



9,000-year-old barley consumption in the foothills of central Asia

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Scholars are increasingly favoring models for the origins of agriculture that involve a protracted process of increasing interdependence within a series of mutualistic relationships between humans and plants, as opposed to a rapid single event or innovation. Nonetheless, these scholars continue to debate over when people first started foraging for grass seeds, when they began to readily utilize sickles, how prominent the early selection pressures were, and when the first traits of domestication fully introgressed into the cultivated grass population. Here, we present complementary archaeobotanical and archaeological (stone tool) evidence for cereal foragers from Toda-1 Cave in the Surkhan Darya, dating to 9200 cal BP. We conclude that early Holocene foragers were processing grains along with nuts and fruits as far north as the rich river valleys of southern Uzbekistan. These data expand the known range that preagricultural cereal foragers covered in the early Holocene, adding to our understanding of the cultural processes that led to farming. Additionally, we present the earliest evidence for people interacting with the progenitors for pistachios and apples (or a close apple relative). The complex foraging behaviors that led to cultivation were being undertaken by people during the early Holocene across a wider area of Eurasia than previously thought.

agriculture origins | holocene | central Asia | barley | climate change

By roughly 10,000 cal BP, a few isolated populations of Triticeae grasses began to evolve the earliest traits of domestication, notably a loss of their natural seed-dispersal mechanism as well as increasing grain size (1–5). The evolutionary transition to tougher rachises allowed these grasses to secure a stronger mutualistic relationship with humans, which facilitated more effective seed dispersal (6–8). From the human perspective, the development of cultural behaviors for harvesting wheat (*Triticum* spp.) and barley (*Hordeum vulgare*) triggered the first Neolithic Demographic Transition (9, 10). The domestication of Triticeae grasses was one of the most significant Holocene phenomena to shape the current economic and genetic standing of humanity (11, 12). Understanding the cultural backdrop of these evolutionary changes is essential for developing a clearer picture of how humanity got to where it is today.

Triticeae grasses have large seeds compared to other wild grasses, likely resulting from a weak dispersal mechanism and intense sibling competition (13, 14). The short-range dispersal mechanism of a brittle rachis caused plants to form dense homogenous stands of annuals, paralleling the structure of agricultural fields and allowing early seed foragers to easily collect wild grains (15). Increasingly, archaeobotanical data are illustrating that there was a long-protracted period of harvesting of wild cereal stands across southwest Asia, which was occurring for millennia prior to the first domestication of crops and presumably long before seed-saving, sowing, or harvesting practices (16–20).

Analysis of usewear on backed geometric lithics from the site of Ohalo II in the Levant shows that by 23,000 cal BP, these multipurpose tools were increasingly being used to harvest wild cereals (21). Additional evidence shows that grains were ground and processed into bread by 14,400 y ago (22). Similar stone artifact assemblages continue at late Pleistocene and early Holocene foraging sites, such as Shubayqa, in northeastern Jordan (14,500 to 11,600 cal BP) (22). However, sickle blades are rare toward the end of the Pleistocene, and foragers at many Natufian sites (15,000 to 11,500 cal BP) likely hand-pulled or beat grains loose, with gradually increasing implementation of sickles occurring after domestication (23). Researchers have previously recognized that backed trapezoidal microliths were used as hafted sickle blades in association with the earliest dispersal of agriculture into central Asia, but there has been little attention to the possibility that earlier foragers there had also begun applying this technology to assist in harvesting wild plant foods (23, 24). Such a shift would indicate Central Asian populations were already engaged in forms of delayed-return strategies that might have

Significance

Here, we present archaeobotanical data for ancient barley grains in association with sickle blades and grinding stones from the cave of Toda in the foothills of southern Uzbekistan. This finding helps shed light on one of the greatest mysteries in central Asian archaeology—how did the Kelteminar people live? We complement our data with a suite of radiocarbon dates, a detailed palynological study, an analysis of wood charcoal remains, and a detailed analysis of all aspects of the archaeological remains. These data, collectively, paint the clearest picture thus far of the prehistory of this poorly studied corner of the ancient world.

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facilitated more rapid adoption of domesticated grains during the Neolithic.

In this paper, we present synthetic evidence from Toda-1 Cave in the Surkhan Darya Valley of southern Uzbekistan, which suggests that the practice of using stone sickles to harvest hulled and naked barley (*Hordeum vulgare* spp.) was more widespread than previously thought. Recent studies of use wear on microliths from other cave sites in the broader region (16, 17) further support our argument that at least some of the microliths were hafted into composite tools and used to process a range of hard materials, such as bone and tough plant fibers. Pitted stones likely resulted from nut cracking; however, they may have served as multipurpose tools, as might the single grinding stone recovered from early layers at the site. These discoveries help frame our understanding of the cultural developments and demic diffusion of the early Holocene.

Results

Toda-1 Cave is located in the foothills of the northwestern corridor of the Surkhan Darya, the largest tributary of the Amu Darya (Fig. 1). A collaborative international research team, including scholars from the Institute for Vertebrate Paleontology and Paleoanthropology (IVPP) in Beijing and the Institute of Archaeology in Samarkand, identified four rock shelters in the area, all of which provided apparent early Holocene cultural material during tests. Toda-1 Cave was the best preserved (Fig. 1 and *SI Appendix, section 1*), leading to excavations during the summers of 2018 and 2019 (*SI Appendix, section 2*).

During the 2 y of excavation, we opened a total of five trenches (T1–T5); T5 contains the most complete strata, including the

earliest phase of the Neolithic Age, and 25 AMS¹⁴C dates from different depths—altogether spanning T5 (n = 17), T1 (n = 3), T2 (n = 4), and T3 (n = 1). An extensive chronology of discontinuous occupation, stretching from 9200 to 1000 cal BP, is marked by the recovery of stone tools, pottery, and plant and animal remains (Fig. 1 and *SI Appendix, Table S1*). We carefully screened all sediments in the cultural layers of Toda-1 Cave, but no pottery was found in the early Neolithic layers of T5 L24–L17 (9000 to 7800 cal BP). However, a large number of pottery fragments were found in the layers above T5–L16 (3000 to 1000 cal BP). In fact, the appearance of pottery at the westernmost point of central Asia, at the Djeitun site, should date back to around 8000 to 7800 cal BP (25). Therefore, we consider that Toda-1 Cave T5 L24–L17 (9000 to 7800 cal BP) belongs to the prepottery age.

The stone artifacts from the earliest occupation layers included blades, blade cores, flakes, flake cores, a grindstone, and fragments of other lithics, and apparent pitted hammer stones (Fig. 2 and *SI Appendix, section 4*). Most of the flakes and blades were made of siliceous limestones, and some are small brown flints, sandstones, siliceous shales, and chalcedony. In a few cases, surface wear was visible on the blades, representing evidence of use—as would be expected from cutting siliceous plant material (*SI Appendix, Fig. S12*). The patterns of use wear on the Toda-1 Cave lithics are similar to those from Obishir, showing polishing on one side of the flake, suggesting use as part of a composite tool to cut hard or abrasive material (16). Ceramic sherds were only recovered in the later occupation layers at the site, suggesting that the earliest occupants at the cave maintained an aceramic economy.

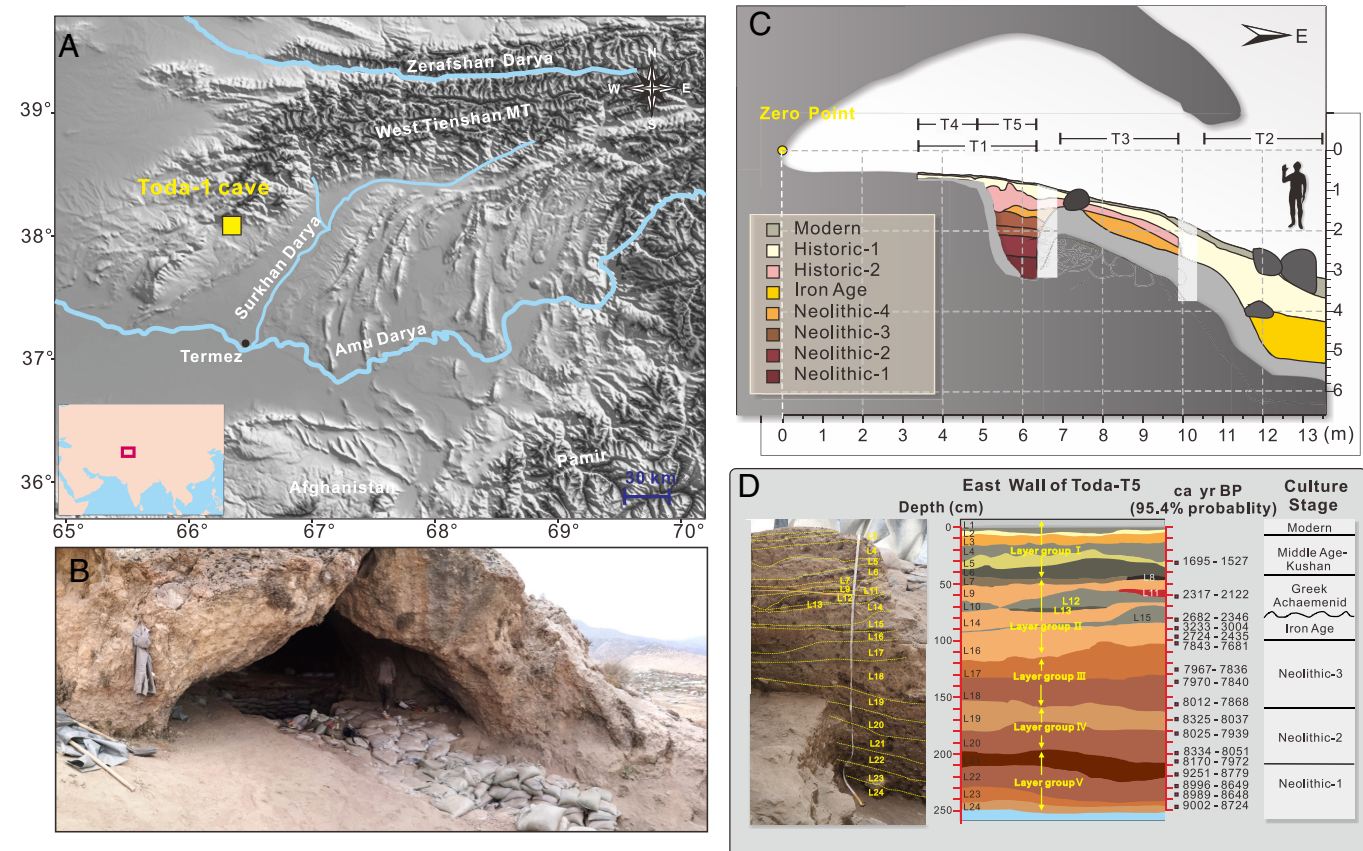


Fig. 1. Location, culture layer distribution, and chronostratigraphy of Toda-1 Cave. (A) Location of Toda-1 Cave and topography of Amu Darya Valley. (B) External photo of Toda-1 Cave (by Xinying Zhou). (C) Cross section and stratigraphic layers of Toda-1 Cave. (D) The culture layer group and sublayer with radiocarbon data of Section-1 of T5, Toda-1 Cave.

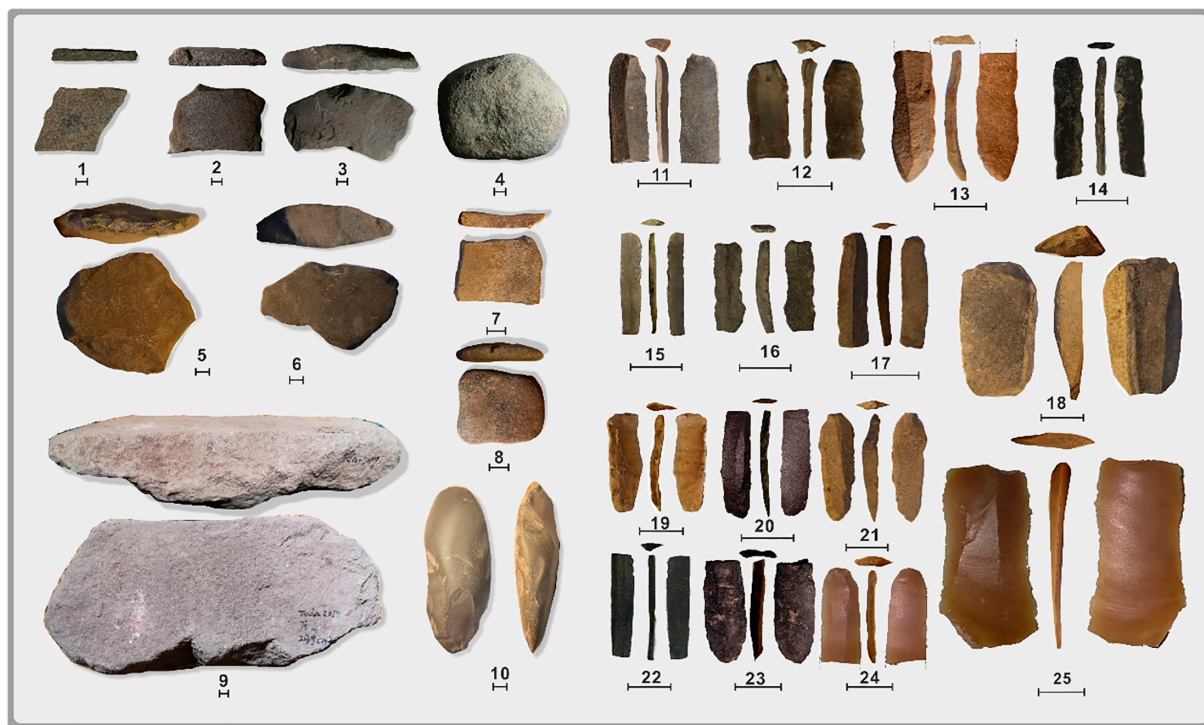


Fig. 2. Stone tools from early Holocene layers of Toda-1 Cave: 1–3, 7. Tabular anvil with pitting (T5-L18, ca. 8000 cal BP); 4. Hammer stone with pitting T5-L17, ca. 7800 cal BP; 5 to 6. Retouched flakes (T5-L18, ca. 8000 cal BP); 8. Polished adze (T5-L18, ca. 8000 cal BP); 9. Grinding stone (T5-L18, ca. 8000 cal BP); 10. Pebble axe (T5-L17, 7800 cal BP); 11 to 13. Microblades with continuous edge damage (T5-L-24, ca. 9000 cal BP); 14 to 17. Microblades with partial edge damage (T5-L18, ca. 8000 cal BP); 18. Blade (T5-L-24, ca. 9000 cal BP); 19 to 24 Microblades with partial edge damage (T5-L-23, ca. 8800 cal BP); 25. Blade with partial edge damage (T5-L23, ca. 8800 cal BP); (Scale bar, 1 cm.)

Archaeobotanical remains were recovered from sediments using flotation and a geological sieve of 0.35 mm. Archaeobotanical analyses were conducted in the labs at the IVPP, and all identifiable remains were systematically reported (Figs. 3 and 4). Ancient cereals are discussed below and the full assemblage of identifiable plant remains is presented in *SI Appendix, section 6*. The chronology of the site was pieced together through an extensive radiocarbon dating program ($n = 25$ dates; *SI Appendix, section 3*). Specialists were brought in to properly analyze all biotic remains and cultural artifacts; a more detailed discussion of the cultural artifacts is presented in *SI Appendix, section 2*. In this paper, we focus on the botanical remains and associated lithics, which we interpret as harvesting and grain processing artifacts from the earliest occupation at the site. Finally, the pollen, organic C^{13} and N^{15} isotope data from sediments are used to reconstruct the changes of the past paleoenvironment and their corresponding relationship with the cultural layer of Toda-1 cave (*SI Appendix, section 5*).

Discussion

The first discoveries of a backed microlithic industry in southern central Asia were reported during the Soviet period and attributed to the poorly understood Kelteminar Culture (26–28). Detailed classifications of these microlith assemblages were made in the 1950s to 1970s, many of which identify linkages between surface-scatter assemblages in the southern Aral Sea region as well as along the foothills of southern central Asia. The Kelteminar-type assemblages are distinguished from other microlithic industries in central Asia based on point typologies, prevalence of bifacial retouch and blade morphologies (29). A similar microlith technology to the Kelteminar extended from Mongolia and western China to Turkmenistan and across the deserts of central Asia (30, 31). Other sixth to fourth millennia BC Kelteminar cave sites have been

reported, all containing blades and ceramics, such as Dzhebel, Dam Dam Cheshme, and Kailiu (30–33).

In the literature, the Kelteminar are often linked to a similar set of cultural remains found at sites in the mountain valleys, stretching from Tajikistan to Afghanistan. Similarly, the Hissar Culture is also largely described based on geometric microliths and is often claimed to start in the region around the eighth millennium BP (34). These traditional culture historic designations may require reassessment, as the Toda-1 material show that the Kelteminar-Hissar Culture stretched across the aceramic/ceramic and foraging/farming boundaries. Collectively, these archaeological remains suggest that there was a broad-reaching tradition of stone microlith production for composite tools and we argue that, at least in some of these cases, they were used for harvesting grains across the front of the Zagros and Taurus Mountains in West Asia.

Taylor et al. (2021) (26) note that the microlithic technology at Obishir dated to 8000 cal BP resembles a broader mid-Holocene tradition identified across southern central Asia, which includes retouched bladelets, trapezoids, scrapers, and grinding stones. Other similar investigations into the microlithic technologies at cave or rockshelter sites in the region were conducted recently at Oshhona and Istikskaya (16, 35, 36). Likewise, bullet-shaped cores have been reported from the well-dated Kelteminarian of Ayakagytm, illustrating more specialized pressure-flaking production techniques in lithic production (37). There are also clear similarities in the lithic assemblage with the slightly later and recently excavated site of Kaynar Kamar in the same region, which has been ascribed to the Hissar complex (38). While these similarities are intriguing, it is also important that we point out the fact that similar microlithic industries were employed across central Asia from the terminal Pleistocene until the mid-Holocene (39–42).

Mesolithic microlithic technologies have been recovered from surface scatter sites across the arid steppe, showing continuity

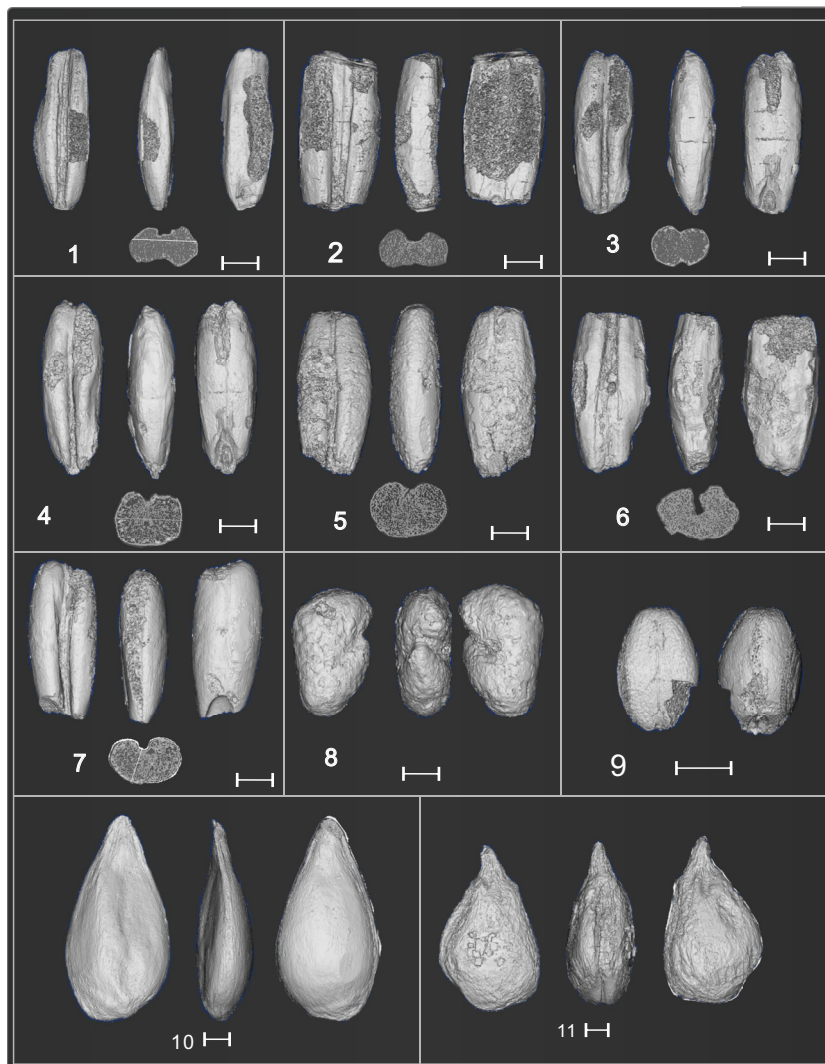


Fig. 3. CT (computed tomography) photo of carbonized seeds from Toda-1 Cave (Scale bar, 1 mm.): 1–7, barley grains: 1. T5-L21, ca. 9000 cal BP; 2. T5-L21, ca. 9000 cal BP; 3. T5-L19, ca. 8000 cal BP; 4. T5-L21, ca. 9000 cal BP; 5. T5-L19, ca. 8000 cal BP; 6. T5-L19, ca. 8000 cal BP; 7. 22B, ca. 9000 cal BP; 8. *Trigonella* (T5-L23, ca. 9000 cal BP); 9. *Piptatherum*; T5-L19, ca. 8000 cal BP; 10. and 11. *Malus/Pyrus* (T5-L18, ca. 8000 cal BP).

through the later Pleistocene, and consisting of blades and points (27). Early Holocene sites in southern Uzbekistan are aceramic and are characterized by the same microlithic technological traditions common across central Asia, but here they have been variously attributed to early farmers, pastoralists, or foragers (43–46). While there are material culture links across a wide area of central Asia, we still lack adequate archaeological evidence for discussing the economy (43). Based on accepted dates and geographic distributions for the Kelteminar tradition, the earliest layers at Toda-1 Cave predate and fall outside the range for Kelteminar, hence the data we present here, through future research, will hopefully allow archaeologists to either describe new assemblage types or to expand the parameters of existing ones. Given that Toda-1 Cave predates the accepted temporal range of Kelteminar and there is a lack of agreement on the geographic distribution, we avoid specifically labeling the Toda-1 Cave industry to any grouping.

Furthermore, paleoclimatic data from the cave were used to complement more detailed published regional studies in an attempt to better fit the early occupants onto an ecological landscape (*SI Appendix, section 1*). As part of a multiproxy approach for reconstructing the paleoenvironment around the cave, we conducted palynological analyses on sediments from the cave, as reported in *SI Appendix, section 5*, wood charcoal analyses, as reported in *SI Appendix, section 6*, geochemical analysis of sediments, as reported in *SI Appendix, section 7*, and sedimentary susceptibility tests, as reported in *SI Appendix, section 8*. We

contrasted our results with several larger-scale previously published datasets, as presented in Figs. 5 and 6, and found clear parallel trends in the data, which were used to loosely reconstruct general climatic patterns during key periods of occupation.

Preserved anthropogenic remains of plants from the earliest occupation layers at the site include carbonized fruit, nut, and grass seeds. The nutshells are primarily from *Pistacia vera*—the progenitor of the domesticated pistachios (*SI Appendix, section 6*). There were also a few undifferentiated shell fragments that might have originated from stone fruits (*Prunus* spp.). Additionally, preserved seeds from a large-fruited species of Maloideae, presumably a wild apple (*Malus sieversii* or a related species) (Fig. 3 and *SI Appendix, section 6*). All of the Triticeae grains from the earliest occupation morphologically match wild barley (*Hordeum vulgare* ssp. *spontaneum*) (Fig. 3). While wild *Triticum* spp. do not grow this far north, other close relatives do, notably *Aegilops* sp., based on morphology, we rule these wild relatives out. Wild barley still grows in dense stands in the region today. Other wild grasses were also present in the assemblage, including a wild Panicoid that we have tentatively identified as *Piptatherum* sp. (rice grass). Wild rice grasses have a modern range spanning the mountain streams and wetlands of northern Pakistan, central Asia, Xinjiang, and Tibet. These grasses produce a large panicle (like rice or millet) and would have hypothetically been a suitable target for foraging, with dense fruiting inflorescences and grains the size of millets. Additionally, *Piptatherum* sp. has been suggested as a grass

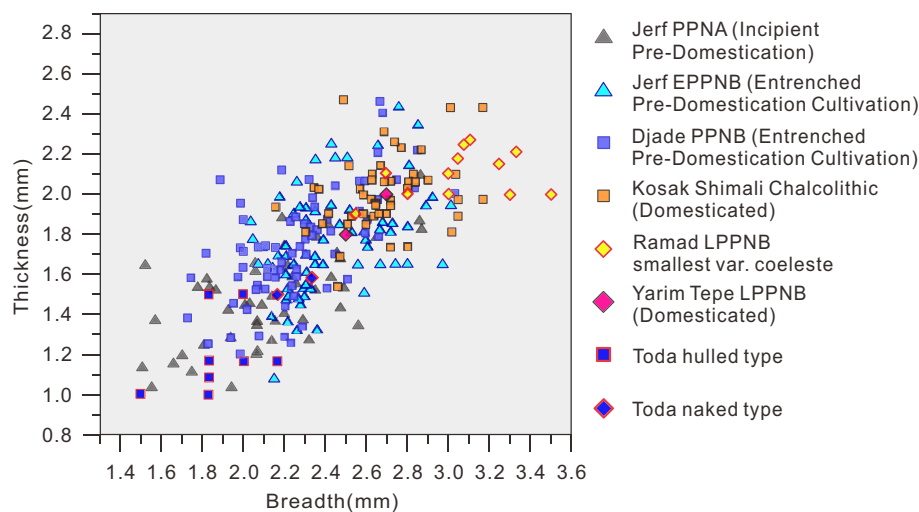


Fig. 4. The best-preserved representative specimens from Toda-1 Cave, breadth, and thickness measurements, compared to early southwest Asian assemblages (data from 2,20,51,52). The Toda-1 Cave barley plots well within the wild range.

harvested by other preagricultural seed foragers in southwest Asia (47).

The assemblage from Toda-1 Cave lacks rachises; the barley appears to be a two-rowed morphotype and there are not enough recovered grains to discuss size changes through time. We have considered the morphology of the Toda-1 Cave grains in relationship to grains from other foraging and early farming sites and it is clear that the grains overlap with wild forms (Fig. 4). Based on the archaeobotanical material, there is no reason to assume that the barley grains are domesticated or were cultivated; although, it is worth considering the possibility of low-investment cultivation or incipient domestication in follow-up studies. Almost all of the Toda grains have a broad furrow and angular cross-section and are narrow and symmetrical grains, which is typical of two-rowed hulled barley.

A few of the specimens (Fig. 2) are well rounded in dorsal profile and they appear to lack transverse striations, features typical of naked types; although, their surface is not well-preserved. A scatter plot of breadth and width measurements is presented in Fig. 4, contrasting the Toda-1 Cave grains with other published roughly contemporaneous assemblages. This figure includes wild assemblages from Syria, as well as fully domesticated assemblages from Syria and Iran. The plotted data also include the two smallest examples reported for early naked barley, found at Ramad in Syria (9300 cal BP). Most of the grains fall clearly in the wild cluster; the two possible naked grains fall at the upper part of the wild range, in the midst of later predomestication cultivation (EPPNB) grains, which are on the early end of the domestication spectrum. These two grains fall well below the minimum dimensions for reported early naked barley grains and outside the fully domesticated cluster. On this basis, all of the grains from Toda-1 Cave are presumed to be from a wild-type barley, i.e., similar with southwest Asian sites dating older than 10,500 cal BP.

The prominence of carbonized wood fragments from short-growth shrubby fruit and nut trees matches interpretations of what the prehistoric woodland of the foothills of central Asia likely looked like. The presence of *Pistacia vera* and Prunoideae wood, along with Maloideae and *Elaeagnus angustifolia* seeds, allows us to better visualize the landscape that the prehistoric foragers occupied. In addition to the wood charcoal data (SI Appendix, section 6), we conducted a palynological analysis (SI Appendix, section 5) of cave sediments, which also illustrates the presence of a Rosaceae and pistachio woodland, likely divided by fields of wild grasses and legumes. In Fig. 5, we contrast four different published paleoclimatic proxies with our localized palynological data from Toda-1 Cave sediments.

The Surkhan Darya Valley is located in the rain shadow of the Pamir Mountains and today is exceptionally arid, despite the extensive irrigated agriculture conducted along the valley basin. Our multiproxy paleoclimatic data support the assessment that, during the early Holocene, these foothills would have been covered in shrubby woodland and seasonal grass-dominant fields (SI Appendix, sections 1 and 5). Notably, the expansion of *Quercus* spp. woodland further north and west might indicate a stronger Indian Summer Monsoon around 9000 cal BP (Fig. 5). This ecology, in many ways, would have mimicked the ecology of the hilly flanks of the Zagros Mountains and the area around the Fertile Crescent. These ecological similarities may have facilitated the dispersal of people sharing a similar suite of economic practices out of southwest Asia and north into central Asia. Additionally, the continental climate may have driven seasonal movements to coincide with wild herd migrations and wild plant seasonality.

The harvesting of wild barley in southwest Asia stretches back at least to Ohalo II (21), and there is reason to believe, based largely on the range of distribution of grinding stones and stone blades, that this practice was widely employed (Fig. 6). Preagricultural assemblages suggest that foragers were using stone blades and, in some cases, sickles to target a wide range of different grasses (47). Current data from southwest Asia indicate size change along a spectrum that began with incipient predomestication around 11,500 cal BP; i.e., average grain thickness of 1.5 mm, breadth of 2.1 mm, in charred assemblages. The grains increased in size to an average of 40 percent by around 9500 to 9000 cal BP; i.e., thickness of 1.8 to 2.7 mm and breadth of 2.5 to 3.4 mm². The earliest grains to express a large domesticated form are two-rowed and hulled, originating from Ganj Dareh (Iran), ca. 10,000 cal BP and Tell Aswad West (Syria), rachises are still partially shattering (ca. 10,500 cal BP) (Fig. 6). Early occurrences of six-rowed and naked forms are reported from Beidha (Jordan), ca. 10,000 cal BP and Aşıklı Höyük (Turkey), ca. 9800 cal BP—predominantly hulled and six-rowed, but including some naked morphotypes (52). These assemblages still contain mostly shattering rachises, representative of the continuing process of evolution (1, 2). Cultivation of six-row naked barley spread eastward early, as it dominated assemblages at Mehrgarh (Pakistan), Sang-i-Chakmakh (northeastern Iran), and Jeitun (Turkmenistan), all dating to ca. 8500 to 8000 cal BP (53).

The data from Toda-1 Cave allows us to expand the known geographic area where wild cereal harvesting was practiced, suggesting that this was a widely implemented behavior and not restricted to the Levant or the broader eastern Mediterranean. The oldest barley seeds from Toda-1 Cave were directly dated to 9133

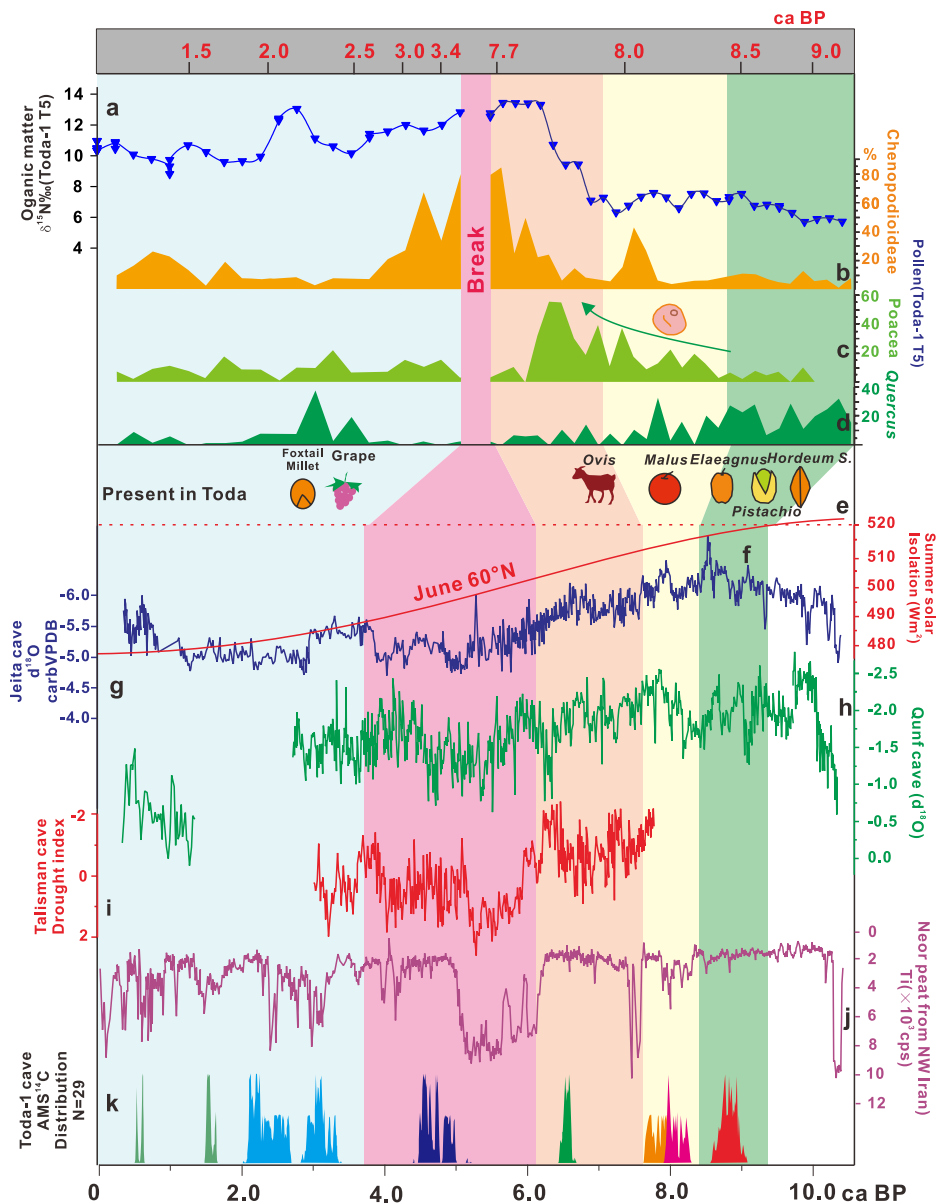


Fig. 5. Comparison of the environmental index of Toda-1 Cave and climate change records: (A) the vegetation (pollen), grazing intensity ($\delta^{15}\text{N}$) change record from Toda-1 Cave T5; (B–D) pollen percentage in Toda-1 Cave sediments from T5; (E) first presence of plant and animal remains in Toda-1 Cave, foxtail millet (*Setaria italica*), grape (*Vitis vinifera*), apple relative (*Malus/Pyrus*), Russian olive (*Elaeagnus* sp.), Pistachio (*Pistacia vera*), barley (*Hordeum vulgare* ssp. *spontaneum*); (F) the summer solar isolation intensity change at 60°N ; (G) the precipitation change record by $\delta^{18}\text{O}$ of Jeita Cave, Levant region (48); (H) the India monsoon intensity change record by $\delta^{18}\text{O}$ of Qunf Cave, Oman (49); (I) middle Asia drought index record by Talisman cave, Fergana, Kyrgyzstan (50); (J) arid events recorded by element Ti concentration of Neor peat, northwestern Iran; (K) radiocarbon data ($n = 29$) possibility distribution of Toda-1 Cave using IntCal20 atmospheric curve (51).

to 8970 cal BP and 8989 to 8652 cal BP. These data help us visualize cereal foraging as part of a wide-ranging set of cultural behaviors that continued for millennia across South and central Asia (Fig. 6). This evidence for wild grass harvesting in the central Asian mountains may also suggest that people were targeting more than just wild barley. Given that increasing evidence attests to multiple parallel trajectories toward domestication for cereals in the Fertile Crescent (19) and speculative proposals have been made of another more eastern parallel domestication of barley (54), it is worth considering the possibility of cultivation. However, if grains started to evolve in response to anthropogenic seed predation, it likely represents a dead end, since domesticated, naked six-rowed barley was introduced to central Asia from the Iranian Plateau around 8,000 y ago as a distinctly domesticated morphotype (53). Recovery of numerous pitted stones likely reflects plant processing, including nut cracking; although hammer stones and pitted stones likely represent multipurpose tools. The forms of edge damage common along the lateral margin of blade/bladelet segments are consistent with expectations for use within composite tools (55, 56) see also (SI Appendix, Figs. S12–S16).

The assemblage also provides the earliest evidence for large-fruited Rosaceae foraging in central Asia. Recent genetic research

has shown that the modern domesticated apple (*Malus pumila*) evolved through hybridization between at least three large-fruited wild species of *Malus* (57, 58). *Malus sieversii*, a wild apple native to the mountains of southern Kazakhstan, Kyrgyzstan, Tajikistan, and Xinjiang, China, is the main progenitor of all domesticated and commercial apples (52, 59). There were also some *Prunus* nutshells and other unidentifiable nutshell fragments. The pistachio shells (SI Appendix, Fig. S19) were found in almost all strata at the site and likely correlated with the pitted stone hammers (Fig. 3 and SI Appendix, Table S4). Out of 352 carbonized specimens of wood charcoal, only *Pistacia* sp. and Prunoideae were present, which supports the results of the archaeobotanical study (SI Appendix, Fig. S18 and Table S5). The Toda-1 Cave data push back the earliest evidence for humans collecting *Pistacia vera* by at least four millennia (60).

Toda-1 Cave provides the first clear evidence of a seed, fruit, and nut foraging economy in central Asia. People living in the cave through time were likely using stone-set composite tools to harvest wild stands of barley as part of a complex foraging system that included the collection of fruits and nuts as well as hunting a wide range of large and small fauna. These foragers entered a landscape that would have shared many parallels to that of the eastern Mediterranean and the Iranian Plateau.

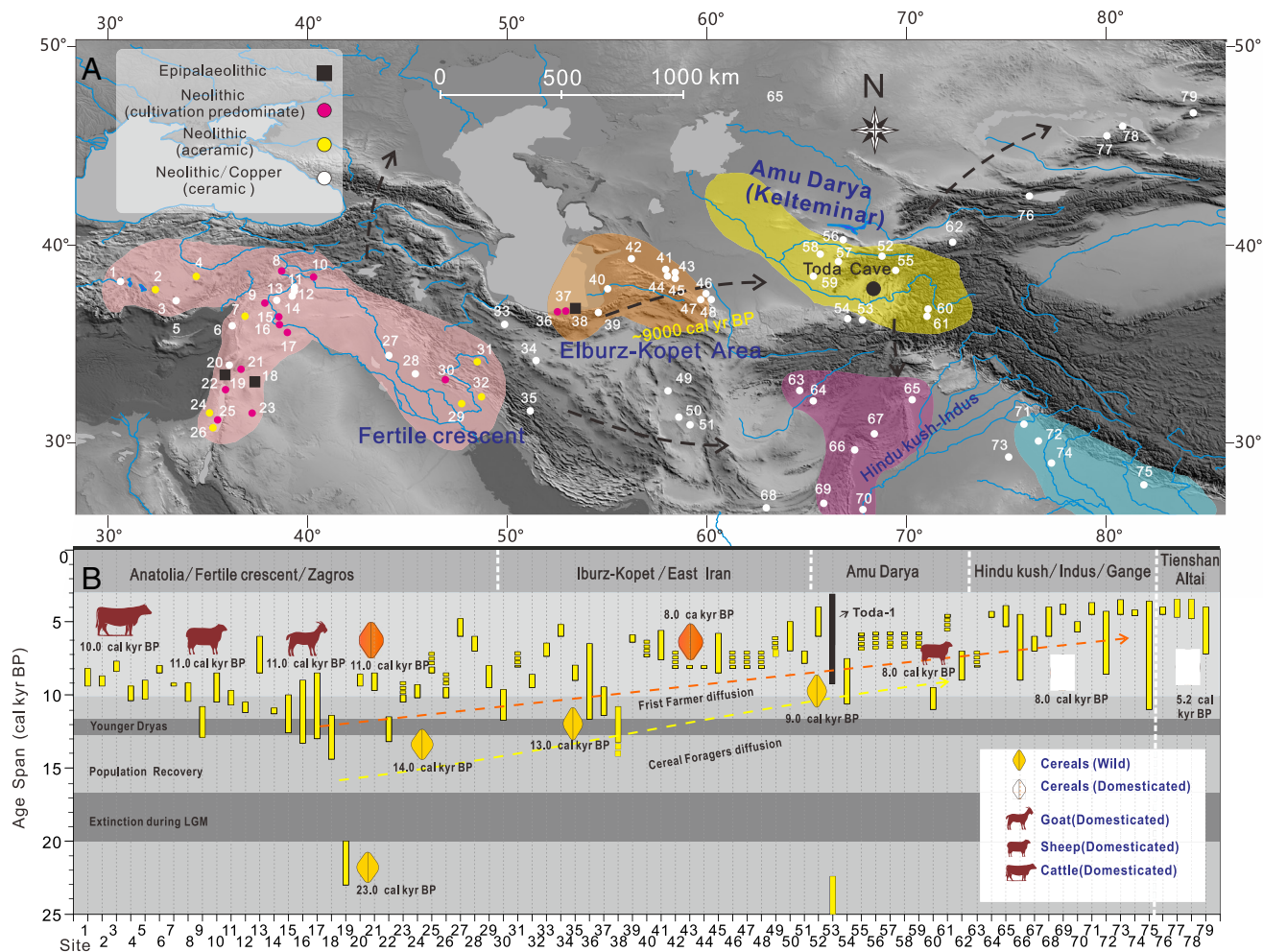


Fig. 6. The diffusion route and the timeline of cereal foragers from west Asia to east. (A) Near East, Iran, central Asia, South Asia early Neolithic site and Toda-1 Cave site distribution. (B) The diffusion timeline of foragers indicated by the age span bar of the numbered sites, the dashed bar represents estimated ages, marked with evidence of wild/domesticated cereal and domesticated animals of the regions (detail of the sites see [Dataset S1](#)).

These data also feed into ongoing debates over what ecological drivers caused evolutionary change in early cultivated fields. If, indeed, wild grain harvesting was practiced across much of West Asia but domestication traits only evolved in the Fertile Crescent and eastern Mediterranean, then maybe a factor other than stone blade or sickle harvesting drove evolution (5, 61). As is well established, in the western and northern parts of the Fertile Crescent and the cultivation and domestication of cereals and legumes predates by at least half a millennium the shift to dependence on cereals (let alone cultivating them) in south Uzbekistan (17, 44, 45). Nevertheless, cereal foraging and nut collection were a viable subsistence practice in foothills of central Asia until domesticated crops were introduced from the western regions.

Materials and Methods

Excavations. The Toda-1 cave was excavated during the summer field seasons of 2018 and 2019, as a joint project between the IVPP, CAS, and the Institute of Archeology of the Academy of Sciences of the Republic of Uzbekistan. The deposits in T5, located in the middle of the cave, were the most abundant and stratified and not significantly disturbed ([SI Appendix, Figs. S3 and S4](#)). Detailed information on the archaeological strata can be found in [SI Appendix, sections 2.5](#).

Radiocarbon Chronology. Samples for radiocarbon dating were collected and plotted using a Total Station. Rough assessments of the cultural layers were determined in the field based on associated material culture and tested using

25 AMS¹⁴C dates from different depths—all together spanning T5 (n = 17), T1 (n = 3), T2 (n = 4), and T3 (n = 1). All samples were sent to Beta LABS in Miami for preprocessing and testing. The strata of T5 were divided into 5 groups (Fig. 2) and 24 substrata ([SI Appendix, Fig. S6](#)). All the C14 age data and the Bayesian depth age model can be referred to [SI Appendix, sections 3](#).

Microbotanical Remains. Sediment samples from T5 were taken at contiguous 5 cm intervals for pollen analysis and processed at the laboratory of the IVPP in Beijing. About 150 g of bulk sediment was treated with a heated 10% aqueous HCl solution for 2 h and then rinsed and dried, then subjected to heavy liquid separation, first with ZnCl₂ (density 2.0 g mL⁻¹) and then with a mixed solution of KI and ZnI₂ (density 2.0 g mL⁻¹). The pollen concentrate was dried and mounted in glycerine for microscopic identification. Pollen grains and spores were identified and counted using a Zeiss MA1 light microscope at a magnification of 400x. Microcharcoal concentration was counted and calculated using the pollen slide method.

Macrobotanical Remains. All samples were floated using a 0.35-mm mesh screen at a work station near the cave. All of the light fraction portions were taken to the archaeobotany laboratory of the IVPP. The archaeobotanical samples were first sorted and weighed, and then wood charcoal and other macrobotanical remains were systematically removed and quantified ([SI Appendix, Tables S4 and S6](#)). Fungal alterations on the wood suggest that people were collecting firewood mainly from dead and rotten wood sources. Charcoal fragments with a diameter >2 mm were selected for identification. First, they were classified under a light microscope mainly according to their cross sections. The characteristics of the cross sections, radial, and tangential sections of charcoal were then observed and photographed under a scanning electron microscope (Zeiss EVO MA10). High-powered light microscopy (Leica 205C) and scanning-electron-microscope imaging were

used to compare the anatomical and morphological features of the archaeological specimens with modern reference material (*SI Appendix, Fig. S17*).

Geochemical Analysis. We tested the organic $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in S1 of T5. The organic $\delta^{13}\text{C}$ was used as an index indicating the proportion of C_4 plants and paleovegetation types near the site, while the $\delta^{15}\text{N}$ values indicate the variation of the source of organic matter in the cultural layer at the site. The sediment samples were dried in an oven at 40 °C. The dried sediments were then ground using a mortar and pestle until the samples could be sieved through a 0.15 μm screen. About 2 g of the sieved sample was treated with 2 M HCl for 24 h at room temperature in order to remove carbonates. Subsequently, the samples were rinsed until it became neutral with deionized water and dried. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the sediment samples were determined at the Institute of Vertebrate Paleontology and Paleoanthropology using a Flash2000 elemental analyzer interfaced with a 253 Plus continuous flow isotope ratio mass spectrometer.

Data, Materials, and Software Availability. All study data are included in the article and/or [supporting information](#).

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