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Abstract

The Middle Pleistocene (MP; ca. 774–129 ka) marks a critical period of human evolution, characterized by increasing behavioral complexity and the first unambiguous evidence of plant-based technologies. Despite this, direct evidence for early wooden tool use remains exceptionally rare. Here, we present the earliest handheld wooden tools, identified from secure contexts at the site of Marathousa 1, Greece, dated to ca. 430 ka (MIS12). Through a systematic morphological, microscopic, taphonomic and taxonomic analysis of the sampled wood macroremains, two specimens were securely identified as modified by hominins: one small alder (*Alnus* sp.) trunk fragment bears clear working and use-wear traces consistent with a multifunctional stick likely used in digging at the paleo-lakeshore; and one very small willow/poplar (*Salix* sp./*Populus* sp.) artifact exhibits signs of shaping and potential use-wear. A third specimen, a large alder trunk segment, shows deep, non-anthropogenic striations interpreted here as claw marks from a large carnivoran. The wooden tools were excavated together with butchered elephant remains, small lithic artifacts and debitage, and worked bone, underscoring the diversity of engagement with a variety of different raw materials for technological purposes at Marathousa-1. These finds extend the temporal range of early wooden tools. They represent both the use of expedient larger handheld tools as well as a much smaller, likely finger-held wooden tool, which is uniquely small for the Pleistocene, expanding known functional purposes of early wood technologies. Moreover, they highlight the Megalopolis Basin's exceptional preservation conditions and its role in understanding the evolution of hominin behavior.

Significance Statement

The specimens presented here represent the earliest known handheld wooden tools, recovered at the Middle Pleistocene site Marathousa 1 (Greece). The site provides evidence of hominin activities in a MIS12 glacial refugium, including the manufacture and use of lithic and bone artifacts, alongside butchery of straight-tusked elephants and other fauna. The wooden tools include a worked alder trunk likely used for digging, and a small willow/poplar tool, possibly used in manufacturing lithics. A further alder trunk fragment with claw marks attests to carnivore presence and possible hominin-carnivore competition at the site. The wooden tools from Marathousa 1 represent the earliest handheld wooden tools, and include a new tool type, together demonstrating the importance of systematic investigation of early wood remains.

Introduction

The Middle Pleistocene (MP; ca. 774-129ka) is notable for encompassing unprecedented diversity of hominin species and concomitant brain expansion, alongside technological innovations (1). Due to preservation conditions, the vast majority of technological information comes from the stone tool record, which likely only comprised a fraction of the myriad materials used by hominins to modify and adapt their engagement with environments and prey.

Starting in the late Middle Pleistocene (Maring Isotope Stages (MIS) 11-6), finds from Clacton-on-Sea (UK, dating to ca. 400ka), Kalambo Falls (Zambia, handheld tools dating to ca. 390-324ka), Schöningen (Germany, dating to ca. 300ka), Gantangqing (China, dating to ca. 300ka) and Poggetti Vecchi (Italy, dating to ca. 171ka) demonstrate the use of wood for a variety of handheld tools (2–9). These include most notably wooden weapons with strategic design features and multi-step woodworking, but also digging sticks, a wooden wedge, and tool handles. Examples of earlier wooden tools are absent, although recent excavations at Kalambo Falls demonstrated the use of large wooden elements for structural purposes by 476ka years ago (5).

Here we systematically investigate the wood assemblage excavated at the MIS12 glacial site Marathousa 1 (MAR-1) in 2015-2019, assessing it for evidence of human modification. We present two wooden artifacts, comprising one clearly humanly modified wooden tool (Category 1) and one likely small wooden tool (Category 2). Dated to ca. 430ka, these specimens represent the earliest known evidence of handheld wooden tools. We also describe a trunk fragment with unusual surface alteration that we propose to be non-anthropogenic, but potentially attributable to the activity of carnivores at the site.

Archaeological Context

The Lower Palaeolithic site MAR-1 is located in the Megalopolis Basin (Greece), known for its fossiliferous deposits and long stratigraphic sequence, spanning from ca. 900-150ka and exposed through lignite mining activities (10). MAR-1 was discovered in 2013 during survey targeting the stratigraphic section profiles in search for stratified Pleistocene remains (11). The site is located at 350m above mean sea level (masl) between lignite seams IIb and IIIa in Marathousa Member (Choremi Formation) sediments, comprising lacustrine clay, silt and sand beds (Fig. S1) (10, 12). Excavations were undertaken from 2013 to 2019 in two areas, designated A and B. Both yielded MP cultural deposits with faunal remains (micro- and macrofauna: insects, ostracods, mollusks, fishes, amphibians, reptiles, birds, mammals) – many of which, including megafauna, have signs of human modification (13–15) – in association with a Lower Palaeolithic lithic assemblage (>2000 artifacts) of microlithic character, worked bone artifacts (16), and micro- and macroflora (17). The latter includes the wood assemblage investigated here.

MAR-1 is one of the oldest currently known stratified open-air archaeological sites in south-east Europe. It is dated to ca. 430ka (Bayesian age model developed from the magnetostratigraphy and chronostratigraphy of the site and from pMET-pIRIR Optically Stimulated Luminescence dates (10, 18, 19), and thus within MIS12, one of the most severe Pleistocene glaciations. The fauna comprises both terrestrial and semi-aquatic mammals, as well as freshwater mollusks, turtles and birds (14, 15), indicating a rich lakeshore environment, an interpretation supported by the botanical remains, which predominantly represent aquatic and waterside plants (17). Pollen analysis found mainly open landscapes but also a persistence of limited forest cover in the surroundings of the basin (20). Additional multi-proxy paleoenvironmental reconstruction indicates the presence of a permanent freshwater body (21), relatively cold mean annual air temperatures (5-6.8°C) (18) coupled with moderate seasonality and the presence of open woodland vegetation (22), highlighting the role of the Megalopolis Basin as a glacial microrefugium. The excellent preservation of a range of different organic remains suggests that the site was subject to rapid burial, and remained in wet contexts thereafter (12).

Results

We conducted a systematic macro- and micro-morphological investigation of the MAR-1 sample of wood remains for signatures of human and other modifications. The assemblage comprises 144 plotted wood pieces (Table S1) excavated from 2015 to 2019 (Fig. S2). Two specimens, 940/673-39 and 935/671-13, both recovered from Area A, were classified as wood artifacts (Category 1 and 2 respectively, Table S2), while a third, 942/677-59, showed evidence of modification by a large carnivoran. We describe the two secure wood tools within a *chaîne opératoire* framework (see Methods, Table S3). Five additional specimens, classified as Category 3 and 4, showed promising morphological characteristics, but lacked diagnostic tool marks, likely due to taphonomic deterioration, and are not described in detail here (Table S2, SI Section 3, 3D models).

Specimen 940/673-39

Specimen 940/673-39 was excavated in 2015 (Fig. 1).

<u>Phase 0: Raw material.</u> The artifact now consists of four refitting fragments of a small worked alder (*Alnus* sp., SI 4) trunk (Fig. 2; SI Section 3, 3D models; Figs. S3 and S4). The total length of the refitted tool is 81cm (as measured from View 3, see Fig. 2), and its maximum diameter is 4.5cm wide (located at 7cm). However, the tool is significantly taphonomically compressed, making its original diameter and annual growth ring count difficult to estimate. Although the object would have originally been broadly round, the

analysis and description of the tool is restricted to Views 1 and 3, as these sides preserved the greatest surface area.

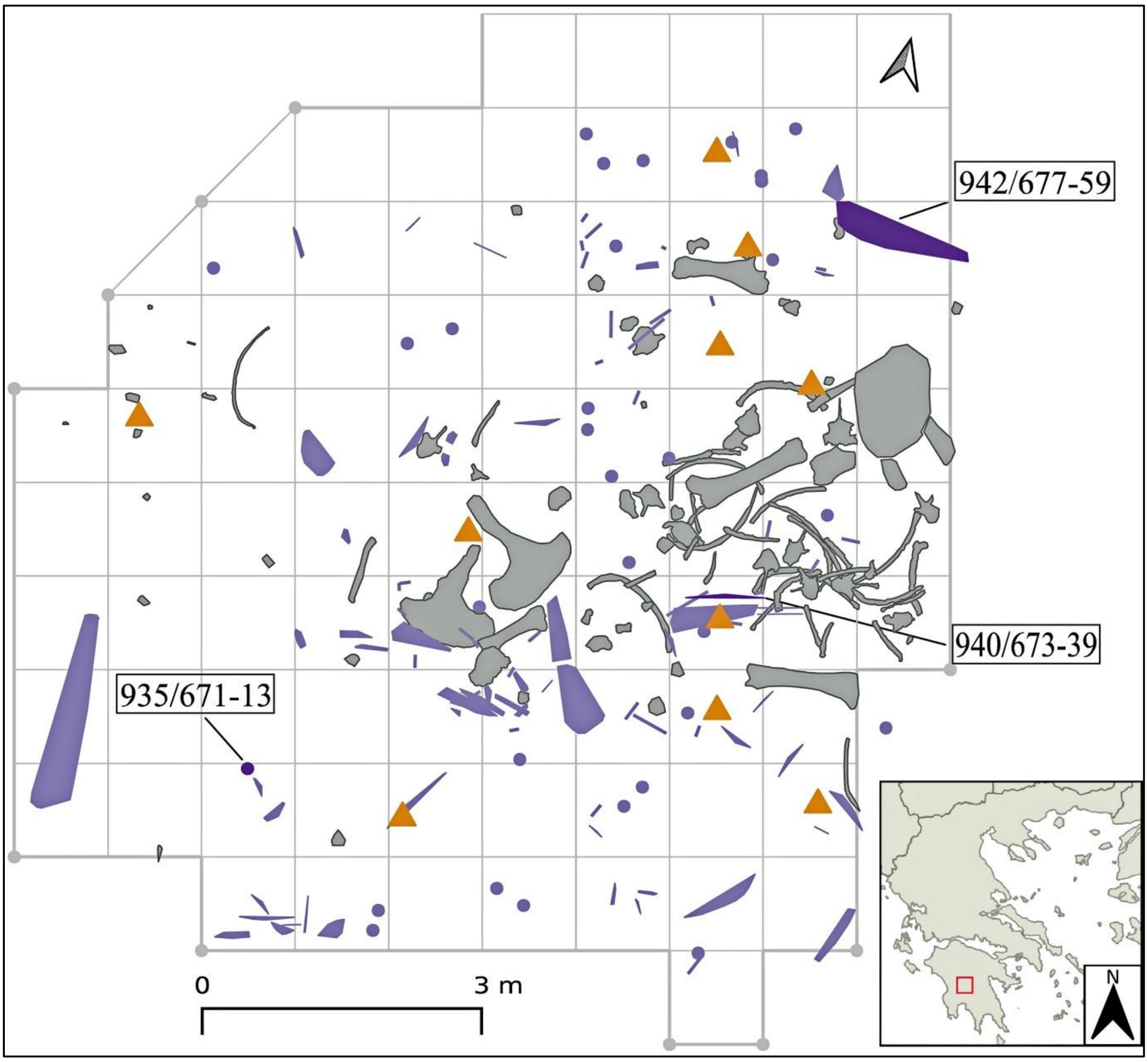

Fig. 1. Area A: Location of the finds plotted in relation to faunal, lithic and other wood remains. Find location of 940/673-39 [MAR-1 2015, Area A, UA4, Spit 1, Z: 349.15masl]; 942/677-59 [MAR-1 2016 Area A, UA4 Spit 2, Z: 349.2masl]; and 935/671-13 [MAR-1 Area A 2018 UA3c Spit 3 Z: 349.48masl]. *Paleoloxodon antiquus* skeletal remains are shown in grey, lithics >2cm are indicated by orange triangles, wood remains shown in purple. Inset box shows the approximate location of MAR-1 on a map of Greece.

The raw material used to make this tool was a small alder trunk. Knots, some with pronounced branch collars and seams, are present along the length of the tool and on all views, indicating this was a roundwood trunk. Branch collars and seams - channel-like depressions that grow underneath branches (23, 24) - indicate the direction of growth, showing that the base of the trunk is toward Fragment 1 (Fig. 2, left). There are dead limbs, as well as worked knots (see Phase 1).

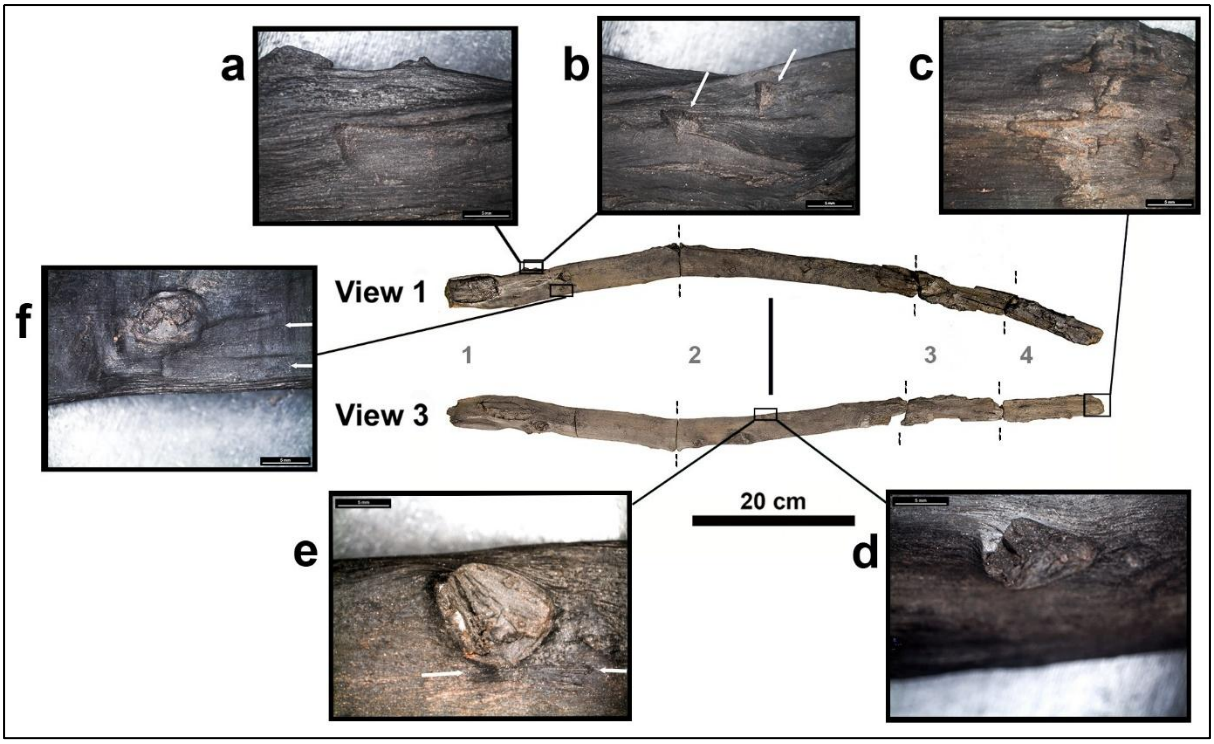

Fig. 2. Center: Overview of 940/673-39. Fragments 1 through 4 numbered in gray. Phase 1 (manufacture) traces identified include carving marks (a, e, f) with stop marks, chopping marks (b, d, e). Phase 2 traces identified on the tool consist of fraying of fibres and micro-splintering concentrated at one end of the tool (c). Cutaway images taken with Leica M10 stereo microscope, with small white arrows showing working traces.

Phase 1: Manufacture: The tool is mostly debarked, with areas (ca 3cm maximum) of outer bark remaining on each of the four fragments. There are clear working traces on fragments 1 and 2. Fragments 3 and 4 are smaller and more heavily degraded, possibly due to sediment erosion or weathering and potentially resulting in loss of working traces. Working traces include carving marks with associated stop marks (Fig. 2a, 2e, 2f), and chopping marks (Fig. 2b, 2d, 2e). Two chopping marks (Fig. 2b) co-occur along the surface of the trunk. One knot was broken off by chopping, which can be seen best in profile (Fig. 2d, but also see the same knot imaged in Fig. 2e). There are carving marks with a faint signature associated with this knot (Fig. 2e, small white arrows). The stop marks associated with carving marks and the chopping marks indicate that the working direction was always towards the base of the tree. There are no visible annual growth rings along the surface, suggesting that the tool was only minimally shaped, likely with the primary aim of removing branches and protruding knots. The location of these working traces around knots may correspond to the areas where the tool would have been held, at the top (toward base of trunk) and middle, and are absent from the functional end (Phase 2).

Phase 2: Use, maintenance, discard: Fragment 1 is slightly rounded and thicker, and with the associated working traces, may represent a simple 'handle'. The thinner end on Fragment 4 also has a rounded termination (Fig. 2, Figs. S5 and S6) with splinter negatives taking the form of micro-splintering focused in the last 2 to 3 cm of the tool (Fig. 2c, Fig. S4). The similar color of this area to the rest of the tool, focused micro-damage at the very end, and rounded morphology are indicative of use-wear. While the area lacks random striations characteristic of use as a digging stick (25), this could be a result of surface preservation. There is more sediment adhering to this area than to the rest of the tool. Together, the concentration of fraying and micro-splintering in association with the rounded tip and sediment suggest a potential function as a digging stick. Alternatively, the stick could have been used as a bark peeler for consuming inner bark (26), or for processing the elephant remains (see Discussion).

Phase 3: Taphonomy: The surface of the artifact is differentially degraded, particularly towards the functional end of the tool. This potentially reflects that the end was shaped, or that during use, wear abrasion occurred and protective outer rings were removed. However, it is also possible that the tool was subjected to slightly different taphonomic environments along its length. Some pitting is observed on the surface of fragment 2 which could be the result of microbial activity (Fig. S7). There are three taphonomic fractures, one of which is sharp while the other two are rough with associated splinter negatives, warping and fibre deformation. Some tangential cracks are also visible on the artifact, which are likely taphonomic in nature. The piece is significantly taphonomically compressed due to the weight of ca. 30 metres of sediment overlying the archaeological layer before mining operations (12), hindering interpretation of microCT scan results.

Phase 4: Excavation and post-excavation: There is a small amount of excavation or post-excavation damage on View 1 (Fig. S8). The color difference associated with this damage is notable and contrasts with carving and chopping marks (Phase 1), and micro-splintering (Phase 2). There is visible warping, in the form of splaying associated with two breaks, which may be post-excavation.

Interpretation: Based on multiple working traces paired with likely use-wear focused at one end, this specimen is a Category 1 tool. The tool has a morphology and size comparable to digging sticks, and fits with other Pleistocene multifunctional sticks retrieved in association with butchered megafauna (see Discussion).

Specimen 935/671-13

935/671-13 is a small wooden artifact (Fig. 3; SI Section 3, 3D models), excavated in 2018 some distance away from the main concentration of elephant remains (Fig. 1).

Phase 0: Raw material: This artifact is a small piece of willow or poplar (*Salix* sp./*Populus* sp., SI Section 4, Figs. S9 and S10), measuring 5.7cm in length, and 1.5cm (measured from View 1-3) and 1.2cm (measured from View 2-4) in diameter (Fig. 3). Small knots are visible around the perimeter of the piece. The microCT scan shows six annual growth rings visible at the base of the object (Fig. 4).

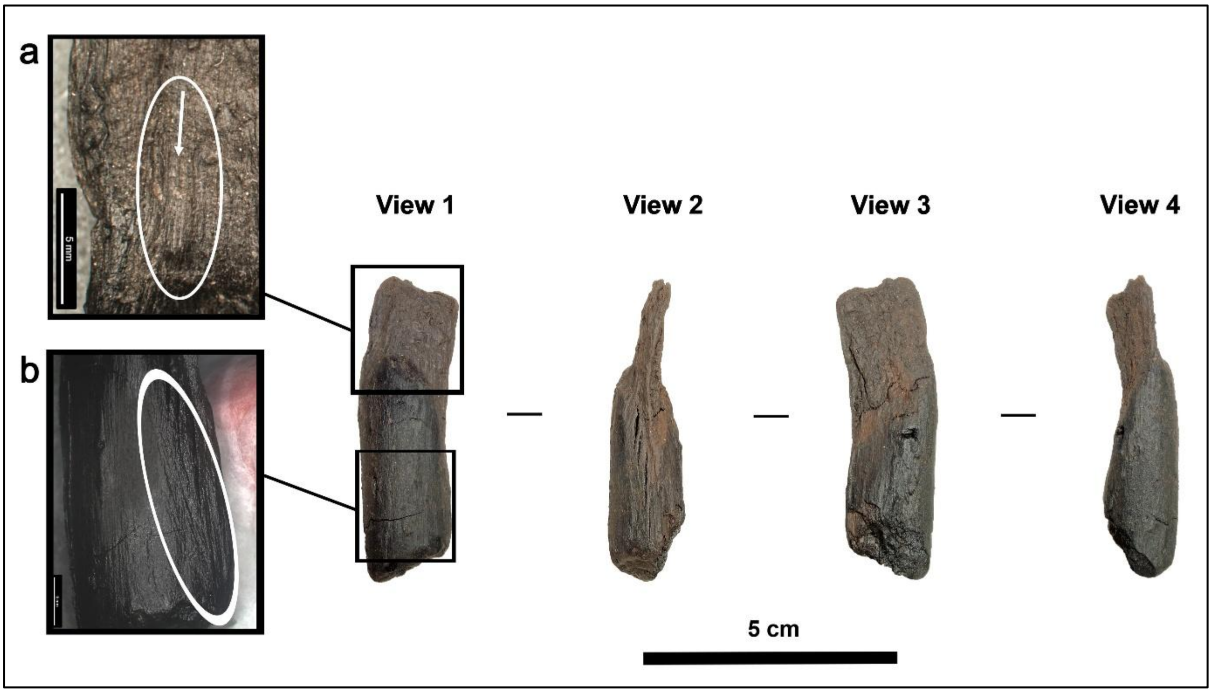

Fig. 3. Overview of 935/671-13. Numbers indicate the Views referred to in the description. Phase 1 (manufacture) traces identified include a tool facet with stop mark (a) and likely scrape mark (b).

Phase 1: Manufacture: The object retains no bark, and a wavy external surface visible on the last annual growth ring suggests the outer surface represents latewood (Fig. 4, box 1). It bears two likely tool facets, suggesting that it was debarked and shaped. A single tool facet with side features, signature, and stop mark is visible on the more heavily shaped part of the object indicating the direction of working (Fig. 3a, Fig. S11). A second tool facet consists of parallel striations running obliquely to the grain of the wood and is likely a scraping mark from debarking the object (Fig. 3b, Fig. S12). The shaping of this small tool is not similar to beaver traces (see Discussion; see also Fig. S13 and further descriptions in SI Section 6; 27, 28). Furthermore, the microCT scans show how the shaping at the narrow end of the object occurred through the removal of annual growth rings on both sides (Fig. 4), which would not be likely to occur naturally.

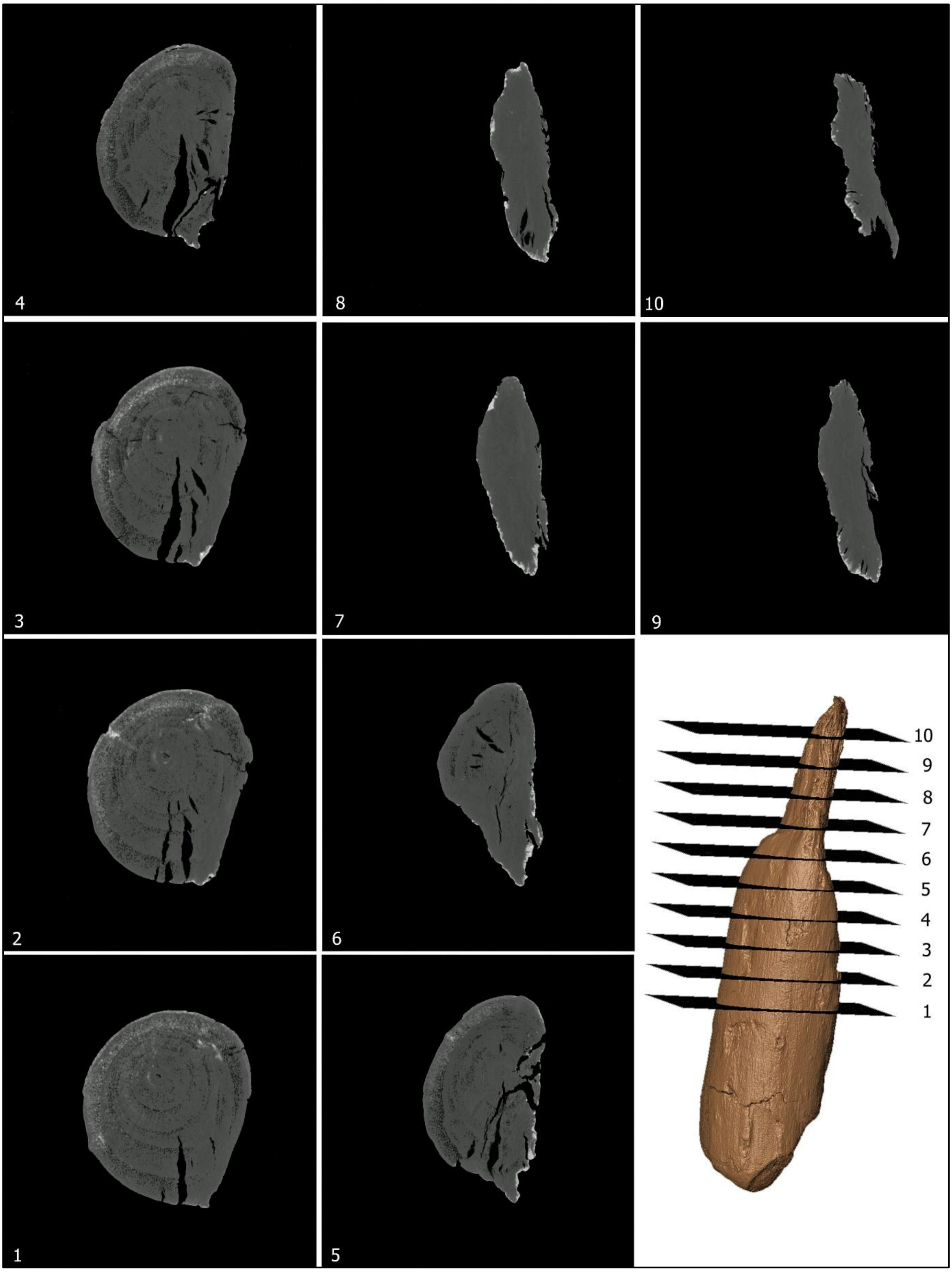

Fig. 4. MicroCT scan slices (1-10) of 935/671-13. The position of the slices on the specimen is illustrated in the lower right corner. Annual growth rings are visible in the middle of the specimen. At one end is the shaped tip, showing the removal of annual growth rings from both directions.

Phase 2: Use, maintenance, discard: The end of the object opposite to the shaped section bears evidence of rounding and pitting (Fig. S14, left) which may constitute use-wear formed by compressing the object. While the rounding could be taphonomic, the lack of rounding on the shaped end, as well as some small splinter negatives on the opposing side (Fig. S14, right) (see Phase 3) points to its formation during Phase 2 rather than Phase 3.

Phase 3: Taphonomy: The object is in excellent condition, with little to no taphonomic compression, and little surface weathering, apart from a small area that could be due to weathering or erosion located on View 3. Some small longitudinal and tangential taphonomic cracks have developed (Figs. 3 and 4). There is a small area of surface flaking on View 3 between 5 and 6 cm.

Phase 4: Excavation and post-excavation: There is no excavation or post-excavation damage.

Interpretation: Based on the two probable working traces, coupled with the working away on one end of annual growth rings from two directions, as well as the rounding at the opposing end of the tool, we interpret this object as a small Category 2 wood tool. The function of this tool is uncertain, but could have been used in lithic retouching activities (see Discussion).

Specimen 942/677-59

942/677-59 is a segment (35cm maximum length, 23cm maximum width) of a large alder (*Alnus* sp., Fig. S15) trunk, excavated in several pieces in 2016 in the periphery and to the north of the main accumulation of the elephant skeleton (Fig. 1, top). Similar to 940/673-39, it has suffered taphonomic compression and flattening. While it shows no anthropogenic modifications, we identified three sub-parallel striations running obliquely to the growth of the trunk (noted as 1, 2, and 3 in Fig. S16, of which striation 3 is formed by two intersecting grooves), ranging from 15.3cm to 20cm in length, with a distance of ca. 10.6cm between the two lateral marks (Fig. S16). The striations are far too wide to represent anthropogenic marks from stone tools. The marks are shallow, wider than deep, with a U-shaped or open V-shaped cross section and in part they exhibit a wavy, crenulated morphology (Figs. S15, S16, Table S4; SI Section 3, 3D models; SI Section 5). Since the surrounding sediments are fine, silty deposits with only very few fine pebbles (granules); the associated lithic and faunal remains show no signatures of trampling (see Discussion); and given that trampling would be unlikely to result in three subparallel striations, we rule out the possibility that these marks were caused by trampling by a large animal. Furthermore, the size and morphology of the striations are not comparable with the feeding traces of xylophagous insects, which leave multi-directional traces characterized by shallow U-shaped profiles (29). We therefore interpret these features as fossilized claw marks (ichnofossils) produced by a large carnivoran (30) (see Discussion). Observed elliptical to subtriangular pits between marks 1 and 2 (Fig. S16) may also be associated with claw marking (31). Some clawing marks appear to overlie cracks on the surface of the specimen that may represent weathering cracks. This suggests that the clawing event possibly occurred on a dead tree.

Discussion

Area A, where the wooden tools and trunk presented here, as well as most of the wood remains at MAR-1, were excavated (Table S1), is dominated by the nearly-complete skeleton of a large adult male straight-tusked elephant (*Palaeoloxodon antiquus*), showing evidence of butchering in the form of cut marks and percussive damage (15). Also present are hippopotamus (*Hippopotamus antiquus*), fallow deer (*Dama* sp.), red deer (*Cervus elaphus*), wild boar (*Sus* sp.), wolf-sized canid (*Canis* sp.), otter (*Lutra simplicidens*) and beaver (*Castor fiber)* (14, 15). The burial conditions allowed for the preservation of micro-fauna, insects, eggshells, molluscs, diatoms and sponges; and macro- and micro-plant remains, including phytoliths, seeds, fruits, spores, as well as the wood remains examined here (17, 32, 33). Lithics recovered in Area A consist of mainly chips and plain flakes, but also some tools, cores and debris, found in direct spatial and stratigraphic association with the elephant remains (Fig. 1) (15, 16). In Area B, where the majority of lithics were recovered, bone artifacts were also found, including possible tools in the form of a bone flake, a denticulated bone flake and a megafauna diaphysis that was likely used as bone percussor. These point to the use of bone not only as blanks for the shaping of tools, but also as tools for the shaping of blanks, broadening the technological repertoire of MAR-1 to include also organic artifacts (16). Additionally, the use of plants by hominins, potentially for woodworking, is indicated by use-wear analysis of the MAR-1 lithics (34). The finds were affected by minimal reworking and are broadly *in situ* (35), consistent with the very fresh condition of the artifacts, the absence of rounding on the faunal remains and the observed faunal refits (15, 16). The fine, silty lakeshore deposits bear very few granules, typically only a few millimetres large, and there are no signs of animal trampling (15). The wood assemblage is therefore likely minimally affected by taphonomic alterations related to these processes. However, the presence of beaver, a riparian and semi-aquatic mammal that feeds on non-woody and woody plants and uses trees and shrubs for dens and dams, necessitates the evaluation of characteristic signatures of beaver traces on the MAR-1 wood. The two specimens identified as wood artifacts show no signs of beaver gnaw marks, and no significant taphonomic alterations, other than the compression observed on 940/673-39. Beaver gnawing is characterized by i) 'cut' branch or trunk ends with one or both ends creating an acutely angled (ca. 30°) beveled point bearing a series of tooth marks across the gnawed surface (Fig. S13, e and g), ii) branches removed from the shaft that also bear tooth marks across the branch/knot surface and iii) shallow grooves running perpendicular to the grain of the wood resulting from consuming the bark (See Fig. S13, e and h; SI Section 6; see also 26, 27). Moreover, no clear signatures of beaver gnawing were identified in any of the wood assemblage examined. Compression affects the majority of the wood assemblage, including the carnivore-modified 942/677-59, and is due to the large volume and weight of sediments originally overlying MAR-1, which was situated ca. 30 m below the earth's surface before mining activities and excavation (12). Only minor excavation damage was observed, and only on 940/673-39. In contrast, several traces of human modification were identified on these specimens (carving, chopping and stop marks, associated with knots, as well as potential use marks in the case of 940/673-39; and two tool facets, removal of annual growth rings on both sides on one end and potential use wear in the form of pitting and rounding for 935/671-13), leading us to identify them as wood artifacts Category 1 and 2, respectively. This classification is consistent with the independent evidence for the use of other organic materials (bone) as raw material and the use of lithics for plant working by hominins at the site (16, 34).

Paleolithic wood artifacts are archaeologically rare due to their perishable nature. Historically they were challenging to identify and analyze, and it is only in the last decade that new methods and systematic approaches have been developed to identify them (2, 3, 5, 8, 24, 36–38). While the use of plant materials is suggested as early as 1-2Ma by residue studies on lithics (39, 40), the earliest direct evidence in the form of securely identified modified wood from stratified contexts comes from Kalambo Falls, Zambia, where a large wooden structure of interlocking logs at least as old as 476ka, was recently excavated (5). A potential fragment of a polished wooden plank from the ca. 780ka old site of Gesher Benot Ya'aqov (Israel) would push this evidence significantly further back in the archaeological record (41, 42). However, this object has not been re-assessed using modern approaches.

Handheld wooden tools dating between 390-324ka were excavated from Kalambo Falls, Zambia (5). In Europe, large MP assemblages of wooden artifacts were identified at Schöningen, Germany, where preservation conditions are similar to MAR-1 (3, 6, 43), dated to ca. 300ka (but see 44, proposing a younger date of ca. 200ka); and at Poggetti Vecchi, Italy, ca. 171ka (8, 37). An additional isolated find of less secure context is a single broken spear tip from Clacton-on-Sea, UK, likely dating to MIS11, ca. 400 ka (45, 46). At ca 430ka, therefore, the MAR-1 MIS12 specimens are the oldest as yet identified handheld wood artifacts known, and the only such evidence from South-East Europe, expanding our knowledge of the cultural adaptations and behavioral repertoire of MP hominins. Interestingly, as in MAR-1, several of the most significant reported wood artifacts were often found in association with small-tool lithic assemblages, including at Schöningen and Poggetti Vecchi (47–49). Specimen 940/673-39 was excavated within the elephant bone accumulation, in the vicinity of several vertebrae and ribs, and close to the cranium (Fig. 1), closely paralleling the position of wood artifacts found among butchered proboscidean skeletons at much later sites, such as the multifunctional boxwood sticks from Poggetti Vecchi (Italy) (37, 49). Moreover, its morphology, with a thicker rounded top potentially representing a 'handle', is similar to the Poggetti Vecchi specimens, while its length is comparable to other 'digging sticks' identified from Pleistocene and early Holocene sites (5, 28, 36, 37). In terms of its functional end, its morphology falls within the variation observed among ethnographic and archaeological digging/multifunctional sticks, which include beveled, pointed, rounded and u-shaped terminations (25, 36, 37, 50, 51). Yet, in contrast to the multi-step woodworking strategies evidenced on wooden tools from later sites such as Schöningen and Poggetti Vecchi, the woodworking strategy here appears to be expedient, with a primary aim of removing branches and some shaping of both ends (2, 3, 37, 52). The tool was shaped from alder, a wetland-loving hardwood species with relatively low density (53), also used to make Mesolithic digging sticks at Star Carr (28). Like the boxwood sticks from Poggetti Vecchi, 940/673-39 may alternatively represent a 'multipurpose' tool, rather than a 'digging stick' in the strict sense (i.e., utilised for digging in soils, primarily for plant extraction). Another possible function could be as a bark peeler, used to extract inner bark for consumption; ethnographic bark peelers can have spatulate ends, but are notably shorter than 940/673-39 (26).

Specimen 935/671-13, found in the periphery of the main elephant bone accumulation, represents a new type of wooden artifact, whose function is as yet unclear. Considering recent evidence of use of organic tools for working lithics during the Lower Palaeolithic (e.g. 54) one possibility could be its use in retouching the small lithic tools at MAR-1, an activity inferred for Area A (14), where small chips and lithic debris are abundant. 935/671-13 is made on willow or poplar (*Salix/Populus*), two species which are challenging to differentiate in archaeological contexts due to similar anatomical features (55). However, the use of willow is well-documented from Holocene archaeological sites with functions including as wood splitting wedges, bows and arrows, handles, digging sticks, fishing technology, stakes and vessels (55–58), and is also the species of the possible polished plank from the early Middle Pleistocene site of Gesher Benot Ya'aqov (42).

Furthermore, the cluster of large fragments of tree trunks in association with the elephant (see Fig. 1), reconstructed to have lain in shallow waters at the edge of the Megalopolis paleolake, could potentially have served some purpose for the hominins engaging in butchering of this large carcass. Although we did not see clear signs of anthropogenic modification on the large wood trunk fragments, such behaviour would be consistent with the modification of wet environments in Kalambo Falls some 50,000 years earlier (5, 38).

Finally, the finding of large, likely carnivore claw marks on specimen 942/677-59, in the periphery of the elephant remains in the archaeological horizon underscores the competition between hominins and carnivores in MP Megalopolis. While cutmarks on the elephant remains in MAR-1 (e.g. ventral side of rib accompanied by peeling) suggest early access to the carcass by hominins, carnivores were not far behind. Indeed, gnawing marks were identified on the same taxa showing cutmarks, including on elephants, indicating intense competition for access to carcasses (15). A variety of mammals, particularly carnivorans, engage in tree-clawing for territorial marking, mating, or sharpening their claws (59, 60). Claw marks can also result from bears climbing a tree, or debarking to feed in the cambium layer. In addition to visual marks, scratching results in scent-marking from their interdigital glands (61). Large carnivorans evidenced in the Megalopolis Basin include bears and felids, who exhibit tree-clawing as an integral part of their social behavior (59), and are the most likely candidates for producing the marks. Although these taxa were not found at MAR-1, bears (*Ursus* sp.), lions (*Panthera* ex gr. *leo*) and possibly leopards (*Panthera* sp.) are documented in other MP Megalopolis localities and would have been members of the greater ecosystem at the site (14). The fact that some of the clawing marks superimpose cracks on the surface would perhaps fit better with the behavior of a bear. Bears may produce such marks with their claws while searching for insects (ants, beetle larvae, termites or grubs) in decomposing and weathered, but still upright standing dead trees (snags) or even in fallen trees and logs (62).

In conclusion, the MAR-1 wood artifacts add to the limited known sample of securely identified Paleolithic wood artifacts from well-dated, controlled excavation contexts. Despite their small number, they expand our knowledge of hominin plant-based technology both temporally and geographically, as well as in terms of repertoire and exploitation of plant species. The expedient shaping of the larger digging tool (940/673-39), its simplicity of morphology, and microscopic nature of tool marks mean it would be easy to miss such tools in archaeological assemblages, and suggest a general lack of recognition of similar early tools from other sites that have good organic preservation. Additionally, the smaller, likely finger-held wooden tool (935/671-13) would also be easily missed due to the microscale of signs of human modification. Yet the potential functions of both tools, and small size of 935/671-13 together have implications for hominin abilities to manipulate different tool types, and exploit a range of different materials for technological purposes. Therefore, these finds significantly extend our framework for understanding the development and use of technologies and materials in human evolution. Our findings further highlight the importance of the Megalopolis Basin not only as a crucial glacial refugium, harboring hominin populations through MP glacial cycles, but also as a flagship region, whose exceptionally long and largely continuous stratigraphic sequence and preservation conditions shed new light on human adaptations, habitats and evolution in Europe.

Methods

The macro- and micro-morphological investigation for signatures of human modification of the sample of wooden remains from MAR-1 was undertaken at the M.H. Wiener Laboratory for Archaeological Science, American School of Classical Studies at Athens. The wood assemblage consists of 144 pieces (Table S1), excavated between 2015-2019 and stored in plastic containers filled with distilled water in industrial refrigerators (chiller). Taxonomic classification was conducted based on diagnostic anatomical features observed under magnification (SI Section 4).

Analytical frameworks and nomenclature follow those recently developed for Pleistocene wood tools (2, 3, 24). Potential tools are categorised from 1 through 4 with Category 1 being certain tools (Table S3). We present the biography of the two tools within a *chaîne opératoire* framework, including Phase 0: raw material, Phase 1: manufacture, Phase 2: use, maintenance, discard, Phase 3: taphonomy and Phase 4: excavation and post-excavation (2, 3, 24).

The functional analysis of wooden tools is still in its infancy, with recent developments including the application of experimental studies for cross-referencing of the nature of surface damage (8, 36, 37, 63, 64). Potential functional parallels are based on existing morphological parallels coupled with lines of evidence including whether a given tool bears a focused area of micro- or macro-damage consistent with potential use. To assist our analysis, we used a suite of imaging techniques to investigate surface and internal features. A hand loupe, oblique lighting and standard stereo microscopy equipped with photomicrography (Leica M10 stereo microscope, with Leica Flexcam C1 camera and LAS X microscope software with Z stack module) enabled an initial assessment of morphology and surface traces of our sample of preserved wood macroremains from MAR-1. MicroCT scans (Brucker SKYSCAN 1273) were undertaken of specimens of interest to investigate internal features relevant to understanding growth characteristics such as annual growth rings and signs of anthropogenic modification (2, 36). Due to the waterlogged nature of the material and taphonomic compression, only 935/671-13 resulted in successful scans (0.5mm Al filter, at 46 kV, 187 μA, 20 μm resolution, rotational angle 0.27°, frame averaging 2, exposure 1350 ms, 1 x 1 binning mode, medium focal spot and 360° rotation). Microscopic images of the beaver wood samples were taken using a Dino-Lite USB microscope (AF3113T).

Finally, we created 3D models of the three specimens presented in this paper with the use of an Artec Space Spider scanner (0.05 mm accuracy and 0.1 mm point resolution, applied uniformly in x, y, and z). 3D models provide readers with a means of examining the specimens from multiple angles, but are also useful analytical and conservation tools: they preserve the object's original form and size prior to post-excavation and post-conservation alterations, and even assist in the analysis of surface features (2, 36). 3D models are available as an open access dataset in Zenodo: https://doi.org/10.5281/zenodo.17414561(65).

Author Contributions

Author contributions: A.M., M.N., G.T., E.P., V.T., P.K., and K.H. designed research; A.M., M.N., S.K., D.M., G.E.K., N.T., and K.H. performed research; A.M., M.N., G.E.K., and D.G. analyzed data; G.E.K. contributed to excavation; D.G., N.T., G.T., and V.T. contributed to excavation, edited final manuscript; E.P. directed the excavation, edited final manuscript; P.K. contributed to excavation, provided equipment and facilities, edited final manuscript; K.H. provided funding, contributed to excavation, provided equipment; and A.M., M.N., G.E.K., and K.H wrote the paper.

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