

# Opal phytoliths found on the teeth of the extinct ape *Gigantopithecus blacki*: Implications for paleodietary studies

(paleoanthropology/paleoecology/Pleistocene/Asia/dietary reconstruction)

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**ABSTRACT** Identification of opal phytoliths bonded to the enamel surface of the teeth of *Gigantopithecus blacki* indicates that this extinct ape had a varied diet of grasses and fruits. By using the scanning electron microscope at magnifications of 2000–6000× specific opal phytoliths were observed and photographed on the fossilized teeth of an extinct species. Since opal phytoliths represent the inorganic remains of once-living plant cells, their documentation on the teeth of *Gigantopithecus* introduces a promising technique for the determination of diet in extinct mammalian species which should find numerous applications in the field of paleoanthropology as well as vertebrate paleontology.

Since the discovery of extinct species, the determination of diet from fossilized teeth has remained a contentious issue. Early paleontologists often drew dietary conclusions from dental cusp patterns, crown height, and overall shape after detailed comparisons with the teeth of living species. Recent studies have focused on more empirical methodologies such as measurement of enamel thickness (1–3), examination of enamel wear striae (4, 5), and the relationship of cusp size, shape, and angulation to biomechanical stresses encountered during mastication (6). All of these techniques share one central theme: the dietary preferences of extinct species are inferred by comparison and analogy with extant species.

An alternative technique based on the identification of opal phytoliths found bonded to the enamel surfaces of the teeth of extinct species allows for identification of the actual plant remains eaten by an animal prior to its death. Thus the vegetative dietary preferences of an extinct species no longer have to be inferred but can be demonstrated directly through the identification of phytoliths, the inorganic remains of plant cells, on the teeth of extinct species.

Opal phytoliths are created when hydrated silica dissolved in ground water is absorbed through the roots of a plant and carried throughout its vascular system. This silica may be precipitated in the lumina, cell walls, and intercellular spaces of any plant organ, although aerial structures, including leaves, fruits, and inflorescence bracts, tend to accumulate solid silica more frequently than do subterranean organs (7, 8). Recent studies have shown that plant families have a strong tendency either to accumulate or not to accumulate silica, and, contrary to traditional expectations, frequency of phytolith production is very high in dicotyledons and Pteridophytes as well as in monocotyledons (7). A marked constancy in both phytolith production and morphology has been demonstrated for many classes of phytoliths, indicating considerable genetic control over these attributes. Furthermore, it has also been shown that numerous woody and herbaceous plant species produce phytoliths identifiable to the familial and generic levels (7–11).

Phytoliths have been shown to have numerous applications in archaeology and paleoecology (7, 9–12). Baker *et al.* (13) showed in 1959 that phytoliths grind and abrade enamel surfaces of teeth. Using scanning electron microscopy, Walker *et al.* (14) demonstrated that it was possible to identify the specific microwear patterns on hyrax teeth produced by opaline phytolith abrasion. They showed that the dietary patterns of two sympatric species of hyrax (one browser and one grazer) could be linked to the consumption of different plant groups, resulting in diverse patterns of wear caused by phytolith abrasion. Finally, Armitage (15) was able to extract and identify opal phytoliths from food residues adhering to the teeth of ungulates from several historic sites in Britain.

The impetus for the present study resulted from a suggestion by one of us (R.G.T.) that the technique of phytolith analysis, useful for determining plant materials adhering to the cutting edges of Paleolithic stone tools, might also be applied to the teeth of the extinct Asian ape *Gigantopithecus blacki*, since this Pleistocene species had a dentition and jaw morphology which is consistent with a diet of hard fibrous vegetation. *Gigantopithecus* has always been an enigma for paleoanthropologists because its body size and weight almost certainly far exceed the range of any other primate, living or extinct (16–18), and it is the only known species of ape to have become extinct during the Pleistocene. Furthermore, its dental proportions, cheek tooth morphology, and robust jaws are unlike those of any extant primate and in some ways more closely resemble those of the giant panda (19–21), a species whose diet consists almost entirely of bamboo. Thus, *Gigantopithecus* was selected for this study because its specific diet was virtually unknown, although its dental morphology indicated a tough diet of plant species that most likely had a high phytolith content.

## MATERIALS AND METHODS

The four teeth of *Gigantopithecus blacki* analyzed in the study, an upper incisor, lower canine, lower premolar, and lower molar, were chosen to provide a representative selection of all areas of the tooth row. These specimens were borrowed from collections housed in the British Museum of Natural History in London and the Forschungsinstitut Senckenberg in Frankfurt. The British Museum specimen [unnumbered] is a partial lower molar collected at Liucheng Cave in Guangxi by Pei Wu-chung and donated to the British Museum in September 1958. The Liucheng Cave site, often referred to as “*Gigantopithecus* Cave,” has produced the largest sample of *G. blacki* fossils, consisting of three lower jaws and approximately 1000 isolated teeth (22). Fossils from this cave have recently been assigned an absolute age of one million years before present by amino acid racemization dating (23), which is consistent with relative dates determined by analysis of the fauna (38). From the Senckenberg Mu-

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Abbreviation: SEM, scanning electron microscope.

seum, three *Gigantopithecus* teeth were studied: an upper incisor [CA 764], a lower canine [CA 752], and a lower fourth premolar [CA 135]. These are part of a sample of 16 *G. blacki* teeth collected from apothecary shops throughout southern Asia in the 1930s by von Koenigswald (24). This sample includes the type specimen of *G. blacki* [CA 733] described in 1935 (25). Since these Chinese apothecary specimens were collected in the 1930s, they almost certainly are from cave localities other than Liucheng Cave, which was not discovered until 1956. Together, this collection of 17 teeth from the British and Senckenberg museums is the only existing sample of *Gigantopithecus* outside of museums in China and Vietnam.

The teeth of other extant and extinct mammalian species were also analyzed for the presence of phytoliths. This sample included the Chacma baboon, *Papio ursinus*; the giant panda, *Ailuropoda melanoleuca*; the red panda, *Ailurus fulgens*; the North American buffalo, *Bison bison*; and two fossil primates, *Sivapithecus darwini* from the middle Miocene site of Pasalar, Turkey, and *Theropithecus oswaldi* from the middle Pleistocene site of Kanjera in Kenya. Phytoliths observed on these specimens were unlike those described here for *Gigantopithecus*.

Before scanning electron microscope (SEM) analysis was conducted, all teeth in the study were cleaned to ensure that any phytoliths discovered had not become incidentally attached to the specimens after the fossilization process. First, the teeth were soaked in an Alconox solution for 24 hr. The second step involved soaking the teeth in a dilute solution of 3% (wt/wt) HCl for 2 hr to remove carbonate-bonded particles and any other residual surface materials. The teeth were then rinsed with distilled water and kept in a similarly cleaned container until SEM examination. Each *Gigantopithecus* tooth was mounted on a stub and blown clean with canned air immediately prior to examination. A Hitachi S-570 electron microscope equipped with a Kevex 8000 x-ray microanalysis

unit was used to study the specimens. Use of this particular model permitted examination of the fossil teeth without having to coat the specimens, since the teeth could be examined at low energies in the range of 5–10 kV. Because of the rare nature of these *Gigantopithecus* specimens, coating the teeth was not an option, since its subsequent removal could have damaged the enamel surfaces.

Whole tooth surfaces were scanned at low magnifications (60–500 $\times$ ). Most phytoliths first became visible in the range of 350 $\times$ . Higher magnifications (2000–6000 $\times$ ) were then used to enlarge and photograph the phytoliths so that diagnostic features could be recorded. Once phytoliths were located on a tooth surface, their positions were noted and it became possible to relocate these same phytoliths on subsequent days of observation. To establish that the structures we were observing were indeed phytoliths, we used x-ray microanalysis to determine the elemental composition of the structures and a silica dot map to pinpoint the structure on the *Gigantopithecus* tooth (see Fig. 1). Phytolith identifications are based on a comparative collection of phytoliths from over 1300 species of tropical plants (7, 8). This collection is oriented toward New World taxa but also included 19 species of plants native to China from three different families: the Moraceae, Ulmaceae, and Gramineae.

One important question is how opal phytoliths are able to adhere so securely to the enamel surfaces of fossil teeth. It appears that two mechanisms may be responsible: (i) Phytoliths become chemically bonded to the enamel in much the same way as they bond to the edges of stone tools used to process plant remains. It is thought that friction and moisture provide the basis for the phytolith chemical bond in stone tools (12, 26, 27). A similar process must also occur during the process of chewing. In some cases, it appeared that the phytoliths were impressed into the enamel surface of the tooth by repeated pressure during mastication and it could be observed that wear striations in the enamel had been made by

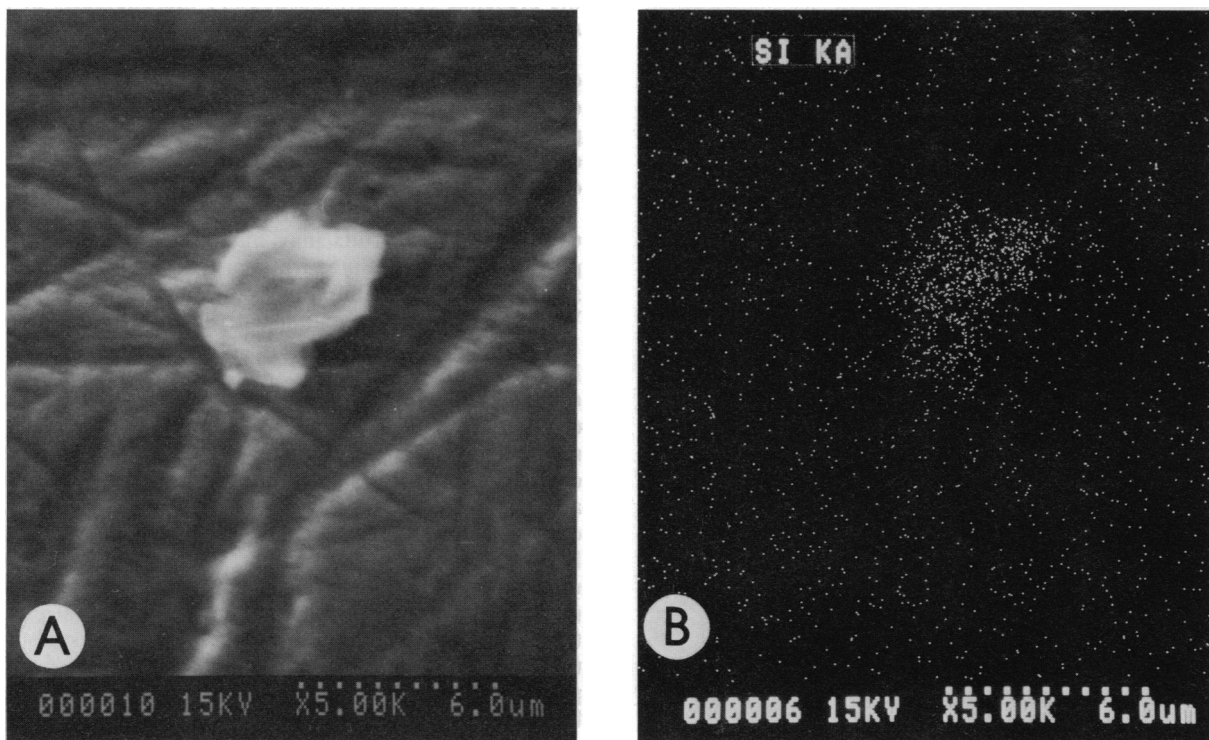


FIG. 1. Determination of the elemental composition of phytolith structure on a *G. blacki* molar. (A) Microphotograph of phytolith on *Gigantopithecus* molar. ( $\times 5000$ .) (B) Silicon dot map of same molar, showing location of phytolith. X-ray microanalysis of this image yielded calcium and phosphorus peaks reflecting the composition of the tooth itself and a silicon peak representing the phytolith impressed into the enamel surface. The scatter of dots outside the phytolith image is created by background radiation.

phytoliths, which were sometimes found sitting astride the tracks (Fig. 2). (ii) Phytoliths become lodged in the numerous depressions and fissures of the enamel surface of a tooth and remain on the surface over long periods of time. The careful cleaning of the fossil teeth prior to SEM analysis, the direct association of wear striations with phytoliths, and evidence for bonding all indicate that the phytoliths found on the teeth of *Gigantopithecus* were from plants consumed during the lifetime of the individual studied.

## RESULTS AND DISCUSSION

At least 30 structures that were indisputably phytoliths were found on two of the four teeth of *G. blacki* in this study, with the greatest concentration appearing on the British Museum molar. The phytoliths appear to derive from two distinct taxonomic groups and from different plant organs: (i) the vegetative parts of grasses and (ii) the fruits and seeds of dicotyledons. Fig. 3A shows a multicelled aggregate of fundamental (long) cell phytoliths from the British Museum molar. On the right side of the middle cell row of the group can be seen part of a prickle hair (28) on which the outline of the nucleus appears visible. Such a phytolith aggregate would derive from either a grass leaf or a culm, probably the former. In addition, on the same tooth a bulliform cell phytolith, also derived from grass leaves, was found (Fig. 3B). These two kinds of grass phytoliths are not identifiable below the family level and hence neither confirm nor deny bamboo consumption by *Gigantopithecus* as suggested previously (19–21).

The two identifiable kinds of grass phytoliths were accompanied by the presence of more numerous conical-to-hat-shaped silica bodies (Fig. 3C). They are small (3–9  $\mu\text{m}$  in diameter) and have a surface that appears to be layered in a series of concentric rings. Some possess a somewhat deco-

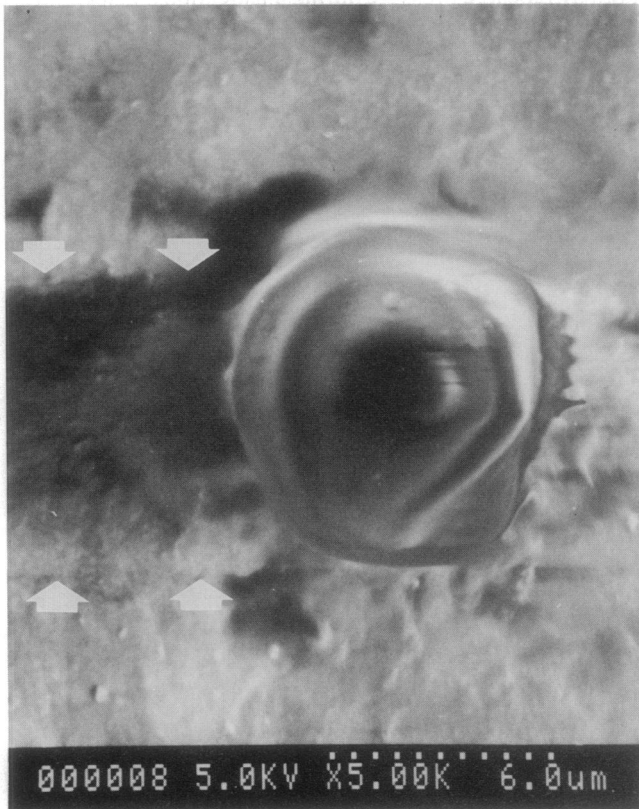


FIG. 2. Microphotograph of conical-to-hat-shaped opal phytolith from *G. blacki* molar. ( $\times 5000$ .) Note track in the enamel left by the phytolith abrading the enamel surface (see arrows).

rated crown (Fig. 3D). Conical-to-hat-shaped bodies occur in four families of the monocotyledons: the Cyperaceae, Gramineae, Palmae, and Marantaceae (7). However, the *Gigantopithecus* phytoliths bear little resemblance in structure and surface decoration of phytoliths of these taxa, all of whose various structures (leaves, fruits, inflorescences, roots) have been well studied (7, 8). We are, therefore, confident in ruling them out as contributing plant species.

Recently, conical phytoliths very similar to those found on the teeth of *Gigantopithecus* have been isolated from fruits of both the Old and New World members of the family Moraceae (8). The phytoliths are derived from hair cells, which occur on the epidermis of the fruit pericarp and seed. They are characterized by a surface layered in concentric rings and sometimes have decorated crowns. We now believe that the *Gigantopithecus* conical phytoliths are indeed from the fruits of a species in the Moraceae or a closely related family. It is expected that additional study of phytoliths from living plants known to have been indigenous to southern Asia in the Pleistocene will result in more precise identification. The phytoliths encountered on the CA 135 premolar were also of the same conical, dicotyledon fruit-type variety, showing that Pleistocene individuals of *G. blacki* sampled from different populations (fossil localities) were consuming the same plants.

Results from this study of phytoliths support the view that Pleistocene populations of *Gigantopithecus*, rather than being solely graminivorous, engaged in more opportunistic feeding strategies that included the consumption of fruits as well as other more varied plant material. Such a dietary pattern has traditionally been thought to be inconsistent with the massive jaw morphology that has been viewed as an adaptation to the specialized consumption of tough graminoid morsels. However, it should be emphasized that the leaves, seeds, and fruits of many nonherbaceous plants possess very high phytolith contents and would therefore compose a tough diet. One need not invoke graminivory alone to account for the presence of robust masticatory morphologies in *Gigantopithecus*.

The relative roles of grasses and fruits in the diet of *Gigantopithecus* are difficult to estimate. However, studies of the teeth of living primates with known diets should provide a reasonable test of the relationship and frequency of observable dental phytoliths to the quantities and proportions of plant remains consumed.

Judging from the present frequency of dental phytoliths in *Gigantopithecus*, fruits may have constituted a significant portion of the diet. Since fruits of the Moraceae have a high sugar content this finding supports earlier observations by Woo (22) that there is an unusually high rate of caries (nearly 11%) represented in the *G. blacki* teeth from Liucheng Cave. More recently, Zhang (29) examined the Liucheng sample of *Gigantopithecus* and reported that there was a high incidence of dental hypoplasia, especially in the second and third molars. This hypoplasia, visible as small uneven pits in the enamel surface or as shallow grooves extending transversely around the tooth, was also studied by one of us (R.L.C.) during a January 1990 examination of the Liucheng sample in Beijing. Zhang (29) concludes that this dental hypoplasia resulted from periodic shortages of food sources and from malnutrition. If bamboo did make up a significant portion of the diet of *Gigantopithecus* as has been suggested (19–21), then the periodic synchronous dieoff of bamboo species that produces environmental stress for the giant panda (30) could have been responsible for the high degree of hypoplasia observed in the Liucheng *Gigantopithecus* sample. However, it should also be noted that Neiburger (31) has recently pointed out that environmental stress is only one of many factors responsible for occurrence of enamel hypoplasia, so other explanations are also possible.

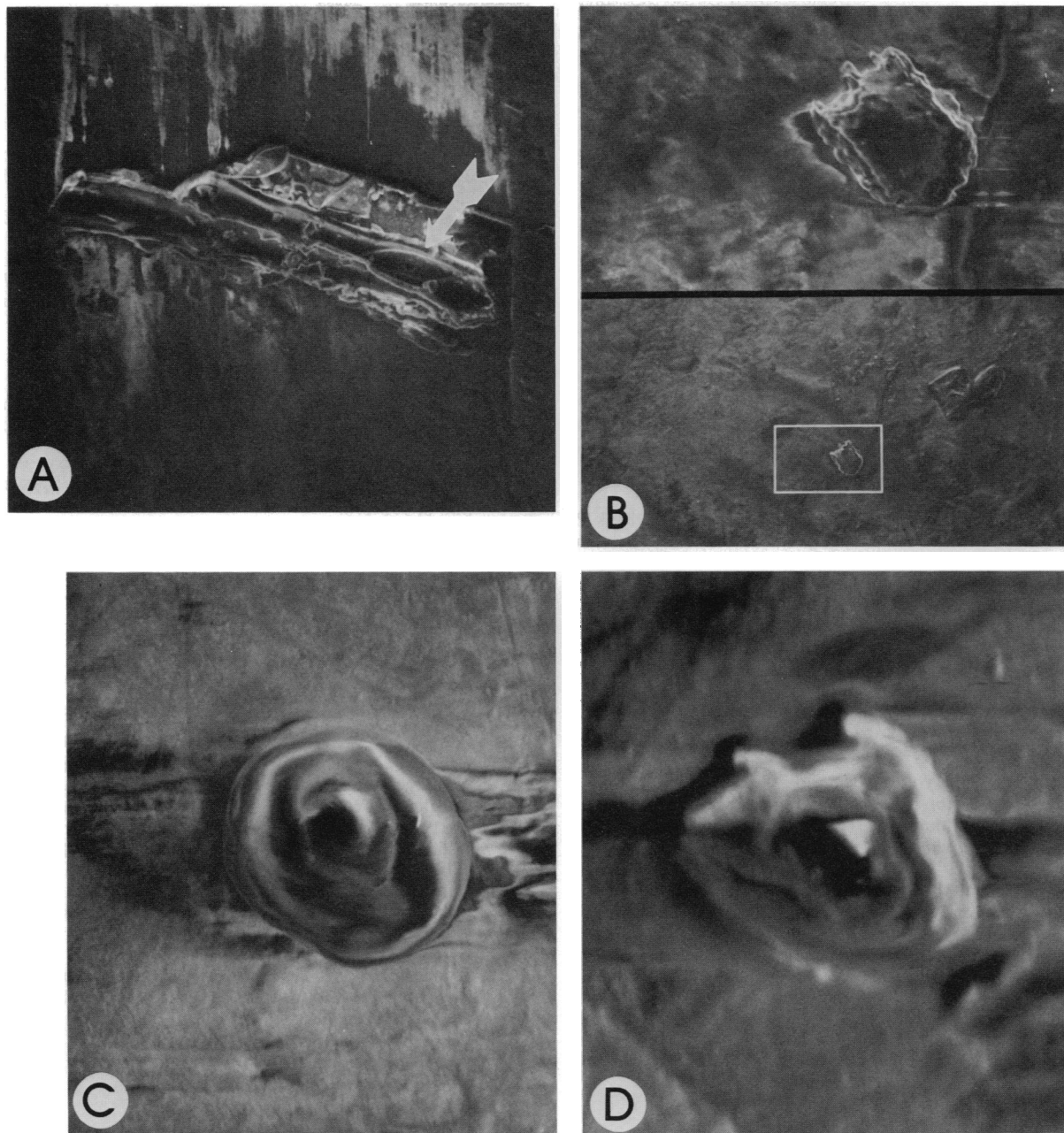


FIG. 3. Microphotographs of opal phytoliths from *Gigantopithecus*. (A) Multicelled aggregate of grass fundamental (long-cell) phytoliths. ( $\times 2000$ .) On the right edge of middle cell row note presence of prickle cell (arrow). (B) Grass bulliform cell phytolith. ( $\times 400$ ,  $\times 2000$ .) (C) Conical-to-hat-shaped phytolith. ( $\times 4000$ .) (D) Conical-to-hat-shaped phytolith. ( $\times 6000$ .) Note presence of somewhat decorated crowns in the two conical-to-hat-shaped phytoliths.

In a separate study of occlusal microwear patterns in *Gigantopithecus*, Daegling and Grine (32) observed microwear on its molars that was most similar to that seen in *Pan troglodytes*. The diet of the common chimpanzee is 60% fruit, 21% leaves, and the remainder variously made up of pith, social insects, and small mammals (17). Daegling and Grine (32) emphasize that neither the mandibular morphology nor the dental microwear observed in *Gigantopithecus* indicate a diet of hard items such as nuts and seeds. Such an adaptation to hard object feeding, which had originally been proposed for *Gigantopithecus*, was based, in part, on an incorrectly inferred open woodland/savanna paleoenvironment (16). The evidence now emerging is that *Gigantopithecus* was an eclectic feeder that concentrated on fruits as well as tough, fibrous vegetation. As White (19) has aptly noted, *Gigantopithecus* "seems to be adapted to a diet both high in

carbohydrates or starches, and requiring heavy mastication" (p. 231). Therefore, a mixed diet as suggested by the phytolith record is in agreement with other lines of evidence concerning the paleoecological adaptations of *Gigantopithecus*.

This phytolith record also invites a comment on the paleoenvironment of *G. blacki*. The presence of Moraceae-type phytoliths would suggest that the exploited habitats were subtropical to tropical forested settings, since this family does not occur in savanna or savanna/woodland habitats. The Moraceae are well known as important components of the Southeast Asian tropical forest ecosystem (33).

This study of dietary components of *G. blacki* based on phytolith analysis is quite preliminary. Many more of the >1000 known teeth of *Gigantopithecus* should also be analyzed. Unfortunately, these teeth are not presently available for SEM analysis, since they are housed in the Institute of

Vertebrate Paleontology and Paleoanthropology in Beijing, in various provincial museums throughout China, and in the Institute of Archaeology in Hanoi, Vietnam. These points aside, this study demonstrates the utility of a promising tool that should prove very useful for determining the paleoecological and paleodietary preferences of extinct species.

In the field of paleoanthropology it may now be possible to empirically test the australopithecine "dietary hypothesis" (34–36) through phytolith analysis of the teeth of *Australopithecus africanus* vs. *Paranthropus robustus* and *Paranthropus boisei*. With regard to Miocene hominoids it should also be possible to better delineate the dietary preferences of *Sivapithecus*, thought to have an "open country" adaptation and a diet of tough foodstuffs such as hard nuts or seeds (2) and to deal with the controversies surrounding the dietary preferences of the supposed forest-dwelling ape *Proconsul* (37). These are but a few of the applications to paleoanthropological issues which result from this initial demonstration of the existence and identifiability of opal phytoliths on the teeth of extinct species.

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