

Quina lithic technology indicates diverse Late Pleistocene human dynamics in East Asia

Qi-Jun Ruan^{ab,1}, Hao Li^{a,c,1,2}, Pei-Yuan Xiao^{a,c,2}, Bo Li^{de,2}, Hélène Monod^{fg}, Alexandra Sumner^h, Ke-Liang Zhaoⁱ, Jian-Hui Liu^b, Zhen-Xiu Jia^a, Chun-Xin Wangⁱ, An-Chuan Fanⁱ, Marie-Hélène Moncel^k, Ben Marwick¹, Marco Peresani^{m,n}, You-Ping Wang^{o,p}, Fa-Hu Chen^{a,c}, and Davide Delpiano^{m,2}

Affiliations are included on p. 8.

Edited by Elsa Redmond, American Museum of Natural History, New York, NY; received September 30, 2024; accepted February 19, 2025

The Late Pleistocene of Eurasia is key for understanding interactions between early modern humans and different types of archaic human groups. During this period, lithic technology shows more diversity and complexity, likely indicating flexible adaptative strategies. However, cultural variability as expressed by technological types remains vague in large parts of eastern Eurasia, like in China. Here, we report a complete Quina technological system identified from the study of the Longtan site in Southwest China. The site has been securely dated to ca. 60 to 50 thousand years ago (ka), with compelling evidence of core exploitation, production of large and thick flakes, shaping and maintenance of scrapers exhibiting the whole Quina concept, typical of contemporary European Middle Paleolithic technologies developed by Neanderthal groups adapted to climatic oscillations during Marine Isotope Stage (MIS) 4 and early MIS 3. The finding of a Quina lithic assemblage in China not only demonstrates the existence of a Middle Paleolithic technology in the region but also shows large-scale analogies with Neanderthal behaviors in western Europe. Longtan substantially extends the geographic distribution of this technical behavior in East Asia. Although its origin remains unclear, implications for Pleistocene hominin dispersal and adaptation to diverse ecological settings are considered. The Longtan lithic evidence also provides perspectives for understanding the cultural evolutionary situation before the large-scale arrivals of early modern humans in East Asia predating ~45 ka.

Middle Paleolithic | fluvial terrace | early MIS 3 | Late Pleistocene | hominins

The Middle Paleolithic or Middle Stone Age (~300 to 40 thousand years ago, ka) marked a crucial period in human evolution. In Africa, the Middle Stone Age is closely associated with both the origin and evolution of early modern humans (1, 2), while in Eurasia, the Middle Paleolithic is linked to the development of various archaic human groups, such as Neanderthals and Denisovans (3–7). The behaviors of a number of human species during this time period are represented by variations of the Mousterian culture, aspects of which signal key developments in lithic technology recognized both in Africa and Eurasia (8–13). The Mousterian is mainly defined by flake-based industries related to different core-reduction technologies and a representative tool set which usually includes scrapers, denticulates, and retouched points (14). The variability within Mousterian assemblages led scholars to identify several technocomplexes characterized by recurring core-reduction strategies, among which the Levallois, the Laminar, the Discoid, and the Quina are most representative, at least in western Eurasia (15–17).

However, in China, one widely held perspective holds that simple core and flake technologies persisted for a long time and were used by diverse hominins, from the Early Pleistocene until the emergence of early modern humans in specific regions by about 45 ka (18, 19). At this point, the use of standardized blade production and microblade technologies became more common in the Upper Paleolithic period (20). This viewpoint had a substantial impact on the international academic community, leading to a widespread perception that lithic technology in China was relatively simple and developed slowly during the majority of the Pleistocene, and in particular, it lacked key elements that typically defined the Middle Paleolithic and its technology (21–25).

Nevertheless, recent discoveries at Jinsitai in Inner Mongolia and Tongtiandong Cave in Xinjiang suggest that typical Mousterian of Levallois technology occurred in the northern frontiers of China at around 50 to 40 ka (26, 27). Additionally, a restudy of the lithic assemblage at Guanyindong Cave in southwestern China revealed the presence of Levallois products dating back to approximately 170 to 80 ka, although there is debate about the frequency and veracity of Levallois technology at this site (28, 29). In addition, discoidal

Significance

Neanderthal adaptation to Marine Isotope Stage 4 cold environments in Europe is reflected by subsistence behaviors and material culture, among which the Quina system of lithic production stands out being easily distinguishable from others. Quina industries are currently confined to European and western Asian countries. Hence, their discovery far outside Western Eurasia challenges the current scenario. The Quina technological system identified in Southwest China, dated to ~55 ka, is culturally in the European range, which challenges popular view that there is no "Middle Paleolithic" in this region and reveals a diversity of technology in the Chinese Middle Paleolithic. Our study further deepens the understanding of biocultural dynamics of Homo sapiens, Denisovans, and possibly other hominins in the Late Pleistocene of East Asia.

The authors declare no competing interest.

This article is a PNAS Direct Submission.

Copyright © 2025 the Author(s). Published by PNAS. This article is distributed under Creative Commons Attribution-NonCommercial-NoDerivatives License 4.0 (CC BY-NC-ND).

Although PNAS asks authors to adhere to United Nations naming conventions for maps (https://www.un.org/ geospatial/mapsgeo), our policy is to publish maps as provided by the authors.

¹Q.-J.R. and H.L. contributed equally to this work.

²To whom correspondence may be addressed. Email: lihao@itpcas.ac.cn, xiaopeiyuan@itpcas.ac.cn, bli@uow. edu.au, or dlpdvd@unife.it.

This article contains supporting information online at https://www.pnas.org/lookup/suppl/doi:10.1073/pnas. 2418029122/-/DCSupplemental.

Published March 31, 2025.

core reductions associated with typical Middle Paleolithic tool types are documented at Lingjing (125 to 90 ka) in the Central Plain of China and Wulanmulun (65 to 50 ka) in the Loess Plateau of northern China (30, 31) (Fig. 1).

Despite growing awareness of the Middle Paleolithic and its variability in China, current available archaeological evidence remains limited. Controversies surrounding some key lithic assemblages further restrict our understanding of this crucial stage in the evolution of hominins in China. It is worth noting that during 300 to 40 ka, a diversity of human fossils have been discovered, such as the Denisovan fossils from the Baishiya Karst Cave site (dated from >160 ka to ~40 ka) (6, 7, 32), the Homo longi cranium from Harbin in Northeast China (>146 ka) (33), and the archaic human cranium exhibiting Neanderthal features found from the Lingjing site (i.e., the Xuchang Man, ~125 to 105 ka) (34). These diverse forms of humans indicate the importance of conducting renewed and thorough study of lithic assemblages found in China. The systematic study of the Middle Paleolithic in China is vital for a robust understanding of the origins and behaviors of Middle and Late Pleistocene hominins, including early modern humans, in the region.

The Longtan site, located in Yunnan Province, Southwest China, is particularly important for expanding our knowledge of the expressions of Middle Paleolithic techno-complexes. The site was excavated in 2019–2020, retrieving a rich collection of stone artifacts (35). Some specimens exhibit characteristics similar to those of the Quina technology, a knapping method solidly correlated with Neanderthals in the European Mousterian. Quina industries are characterized by a discrete core reduction system aimed at detaching thick flakes that are often modified into scrapers, subjected to frequent rejuvenation of the edges and commonly related to multifunctional purposes on material of different nature (36–39). This technology is well known in western Europe during the Marine Isotope Stage (MIS) 4 and early MIS 3, despite some early occurrence of isolated features appearing in both Levant and Europe as early as MIS 11 (40–43) (Fig. 1 and *SI Appendix*, Table S1). Overall, the Quina Mousterian represents one of the most well-defined Middle Paleolithic cultural entities in Eurasia. It is systematically associated with Neanderthals and usually characterized by the adoption of specialized subsistence strategies and innovative technical behaviors aimed at facing ecological shifts and turnovers (12).

This paper reports our chronological, environmental, taphonomic, and technological analyses of the lithic assemblage at Longtan, demonstrating the presence of a complete and well-defined Quina system in eastern Eurasia during the Late Pleistocene. The study aims to contribute to our understanding of the complex technological behaviors of the Middle Paleolithic and expand our knowledge of the global spatial-temporal distribution of technocomplexes during this period. In addition, findings at Longtan provide a rare opportunity to understand the technological contexts and population dynamics during the period that diverse human groups potentially coexisted in China.

Results

Site, Stratigraphy, Chronology, and Paleoenvironment. Longtan is an open-air site located on the southern margin of the Hengduan Mountains of the Tibetan Plateau (N26°1′47″, E100°24′54″, ~1,540 m above sea level) (Fig. 2 *A* and *B*). Situated on the third terrace of the Caifeng river's right bank, it is about 600 m away from the riverbank and stands about 100 m above the river surface (*SI Appendix*, Figs. S1–S4). In the Caifeng river basin, a total of six Paleolithic sites have been found, comprising five open-air sites and a cave site (Fig. 2*A* and *SI Appendix*, Table S2). Among them, Longtan and Tianhuadong Cave are the only ones that



Fig. 1. Distribution of Middle Paleolithic sites in Eurasia. Different colors and symbols indicate the geographical spread and chronology of Levallois, Discoidal, and Quina systems, respectively. Each site was color-coded based on its earliest known age. Detailed information for each site pointed on the map is provided in *SI Appendix*, Table S1.



Fig. 2. Location, stratigraphy, and chronology of the Longtan site. (*A*) Locations of the site and the other five sites in the Caifeng river valley. (*B*) Landscape surrounding the site viewed from Southeast. (*C*) Stratigraphy of the east wall of T2 and locations of OSL samples. (*D*) Schematic stratigraphy of the sediment profile. (*E*) OSL dating results. The error bars represent one sigma error. The red point represents the age of Longtan-OSL8 and is considered as an outlier (see *SI Appendix*, section 2 for details of the dating analysis).

preserve intact cultural deposits, all others have been extensively eroded and/or disturbed. Interestingly, at Tianhuadong Cave, which is about 4 km east of Longtan, two Quina-like scrapers were uncovered from the intact cultural layers 2 and 3 dated to ~90 to 50 ka (44, 45). However, as Tianhuadong Cave was not systematically excavated (i.e., only a 1×2 m trench and ~2 m depth was excavated) and most of the stone artifacts were collected from the surface, that site provides only limited insights into the Quina system.

With respect to Longtan, two side-by-side trenches (T1 and T2, 5×5 m each) and a test trench (TG3, 2×7 m) were excavated, covering a total area of 64 m² (*SI Appendix*, section 1 and Fig. S5). The sediments of the site are characterized by reddish or brownish silty clay. The stratigraphy is divided into four layers based on sedimentary characteristics and the presence of artifacts (Fig. 2 C and D and SI Appendix, section 1). Layers 1 and 2 were highly disturbed due to modern cultivation activities, with a relatively loose structure containing abundant small rock fragments and some modern items. A total of 1,346 stone artifacts was found from these layers. Layer 3 is characterized by a much more compact structure and appears to preserve intact and undisturbed cultural materials. The main excavation area (T1 and T2) produced 3,464 stone artifacts, which were unearthed from Layer 3, while the test trench (TG3) yielded 23 stone artifacts from the same layer, for a total of 3,487 artifacts from Layer 3. Layer 4 is archaeologically sterile. Below Layer 4 is a highly calcareous layer, which was not excavated and is exposed as the current excavation floor (Fig. 2*C*).

To establish the chronological context of the site, we dated the sediments using optically stimulated luminescence (OSL) on quartz grains. Nine OSL samples were collected from Layers 2 to 4 (Fig. 2 C and D), including two from Layer 2 (Longtan-OSL1 and Longtan-OSL2; only Longtan-OSL2 was measured), four from Layer 3 (Longtan-OSL3 to -OSL6) and three from Layer 4 (Longtan-OSL7 to -OSL9). To assess stratigraphic integrity and identify potential postdepositional disturbance, we dated the samples using the single-grain technique. Details about sampling, sample preparation, measurements, and analysis are provided in SI Appendix, section 2. The large scatter in the single-grain D_e distribution of sample Longtan-OSL2 further confirms that Layer 2 is affected by disturbance (SI Appendix, section 2 and Fig. S7A). The pattern of D_e distribution of sample Longtan-OSL3 suggests that the upper part of Layer 3 was also influenced by the cultivation activities on the upper layers, which resulted in intensive intrusion of younger grains. Such downward intrusion of younger grains appears to impact the deeper layers to a lesser extent, which is expected and evident by the D_e distribution patterns of the lower samples that show smaller numbers of younger grains (SI Appendix, section 2 and Fig. S7).

Given the intrusion of younger grains, we have applied a maximum age model to estimate the age of our samples from Layers 3 and 4. This was achieved using the Bayesian Hierarchical Age Model (BHAM) (46), which is designed to deal with sediments deposited in a variety of depositional settings, including those affected by postdepositional disturbance. A detailed description of the application of BHAM and results are provided in *SI Appendix*, section 2 and Figs. S8-S18. Our BHAM results show that all the samples from Layer 3 date back to ~60 to 50 ka, and the ages of the samples are statistically consistent with each other (Fig. 2E and SI Appendix, Tables S3–S5). Assuming a fast deposition-rate scenario, we obtained an age of 55.0 ± 2.5 ka based on the weighted mean age of the samples from this layer, which corresponds to the early stage of the MIS 3. For the samples from Layer 4, two of them (Longtan-OSL7 and -OSL9) yielded indistinguishable ages at 57.1 \pm 2.8 ka and 58.4 \pm 2.3 ka, respectively. However, the other sample, Longtan-OSL8, gave a significantly older age of 77.0 ± 3.1 ka, which we consider as an overestimation, probably due to the intrusion of old grains from rock fragments in the sediments, and, hence, we rejected this sample as an outlier (see SI Appendix, section 2 for justification). Based on the ages of Longtan-OSL7 and -OSL9, we obtained a depositional age of 57.9 ± 1.8 ka for Layer 4, which in general corresponds to the late stage of MIS 4.

Our dating results suggest that the deposit at Longtan was formed during the transitional period from MIS 4 to MIS 3, and hominin occupation most likely occurred during the early stage of MIS 3. To further understand the environmental context of the hominin occupation at Longtan, sediments from Layers 3 and 4 on the east wall were collected for pollen analysis. The pollen record can be divided into three distinctive zones (I, II, and III) (SI Appendix, section 3 and Fig. S19). Zone I correlates with the lower part of the Layer 4, where the high Amaranthaceae content indicates a relatively arid climatic condition, consistent with the MIS 4 age of the layer. Zone II is associated with the upper part of Layer 4 and lower part of Layer 3, and it is characterized by a Pinus-Tsuga-Poaceae pollen assemblage, indicating a shift to a coniferous forest environment. Zone III corresponds to the upper part of Layer 3, which has a substantial increase in herbaceous pollen content and a decrease in woody plants. Overall, the pollen assemblage in Layer 3 suggests that the hominins inhabited Longtan in a relatively open mountainous forest-grassland landscape, likely with scattered pine forests and small lakes or ponds in the surrounding area.

Lithic Analysis. Due to the disturbance of Layers 1 and 2, this study focuses only on lithics from Layer 3 (n = 3,487). The Layer 3 assemblage includes 179 cores (5.1%), 878 flakes (25.2%), 242 retouched tools (6.9%), 2,038 chunks and debris (58.4%), and 150 manuports (4.3%) (SI Appendix, section 4 and Table S6). The prevalent raw materials exploited at Longtan include trachyte (n = 2,382, 68.3%), hornfels (n = 423, 12.1%), and chert (n = 241, 6.9%, see *SI Appendix*, Table S6 for the other raw materials). Trachyte is present in the form of river cobbles from the Caifeng riverbed and is easily collectable within approximately 600 m from the site (SI Appendix, section 4 and Fig. S20). The taphonomy, size distribution, and fabric patterns (e.g., orientation and plunge) of the stone artifacts (SI Appendix, section 4 and Fig. S21) indicate that the lithic assemblage at this site was deposited in situ and subjected to limited postdepositional modifications, giving confidence to our chronological and technological study.

Core reduction strategies. Several core reduction patterns were identified at Longtan, including both expedient and organized types. Expedient cores are in relative abundance (n = 116, 64.8%) and were exploited in short reduction sequences that produced both thin and thick blanks optimal for retouching. On the other hand, what we refer to as organized cores demonstrate the application of relatively diverse flaking methods such as Quina, Discoid, and core-on-flake reductions.

Quina cores (n = 14; mean $L \times W \times T$: 51 × 41 × 33 mm) (Fig. 3 *E*-*G* and *SI Appendix*, Fig. S24) are a diagnostic component of the Quina system at Longtan. These cores feature a plan-secant

volume structure and acute platform angles (mean = 62.4°; SD = 10.8°) (SI Appendix, Fig. S39), consistent with the volumetric structure observed on Quina cores from western Mousterian sites. These criteria are evident at Longtan both on cores organized on two secant planes and on more developed specimens attesting to the frequent reorientation in surface exploitation, which led to the shaping of multifacial cores (Fig. 3 *E* and *F* and *SI Appendix*, Fig. S24D). Consistently associated with these cores' reduction are the unretouched Quina flakes (n = 15), showing significantly larger dimensions on both the overall size and the striking platform compared to other types of flakes (*Pillai's Trace* = 0.77, *F*(28, 516) = 4.36, P < 0.001) (SI Appendix, Fig. S40). These products are generally wedge-shaped and asymmetric in cross-section and frequently bear remnants of the cortex on one side of the dorsal surface, all typical attributes as described by others (36, 47) (SI Appendix, Fig. S28).

Discoidal cores (n = 15; L × W × T: 47 × 39 × 28 mm) (Fig. 4*E* and *SI Appendix*, Figs. S25 and S26) at Longtan exhibit a high degree of variation, especially regarding the extension of the exploited peripheral edge. The most developed cases show continued centripetal flaking along the intersecting plane formed by two convex surfaces, while others just exhibit bifacial alternating detachments on part of the periphery. Flakes with centripetal dorsal scars (n = 21; L × W × T: 37 × 31 × 13 mm) (*SI Appendix*, Fig. S42) and core-edge flakes (n = 16; L × W × T: 34 × 29 × 13 mm) are closely associated with the discoidal core flaking strategy (*SI Appendix*, Fig. S29 *A*–D), especially the latter which were used to manage the core angles and convexities and to maintain the flaking system.

Surface-oriented cores (n = 7; L × W × T: 49 × 40 × 27 mm) (*SI Appendix*, Fig. S27 *D*–F) feature a flat and large face used as the flaking surface, revealing a hierarchical volumetric design similar to the Levallois concept. However, the knapping on the main surface lacks a clear predetermination of flakes and core platform preparation is absent, making them different from the Levallois cores. Flakes detached from these cores (n = 5; L × W × T: 40 × 30 × 10 mm) show significantly smaller interior platform angles than other types of flakes, approaching 90° (*F*(4, 26.84) = 16.01, *P* < 0.001; *SI Appendix*, Fig. S41 and Table S8), and small and flat platform (*SI Appendix*, Fig. S29 *E* and F).

Cores-on-flakes (n = 20; L × W × T: 48 × 44 × 23 mm) (*SI Appendix*, Fig. S27 *A*–C) mostly resemble Kombewa-type production (n = 17) which is found in some Middle Paleolithic assemblages, with the ventral faces used to detach flakes. Flakes removed from cores-on-flakes are generally small in size (n = 27; L × W × T: 27 × 22 × 8 mm; comparative results can be found in *SI Appendix*, Fig. S40) (*SI Appendix*, Fig. S30 *D*–F).

Tool production strategies. A total of 242 tools was identified, including 81 miscellaneously retouched tools (33.5%), 79 ordinary scrapers (32.6%), 53 Quina scrapers (21.9%), 16 notches (6.6%), and 13 denticulates (5.4%) (*SI Appendix*, Fig. S34). Among these tools, Quina scrapers are the most diagnostic type and often show significantly larger thickness values than other types of tools (mean = 24 mm; F(3, 36.38) = 19.20, P < 0.001, *SI Appendix*, Fig. S43), due to the use of thick flake blanks.

Quina scrapers at Longtan can be divided into three subtypes, including single-edged (n = 33), double-edged (n = 16), and multiedged (n = 4) (Fig. 3 A-D and SI Appendix, Figs. S31–S33). Regardless of the types, all retouched edges of Quina scrapers exhibit multiscalar retouch, structured in multiple orders of scars (mean = 2.9), in contrast to the ordinary scrapers (mean = 1.2). In addition, scars distributed on the innermost order have a more convex shape than those distributed on the outer orders, the latter having often been referred to as concavity scars, which served to



Fig. 3. Products of the Quina system at the Longtan site. (*A–D*) Quina scrapers, illustrations provide details on the transverse layout of the tools. Note that the innermost order of retouching scars shows convex outlier shape, while the outer orders often show concave shape. Also note that the large removal on specimen C (*Middle* and *Right* pictures) indicates the "Clactonian notch." (*E–G*) Quina cores, illustrations highlight the acute angle between intersecting flaking surfaces. (*H–J*) Resharpening flakes showing Quina retouch at the proximal end of the dorsal face. (*K*) Small tool made on resharpening flake.

obtain appropriate functional edges (see Fig. 3 A–D for examples). Quina scrapers generally have larger edge angles (mean = 70.6°; SD = 7.0°), which are significantly greater than those of ordinary scrapers (mean = 59.3°; t (128.86) = 8.35, P < 0.001) (Fig. 4B). Using the Geometric Index of Unifacial Reduction [GIUR; (48)] to quantify the reduction intensity of Quina scrapers shows a mean GIUR value of 0.76, significantly higher than that of ordinary scrapers (mean = 0.37; t (104.03) = 11.91, P < 0.001), indicating the extensive reduction of Quina types (Fig. 4C and SI Appendix, Table S9).

In general, Quina scrapers at Longtan show a diagnostic feature of asymmetrical cross-sections, which is clearly present on the single-edged Quina scrapers (mean = 0.40) whose original morphologies were less modified. This is consistent with the high asymmetry observed on Quina flakes (mean = 0.39, details of asymmetry analysis in *SI Appendix*, section 4.3 and Table S10). When the cortex was preserved, most single-edged Quina scrapers retained the cortex on the lateral edge (73.7%), consistent with the location of the cortex on Quina flakes (100% on the lateral edge) (*SI Appendix*, Table S11). In contrast, perhaps due to the substantial modification of the original shape of blanks, asymmetry is lower in cross-sections of double-edged (mean = 0.68) and multiedged (mean = 0.84) Quina scrapers, and the residual cortex is often located on the central part of the dorsal surface (72.7%).

Edge resharpening was a key strategy to maintain the long use-life of Quina scrapers, and this phenomenon is indicated by the high number of resharpening flakes identified from the



Fig. 4. Features of Quina products compared to ordinary scrapers. (*A*) Thickness of Quina scrapers. (*B*) Edge angles of Quina scrapers. (*C*) Reduction intensity (GIUR) of Quina scrapers. (*D*) Similarity between edge angles of Quina scrapers and the exterior platform angles of resharpening flakes. (*E*) The sequence of the discoidal production system. (*F*) The sequence of the Quina production system, which is longer than in the discoidal system. In the box-and-whisker plots, black circles in the boxes represent the mean value, thick solid lines indicate the median value, bottom and top edges show the 1st and 3rd quartiles, and whiskers extend to 1.5 times the interquartile range.

assemblage (n = 57; L × W × T: 29 × 22 × 8 mm, Fig. 3 H–J and SI Appendix, Fig. S30 A-C). The mean exterior platform angle for flakes used to rejuvenate the scraper edge is 71°, with no significant difference observed from the edge angle of Quina scrapers (t (73.15) = -0.61, P = 0.542). Multiple orders of scars can be observed at the proximal end of the dorsal face of those flakes, with 26 specimens having two orders and 27 specimens having three orders. Altogether, these features indicate that resharpening flakes were detached from the previous functional edges of the scrapers. On the one hand, these flakes renewed the edges of Quina scrapers, and on the other hand, as also seen elsewhere (42, 49), some may also be used as tool blanks, as indicated by further retouch on the distal ends and margins of the flakes (Fig. 3K). Some Quina scrapers show the detachment of large removals in the final stage of retouch which are consistent with the procedure known as the Clactonian notch [(50); see Figs. 3C and 4F and *SI Appendix*, Fig. S31*C* for examples].

Compared with Quina scrapers, other types of tools at Longtan, for instance, notches and denticulates, are generally small in size and were less reduced, considering the number of scars and GIUR values (*SI Appendix*, Fig. S43 and Table S9). The obviously short use-life of non-Quina tools can be regarded as an important complementarity to form an integral toolkit at the site.

Use-wear analysis of Quina scrapers. Six Quina scrapers with clear use-wear traces were identified at Longtan (SI Appendix, section 4.4 and Figs. S44-S50). Of these, four Quina scrapers have one or two working edges, which display macro, large, and deeply invasive striations and scars, indicating contact with hard materials (SI Appendix, Figs. S45-S48). This suggests that the users may have employed scraping and scratching actions on bones, antlers, or wood. The remaining two Quina scrapers have three working edges, all of which exhibit polish along the edges (SI Appendix, Figs. S49 and S50). This observation suggests these two tools were used for processing soft materials, likely involving unidirectional or bidirectional scraping actions on meat, hides, or nonwoody plants. Overall, the diversity in materials and tool functions indicates that Quina scrapers from the Longtan site were employed in various subsistence activities and for processing different materials.

Discussion

Longtan exhibits a diversity of flaking technologies, with the Quina strategy as a unique feature with respect to the Discoid and other technologies. All the parameters known to define the Quina concept in studies from western Europe are consistently documented here

as a complete package. In particular, both the core reduction strategy and the production trajectories of Quina scrapers at Longtan are comparable with the well-defined Quina techno-complex in the European Mousterian (36, 37, 42, 47, 51). Furthermore, the production versatility implied in the functional ambivalence and the recycling of blanks as both cores and tools, known as the Quina ramification or branching cycles, can be assumed from the tools' resharpening stages and the use of flakes as cores (52). All these attributes are here interrelated in a coherent techno-economic system: this flaking strategy adopts the plan-secant concept for the volume structure, involving alternated knapping on different surfaces to obtain thick asymmetric short flakes and large flakes, i.e., Quina flakes. The thick flakes can provide large volumes and were intentionally selected to produce Quina scrapers intensively retouched with multiscalar scars, sometimes to provide new cutting blanks or edges with different functions. The relatively low number of Quina cores and unretouched flakes compared to tools could be explained by the high rate of blank retouching and by the fact that suitable flakes for Quina scrapers could have also been produced by the initial exploitation of single-platform, expedient cores, which are consistent with the generally unprepared and nonhierarchical nature of Quina cores (36, 37).

Regardless of the local abundance of lithic raw materials, the high reduction intensity of Quina scrapers at Longtan was not influenced by the scarcity and/or transportation distance of knappable cobbles, but rather it reflects a purposeful technological strategy. Indeed, the Quina system has been noted in other contexts as being versatile with respect to the range of lithologies (e.g., quartzite, shell) that can be exploited and/or favorably accessible (43, 49, 53). In relation to the long potential use-life of Quina blanks in Longtan, it is noted that scars on the innermost order (i.e., the initial retouching sequence) often show convex profiles that can facilitate the resharpening of the edge, while scars on the outer orders generally show concave profile that can provide usable edge angles. The morpho-technical consistency of resharpening flakes, which sometimes were additionally retouched, further supports this observation. In addition, Quina-related products at Longtan constitute a notable amount within the diagnostic lithic types; for instance, Quina scrapers account for 1/3 (32.9%) of the whole formal tools assemblage. Overall, these features permit us to clearly identify a comprehensive Quina concept and to differentiate it from other Middle Paleolithic systems.

The late MIS 4 or early MIS 3 age of the Longtan assemblage is contemporary with the Quina-based Mousterian culture primarily identified in Western and Southern Europe, which has a chronological concentration in MIS 4 and early MIS 3 stages (41). The Quina system has commonly been considered as a technological strategy responding to dry, cold, and open woodland environment, where a high mobile lifestyle, suggested by lithics' long use-life, recycling, and raw material circulation, was meant to deal with low density and patchy resources (12). Pollen analysis at Longtan indicates that the inhabitants of Longtan lived in a relatively open forest-grassland environment, along with dry and cool paleoclimatic conditions. This environmental context is similar to Quina sites in Europe, where this technocomplex has been connected to the hunting of seasonally migrating herds, specifically reindeer, giant deer, horse, and bison (54, 55). Unfortunately, the absence of faunal remains at Longtan limits reconstruction of subsistence strategies, restricting the comparison to cultural and environmental data. More robust regional environmental evidence is needed to better understand the dynamics which led to the adoption of the Quina strategy at Longtan.

The evidence from Longtan makes a substantial contribution to debates about the presence of Middle Paleolithic technologies in China. First, we present a distinct and coherent technology which has not been identified before in East Asia. Second, the entire technological concept documented at Longtan is unequivocally Middle Paleolithic. Furthermore, it reveals the remarkable variability of techno-complexes in the Chinese Middle Paleolithic (CMP, as first referred to by ref. 30), consistent with variability well documented in other regions of the Old World. On the one hand, the earliest claimed Middle Paleolithic with Levallois traits is from the Guanyindong Cave site, which has been dated to ca. 170 to 80 ka [(28), but see ref. 29], while the more robust evidence of Levallois in northern China (e.g., Jinsitai and Tongtiandong) only appeared at ca. 50 ka and may have different origins (26, 27). On the other hand, Longtan, together with the nearby site Tianhuadong Cave, were occupied in between Guanyindong and Jinsitai at ca. 90 to 50 ka. Within this time span, other technological behaviors were expressed elsewhere, such as the discoidal cores and discrete flake-based tool set from the Middle Paleolithic of Lingjing dated to ca. 125 to 90 ka (30). Furthermore, during this period, some sites have been claimed to represent the late persistence of the relatively simple core-and-flake traditions, e.g., Huangniliang (ca. 59 to 54 ka) (56) and Banjingzi (ca. 86 ka) (57) in northern China and Jingshuiwan (ca. 70 ka) (58) and Huanglong Cave (ca. 104 to 79 ka) (59) in southern China. Considering these cases, we challenge the traditional view of a long-lasting stable and relatively simple development of lithic technology in China. Rather, the evidence demonstrates striking complexity and diversity during the CMP.

Identifying Middle Paleolithic technologies in southern China is potentially crucial for understanding the southern dispersal route of new hominin lineages such as early modern humans. Currently, several early modern human fossils dating to the early Late Pleistocene have been discovered in southern China, such as the mandible from Zhirendong, Mulanshan, Guangxi (~113 to 100 ka) (60), the teeth from Luna Cave (~126 to 70 ka) (61), and the teeth from Fuyan Cave, Daoxian, Hunan (~120 to 80 ka) (62). However, no cultural package was associated with these fossils, and the chronology of some of these remains has been debated (63). From a broader perspective, cultural evidence supporting an early dispersal model (>45 ka) of early modern humans mainly comes from South Asia, where Middle Paleolithic technologies similar to those in Africa have been found, particularly the Aterian points and the Nubian Levallois cores (64). Middle Paleolithic sites in southern China exhibiting distinct African Middle Stone Age technological elements remain undocumented. Consequently, from a material cultural perspective, we suggest that it is currently premature to support the early dispersal model along the southern route with the arrival in China before ca. 45 ka.

The emergence of the Quina technological concept at Longtan remains an open question, with two opposing dynamics potentially relevant. On the one hand, local ecological adaptation may be responsible for a context-specific convergence of technological traits, conceptually linking Longtan to the framework of western European Neanderthals. The evidence of multiscalar retouching and the existence of matrices on tools at Longtan represents a strategy to satisfy the versatility and portability required by a system designed for high mobility behaviors in a dry and cool environment. In this way, Quina technological aspects could have been locally developed by eastern Asian hominin groups, from a cognitive and technical background shared with Eurasian Late Pleistocene populations. In support of this convergence model is the finding of Quina-type retouch tools from Denisova at ca. 200 ka when only Denisovans occupied the site (65). Similarly, an early appearance of Quina scrapers is documented in the Levant within the Acheulo-Yabrudian complex, dated between 400 and 200 ka and associated with taxonomically

uncertain new human forms in the region (66). This precursory production has been connected to the need to adapt through new strategies to major shifts in subsistence such as the unique procurement strategies for specific raw material and the extensive exploitation of animal hides (43, 67). In each of these geographically distinct contexts, Quina scrapers would have provided new, highly effective, and flexible butchery/scraping kits.

On the other hand, Longtan Quina may have originated via dispersion, implying dynamics of knowledge transmission and/or population dispersal from western Eurasia. Dispersion may be supported by evidence of the coexistence of Denisovans and Neanderthals in southern Siberia since ca. 200 ka (the earliest appearance of Neanderthals just overlies the earliest layer occupied by Denisovans), which has not only indicated the early eastward migration event of Neanderthals but also the genetic exchanges between the two distinct human groups (68, 69). In terms of the evidence from China, the identification of Levallois technology at Guanyindong Cave (but see ref. 29) from 170 to 80 ka may indicate demographic events across Eurasia (28), and a much later finding of the Levallois-featured lithic assemblage at Jinsitai (ca. 50 ka) in northeastern China bears more potential to demonstrate a younger long-distance expansion of Neanderthals into East Asia and the accompanied transmission of their technology (26). In addition to the cultural evidence, human crania found from the early Late Pleistocene Xuchang Lingjing site show some notable anatomic features (e.g., occipital, temporal labyrinthine) close to Neanderthals, which might indicate that human interactions occurred between the West and the East (34). Altogether, this evidence underlines the necessity to give careful consideration of the direct population dispersal or the cultural transmission and exchange model to explain the emergence of Quina technology at Longtan. If dispersal or migration is relevant to the Longtan Quina, we would expect evidence of Quina systems in wide areas of Central and South Asia; however, none have been reported to date. Further evidence is required to test the above proposed hypotheses.

Materials and Methods

The detailed procedures and statistical approach used for OSL dating are provided in *SI Appendix*, section 2. Standards for preparation and identification of pollen samples are demonstrated in *SI Appendix*, section 3. Indices used for evaluating the integrity of lithic assemblage, technological attributes and

- J. J. Hublin et al., New fossils from Jebel Irhoud, Morocco and the pan-African origin of Homo sapiens. Nature 546, 289–292 (2017).
- A. S. Brooks et al., Long-distance stone transport and pigment use in the earliest Middle Stone Age. Science 360, 90-94 (2018).
- J. L. Arsuaga et al., New Neandertal remains from Cova Negra (Valencia, Spain). J. Hum. Evol. 52, 31–58 (2007).
- D. Reich et al., Genetic history of an archaic hominin group from Denisova Cave in Siberia. Nature 468, 1053–1060 (2010).
- M. H. Moncel, A. M. Moigne, Y. Sam, J. Combier, The emergence of Neanderthal technical behavior: New evidence from Orgnac 3 (Level 1, MIS 8), southeastern France. *Curr. Anthropol.* 52, 37–75 (2011).
 F. H. Chen et al., A late middle Pleistocene Denisovan mandible from the Tibetan Plateau. *Nature*
- 569, 409-412 (2019).
 D. J. Zhang *et al.*, Denisovan DNA in late pleistocene sediments from Baishiya Karst Cave on the
- Tibetan Plateau. Science **370**, 584–587 (2020). 8. S. Wurz, Technological trends in the Middle Stone Age of South Africa between MIS 7 and MIS 3.
- Curr. Anthropol. 54, S305-S319 (2013). 9. E. M. Scerri, The North African Middle Stone Age and its place in recent human evolution. 5. Fund Asthropol. Hum Days 21, 119, 132 (2013).
- Evol. Anthropol. Issues News Rev. 26, 119–135 (2017).
 R. Potts et al., Environmental dynamics during the onset of the Middle Stone Age in eastern Africa. Science 360, 86–90 (2018).
- 1. J. I. Rose et al., The Nubian complex of Dhofar, Oman: An African middle stone age industry in southern Arabia. PLoS ONE 6, e28239 (2011).
- A. Delagnes, W. Rendu, Shifts in Neandertal mobility, technology and subsistence strategies in western France. J. Archaeol. Sci. 38, 1771–1783 (2011).
- K. A. Kolobova *et al.*, Archaeological evidence for two separate dispersals of Neanderthals into southern Siberia. *Proc. Natl. Acad. Sci. U.S.A.* **117**, 2879–2885 (2020).
- 14. S. L. Kuhn, Roots of the middle Paleolithic in Eurasia. Curr. Anthropol. 54, S255–S268 (2013).

statistical methods used for the quantitative study of lithic assemblage, and procedures and microscope instruments used for use-wear analysis of Quina scrapers are described in *SI Appendix*, section 4. All archaeological specimens analyzed in this study are stored in the Yunnan Provincial Institute of Cultural Relics and Archaeology, China.

Data, Materials, and Software Availability. Raw data and R code for the stone artifact analysis are openly available at OSF (https://doi.org/10.17605/osf.io/mzn9b) (70). All other data are included in the manuscript and/or SI Appendix.

ACKNOWLEDGMENTS. This research was supported by the National Natural Science Foundation of China BSCTPES (project 41988101 to F.-H.C.), Open Research Fund of TPESER (No. TPESER202210 to Q.-J.R.), the National Natural Science Foundation of China (project 42471180 to H.L. and project 42471185 to K.-L.Z.), the Australian Research Council (project DP210100717 to B.L.), the Research Academy of Songshan Civilization in Zhengzhou (No. DZ-7 to Y.-P.W.), and the University of Ferrara (project FAR2023 to M.P.). Thanks go to Dr. Qing-Jiang Yang for pollen samples collection and analysis, researchers Xu Liu and Jian Sun for support of excavation, and Jun-Yi Li, Jin-Mei He, Jian-Wei Zhou, Chang-Cheng Yang, Xing-Rong Luo, Hai-Ning Wang, and Zhi-Juan Song for their participation of field survey, excavation, and materials arrangement. We also thank the Cultural Relics Administrations at Dali and Heqing for support of the excavation and research work at Longtan.

Author affiliations: ^aState Key Laboratory of Tibetan Plateau Earth System, Resources and Environment, Institute of Tibetan Plateau Research, Chinese Academy of Sciences, Beijing 100101, China; ^bVunnan Provincial Institute of Cultural Relics and Archaeology, Kunming 650118, China; ^bUniversity of Chinese Academy of Sciences, Beijing 101408, China; ^aSchool of Science, University of Wollongong, Wollongong, NSW 2522, Australia; ^eEnvironmental Futures Research Centre, University of Wollongong, NSW 2522, Australia; ^bEnvironmental Futures Research Centre, University of Art, Universitat Rovira i Virgili, Tarragona 43002, Spain; ^bUMR7194, Natural History of Prehistoric Man, CNRS, Nomad Team, Department of Man and Environment, National Museum of Natural History, Paris 75007, France; ^hDepartment of Anthropology, DePaul University, Chicago, IL 60604; ^lInstitute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China; ^lDepartment for the History of Science and Scientific Archaeology, University of Science and Technology of China, Hefei 230026, China; ^kUMR 7194 CNRS, National Museum of Natural History, Paris 75007, France; ^lDepartment of Anthropology, University of Washington, Seattle, WA 98195; ^mDepartment of Human Studies, Prehistoric and Anthropological Science Unit, University of Ferrara, Ferrara 44121, Italy; ⁿConsiglio Nazionale delle Ricerche-Institute of Environmental Geology and Geoengineering, Laboratory of Palynology and Palaeoecology, Research Group on Vegetation, Climate and Human Stratigraphy, Milan 20126, Italy; ^sSchool of Archaeology, and Museology, Peking University, Beijing 100871, China; and ^pZhengzhou Municipal Institute of Cultural Relics and Archaeology, Zhengzhou 450052, China

Author contributions: Q.-J.R., H.L., and F.-H.C. designed research; Q.-J.R., H.L., P.-Y.X., A.S., J.-H.L., Z.-X.J., M.-H.M., B.M., M.P., Y.-P.W., and D.D. performed lithic analysis; B.L., C.-X.W., and A.-C.F. performed dating analysis; H.M. performed use wear analysis; K.-L.Z. performed pollen analysis; and Q.-J.R., H.L., P.-Y.X., and D.D. wrote the paper, with contributions from all other authors.

- F. Bordes, Mousterian Cultures in France: Artifacts from recent excavation dispel some popular misconceptions about Neanderthal man. Science 134, 803–810 (1961).
- 16. M. Peresani, Ed., Discoid Lithic Technology (BAR International Series, 2003)
- A. Delagnes, L. Meignen, "Diversity of lithic production systems during the Middle Paleolithic in France: Are there any chronological trends?" in *Transitions Before the Transition: Evolution and Stability in the Middle Paleolithic and Middle Stone Age*, E. Hovers, S. L. Kuhn, Eds. (Springer US, Boston, MA, 2006), pp. 85–107.
- 18. X. Gao, C. J. Norton, A critique of the Chinese 'Middle Palaeolithic'. Antiquity 76, 397-412 (2002).
- 19. Y. P. Wang, Late Pleistocene human migrations in China. Curr. Anthropol. 58, S504–S513 (2017).
- 20. F. Peng, J. L. Guo, S. Lin, H. M. Wang, X. Gao, The onset of Late Paleolithic in North China: An
- integrative review of the Shuidonggou Site Complex, China. Anthropologie **122**, 74-86 (2018).
- R. G. Elston, G. H. Dong, D. J. Zhang, Late Pleistocene intensification technologies in northern China. O. Int. 242, 401–415 (2011).
- P. Marrero, K. K. Abu-Amero, J. M. Larruga, V. M. Cabrera, Carriers of human mitochondrial DNA macrohaplogroup M colonized India from southeastern Asia. *BMC Evol. Biol.* 16, 1–13 (2016).
- B. Marwick, "The Hoabinhian of Southeast Asia and its relationship to regional Pleistocene lithic technologies" in *Lithic Technological Organization and Paleoenvironmental Change: Global and Diachronic Perspectives*, E. Robinson, F. Sellet, Eds. (Springer International Publishing AG, Cham, Switzerland, 2018), pp. 63–78.
- C. J. Bae, Late Pleistocene human evolution in eastern Asia: Behavioral perspectives. *Curr. Anthropol.* 58, S514–S526 (2017).
- C. Morgan, L. Barton, R. L. Bettinger, Looking for behavioral modernity in Pleistocene northwestern China. Archaeol. Res. Asia. 17, 70–78 (2019).
- F. Li et al., The easternmost middle paleolithic (Mousterian) from Jinsitai cave, north China. J. Hum. Evol. 114, 76–84 (2018).
- T. L. Qu, J. J. Yu, New evidence on the subsistence of Middle Paleolithic from Tongtian cave, Northwestern China. Archaeol. Anthropol. Sci. 16, 88 (2024).

- Y. Hu *et al.*, Late Middle Pleistocene Levallois stone-tool technology in southwest China. *Nature* 565, 82–85 (2019).
- F. Li et al., A refutation of reported Levallois technology from Guanyindong Cave in south China. Natl. Sci. Rev. 6, 1094–1096 (2019).
- H. Li, Z. Y. Li, X. Gao, K. Kuman, A. Sumner, Technological behavior of the early Late Pleistocene archaic humans at Lingjing (Xuchang, China). Archaeol. Anthropol. Sci. 11, 3477-3490 (2019).
- Y. Liu, The Lithic Industry of Wulanmulun Site in Ordos, North China (University of Chinese Academy of Sciences, 2013).
- H. Xia *et al.*, Middle and Late Pleistocene Denisovan subsistence at Baishiya Karst Cave. *Nature* 632, 108–113 (2024).
- X. J. Ni et al., Massive cranium from Harbin in northeastern China establishes a new Middle Pleistocene human lineage. *Innovation* 2, 100130 (2021).
- 34. Z.Y. Li et al., Late Pleistocene archaic human crania from Xuchang, China. Science 355, 969–972 (2017).
- Q. J. Ruan *et al.*, A preliminary excavation report of the Longtan site during 2019-2020 in Heqing county, Yunnan Province. *South China Cultural Relics* **121**, 105-118 (2021).
- L. Bourguignon, Le Moustérien de Type Quina: Nouvelle Définition d'une Technique (Université de Paris X, Nanterre, France, 1997).
- P. Hiscock, A. Turq, J. P. Faivre, L. Bourguignon, "Quina procurement and tool production" in *Lithic Materials and Paleolithic Societies*, A. Brian, B. Brooke, Eds. (Blackwell Publishing Ltd., 2009), pp. 232–246.
- C. Lemorini et al., A scraper's life history: Morpho-techno-functional and use-wear analysis of Quina and demi-Quina scrapers from Qesem Cave, Israel. Q. Int. 398, 86–93 (2016).
- S. C. Lin, J. Marreiros, Quina retouch does not maintain edge angle over reduction. *Lithic Technol.* 46, 45–59 (2021).
- W. J. Rink, H. P. Schwarcz, A. Ronen, A. Tsatskin, Confirmation of a near 400 ka age for the Yabrudian industry at Tabun Cave, Israel. J. Archaeol. Sci. 31, 15–20 (2004).
- M. Frouin et al., Dating the middle Paleolithic deposits of La Quina Amont (Charente, France) using luminescence methods. J. Hum. Evol. 109, 30–45 (2017).
- D. Delpiano et al., Flexibility within Quina lithic production systems and tool-use in Northern Italy: Implications on Neanderthal behavior and ecology during early MIS 4. Archaeol. Anthropol. Sci. 14, 219 (2022).
- V. Litov, R. Barkai, The Stone, the Deer, and the Mountain: Lower Paleolithic scrapers and early human perceptions of the Cosmos. *Archaeologies* 20, 106–146 (2024).
- Q. J. Ruan *et al.*, A study of stone artifacts found in the Tianhuadong Paleolithic site, Heqing, Yunnan. *Acta Anthropol. Sin.* 38, 166–181 (2019).
- Y. Hu, Q. J. Ruan, J. H. Liu, B. Marwick, B. Li, Luminescence chronology and lithic technology of Tianhuadong Cave, an early Upper Pleistocene Paleolithic site in southwest China. Q. Res. 94, 121–136 (2020).
- B. Li, Z. Jacobs, R. G. Roberts, A Bayesian hierarchical age model for optical dating of single grains of quartz. Q. Geochronol. 77, 101455 (2023).
- A. Turq, Approche technologique et économique du faciès Moustérien de type Quina: Étude préliminaire. Bull. Soc. Prehist. Fr. 86, 244-256 (1989).
- S. L. Kuhn, A geometric index of reduction for unifacial stone tools. J. Archaeol. Sci. 17, 583–593 (1990).
 J. Baena Preysler, E. Carrión Santafé, "Experimental approach to the function and technology
- of Quina side-scrapers" in Experiments and Interpretation of Traditional Technologies: Essays in Honor of Errett Callahan, H. G. Nami, Ed. (Ediciones de Arqueología Contemporánea, Buenos Aires, Argentina, 2010), pp. 171–202.
- M. Peresani, L. Bourguignon, D. Delpiano, C. Lemorini, Quina on the edge. Insights from a Middle Palaeolithic lithic assemblage of Grotta di Fumane, Italy. J. Archaeol. Sci. Rep. 49, 103998 (2023).

- J. P. Faivre, E. Discamps, B. Gravina, A. Turq, L. Bourguignon, Cleaning up a Messy Mousterian: How to describe and interpret Late Middle Palaeolithic chrono-cultural variability in Atlantic Europe. *Q. Int.* 433, 1–3 (2017).
- L. Bourguignon, J. P. Faivre, A. Turq, Ramification des chaînes opératoires: Une spécificité du Moustérien. Paléo 16, 37-48 (2004).
- F. Romagnoli, J. Baena, L. Sarti, Neanderthal retouched shell tools and Quina economic and technical strategies: An integrated behaviour. Q. Int. 407, 29-44 (2016).
- K. Britton *et al.*, Strontium isotope evidence for migration in late Pleistocene Rangifer: Implications for Neanderthal hunting strategies at the Middle Palaeolithic site of Jonzac, France. J. Hum. Evol. 61, 176–185 (2011).
- A. Livraghi, F. Rivals, W. Rendu, M. Peresani, Neanderthals' hunting seasonality inferred from combined cementochronology, mesowear and microwear analysis: Case studies from the alpine foreland in Italy. Archaeol. Anthropol. Sci. 14, 51 (2022).
- M. J. Yi, F. Y. Chen, F. Li, Y. Li, G. Li, New discoveries of the Huangniliang site and cultural diversity in North China during early MIS 3. *Q. Int.* 535, 13–20 (2020).
- Y. J. Guo et al., Luminescence ages for three 'Middle Palaeolithic'sites in the Nihewan Basin, northern China, and their archaeological and palaeoenvironmental implications. O. Res. 85, 456–470 (2016).
- S. W. Pei, X. Gao, X. W. Feng, F. Y. Chen, R. Dennell, Lithic assemblage from the Jingshuiwan Paleolithic site of the early Late Pleistocene in the Three Gorges, China. *Q. Int.* **211**, 66–74 (2010).
- W. Liu, X. Z. Wu, S. W. Pei, X. J. Wu, C. J. Norton, Huanglong cave: A Late Pleistocene human fossil site in Hubei Province, China. *O. Int.* **211**, 29-41 (2010).
- W. Liu et al., Human remains from Zhirendong, South China, and modern human emergence in East Asia. Proc. Natl. Acad. Sci. U.S.A. 107, 19201–19206 (2010).
- C. J. Bae et al., Modern human teeth from late Pleistocene Luna cave (Guangxi, China). O. Int. 354, 169–183 (2014).
- W. Liu et al., The earliest unequivocally modern humans in southern China. Nature 526, 696–699 (2015).
- Y. Kaifu et al., Modern human teeth unearthed from below the ~128,000-year-old level at Punung, Java: A case highlighting the problem of recent intrusion in cave sediments. J. Hum. Evol. 163, 103122 (2022).
- J. Blinkhorn, H. Achyuthan, M. Petraglia, P. Ditchfield, Middle Palaeolithic occupation in the Thar Desert during the Upper Pleistocene: The signature of a modern human exit out of Africa? *O. Sci. Rev.* 77, 233-238 (2013).
- M. V. Shunkov, M. B. Kozlikin, A. P. Derevianko, Dynamics of the Altai Paleolithic industries in the archaeological record of Denisova Cave. Q. Int. 559, 34–46 (2020).
- I. Hershkovitz et al., New middle Pleistocene dental remains from Qesem cave Israel. Q. Int. 398, 148-158 (2016).
- A. Agam, A. Zupancich, Interpreting the Quina and demi-Quina scrapers from Acheulo-Yabrudian Qesem Cave, Israel: Results of raw materials and functional analyses. J. Hum. Evol. 144, 102798 (2020).
- V. Slon et al., Neandertal and Denisovan DNA from Pleistocene sediments. Science 356, 605–608 (2017).
- V. Slon et al., The genome of the offspring of a Neanderthal mother and a Denisovan father. Nature 561, 113–116 (2018).
- Q. J. Ruan *et al.*, Research Compendium for: "Quina lithic technology indicates diverse Late Pleistocene human dynamics in East Asia." OSF. https://doi.org/10.17605/osf.io/mzn9b. Deposited 20 January 2025.