Diet of the earliest modern humans in East Asia

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Abstract

Reconstructing diet can offer an improved understanding of the origin and evolution of modern humans. However, the diet of early modern humans in East Asia is poorly understood. Starch analysis of dental calculus is harmless to precious fossil hominins and provides the most direct evidence of plant food sources in early modern human dietary records. In this paper, we examined starch grains in dental calculus from Fuyan Cave hominins in Daoxian (South China), which were the earliest modern humans in East Asia. Our results reveal the earliest direct evidence of a hominin diet made of acorns, roots, tubers, grass seeds, and other yet-unidentified plants in marine isotope stage 5 between 120–80 ka. Our study also provides the earliest evidence that acorns may have played an important role in subsistence strategies. There may have been a long-lasting tradition of using these plants during the Late Pleistocene in China. Plant foods would have been a plentiful source of carbohydrates that greatly increased energy availability to human tissues with high glucose demands, such as the brain, red blood cells, and developing fetuses. Furthermore, a variety of starch grains retrieved from dental calculus revealed that Fuyan cave hominins were able to consume a diet that fulfilled their physiological requirements in the late Middle and early Upper Pleistocene. Our study both provides the earliest direct dietary evidence from modern humans in China and helps elucidate the evolutionary advantages of early modern humans in the late Middle and early Upper Pleistocene.

1. Introduction

Scientific interest in the origin and evolution of modern humans has a long history. Since the emergence of *Homo erectus*, China has been an important area of human evolution, and East Asia is considered by some to be the birthplace of modern humans^{1,2}. Recent studies more clearly demonstrated details regarding the origin and evolution of modern humans. New fossils were found in Huanglong Cave in Hubei³, Zhiren Cave in Guangxi⁴, Panxian Dadong in Guizhou⁵, and at the Lingjing site in Henan⁶. Moreover, 47 human teeth dating back to more than 80 ka (with an inferred maximum age of 120 ka) were found in Fuyan Cave in Hunan⁷, which provided the earliest fossil evidence of modern people in South China. These findings indicated that fossil hominins with full early modern human morphology were present in South and Central China as early as 100 ka⁸.

Diet is key to understanding the origin and evolution of modern humans. Diet is a direct reflection of human adaptation and transformation of the natural environment. Much of human evolutionary success can be attributed to our ability to consume a wide range of foods⁹. Reconstructing paleolithic diets can offer an improved perspective on human adaptation and may help elucidate modern human dietary physiology.

Plants are an important dietary source for humans. Few macro-botanical remains have been found in Paleolithic sites. The study on the utilization of ancient human plant resources comes more from micro-botanical remains. However, plant residue from stones cannot accurately reflect the food sources of ancient humans. The research on the role of plant food in human evolution and survival is limited. Dental

calculus is made of calcium phosphate deposits on teeth that captures many food particles and therefore contains the dietary information of ancient humans. Analysis of early Paleolithic dental calculus is particularly valuable^{10,11}; it is both harmless to precious hominin fossils and the data recovered may be the only evidence of plant consumption. Starch grains sealed within the calculus can provide the most direct evidence of items ingested in the past¹².

Recently, the recovery of starch grains from dental calculus has become increasingly used for revealing diets of Neanderthals and early modern humans. On the basis of starch grain analysis, palms, beans, and grasses were found from Neanderthal dental calculus, which revealed a wide spectrum of plant foods sources¹³. Further analyses of plant derived diets were compared between Neanderthals and other early modern humans from several populations in Europe, the Near East, and Africa¹⁴. In East Asia, starch grain analysis studies at Zhuannian (~10.0 ka), Nanzhuangtou (>11.0 ka), and Shizitan (~28 ka) confirmed plant foods exploitation strategies by the last hunter–gatherers^{15–17}; however, these sites are all less than 30,000 years old and located in northern China. Research in East Asia has not been carried out for early modern humans older than 30 ka. Thus, this paper investigates starch grains on the dental calculus of human teeth dated 120–80 ka from Fuyan Cave in South China to provide important information for studying the emergence and dispersal of early modern humans in East Asia.

2. Methods

2.1 Fuyan Cave

Fuyan Cave is located in Tangbei Village, Daoxian County, Hunan Province, South China (E 111°28'49.2", N 25°39'02.7") (Fig. 1a). Fuyan Cave is a karst system that comprises several connected and stacked caves (Fig. 1b), and covers a total area of more than 3,000 m² (Fig. 1b). Three seasons of systematic excavation at Fuyan Cave in Daoxian were carried out between 2011 and 2013, and yielded 47 human teeth and an abundant fossil mammalian assemblage (Fig. 1d). The morphological and metric assessment of those teeth supports their unequivocal assignment to *Homo sapiens*⁷. U-series dating indicated that early modern humans most likely colonized the site in the late Middle and early Upper Pleistocene (ca. 120–80 ka); this is the earliest and soundest evidence of modern humans in South China⁷.

2.2 Starch grain extraction from dental calculus

Adhered soil and other particles on 47 human teeth from Fuyan Cave in Daoxian were cleaned with a soft tooth brush. Microwear and dental calculus were observed under a digital microscope (VHX-600) using the extended depth of focus (EDF) technology. Fifteen teeth had obvious calculus (Fig. 2), and a dental pick was used to scrape visible calculus following the non-destructive protocols outlined by Piperno and Henry^{18,19}. Calculus fragments were transferred into centrifuge tubes; 2 ml 10% HCl was then added and the tubes were left for several hours until there were no more bubbles. Then, distilled water was added and the solution was centrifuged at 3000 rpm for 10 min, the supernatant was removed and the residue

at the bottom was retained. This step was repeated three times. The samples were then mixed with 5% Calgon for 24 h. After two washes with distilled, a heavy liquid flotation with a dense solution of CsCl ($d=1.8\text{g/ml}$) was added to the sample to float the starch grains. After adding distilled water into the new centrifuge tube and centrifuging it at 3000 rpm for 10 min, the supernatant was pipetted and removed; this step was repeated a second time, and the remaining residue was kept for microscopic observation. The remaining sample was mounted in 1:2 glycerin/water on a slide and examined under polarized and transmitted light with a Nikon Eclipse LV100POL at 500 $\times$ magnification. Each starch grain was photographed, described, and counted, and the entire slide was examined. We observed and analyzed microwear under a digital microscope (VHX-600) using the extended depth of focus (EDF) technology. Published literature on diagnostic criteria for starch grains was consulted^{20–29}.

3. Results

A total of thirty-two starch grains were recovered from the dental calculus of thirteen Daoxian human teeth. In addition, two wood fragments with characteristic conifer tracheid fibers were identified in the dental calculus of two Daoxian human teeth (see Table S1 for detailed starch and wood fragments counts). The source of starch granules was detected by comparing the size, shape, presence, and prominence of lamellae; hilum morphology; formation characteristics; cross sections; cracks; and other surface features. Twenty-two starch grains could be assigned to four main types. The others could not be identified because of damage or a lack of diagnostic features. The morphological characteristics of identified starch types and wood fragments are described below.

Type 1. Thirteen starch granules consistent with acorns represented this type. The starch grains from acorns have different morphologies according to their species and genera^{22,23,30}. Seven starch granules of these were large (size range, 14.31–22.98 μm). As shown as Fig. 3a, b., the granule was oblong with rounded corners and a centric hilum with visible fissures. The length of the major axis was 20.1 μm , and the minor axis was 15.3 μm . The size and morphology of the starches matched those of *Castanopsis* spp.³¹. Starch grains from *Cyclobalanopsis* are semi-compound²³. Six larger single starch grains were also found that may have fallen off from compound starch grains. These starch grains (Fig. 3c–f) are consistent with *Cyclobalanopsis* spp.^{22,23}.

Type 2. Six starch granules of this type were found. One starch grain was nearly oval with an eccentric hilum and showed faint extinction crosses under a polarized microscope (Fig. 3g, h). This type of starch grain is possibly a root or tuber starch, as it exhibited an eccentric hilum^{28,29}. Two more starch granules were sub-spherical and displayed a distinctive dark central vacuole (Fig. 3i, j). The length of the major axis was about 11.3 μm , and that of the minor axis was about 8.6 μm . According to Tromp and Dudgeon (2015)²⁴, this type of starch grain possibly originated from roots and tubers. Three starch granules were polygonal with multiple extrusion surfaces. Under the polarized light the extinction arm was vertical (Fig. 3k, l). Those are similar to modern starch grains from roots of *Pueraria lobata*, *Amorphophallus* sp., with

characteristic pressure facets^{28,29}. Although it is difficult to identify these starches at the species level, the shapes suggest they might come from roots and tubers.

Type 3. This group contained nearly round starch grains in which an open and centric hilum, without any lamellae showing an extinction cross under the polarized light (Fig. 3m, n). These starch granules were larger; the lengths of the A axis were 16 and 18 μm and those of the B axis were 15.1 and 17 μm . On the basis of published records [25,26] we identify these grains as belonging to the tribe Triticeae, easily distinguishable from tribe Poaceae.

Type 4. One polygonal starch grain had a centric hilum, without any lamellae showing an extinction cross under the polarized light. The length of the major axis was 15.3 μm and that of the minor axis was 15.2 μm (Fig. 3o, p). Modern reference²⁶ revealed that starch grains with polygonal shapes usually come from the caryopsis of Poaceae.

Type 5. Ten starch granules were included into this type because they lacked any known diagnostic features from previously published starch morphology (Fig. 3q-x). Four starch granules were defined by having a shared unique shape and probably represented a single plant taxon (Fig. 3q-t). In addition, there were six starch granules (Fig. 3u-x) that may have experienced processing or cooking damage based on previously published characteristics^{32,33}.

In addition, two wood fragments with characteristic conifer tracheid fibers were identified in the dental calculus of Daoxian human teeth (Fig4a). Identifying features included tubular cells with parallel lines of small, regular, circular bordered pits that often display a 'cross' feature in cross polarized light (Fig. 4b, c and FigS1). The identifying features were very similar to those described in Hardy and Radini^{34,35}, which support that this evidence is indeed preserved in dental calculus. In one of Daoxian teeth (No.DX4) a coniferous calculus was found under a digital microscope (VHX-600) and showed a groove in the crown with numerous fine and parallel scratches (Fig4d-g).

4. Discussion

Despite the modest amount of starch grains found in the dental calculus samples, the results revealed direct evidence that early modern human ate acorns, roots, tubers, grass seeds, and other yet-unidentified plants as food in marine isotope stage 5 (MIS5) approximately 100 ka. Forty percent of the starch grains analyzed were from acorns. These findings show that acorns were potentially an abundant food resource. Acorns generally refer to the nuts of *Quercus*, *Lithocarpus*, *Castanopsis*, *Cyclobalanopsis*, and other plants of Fagaceae. Acorns today are widely distributed in China^{30,31}, including around Fuyan Cave. Exploitation of acorns as a carbohydrate source is well documented in prehistoric and recent times. Starch grains on grinding stones and pottery from numerous sites in China have been reported from the Upper Paleolithic to the Middle Neolithic^{17,23,30,36}.

Our study provides the earliest evidence that acorns may have played an important role in human subsistence strategies approximately 80 ka in late Paleolithic China. We also provide evidence that these plants have been exploited for a long time, and that humans started using this food resource earlier than previously estimated. Some species of acorns, such as *Castanopsis* and *Cyclobalanopsis*, constitute a particularly valuable nutritional source. These plants probably increased intake of vegetable fat and would likely have facilitated early modern humans' access to food energy. Modern humans also require a reliable source of glycemic carbohydrates to support the normal functioning of the brain, kidney medulla, red blood cells, and reproductive tissues³⁷. Under normal circumstances, a glucose requirement of approximately 170 g/day is met by a mixture of dietary carbohydrates³⁸. Roots and tubers are high in carbohydrates¹¹. Therefore, roots and tubers, as important food sources, are an important factor in early human body evolution. However, roots and tubers are perishable and difficult to preserve, and it is difficult to obtain their macro remains. In contrast, starch grains extracted from dental calculus are good direct evidence of root and tuber consumption^{18,21}. Starch granules of roots and tubers have been reported from numerous sites dating from the Paleolithic to the Neolithic^{28,29,39,40}.

Dioscorea starches have been found from grinding stones at the Shizitan site, which dates back to 28–18 ka^{15,16}. Our evidence indicates that humans in South China ate carbohydrates from roots and tubers, at least 80 ka. In particular, our findings greatly advance our understanding of the history of roots and tubers.

Triticeae plant remains were first found at the Shizitan site as far back as 28 ka¹⁶. Two Triticeae starch grains were also recovered from the dental calculus of human teeth from Fuyan Cave in Hunan, South China; although only two grains were recovered, this indicated that the use of Triticeae plants began at least 80 ka. In addition to Triticeae, possible seeds of other grasses were also found.

Our results showed that the earliest direct evidence for human use of these wild grass seeds for food in the MIS5 period was approximately 80 ka, which indicates a long-lasting tradition of using Triticeae plants for subsistence during the Late Pleistocene in China. These findings also suggest a very long history of Triticeae exploitation as part of broad-spectrum subsistence strategies prior to its domestication.

Humphrey et al. (2014)⁴¹ showed that high intake of starch plants (such as acorns) can lead to a certain degree of dental caries because frequent consumption of carbohydrates is a key factor in the initiation and progression of this disease. One early modern human in Daoxian had obvious dental caries (Fig2c) and starch grains from acorns such as *Castanopsis* spp. were also found in this individual's dental calculus (No.DX7). This occurrence of dental caries may have been related to the carbohydrates found in acorns.

Acorns have tannin and need to be processed before human consumption^{15,42}. It is worth mentioning that some starch grains displayed damage possibly caused by food processing. Food processing

technology seems to have developed much earlier than previously detected, and early modern humans in Daoxian may have had this technology 80 ka.

Coniferous fragments were also found in the dental calculus of two Daoxian human teeth 80 ka. Similar evidence was also found in the remains of pottery from the Kuahuqiao site (more than 8 ka) in China ²⁷ and in the dental calculus of a Neanderthal population from a 49,000-year-old site in Spain ³⁵. In addition to coniferous calculus (Fig4a-c) extracted from Daoxian teeth (No.DX4), a groove with numerous fine and parallel scratches was also found from the same tooth of its crown (Fig4d-g). The coniferous fragments (Fig4b, c) and parallel micro scratches in the groove (Fig4d-g) indicate that Daoxian humans habitually rubbed material between their teeth, similar to Neanderthals. Comparison of plant foods in the diets of Neanderthals and early modern humans from several populations in Europe, the Near East, Africa, and East Asia revealed that early modern humans similarly consumed a wide array of plant foods worldwide¹⁴. Early modern humans ate more plant foods, and some analyzed starch grains show evidence of cooking damage. The survival and adaptability of Neanderthals may not have been as successful as those of early modern humans. Neanderthals primarily consumed plant foods that required little processing. Our results further indicate that a broader dietary spectrum already existed in early modern humans by the MIS5 period in East Asia.

Our results support that consumption of increased amounts of starch may have provided a substantial evolutionary advantage for early modern humans in the late Middle and early Upper Pleistocene in East Asia because of the energy it supplied to their increasingly large brain and other glucose-dependent tissues.

5. Conclusions

We found acorns, roots and tubers, grass seeds, and other yet-unidentified starch grains from the dental calculus of Fuyan Cave hominins approximately 80 ka. This direct evidence indicates that these foods played important roles in subsistence of the earliest modern humans in East Asia. Our study provides evidence of starch grains from acorns in dental calculus dating back at least 80 ka in South China. Additionally, starch grains that likely represent Triticeae were also found; although few were found, we should not underestimate the potential importance of these foods as early as 80 ka in South China. The starch analysis of the earliest modern human dental calculus from Fuyan Cave documents diversity in plant food resources approximately 80 ka in the late Paleolithic China. Plant food is a rich source of carbohydrates, which greatly increase the availability of energy for human tissues with high glucose requirements and therefore provided an advantage for early modern human evolution. Indeed, our study both reveals novel information about the diet of early modern humans in late Paleolithic China and provides the earliest direct evidence for understanding the lifestyle of early modern humans in the late Middle and early Upper Pleistocene.

Declarations

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Author contributions: Y.W. designed research; Y.W., D.T., X.W., and W.L. performed research and analyzed data; Y.W. wrote the paper.

The authors declare no conflict of interest.

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Figures

Figure 1

Geographical location and stratigraphy of Fuyan Cave in Daoxian. A, Location of Fuyan Cave. B, Panoramic view of Fuyan Cave. C and D, Stratigraphic layers of region II of Fuyan Cave. All human fossils came from layer 2. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

Figure 2

Images showing deposition of dental calculus on Daoxian human teeth (Sample No. A, DX4. B, DX.2. C, DX13. E, DX6).

Figure 3

Microfossils of starch grains observed in the dental calculus of Daoxian human teeth. Scale, 20 µm.

Figure 4

Wood fragments with characteristic conifer tracheid fibers in the dental calculus and parallel micro scratches in the groove of Daoxian human teeth. A, No. DX4 human teeth; B, Bordered pits of tracheid under unpolarized light from dental calculus; C, bordered pits of tracheid and the 'cross' feature under polarized light from dental calculus. (Scale, 50 µm). D parallel micro scratches in the groove of teeth, E-G parallel micro scratches in Fig. 4D at magnification 50x, 200x (Scale, 250 µm).

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