Regional diversity on the timing for the initial appearance of cereal cultivation and domestication in southwest Asia

Amaia Arranz-Otaegui[a,1], Sue Colledge[b], Lydia Zapata[c], Luis Cesar Teira-Mayolini[d], and Juan José Ibáñez[e]

[a]Department of Cross-Cultural and Regional Studies, University of Copenhagen, 2300 Copenhagen, Denmark; [b]Institute of Archaeology, University College London, London WC1H 0PY, United Kingdom; [c]Department of Geography, Prehistory and Archaeology, University of the Basque Country–Euskal Herriko Unibertsitatea, 01006 Vitoria-Gasteiz, Spain; [d]Instituto Internacional de Investigaciones Prehistóricas de Cantabria, 39005 Santander, Spain; and [e]Consejo Superior de Investigaciones Científicas, Instituto Milá y Fontanals, 08001 Barcelona, Spain

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Recent studies have broadened our knowledge regarding the origins of agriculture in southwest Asia by highlighting the multiregional and protracted nature of plant domestication. However, there have been few archaeobotanical data to examine whether the early adoption of wild cereal cultivation and the subsequent appearance of domesticated-type cereals occurred in parallel across southwest Asia, or if chronological differences existed between regions. The evaluation of the available archaeobotanical evidence indicates that during Pre-Pottery Neolithic A (PPNA) cultivation of wild cereal species was common in regions such as the southern-central Levant and the Upper Euphrates area, but the plant-based subsistence in the eastern Fertile Crescent (southeast Turkey, Iran, and Iraq) focused on the exploitation of plants such as legumes, goatgrass, fruits, and nuts. Around 10.7–10.2 ka Cal BP (early Pre-Pottery Neolithic B), the predominant exploitation of cereals continued in the southern-central Levant and is correlated with the appearance of significant proportions (~30%) of domesticated-type cereal chaff in the archaeobotanical record. In the eastern Fertile Crescent exploitation of legumes, fruits, nuts, and grasses continued, and in the Euphrates legumes predominated. In these two regions domesticated-type cereal chaff (>10%) is not identified until the middle and late Pre-Pottery Neolithic B (10.2–8.3 ka Cal BP). We propose that the cultivation of wild and domesticated cereals developed at different times across southwest Asia and was conditioned by the regionally diverse plant-based subsistence strategies adopted by Pre-Pottery Neolithic groups.

plant domestication | agriculture | southwest Asia | Pre-Pottery Neolithic | archaeobotany

Plant domestication is defined as an evolutionary process that resulted from the systematic cultivation of morphologically wild plants and eventually led to the appearance of agriculture (1, 2). In southwest Asia, the archaeobotanical evidence indicates that during the Epipaleolithic (*c*. 23–11.6 ka Cal BP), the plant-based subsistence focused primarily on the collection of wild plant species, including several species that are the ancestors of modern-day domesticated cereals and legumes (3–6). Around 11.5 ka Cal BP, during the Pre-Pottery Neolithic A (PPNA) in the Levant (11.6–10.7 ka Cal BP), there is evidence for the development of plant food production with the cultivation of various wild cereals such as wheat (*Triticum*) and barley (*Hordeum*) (7–10). Morphologically domesticated cereal species first appeared in the early Pre-Pottery Neolithic B (EPPNB, *c*. 10.5 ka Cal BP) (11, 12). However, agriculture, defined as a system based on the production and consumption of and high reliance on domesticated plants (1), did not developed in southwest Asia until around 9.8 ka Cal BP, during the middle and late Pre-Pottery Neolithic B (M/LPPNB) (1, 2, 13, 14).

In the last 25 y several hypotheses have been put forward to explain when and where plant cultivation and domestication started in southwest Asia. The "core-area" hypothesis, which was developed during the 1990s and early in the following decade (15–17), suggested that eight plant species, collectively referred to as the "founder crops" (18), had been selected and domesticated once in a single region or core area located in southeast Turkey. According to modern experimental work, the process of plant domestication was a rapid event that occurred as a result of human selection for morphologically domesticated species (19, 20). However, recent archaeobotanical data have demonstrated that before the establishment of domesticated plants in southwest Asia there was a period of cultivation of morphologically wild plants (7–10, 21). The new evidence indicates that predomestication cultivation occurred broadly at the same time in different regions (22, 23). Genetic evidence indicates that cultivation practices involved multiple wild progenitor populations located across different regions, and therefore it is not possible to pinpoint the exact origins of domesticated plants (24–29). Domesticated cereals first emerged during the EPPNB (*c*. 10.5 ka Cal BP), but they did not become dominant until 1,000 y later (11, 12), indicating that domesticated species evolved slowly (21) and that the rates of evolution during domestication were similar to those observed in wild species subject to natural selection (30, 31). In light of the data compiled in the last 30 y, plant domestication now is regarded as a protracted evolutionary process that occurred in multiple regions (32).

Archaeological evidence indicates that marked social, technological, and economic differences existed between the Epipaleolithic and Pre-Pottery Neolithic (PPN) groups that inhabited southwest Asia (33–36). Several scholars argue that, given the lack of consistency in the archaeological record, terms such as "PPNA" and "PPNB" cannot be used to define all the aceramic groups that

Significance

Recent studies show that cultivation of wild and domesticated plants was a protracted process that developed across southwest Asia. However, there have not been sufficient data to evaluate whether cereal cultivation and domestication developed in parallel in all the regions or at different times. Our findings indicate that cultivation of wild cereal forms during Pre-Pottery Neolithic A was common only in specific regions such as the southern-central Levant. Domesticated-type cereal chaff (>10%) is found in southern Syria around 10.7–10.2 ka Cal BP but appears around 400–1,000 y later in the other regions. Regionally diverse plant-based subsistence during the Pre-Pottery Neolithic could have contributed to (if not caused) chronological dissimilarities in the development of cereal cultivation and domestication in southwest Asia.

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[1]To whom correspondence should be addressed. Email: kch860@hum.ku.dk.

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inhabited southwest Asia, especially those located in the eastern Fertile Crescent (modern-day Turkey, Iran, and Iraq) (33, 36–41). Recent excavations in the eastern Fertile Crescent have revealed significant differences in terms of architecture (42–45), lithic industries (39, 41, 46), burial customs (36), and animal (47–50) and plant exploitation (51–53) in comparison with sites in the Levant. Because of these differences, the aceramic Neolithic groups of the eastern Fertile Crescent are often referred to as "sedentary hunter/herder-gatherer groups" as opposed to the farming societies of the Levantine area (36, 54).

We hypothesize that these socio-cultural and economic differences between PPN sites in southwest Asia are reflected in the plant-based subsistence, as already shown by some authors (14, 32, 51–53), and could have influenced the development of plant cultivation and domestication in southwest Asia. Because thus far cereals have provided the most reliable data for characterizing the process of plant domestication, the aim of this paper is to explore the regional timing for the cultivation of wild and domesticated cereals across southwest Asia. To do so, the available archaeobotanical evidence from PPNA (11.7–10.7 ka Cal BP) and PPNB (10.7–8.2 ka Cal BP) sites is considered. In addition, we provide data for cereal domestication in the southern-central Levant area. This paper contributes to the understanding of the origins of agriculture, exploring the regional timing for the two main developments that occurred before the emergence of agriculture: the cultivation of morphologically wild cereal species and their subsequent domestication.

Cereal Cultivation vs. Wild Plant Gathering During the PPNA

One precondition for the emergence of morphologically domesticated plants is the adoption of cultivation practices involving wild plant species. Wild cereal cultivation was identified in archaeological sites during the 1980s and 1990s (7, 55, 56) and since then has been demonstrated at several PPN sites (the available evidence is summarized in ref. 57). The identification of wild plant cultivation is based on (*i*) the presence of cultivated-type grains (distinguished by their morphology and size; *SI Text*) and the gradual increase in grain size over time (58), both of which are associated with husbandry activities such as tillage (21, 59, 60), and (*ii*) the presence in archaeological sites of weeds characteristic of cultivated fields (56, 61) (see refs. 9 and 10 for additional criteria for identifying the early cultivation of wild cereals). Despite the limitations of any archaeobotanical record (see ref. 62), we consider that the types of plants represented in archaeological sites (e.g., cereals, legumes, fruits and nuts, other wild plants) and their proportions provide insights into the plants on which prehistoric groups relied for their subsistence and therefore should be considered, along with the abovementioned characteristics, when evaluating the presence and importance of practices such as cereal cultivation.

Several studies have shown that predomestication cultivation practices emerged around 11.7–10.7 ka Cal BP (the PPNA period in the Levant) in regions such as the southern-central Levant (7–9, 63–65), the Euphrates area (10, 56, 58), and the Zagros in Iran (23). However, the numbers of sites with evidence of predomestication cultivation (i.e., combined presence of cultivated-type grains and weeds of cultivated crops, along with the predominance of cereals in the archaeobotanical assemblage) varies considerably from one region to another (Fig. 1, based on Tables S1 and S2). The largest number of sites providing evidence for this practice are found in the southern-central Levant. Here cereals (mainly wild barley, *Hordeum spontaneum*) outnumber all other types of plants (Table S2), indicating they were preferentially exploited over other plant resources (7–9, 63–65). The PPNA sites in the Euphrates also show the prevalent exploitation of cereals, which we believe indicates their importance in the plant-based subsistence economy (10, 56). However, evidence for the cultivation of wild cereals has been identified so far only at Jerf el Ahmar and comprises wild barley and two-grained einkorn/rye (*Triticum boeoticum*/*Secale*) (10). In the eastern Fertile Crescent (southeast Turkey, Iran, and Iraq), the archaeobotanical evidence indicates a completely different subsistence strategy based on the exploitation of legumes and other wild plants (Table S2) (23, 51–53, 66, 67). At Chogha Golan (phases X–XI dated to 11.5–10.6 ka Cal BP) small-seeded legumes predominate, and within the large-seeded grasses goatgrass (*Aegilops*) outnumbers all other species including wild barley and wheat (23). At the neighboring site of Sheikh-e Abad plant exploitation focused on taxa such as club-rush (*Scirpus*), small-seeded wild grasses, and legumes (67). At sites in northern Iraq such as M'lefaat and Qermez Dere, large-seeded legumes and small-seeded wild grasses were mainly exploited, whereas wild barley and wheat were found in considerably lower proportions (51, 52). Contemporary sites such as

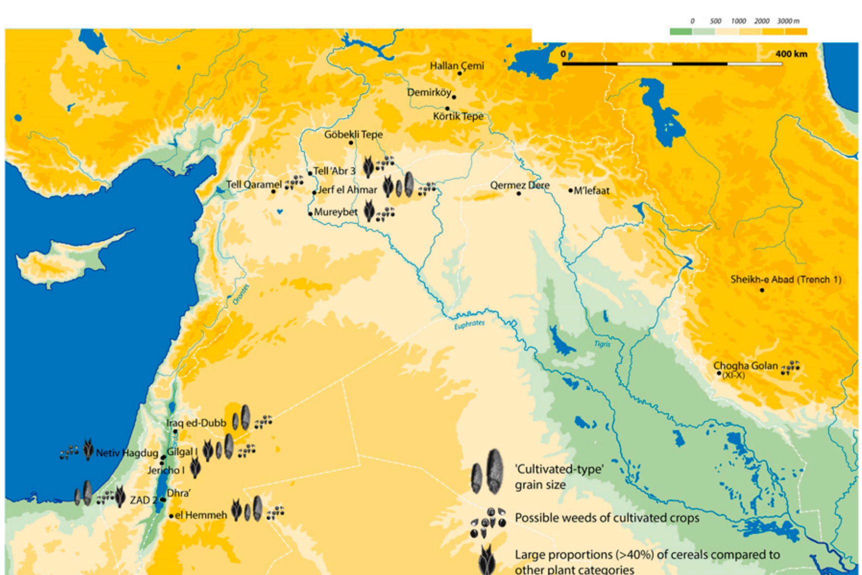

Fig. 1. Archaeological sites dated to 11.7–10.7 ka Cal BP (PPNA in the Levant) with published archaeobotanical evidence. Sites with combined presence of cultivated-type grains and arable flora, along with predominance of cereals over other plant categories, are considered to indicate wild cereal cultivation practices (based on Tables S1 and S2).

Hallan Çemi and Demirköy in southeast Turkey show the prevalence of wild plants of the Cyperaceae, Brassicaceae, Chenopodiaceae, and Polygonaceae family, but few barley and einkorn remains were found (52, 53). At the nearby site of Körtik Tepe, seeds of the wild relatives of domesticated plants account for less than 6% of the plant assemblage (66).

In accordance with the differences observed in the archaeological record between sites in the Levant and the eastern Fertile Crescent (33–50), the archaeobotanical evidence also highlights regional diversity in the plant-based subsistence around 11.7–10.7 ka Cal BP (PPNA in the Levant) (51–53). With few exceptions, wild cereals were the preferred type of plant exploited at sites in the southern-central Levant and the Euphrates area, and there is substantial evidence of cultivation at several sites. In the eastern Fertile Crescent, the plant-based subsistence focused instead on the exploitation of legumes and wild plants, with no clear evidence for wild cereal cultivation. The archaeobotanical data compiled in the last 30 y highlight the complexity of the subsistence strategies during this time, with cultivation of wild cereals being carried out only in specific locations (57).

Cultivation of Wild vs. Domesticated-Type Cereals During the PPNB

The domestication syndrome is defined as the set of features that differentiate domesticated crops from their wild ancestors (18, 21, 59). In grain crops, the domestication syndrome includes six major changes (21). Among these changes, the increased grain size and the loss of dispersal appendages (e.g., hairs and awns) represent evidence for semi-domestication, and the elimination or reduction of natural seed-dispersal mechanisms (e.g., nonshattering rachises) is regarded as the most reliable trait for the identification of morphologically domesticated cereals in archaeobotanical assemblages (68), that is, full domestication (21, but see ref. 19 for an alternative definition of plant domestication). Wild cereal species have brittle rachises with smooth scars (here referred to as "wild-type"), which enable the plant to shatter when ripe, thus shedding the grains. Domesticated cereal species, in contrast, are characterized by the presence of nonbrittle rachises with tough abscission scars (here referred to as "domesticated-type"). This trait hampers the natural reproduction of the plant (i.e., the spikelets remain attached to the ear and do not shatter spontaneously when mature), and they therefore require human intervention for their reproduction.

However, the occurrence of domesticated-type nonbrittle rachises in archaeological sites does not directly imply the exploitation of domesticated plant species. Observations in modern wild cereal stands indicate that genetically mutant plants that produce nonbrittle rachises are present in stands of morphologically wild species, at low proportions (one or two of every 2–4 million brittle-rachised plants) (19, 69). Additionally, in wild cereal species such as barley, around 10% of the basal rachises located in the lowest end of the ear produce domesticated-type scars (7). This evidence points out the need for detailed identification (i.e., wild- and domesticated-type, basal or nonbasal chaff) and quantification (i.e., examination of the proportions of wild- and domesticated-type scars) of the rachis remains to evaluate the development of domesticated cereals in archaeological sites.

The Evidence of Cereal Domestication at Tell Qarassa North

Tell Qarassa North (TQN) is a site located to the west of the Jebel el Arab region in southern Syria (Fig. 2), and eight radiocarbon dates from excavation area XYZ-67/68/69 indicate it was occupied during the EPPNB (Table S3) (70). Along with Tell Aswad in the Damascus Basin (71), TQN is one of only two sites in the southern-central Levant that provide a substantial archaeobotanical assemblage dated to this time period (72).

The cereal assemblage from TQN (area XYZ-67/68/69) comprises wild and domesticated-type species of emmer wheat (*T. dicoccoides/dicoccum*), one- and two-grained einkorn wheat (*T. boeoticum/monococcum/urartu*), and barley (*Hordeum spontaneum/vulgare*) (Fig. S1), which account for 56.8% of the assemblage (72). In the case of einkorn, the results indicate the predominance of two-grained forms [61.2% based on minimum number of individuals (MNI)] over one-grained ones (38.8% based on MNI) (72). The size ranges (i.e., breadth and thickness) of the wheat and barley grains are comparable to those observed in modern reference specimens from wild uncultivated and cultivated populations (the latter including wild and domesticated species) (*SI Text* and Table S4). Emmer, two-grained einkorn, and barley show a majority of cultivated-type specimens (>70.0%), whereas only 12.1% of the one-grained einkorn corresponds to cultivated-type grains. The final analysis of the rachis remains from TQN includes a total of 732

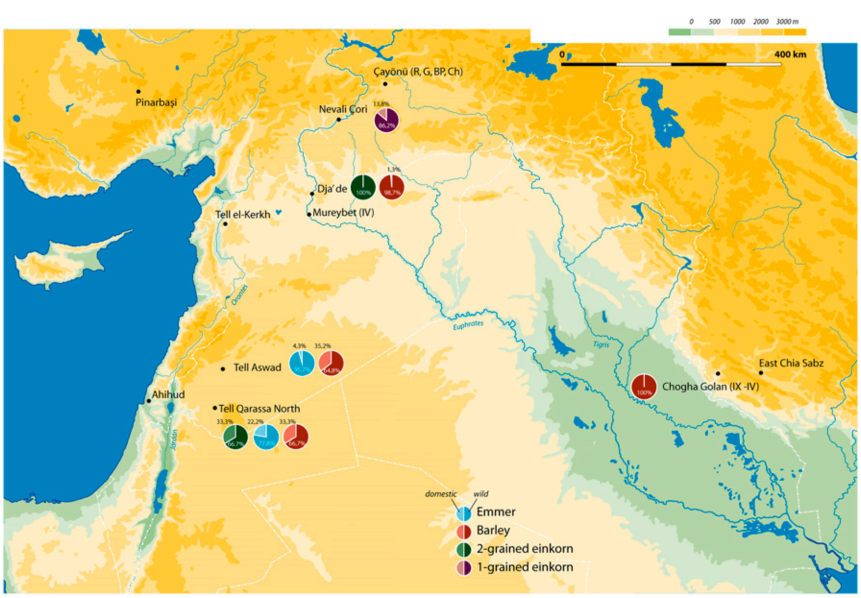

Fig. 2. Archaeological sites dated to 10.7–10.2 ka Cal BP (EPPNB in the Levant) with published archaeobotanical records. Sites where domesticated-type rachis scars comprise >10% of the assemblage are considered to represent evidence of incipient cereal domestication (based on Table S6).

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spikelet forks and rachis fragments (basal and nonbasal) from emmer, einkorn, and barley (Fig. S2). Of these, 305 could be identified as either wild-type or domesticated-type, but it was not possible to distinguish this trait on the remaining 427 remains (Table S5). Domesticated-type scars were identified on the emmer, einkorn, and barley chaff, and the proportions (21.1–41.2%) are larger than expected in wild cereal species (which is around 10%, as noted in ref. 7). The analysis on chaff remains identified to genus (i.e., *Triticum*) also shows large proportions of domesticated-type remains (35.8%).

On the basis of these results it can be concluded that by 10.7–10.2 ka Cal BP there are positive signs that barley, emmer, and einkorn were being cultivated at TQN (72) and that at least some of the remains of grains and/or chaff bear the characteristics of fully evolved domesticated specimens. The evidence of einkorn domestication at TQN probably involves two-grained einkorn species (i.e., *T. boeoticum thaoudar* or *T. urartu*). In terms of the numbers of grains, two-grained einkorn forms were predominant, and morphometric analyses suggested that, unlike the one-grained forms, they had characteristics similar to cultivated-type forms. The overall proportions of domesticated-type cereal chaff are <50% of the total sample for each of the three cereals and therefore indicate that the site represents an early stage in the process of cereal domestication. The presence of considerable proportions of uncultivated-type cereal grains suggests that at TQN, in addition to cultivation, cereals could have been gathered from wild stands.

The Regional Evidence for Cereal Domestication (Early/Middle Pre-Pottery Neolithic B)

The archaeobotanical evidence for the EPPNB period (10.7–10.2 ka Cal BP) indicates regional differences in the proportions of wild and domesticated-type cereals (Fig. 2). In southern Syria, there are clear signs of cultivation of domesticated-type barley at Tell Aswad (12) and of emmer, einkorn, and barley at TQN (i.e., the presence of *c.* 30% of domesticated-type cereal chaff). However, in the rest of contemporary sites domesticated-type chaff accounts for *c.* 10% or even less, indicating continued exploitation of morphologically wild species (10, 12, 23, 66, 67, 73–77). The evidence suggests that the pace with which morphologically domesticated cereals appeared during the EPPNB in southwest Asia varied regionally.

The lack of evidence for cereal domestication during the EPPNB on the Upper Euphrates, in southeast Turkey, and the Zagros is not surprising if we consider that the plant-based subsistence focused primarily on the exploitation of plants other than cereals (Table S2). In the Euphrates area, a change in the subsistence is found during this time. The widespread exploitation of cereals during the PPNA is replaced by the exploitation of lentils (*Lens*), pea/vetch/grass pea (*Pisum*/*Vicia*/*Lathyrus*), and small-seeded legumes as suggested by their predominance in the archaeobotanical assemblages (10, 76, 77). In southeast Turkey, archaeobotanical (73–75) and isotope (78, 79) evidence indicates that legumes such as lentil, bitter vetch (*Vicia ervilia*), and pea seem to have been consumed preferentially during the EPPNB. The importance of legumes in the subsistence is also shown at other contemporary sites such as Tell el-Kerkh in northwest Syria (80) and Ahihud in Israel (81), where domesticated-type chickpea and faba bean (*Vicia faba*) have been found. In the Zagros, continued exploitation of wild plants, including goatgrass and small-seeded wild grasses and legumes, is attested (23, 66). The presence of these particular species might be linked to caprine-management activities identified in the area (49), because goatgrass and small-seeded legumes are commonly regarded as fodder plants (82).

With the onset of the middle Pre-Pottery Neolithic B (MPPNB) in the Levant (10.2–9.5 ka Cal BP), domesticated-type cereal species (>10%) are identified in most of the regions across southwest Asia (Fig. 3, based on Table S6). In Turkey, the earliest evidence includes domesticated-type emmer, barley, and one-grained einkorn, which are found around 10.3–10.2 ka Cal BP in central Anatolia (83–85) and the southeast area (86). In the Euphrates and northwest Syria domesticated free-threshing wheat (*Triticum aestivum*/*durum*) is found *c.* 9.8–9.3 ka Cal BP (87), although there is no evidence for domesticated-type hulled cereals (barley in this case) until *c.* 9.3 ka Cal BP (12). In the Zagros, the earliest record for domesticated-type cereals found so far, *c.* 9.8 ka Cal BP, involves emmer (23). The spread of domesticated-type cereals is correlated with an overall increase in the presence of cereals as opposed to other plants in archaeobotanical assemblages, although exceptions exist (8, and see data in ref. 46). The information compiled so far indicates that cereals constituted 46.2% of the archaeobotanical assemblages at sites dated to 10.2–7.4 ka Cal BP, in comparison with the average of 22.4% found at sites dated to 13.8–10.2 ka Cal BP (based on ref. 46). However, the evidence suggests that there is not a directional change toward increased proportions of domesticated-type chaff, because these proportions are sometimes similar to or even lower than those seen during the EPPNB in southern Syria (*c.* 30%) (Figs. 2 and 3). That crops may have moved outside their natural area of distribution

Fig. 3. Archaeological sites dated to 10.2–8.3 ka Cal BP (M/LPPNB in the Levant) with published archaeobotanical evidence. Sites where domesticated-type rachis scars comprise >10% of the assemblage are considered to represent evidence of incipient cereal domestication (based on Table S6).

at different stages (i.e., wild, wild-cultivated, domesticated, or a mixture) and hybridized with local wild genetic lineages (24–27), as well as the continued exploitation of wild cereal stands, should be considered as possible explanations for the protracted establishment of domesticated cereals in southwest Asia.

Conclusions

Several studies have shown that strong socio-cultural differences existed among PPN groups in southwest Asia (33–54). This work shows that the plant-based subsistence strategies were regionally diverse during the PPNA and the EPPNB. Cereal exploitation was predominant in regions such as the southern-central Levant and the Euphrates, whereas in the eastern Fertile Crescent the exploitation of other plant resources predominated. Thus we must reconsider the importance that is often uncritically attributed to cereals when evaluating the plant-based subsistence strategies of the PPN and should emphasize the key role that other plant taxa, such as legumes and large-/medium-seeded wild grasses (e.g., goatgrass), played during this time.

The archaeobotanical evidence shows that some domesticated-type crops (e.g., einkorn, emmer, barley, faba bean) appeared in the southern-central Levant, and others (e.g., chickpea) occurred in other regions such as northwest Syria. This diversity indicates that plant domestication (in the broadest sense of the term) is a process that occurred in multiple regions across southwest Asia and cannot be linked with a single core area. For cereals such as wheat and barley, we propose that the domestication process was protracted (21, 30) and was regionally diverse in terms of timing. The results indicate chronological dissimilarities in the adoption of predomestication cultivation practices and in the emergence of domesticated species in various regions. However, we believe that in the regions where cereal exploitation was not common practice during the PPN, similar management processes involving different plant species could have existed. Studies that explore the cultivation and domestication processes of plants other than cereals will contribute to a more comprehensive understanding of the scale and nature of agriculture in southwest Asia.

Materials and Methods

Nonwoody plant macroremains from TQN were identified using the reference collection housed at the Institute of Archaeology, University College London. The identification of domesticated species was undertaken only in the case of chaff remains and was based on the presence of nonbrittle or tough rachises (Fig. S2) (12). The identification of domesticated emmer chaff (Fig. S2*A*) was based on ref. 88. The identification of cultivated- and uncultivated-type grains was based on grain size and morphology (*SI Text* and Fig. S1) (89). The raw data from TQN are presented in *SI Text* and Tables S4 and S5.

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