. 159–180.
Lowe, J., Barton, N., Blockley, S., Bronk Ramsey, C., Cullen, V., Davies, W., et al., 2012. Volcanic ash layers illuminate the resilience of Neanderthals and early modern humans to natural hazards. Proc. Natl. Acad. Sci. (USA) 109 (34), 13532–13537.
Löhnert, E., Nowak, H., 1965. Die Braunkohlenlagerstätte von Khoremi im Becken von Megalopolis/Peloponnes. Geol. Jahrbuch 82, 847–868.
Lykousis, V., 2009. Sea-level changes and shelf break prograding sequences during the last 400 ka in the Aegean margins: subsidence rates and palaeogeographic implications. Cont. Shelf Res. 29, 2037–2044.
Macleod, D.A., Vita-Finzi, C., 1982. Environment and provenance in the development of recent alluvial deposits in Epirus, NW Greece. Earth Surf. Process. Landforms 7, 29–43.
Madella, M., Jones, M.K., Goldberg, P., Goren, Y., Hovers, E., 2002. The exploitation of plant resources by Neanderthals in Amud Cave (Israel): the evidence from Phytolith studies. J. Archaeol. Sci. 29, 703–719.
Marinos, P., Herman, J.S., Back, W., Xidakis, G., 1985. Structural control and geomorphic significance of groundwater discharge along the coast of the Mani Peninsula, Peloponnese, Greece. Karst Water Resources. In: Proceedings of the Ankara-antalya Symposium, July 1985. IAHS Publl. no. 161.
Melentis, J.K., 1961. Studien über fossile Vertebraten Griechenlands: 2. Die Dentition der plestozänen Proboscidier des Beckens von Megalopolis im Peloponnes (Griechenland). Ann. Géol. Des. Pays Hell. XII, 154–262.
Mountrakis, D., 1985. Geology of Greece. University Studio Press (in Greek), Thessaloniki.
Ntinou, M., 2010. Wood charcoal analysis at Klissoura cave 1 (Prosymna, Peloponnese): the upper Palaeolithic vegetation. Eurasian Prehist. 7 (2), 47–69.
Okuda, M., van Vugt, N., Nakagawa, T., Ikeya, M., Hayashida, A., Yasuda, Y., Setoguchi, T., 2002. Palynological evidence for the astronomical origin of lignite-detritus sequence in the middle Pleistocene Marathousa Member, Megalopolis, SW Greece. Earth Planet. Sci. Lett. 201, 143–157.
Palli, O., Papadea, A., 2004. Le nouveaux sites paléolithiques en Thesprotie. In: Cabanes, P., Lamboley, J.-L. (Eds.), L' Illyrie Meridionale et l' Epire dans l' Antiquite IV: Actes du IV colloque international de Grenoble (10-12 octobre 2002), pp. 17–22 (Paris: De Boccard).
Papakonstantinou, V., Vassilopoulou, D., 1997. The middle Palaeolithic industries of Epirus. In: Bailey, G.N. (Ed.), Klithi: Palaeolithic Settlement and Quaternary Landscapes in Northwest Greece, Vol. 2: Klithi in its Local and Regional SettingMcDonald Institute for Archaeological Research, Cambridge, pp. 459–480.
Panagopoulou, E., 1999. The Theopetra Middle Palaeolithic assemblages: their relevance to the middle Palaeolithic of Greece and adjacent areas. In: Bailey, G.N., Adam, E., Panagopoulou, E., Perlès, C., Zachos, K. (Eds.), The Palaeolithic Archaeology of Greece and Adjacent Areas: Proceedings of the ICOPAG Conference, Ioannina, September 1994. British School at Athens Studies 3, London, pp. 252–265.
Panagopoulou, E., 2000. The middle Palaeolithic assemblages of Theopetra cave: technological evolution in the upper Pleistocene. In: Kyparissi-Apostolika, N. (Ed.), The Theopetra Cave: 12 Years of Excavation and Research1987–1998. Proceedings of the International Conference, Trikala, 6 -7 November1998. Greek Ministry of Culture, Athens, pp. 139–161.
Panagopoulou, E., Karkanas, P., Tsartsidou, G., Harvati, K., Ntinou, M., 2002-2004. Late Pleistocene archaeological and fossil human evidence from Laconis Cave, southern Greece. J. Filed Archaeol. 29 (3–4), 323–349.
Panagopoulou, E., Kotjabopoulou, E., Karkanas, P., 2001. Geoarchaeological research in Alonnisos: new evidence on the Palaeolithic and Mesolithic in the Aegean region. In: Sampson, A. (Ed.), The Archaeological Research in Northern Sporades, 121–51. Alonnisos: Municipality of Alonnisos (In Greek).
Panagopoulou, E., Tourloukis, V., Thompson, N., Athanassiou, A., Tsartsidou, G., Konidaris, G.E., Giusti, D., Karkanas, P., Harvati, K., 2015. Marathousa 1: a new middle Pleistocene archaeological site from Greece. Antiquity 343 (Project Gallery).
Papoulia, Ch, 2017. Seaward dispersals to the NE Mediterranean islands in the Pleistocene: the lithic evidence in retrospect. Quat. Int. 431 (Part B), 64–87.
Papoulia, Ch, 2011. Mikro Karvounari in context: the new lithic collection and its implications for middle Palaeolithic hunting activities. In: Forsén, B., Tikkala, E. (Eds.), Thesprotia Expedition II: Environment and Settlement Patterns. Papers and Monographs of the Finnish Institute at Athens, vol. XVI, pp. 123–158. Helsinki.
Pearson, O., 2013. Hominin evolution in the middle-late Pleistocene: fossils, adaptive scenarios and alternatives. Curr. Anthropol. 54, 221–233.
Perlès, C., 1999a. Long-term perspectives on the occupation of the Franchthi Cave: continuity and discontinuity. In: Bailey, G.N., Adam, E., Panagopoulou, E., Perlès, C., Zachos, K. (Eds.), The Palaeolithic Archaeology of Greece and Adjacent Areas: Proceedings of the ICOPAG Conference, Ioannina, September 1994. British School at Athens Studies 3, London, pp. 311–318.
Perlès, C., 1999b. Greece, 30,000-20,000 bp. In: Roebroeks, W., Mussi, M., Svoboda, J., Fennema, K. (Eds.), Hunters of the Golden Age: the Mid Upper Palaeolithic of Eurasia 30,000-20,000 BP, Analecta Prehistorica Leidensia. University of Leiden, Leiden, pp. 375–397.
Pettitt, P.B., 2003. The Mousterian in action: chronology, mobility, and Middle Paleolithic variability. In: Moloney, N., Schott, M.J. (Eds.), Lithic Analysis at the Millennium. Left Coast Press, London, pp. 29–43.
Picin, A., Peresani, M., Falguères, C., Gruppioni, G., Bahain, J.-J., 2013. San Bernardino Cave (Italy) and the appearance of Levallois technology in Europe: results of a radiometric and technological reassessment. PLoS One 8 (10), e76182. http://dx.doi.org/10.1371/journal.pone.0076182.
Reisch, L., 1980. Pleistozän und Urgeschichte der Peloponnes. University of Erlangen, Erlangen.
Rocca, R., Abruzzese, C., Aureli, D., 2016. European Acheuleans: critical perspectives from the east. Quat. Int. 411 (Part B), 402–411.
Runnels, C., 1988. A prehistoric survey of Thessaly: new light on the Greek middle Palaeolithic. J. Field Archaeol. 15, 277–290.
Runnels, C., 1995. Review of Aegean prehistory IV: the stone age of Greece from the Palaeolithic to the advent of Neolithic. Am. J. Archaeol. 99, 699–728.
Runnels, C., 2014. Early Palaeolithic on the Greek islands? J. Mediterr. Archaeol. 27, 211–230.
Runnels, C., van Andel, T.H., 1993a. A handaxe from Kokkinopilos, Epirus, and its implications for the Palaeolithic of Greece. J. Field Archaeol. 20, 191–203.
Runnels, C., van Andel, T.H., 1993b. The lower and middle Palaeolithic of Thessaly, Greece. J. Field Archaeol. 20, 299–317.
Runnels, C., van Andel, T.H., 2003. The early stone age of the Nomos of Preveza: landscape and settlement. In: Wiseman, J., Zachos, K. (Eds.), Landscape Archaeology in Southern Epirus, Greece I, Hesperia Supplement 32. American School of Classical Studies at Athens, Athens, pp. 47–133.
Runnels, C., Karimali, E., Cullen, B., 2003. Early upper Palaeolithic spilaion: an artifact-rich surface site. In: Wiseman, J., Zachos, K. (Eds.), Landscape Archaeology in Southern Epirus, Greece I, Hesperia Supplement 32. American School of Classical Studies at Athens, Athens, pp. 135–156.
Runnels, C., DiGregorio, C., Wegmann, K.W., Gallen, S.F., Strasser, T.F., Panagopoulou, E., 2014a. Lower Palaeolithic artifacts from Plakias, Crete: implications for hominin dispersals. Eurasian Prehist. 11, 129–152.
Runnels, C., McCoy, F., Bauslaugh, R., Murray, P., 2014b. Palaeolithic research at Mochlos, Crete: new evidence for Pleistocene maritime activity in the Aegean. Antiq. Proj. Gallery 88, 342.
Sickenberg, O., 1975. Eine Säugertierfauna des tieferen Bihariums aus dem Becken von Megalopolis (Peloponnes, Griechenland). Ann. Géologiques Des. Pays Helléniques 27, 25–73.
Sitlivy, V., Sobczyk, K., Karkanas, P., Koumouzelis, M., 2007. Middle Palaeolithic lithic assemblages of the Klisoura cave, Peloponnesus, Greece: a comparative analysis. Archaeol. Ethnol. Anthropol. Eurasia 3, 2–15.
Smith, T.M., Harvati, K., Olejniczak, A.J., Reid, D.J., Hublin, J.J., Panagopoulou, E., 2009. Dental development and enamel thickness in the Lakonis Neanderthal molar. Am. J. Phys. Anthropol. 138 (1), 112–118.
Starkovich, B.M., 2011. Trends in Subsistence from the Middle Paleolithic through Mesolithic at Klissoura Cave 1 (Peloponnese, Greece). PhD Dissertation. University of Arizona.
Starkovich, B., 2014. Optimal foraging, dietary change, and site use during the Paleolithic at Klissoura Cave 1 (southern Greece). J. Archaeol. Sci. 52, 39–55.
Starkovich, B., Ntinou, M., 2017. Climate change, human population or both? Upper Paleolithic subsistence shifts in southern Greece. Quat. Int. 428 (Part B), 17–32.
Stewart, J.R., Stringer, C.B., 2012. Human evolution out of Africa: the role of refugia and climate change. Science 335, 1317–1321.
Strasser, T.F., Panagopoulou, E., Runnels, C., Murray, P., Thompson, N., Karkanas, P., McCoy, F., Wegmann, W., 2010. Stone age seafaring in the Mediterranean: evidence from the Plakias region for lower Palaeolithic and Mesolithic habitation of Crete. Hesperia 79 (2), 145–190.
Strasser, T.F., Runnels, C., Wegmann, K., Panagopoulou, E., McCoy, F., DiGregorio, C., Karkanas, P., Thompson, N., 2011. Dating lower Palaeolithic sites in southwestern Crete, Greece. J. Quat. Sci. 26, 553–560.
Tourloukis, V., 2016. On the spatio-temporal distribution of Mediterranean lower Paleolithic sites: a geoarchaeological perspective. In: Harvati, K., Roksandic, M. (Eds.), Paleoanthropology of the Balkans and Anatolia: Human Evolution and its Context. Springer, Dordrecht, pp. 303–323.
Tourloukis, V., 2010. The Early and Middle Pleistocene Archaeological Record of Greece: Current Status and Future Prospects. Archaeological Studies Leiden University 23, Leiden University Press, Leiden.
Tourloukis, V., Karkanas, P., 2012. The Middle Pleistocene archaeological record of Greece and the role of the Aegean in hominin dispersals: new data and interpretations. Quat. Sci. Rev. 43, 1–15.
Tourloukis, V., Karkanas, P., Wallinga, J., 2015. Revisiting Kokkinopilos: middle Pleistocene radiometric dates for stratified archaeological material in Greece. J. Archaeol. Sci. 57, 355–369.
Tourloukis, V., Thompson, N., Garefalakis, Ch, Karkanas, P., Konidaris, G., Panagopoulou, E., Harvati, K., 2016. New middle Palaeolithic sites from the Mani peninsula, southern Greece. J. Field Archaeol. 41 (1), 68–83.
Tsartsidou, G., Karkanas, P., Marshall, G., Kyparissi-Apostolika, N., 2015.

Palaeoenvironmental reconstruction and flora exploitation at the Palaeolithic cave of Theopetra, central Greece: the evidence from phytolith analysis. Archaeol. Anthropol. Sci. 7 (2), 169–185.

Tzedakis, P.C., 1994. Vegetation change through glacial-interglacial cycles: a long pollen sequence perspective. Philos. Trans. R. Soc. Lond. B 345, 403–432.

Tzedakis, P.C., 2005. Towards an understanding of the response of southern European vegetation to orbital and suborbital climate variability. Quat. Sci. Rev. 24, 1585–1599.

Tzedakis, P.C., 2007. Seven ambiguities in the Mediterranean palaeoenvironmental narrative. Quat. Sci. Rev. 26, 2042–2066.

Tzedakis, P.C., Hooghiemstra, H., Pälike, H., 2006. The last 1.35 million years at Tenaghi Philippon: revised chronostratigraphy and long-term vegetation trends. Quat. Sci. Rev. 25 (23–24), 3416–3430.

Tzedakis, P.C., Lawson, I.T., Frogley, M.R., Hewitt, G.M., Preece, R.C., 2002. Buffered tree population changes in a Quaternary refugium: evolutionary implications. Science 297, 2044–2047.

Tzedakis, P.C., McManus, J.F., Hooghiemstra, H., Oppo, D.W., Wijmstra, T.A., 2003. Comparison of changes in vegetation in northeast Greece with records of climate variability on orbital and suborbital frequencies over the last 450 000 years. Earth Planet. Sci. Lett. 212, 197–212.

Valladas, H., Mercier, N., Froget, L., Joron, J.-L., Reyss, J.-L., Karkanas, P., Panagopoulou, E., Kyparissi-Apostolika, N., 2007. TL age estimates for the middle Palaeolithic layers at Theopetra cave (Greece). Quat. Geochronol. 2, 303–308.

Van Andel, T.H., 1998. Paleosols, red sediments and the old stone age in Greece. Geoarchaeology 13, 361–390.

Van Andel, T.H., Runnels, C., 2005. Karstic wetland dwellers of middle Palaeolithic Epirus, Greece. J. Field Archaeol. 30 (4), 367–384.

Van Vugt, N., de Bruijn, H., van Kolfschoten, T., Langereis, C.G., 2000. Magneto- and cyclostratigraphy and mammal-fauna's of the Pleistocene lacustrine Megalopolis basin, Peloponnesos, Greece. Geol. Ultraiectina 189, 69–92.

Vinken, R., 1965. Stratigraphie und Tektonik des Beckens von Megalopolis (Peloponnes, Griechenland). Geol. Jahrbuch 83, 97–148.

White, M., Pettitt, P., Schreve, D., 2016. Shoot first, ask questions later: interpretative narratives of Neanderthal hunting. Quat. Sci. Rev. 140, 1–20.

Woodward, J.C. (Ed.), 2009. The Physical Geography of the Mediterranean. Oxford University Press, Oxford.

Woodward, J.C., Lewin, J., Macklin, M.G., 1995. Glaciation, river behavior and the Palaeolithic settlement of upland northwest Greece. In: Lewin, J., Macklin, M.G., Woodward, J.C. (Eds.), Mediterranean Quaternary River Environments, Balkema, Rotterdam, pp. 115–129.

Please cite this article in press as: Tourloukis, V., Harvati, K., The Palaeolithic record of Greece: A synthesis of the evidence and a research agenda for the future, Quaternary International (2017), http://dx.doi.org/10.1016/j.quaint.2017.04.020