Identification of ancient starch grains from the tribe Triticeae in the North China Plain

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A B S T R A C T

Both macrofossil and microfossil plant remains from the grass family (Poaceae) have been recovered from Neolithic and historic sites in China. Basing our work on the plant taxa that were previously recovered, we analyzed the economically significant genera for modern starch grain analysis with a focus on the important tribe Triticeae. Modern starch grains from the tribe Triticeae were compared with those from other grasses, and criteria for identification were determined. In total, 38 species within 28 genera, 13 tribes and 4 subfamilies were selected for analysis. Results demonstrate that starch grains from members of the tribe Triticeae are discernible from those of other tribes by their distinctive lenticular morphologies and surfi cal pressure craters. A dichotomous key covering 10 species within 7 genera of the Triticeae was created, thus allowing identification of members of the tribe to the level of genus. Application of the dichotomous key to the ancient starch assemblage recovered from lithic tools excavated from the early Neolithic site of Donghulin demonstrates that plants from the genera Hordeum and Agropyron were exploited alongside millets at this site.

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1. Introduction

The grass family Poaceae is one of, if not the most, economically important plant families to modern humans, and the domestication of cereal crops by ancient humans is directly linked to the development of social complexity in several areas of the world. Consequently, seeds of grasses have received a great deal of attention from archaeobotanists who are interested in ancient starch research, the methods of which allow for the recovery of these important plant foods in contexts where macroremains may not survive. Starch grains from maize in the Americas (Holst et al., 2007), wheat-related grasses in Southwest Asia (Piperno et al., 2004) and millets in East Asia (Yang et al., 2012a) are among the most carefully studied groups of cereal crops, and researchers have focused on methods by which we can 1) distinguish starch grains of these crops from those of other plants, and 2) distinguish domesticated forms from wild types. Both these important goals have been reached in studies of starch grains from maize in Mesoamerica and millets in East Asia (Holst et al., 2007; Yang et al., 2012a). These studies add to what is already known about grass starches in the tribe Triticeae (e.g., Reichert, 1913), the group that includes barley, wheat and rye.

The morphological and physical characteristics of starch grains from modern, domesticated plants of wheat and barley as well as wild goat-grass are well described in the literature from both the food sciences and plant physiology (e.g. Geera et al., 2006; Ao and Jane, 2007; Stoddard and Sarker, 2000). Archaeobotanical investigators have built upon that foundation with studies that focus on diagnostic characteristics that are recognizable within ancient assemblages of starch grains. Piperno et al. (2004) analyzed 11 species of grasses classified within three genera of the Triticeae native to southwestern Asia when they studied the ancient starches from a slab at the site of Ohalo II (23–22ka cal yr BP) in Israel. Henry et al. (2011) analyzed and described 5 more members of the Triticeae, from 4 genera, to identify the starches recovered from dental calculus lodged within Neanderthal’s teeth (~46ka and ~36ka cal yr BP). While studying the use of wildrye (Elymus) in North America by ancient Native Americans, starch grains from 13 species within 4 genera were studied and described by Perry and Quigg (2011). These studies all focused on the plants native to North America and southwestern Asia.

Starch grains from the tribe Triticeae have recently been recovered from sites dating from the Late Paleolithic to Middle Neolithic in North China (Liu et al., 2011, 2013; Zhang et al., 2011;
Yang et al., 2012b), and the plants in this tribe occur alongside grasses from the Paniceae and millets during the origins and spreads of cereal agriculture in this region. The lack of detailed work on modern reference collections of species from this tribe in East Asia, however, has hampered the secure identification of these remains. For example, in total 72 starch grains recovered from lithic tools excavated from the Late Paleolithic site of Shizitan in North China were identified as Pooid grasses, possibly from the tribe Triticeae (Liu et al., 2011, 2013). The authors compared the ancient starches with 4 modern reference species, 3 of the genus Agropyron and one possibly from Elymus (Liu et al., 2011). Zhang et al. (2011) analyzed residues from eight slabs excavated from Peiliguan sites (older than 11,000 cal yr BP) in Central China, and found that almost one fourth of the starch assemblage was derived from members of the tribe Triticeae. In our previous study at the sites of Nanzhuangtou (older than 11,000 cal yr BP) and Donghulin (11.0–9.5 cal yr BP) in the North China Plain, numbers of identifiable starch grains from the Triticeae were second only to the millets in the assemblage (Yang et al., 2012b). As the data on these grasses accumulate, the need for secure identification increases. To address this gap in the literature, careful morphological studies of key members of the tribe Triticeae were undertaken.

Here we present an analysis of modern starch grains from both Triticeae that are both native to and introduced in China. The characteristics of these types are then compared with starches from other economically significant grasses in East Asia, and a dichotomous key is presented to provide archaeobotanists with a tool for genus and species-level identification. Finally, we employed the dichotomous key to identify the ancient starches previously recovered from the Donghulin site, demonstrating that plants within the genera Hordeum and Agropyron were likely exploited in early Neolithic North China.

2. Material and methods

Grasses classified within 28 tribes, 226 genera (seven endemic), and 1795 species (809 endemic) occur throughout China (Flora of China Online, 2013). For the purposes of this work, we focused on the economically significant species and their genera that have been previously recovered as both macrofossil and microfossil plant remains in both Neolithic and historic sites in China (Liu et al., 2008; Zhao, 2010). Members of the genera Oryza, Panicum, Setaria, Triticum, Hordeum, Digitaria, Sorghum, Coix and Eriochloa were exploited widely, so samples from these genera and their relatives, 38 species in total, covering 28 genera, 13 Tribes, and 4 subfamilies were selected for study (Table 1).

There are 175 species and 13 genera within the tribe Triticeae in China, including 95 endemic and 8 introduced species (Flora of China Online, 2013). More than 50% of these species are members of the genus Elymus, and they are typically used in modern times as forage plants. Chinese genera of known economic value include Triticum, Hordeum, Agropyron, Elymus, Elpingria and Leymus. Weeds and barley are the members of the first two genera, and members

<table>
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<th>Tribe</th>
<th>Genus</th>
<th>Species</th>
<th>Geographic origin</th>
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Notes: IM: Crop Gene Bank of Institute of Miliets, Hebei Provincial Academy of Agricultural Sciences; HUH: Harvard University Herbaria; IGG: Institute of Geology and Geophysics, Chinese Academy of Sciences. IGSNRR: Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences.
within the last four are used as forage plants by modern humans. Ten species from seven genera within the tribe Triticeae were examined here (Table 1), including modern, domesticated wheat and barley (Hordeum vulgare and H. vulgare var. coeleste) and rye (Secale cereale), the wild relatives of wheat, goat-grass (Aegilops tauschii and Aegilops speltoides), and four typical forage plants from Agropyron, Elymus and Leymus. Ae. speltoides is not present in China. The sample is from Caucasus for comparison.

The protocol for extraction of starch grains from seeds was undertaken according to Yang et al. (2012a). Depending on the size of seeds, one to three seeds were broken and placed in a new, sterile test tube with ultra-pure water for 12 h to soak. They were then gently crushed with clean, glass stirring rods to release the starches. The solution of water and starch was pipetted onto a clean glass slide, mounted in 10% glycerine and 90% ultra-pure water, and the cover glass was sealed with nail polish. The prepared slides from all samples were examined using compound light microscopy at a magnification of 400×. 100–200 starch grains from each sample were photographed and measured. Morphological characteristics of 100 grains were recorded.

Because all archaeological starches from the Triticeae were recovered from groundstone tools in East Asia, thus indicating processes of pounding or grinding, seeds of bread wheat (Triticum aestivum), barley (H. vulgare) and goat-grass (Ae. tauschii) were ground and pounded in ceramic mortars with pestles to create modern analogs for comparative purposes. Then the ultra-pure water was added to the mortar. The solution of water and starch was pipetted onto a slide, mounted, sealed and examined according to the above protocol.

Morphological features of the starch grains were examined for comparison, including overall grain shape, contour and surface features, position and form of the hilum and fissure, number and characteristics of pressure facets, presence or absence of demonstrable lamellae and mean maximum length averaged from the measurement of 100–150 starch grains.

3. Results

3.1. Starch grains from Poaceae

The starch grains from species within the grass family are typically, but not always, polyhedral (Fig. 1). Of the 38 studied species, 23 are characterized by simple, polyhedral starch grains, e.g. foxtail millet (Setaria italica) (Fig. 1-9), but compound starch grains occur in some species, e.g. naked oat (Avena nuda) (Fig. 1-37). Lenticular or discoidal starch grains occur in 11 of the studied species in the tribes Triticeae and Bromeae. The remaining 4 species contained spherical grains. The hila of starch grains from the studied grasses are centric with occasional fissures. The sizes range widely (Table 2), from a few microns to more than 40 μm in maximum length. The mean of starches from seeds of forage grasses are often less than 5 μm, while the mean of starch grains from rye is greater, up to 28.9 ± 13.3 μm (Table 2).

3.2. Starch grains from the tribe Triticeae

Starches that occur in the seeds of species within the tribe Triticeae typically have a bimodal assemblage with two distinct size classes, small and large (Lindeboom et al., 2004) (Fig. 2a, b). The small grains tend to be rather uniform in morphology when observed at a magnification of 400×. Previous studies demonstrate that these small grains are difficult to detect via compound light microscopy, are rarely diagnostic to taxa, and occur in many plant tissues (Moss, 1976; Czaja, 1978; Barton, 1991; Loy et al., 1992; Therin et al., 1997; Perry and Quigg, 2011). In contrast, the larger lenticular grains are recovered with regularity, and they possess unique diagnostic characteristics. The identification and differentiation of archaeological starches from this group, therefore, will necessarily depend upon the larger, lenticular grains (Piperno et al., 2004; Henry et al., 2011; Perry and Quigg, 2011). For these reasons, the large size class of starches was measured and studied for this investigation while the small class was disregarded.

Typical morphological characteristics of the starch grains from the tribe Triticeae are a lenticular or discoid shape, an olivary side view (Fig. 2c) and pressure craters on the surfaces of grains that appear as small depressions (Fig. 1-21). The mean maximum length of measurements of 10 species in this group ranges from 12.1 μm to 28.9 μm and the largest starch grain, with a maximum dimension of 45.2 μm, comes from rye. Viewed with a polarizing microscope, the starch grains show strong birefringence, with the extinction crosses appearing strongly black against a bright, white background. Some starch grains from the tribe Triticeae are unique in that the four bright white areas divided by the extinction cross change from brighter at the center of the grain, to dark, then brighter again at the edge (Fig. 2d).

3.3. Processing damage to starch grains from the tribe Triticeae

After pounding and grinding, intact starch grains from bread wheat, barley and goat-grass were observed in the assemblages, but damaged starches with newly visible lamellae were much more common (Fig. 3), and birefringence became reduced or was even absent (Fig. 3c, h). The damaged starch grains from these three species are similar in morphological characteristics to each other, but their large, lenticular shapes still effectively demonstrate that they are from the tribe Triticeae.

3.4. Further identification of starch grains from the Triticeae

The starch grains from the tribe Triticeae in our study are first divided into two groups according to size (Table 2). One is the “large group”, including the genera Triticum, Hordeum, Aegilops, Agropyron and Secale, whose mean size is typically larger than 20 μm, with the exception of barley. The other is the “small group”, including the genera Elymus and Leymus, whose mean size is less than 16 μm. The sizes of the starch grains of species within the large group overlap each other, and, because it has been demonstrated that size can vary between populations of grasses in this tribe, diagnostic starch grains in each taxon are securely identified using other morphological features (Table 2).

3.4.1. Starch grains from rye (Secale)

Starch grains that are larger than 20 μm make up 77.8% of the population. Diagnostic rye starch grains bear Y-shaped or stellate fissures through the hila, and they are sometimes surrounded by very faint concentric lamellae and delicate radiating lines (Fig. 4a). The craters on the surface often appear in reticulate patterns.

3.4.2. Starch grains from crested wheatgrass (Agropyron cristatum)

These starches are the second largest in size following rye, and grains larger than 20 μm make up 70.3% of the population. Diagnostic rye starch grains have Y-shaped or stellate fissures through the hila, and they are sometimes surrounded by very faint concentric lamellae and delicate radiating lines (Fig. 4a). The craters on the surface often appear in reticulate patterns.

3.4.3. Starch grains from goat-grass (Aegilops)

Two goatgrasses were studied, Ae. speltoides and Tausch’s goatgrass (Ae. tauschii). Ae. speltoides is often considered to be ancestral to emmer wheat (Triticum dicoccum). The diagnostic starch grains from this species have dense groups of craters in a
Fig. 1. Characteristic starch grains from the studied members of the family Poaceae, 1, Oryza sativa; 2, Oryza rufipogon; 3, Zizania caduciflora; 4, Sorghum bicolor; 5, Eriochloa villosa; 6, Echinochloa colona; 7, Panicum miliaceum; 8, Panicum bisulcatum; 9, Setaria italica; 10, Setaria Fabeli; 11, Setaria viridis; 12, Setaria pumila; 13, Setaria chondrachne; 14, Setaria parviflora; 15, Setaria plicata; 16, Digitaria sanguinalis; 17, Coix lacryma-jobi; 18, Elymus dahuricus; 19, Roegneria kamoji; 20, Leymus chinensis; 21, Triticum aestivum; 22, Hordeum vulgare; 23, Hordeum vulgare var. coeleste; 24, Aegilops tauschi; 25, Aegilops ssp. spelta; 26, Agropyron cristatum; 27, Secale cereal; 28, Bromus japonica; 29, Alopecurus aequalis; 30, Lolium perenne; 31, Milium effusum; 32, Milium effusum; 33, Melica scabrosa; 34, Poa annua; 35, Poa annua 36, Avena nuda; 37, Elymus coracana; 38, Elymus coracana. Scale bar, 1–16 and 28–38, 10 μm; others, 20 μm.
with those published by other authors. The large, discoidal grains among crop plants in the Triticeae, and our observations are in line with previous archaeobotanical studies (Piperno et al., 2004; Henry et al., 2011; Perry and Quigg, 2011). Of them, two species, *Hordeum spontaneum* and *Hordeum bulbosum*, are present in China. Starch grains from the previously studied seven species always measure less than 30 μm when lamellae are absent, which is similar to our samples of barley (*H. vulgare*) and naked barley (*H. vulgare* var. *coeleste*), where the largest grain measured 27.4 μm. Starch grains from naked barley are a little larger than barley, and 35.0% of the starch grains are larger than 20 μm; while 57.1% of starch grains from naked barley are larger than 20 μm. The granules from barley and naked barley often present as deformed, lenticular shapes in plan view including ellipses, subcircles, semicircles, rounded-corner triangles and others (Fig. 1-22 and 23, Fig. 4d). Some starches from both samples have faint craters in reticulate patterns on their surfaces. Lamellae are extremely rare to absent.

### 3.4.5. Starch grains from barley and naked barley (Hordeum)

Seven species within the genus *Hordeum* were examined in previous archaeobotanical studies (Piperno et al., 2004; Henry et al., 2011; Perry and Quigg, 2011). Of them, two species, *Hordeum spontaneum* and *Hordeum bulbosum*, are present in China. Starch grains from the previously studied seven species always measure less than 30 μm when lamellae are absent, which is similar to our samples of barley (*H. vulgare*) and naked barley (*H. vulgare* var. *coeleste*), where the largest grain measured 27.4 μm. Starch grains from naked barley are a little larger than barley, and 35.0% of the starch grains are larger than 20 μm; while 57.1% of starch grains from naked barley are larger than 20 μm. The granules from barley and naked barley often present as deformed, lenticular shapes in plan view including ellipses, subcircles, semicircles, rounded-corner triangles and others (Fig. 1-22 and 23, Fig. 4d). Some starches from both samples have faint craters in reticulate patterns on their surfaces. Lamellae are extremely rare to absent.

### 3.4.6. Starch grains from Leymus chinensis

Just 15.0% of starch grains from this species are larger than 20 μm. Starch grains are typically lenticular or deformed lenticular...

![Fig. 2](image2.png)

**Fig. 2.** Morphological features of starch grains from the tribe Triticeae, a, bimodal assemblage of starch grains from barley; b, bimodal assemblage of starch grains from *Leymus chinensis*; c, side view of starch grains from goat-grass, *Aegilops tauschii*; d, characteristic birefringence of starch grains from the Triticeae. Scale bar, 20 μm.

![Fig. 3](image3.png)

**Fig. 3.** Damaged starch grains from ground seeds. a, damaged starch grains from bread wheat; b–c, damaged starch grains from goat-grass (*Ae. tauschii*) under bright field and polarized light; d–g, damaged starch grains from barley; h, damaged starch grain under polarized light. Scale bar, 20 μm.
in morphology, and some granules have scattered, large craters on the surfaces (Fig. 4e and f). Lamellae are usually absent.

3.4.7. Starch grains from wild rye (Elymus)

Starches from seeds of 12 species of Elymus native to North America have been previously described (Reichert, 1913; Messner, 2008; Perry and Quigg, 2011). Perry and Quigg (2011) analyzed the crater (depression) patterns on the surfaces of starch grains and were able to use these criteria to identify archaeobotanical samples to species. Since no wild rye remains have been reported from archaeological sites in China, here we chose only two species, Elymus dahuricus and Elymus kamaoji, to study. The largest starch grain from seeds of these two species measures less than 20 μm. The craters of starch grains from E. dahuricus occur in reticulate patterns throughout the surface (Fig. 4g and h), while the craters on starch grains from E. kamaoji are rare or absent (Fig. 1-19).

3.4.8. Summary of findings

When size classes, fissuring and crater patterns are taken into consideration, starch assemblages with characteristics typical of Triticaceae in this study can be partitioned into taxonomic groups using the following dichotomous key.

1. No starch grains larger than 20 μm
2. Craters scattered
3. Less than 20% of starch grains larger than 20 μm, craters scattered
4. Less than 20% of starch grains larger than 20 μm
5. Less than 70% of starch grains larger than 20 μm
6. Craters reticulate
7. None of starch grains more than 30 μm, reticulate craters and deformed shapes common
8. Starch grains with well-defined lamellae, scattered craters
9. No lamellae or craters
10. Faint lamellae and reticulate craters
11. Starch grains with well-defined lamellae
12. Scattered craters
13. More than 70% of starch grains larger than 20 μm
14. Less than 50% of starch grains larger than 20 μm
15. More than 70% of starch grains larger than 20 μm
16. Craters reticulate
17. None of starch grains more than 30 μm, reticulate craters and deformed shapes common
18. Starch grains with stellate fissures, and faint concentric rings at the edge of granule
19. Starch grains lack stellate fissures

4. Discussions

4.1. Comparison the Triticaceae with other tribes within the Pooidae

Ten species from seven other tribes within the Pooidae were studied for comparison with the starches from the tribe Triticaceae. With the exception of Japanese brome (Bromus japonica) within the tribe Bromeeae, which overlaps somewhat with starch grains from members of the tribe Triticaceae, the other nine species differ significantly in that their starch grains are minute and are often present in compound forms (Fig. 1-29–37).

Perry and Quigg (2011) studied two species from the tribe Bromeeae, and found the sizes of their starch grains to be quite small. There are two genera, Bromus and Littelalea classified within this tribe of grasses in China. The members of the latter genus are forage plants that occur in the alpine meadow vegetation of Himalaya-Tibet. The type species of the genus Bromus, Japanese brome, was selected for study. As was observed in the species from the Americas, starch grains from Japanese brome have a bimodal morphological distribution. The large grains have a lenticular or deformed lenticular shape, the mean size is 13.2 ± 4.1 μm, and 10.9% of the starch grains are larger than 20 μm. These morphological features are similar to those of L. chinensis, but the two species are easily distinguishable from one another using other criteria. Faint concentric lamellae and a central cluster of craters occur on the surfaces of some starch grains from Japanese brome (Fig. 1-28), while the lamellae are absent and craters are scattered when they occur in L. chinensis. Thus, with a sufficient sample size that includes grains with cratering, the two cannot be confused.

4.2. The tribe Triticaceae in the archaeobotanical record

Our studies indicate that, given an adequate assemblage, starch grains from the tribe Triticaceae are identifiable to genus and species. As ancient starch assemblages from the tribe Triticaceae recovered from East Asia, and China in particular, are studied for identification, the following factors bear consideration.

For assemblages recovered in China, 1) the genera Triticum and Aegilops can at this time be excluded from sites that date earlier than 4500 years ago at which time current archaeobotanical data indicate the introduction of these cereal crops into China (Li et al., 2008; Flad et al., 2010). Future studies may alter this date. 2) The genus Secale can be eliminated from consideration in prehistoric sites due to the fact that the species was put into use much later than wheat (Zohary and Hopf, 2000). 3) Recent studies have confirmed the existence of Tibetan wild barleys, and the data suggest that the evolutionary split between the wild barleys in the Near East and those in Tibet occurred around 2.76 million years ago, with local barley being domesticated in Tibet and the surrounding area (Dai et al., 2012). Hordeum plants can be grown in cold and dry areas including Tibet, Qinghai, Sichuan, Inner Mongolia, Gansu and some areas of the North China Plain. After domestication, barley was cultivated in temperate areas. Therefore, plants of the genus Hordeum, both wild and domesticated, cannot be excluded from consideration.

Fig. 4. Characteristic starch grains from different species within the Triticaceae: a, Secale cereale; b and c, Agropyron cristatum; d, Hordeum vulgare var. coeleste; e and f, Leymus chinensis; g and h, Elymus dahuricus. Scale bar, 20 μm.
The following factors should be considered in both these and other contexts in which these taxa may occur. 4) Ancient starch residues recovered from grinding stone tools almost always exhibit damage. Our experiments grinding seeds demonstrate that damaged starch grains within three genera, Aegilops, Triticum and Hordeum, are not distinguishable from each other at the genus level. 5) Perry and Quigg (2011) noted that surface craters do not occur on every starch grain from any species of grass in the tribe Triticeae, and secure identifications may require larger assemblages of microfossils. Therefore, depending upon the size of the assemblage, and whether or not diagnostic grains are present, genus-level identifications may be more secure than species-level IDs. Investigators should note when diagnostic forms are present.

We applied these principles as we identified starches that were previously recovered from the early occupation (11,150–10,500 cal kyr BP) of the Donghulin site located at the edge of the North China Plain (Yang et al., 2012b). Of the 137 grains initially believed to be derived from grasses in the Triticeae, 78 starch grains from two lithic mullers can now be securely identified as derived from the Tribe Triticeae. Using the data derived from the new modern comparative studies, and with application of the dichotomous key, we are now able to make further identifications.

The majority of the residues recovered from the site, 54 of the 78 grains, bore damage consistent with grinding including exposed surface lamellae and weak or fragmentary birefringence (Fig. 5a–e). The other 26 starch grains, in contrast, were nearly to completely intact with relatively strong birefringence present (Fig. 5f–j). We classified this component of the assemblage as near-intact grains. Among these near-intact grains, two starch grains, measuring 30.1 μm and 30.6 μm in size, respectively, have concentric, equidistant lamellae occurring from the hilum to the edge of the grain, and craters are scattered on the surfaces of the grains (Fig. 5j). Both the size and the diagnostic morphological features are identical with those of modern starch grains from crested wheatgrass (A. cristatum).

The remaining 24 grains range from 12.6 to 29.4 μm in length, with a mean size of 23.1 ± 4.2 μm. The majority of these starch grains have a deformed lenticular shape that appears subcircular or semicircular in plan view. The craters on the surface occur in reticulate patterns on both intact and slightly damaged grains (Fig. 5a, b). The diagnostic morphological features are consistent with starch grains from Hordeum, but the mean size is a little larger than our modern samples, perhaps resulting from the grinding damage. Given that previous research has indicated that starch grains can vary in size according to environmental conditions (Nikuni, 1978; Haase and Plate, 1996; Oliverira et al., 1994; Lindeboom et al., 2004), and taking into consideration the fact that the key diagnostic characteristics are independent of size, we are quite secure in this identification.

The modern distributions of these two grasses span throughout the arid and semi-arid regions in North China where the climate is dry and warm through the summer and quite cold and harsh during the winter. Studies in both Greenland and China document a gradual increase in temperature beginning 15,000 cal yr BP, though the progression was interrupted by the Younger Dryas (Wang et al., 2001; Yuan et al., 2004). From ca. 11,000 cal yr BP to the early Holocene, the climate in the North China Plain was both dry and warm (Wen et al., 2010), and, thus, ideal for cultivation of these grasses. Thus, it is not surprising that Hordeum and Agropyron grasses were exploited alongside the staple millets in early prehistoric North China.

5. Conclusions

To better determine the role of grasses from the Triticeae in ancient China, modern starch grains from both local and a few exotic species were studied and compared with grasses from other taxonomic groups in the Poaceae. Our observations allowed us to develop criteria for the identification of residues from the Triticeae based upon their distinctive lenticular-shaped morphologies and diagnostic patterns of pressure craters on the surfaces. A dichotomous key applicable to 10 species within 7 genera demonstrates that members of the tribe Triticeae can be identified further to genus and even to the level of species. The application of the dichotomous key to the ancient starches recovered from the early Neolithic site of Donghulin demonstrates that Hordeum and Agropyron plants were exploited synchronously with millets during this key time in the domestication of cereal crops in the North China plain.

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