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Journal of Archaeological Science 34 (2007) 526–531

Journal of Archaeological SCIENCE

http://www.elsevier.com/locate/jas

Do silica phytoliths really wear mammalian teeth?

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Received 7 October 2005; received in revised form 10 May 2006; accepted 13 June 2006

Abstract

There is considerable literature suggesting that silica (opal) phytoliths cause dental enamel microwear in mammals. Much of this literature cites a single study from 1959 as evidence that silica phytoliths are harder than mammalian tooth enamel and so have the potential to cause dental microwear. No other studies using similar methodology have actually confirmed whether phytoliths are harder than dental enamel.

The hardness of silica phytoliths from four species of grass and mammalian tooth enamel from sheep was tested using a modern nanoindentation tool. We found that silica phytoliths are considerably softer (51−211 Vickers Hardness, HV) than tooth enamel (257−397 HV) and therefore must be re-evaluated as a major source of dental microwear.

The hardness results indicate that silica phytoliths do not contribute as much to mammalian dental microwear as previously reported and that exogenous grit and dust are a more likely cause. This premise has implications for interpretations of the causal agents of microwear phenomena in areas such as the evolution of high-crowned teeth in grazing mammals during the Miocene, and the inference of diet from fossilized mammal teeth as reported by some studies in physical anthropology and archaeology.
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Keywords: Silica phytoliths; Dental enamel; Abrasion; Microwear; Hardness; Nanoindentation

1. Introduction

Many plants absorb silica from soil solution as monosilicic acid (H_4SiO_4) and deposit it as hydrated amorphous silica ($SiO_2 \cdot H_2O$) either between the cell membrane and cell wall, as infillings of the cell lumen, or as extracellular secretions in various tissues [3,7,8,30]. These deposits, commonly referred to as opal or silica phytoliths, are found in many plant taxa but are most abundant and morphologically diverse in the monocotyledons, particularly the families Poaceae and Cyperaceae [32,34,42].

Many plants have silica phytoliths with morphologies unique to a particular family, subfamily or even genus, making them useful in taxonomic studies [29,33,42]. This feature, together with the longevity of phytoliths in the soil strata, have made them valuable in the disciplines of paleontology, archaeology and physical anthropology for a wide range of applications such as the reconstruction of past vegetation assemblages [40] or identifying specific plant usage by ancient human cultures [12,20−23]. One particular field where phytoliths have received considerable recent attention is the reconstruction of the mammalian paleodiet, including the human diet, based on their supposed influence on patterns of dental enamel microwear.

Dental microwear in mammalian grazers, in which the diet may consist exclusively of grasses, is often characterized by a high density of parallel linear striations [44]. These striations are often attributed to the abrasive action of silica phytoliths on the dental enamel during mastication of grasses [38,39,44]. By analogy, similar patterns of dental microwear in mammalian fossil teeth are also assumed to have diets with high grass and/or plant matter content. This interpretation is largely based on the assumption that silica phytoliths are harder than dental enamel and therefore readily abrade the

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0305-4403/$ - see front matter © 2006 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jas.2006.06.009

tooth surface, leading to the characteristic patterns of dental microwear.

The premise that silica phytoliths are harder than tooth enamel is widely accepted and often cited in physical anthropological literature. However, almost all citations refer to a single experiment on tooth wear in sheep conducted by Baker et al. [2]. Using a microhardness tester Baker et al. studied the hardness of silica phytoliths from oats (*Avena* sp.) and compared it with tooth enamel from sheep and inorganic opal. They showed that the silica phytoliths were harder than enamel, and therefore likely to cause abrasion and be a major cause of tooth wear in sheep. To date there have been no studies using similar methodology to independently verify Baker et al.'s reported hardness of silica phytoliths. Here we report the findings of a new study using a more sensitive hardness tester to accurately determine the hardness of silica phytoliths and mammalian teeth enamel.

2. Methods

We considered it extremely important to test phytoliths in the same physical and chemical condition as they would exist *in situ* in grass leaves. Indeed, it has been demonstrated that certain extraction treatments, such as dry-ashing, can alter the physical and chemical properties of plant silica [15]. Thus our extraction method of silica phytoliths avoids any chemical treatment or extreme physical conditions.

Silica phytoliths from four globally widespread species of grass (Poaceae), the pasture grasses *Paspalum dilatatum* and *Setaria viridis* (both subfamily Panicoideae, tribe Paniceae), and *Phragmites australis* and *Arundo donax* (both subfamily Arundinoideae, tribe Arundineae), were tested.

Fresh leaves of these species were scraped with a blade to produce fine tissue fragments which were then screened under a microscope for liberated silica phytoliths. As we found it impossible to completely liberate individual phytoliths from the leaves without chemical and/or extreme physical treatment, it was necessary to use phytolith chains with a minimal amount of cellular material still attached (Fig. 1). Selected phytolith chains were then removed and immediately mounted in transparent epoxy resin (Epofix© Struers) in a small mould. Using an automatic polisher, the mounted phytoliths were brought to the surface of the epoxy mould through a series of abrasives before being further polished flat with a 1 μm diamond suspension.

Fig. 1. Two phytoliths connected by strands of tissue from *Paspalum dilatatum*. Scale bar = 20 μm.

Three fragments of clean sheep teeth were mounted and polished in an identical fashion to that of the silica phytoliths. Care was taken to ensure that only the enamel was exposed and polished.

The polished phytoliths and teeth were then tested for hardness on an Ultra Micro Indentation System (UMIS©, CSIRO), fitted with a tri-faced Berkovich indenter (65.3°) using a maximum load of 5 mN. The UMIS system has a positional accuracy of 0.1 μm and can apply forces of <1 mN allowing for accurate control of indentation positioning and recording of indent depth. While the phytoliths were asymmetrically attached to a relatively thin strand of organic material, the bulk of each phytolith was tightly supported by the encasing resin. SEM analysis of the phytoliths after the indentation did not indicate any cavities or spaces between the phytolith and the resin.

Between four and eight replicate plants were tested per species and between one and six phytoliths indented per replicate plant. The number of phytoliths indented per replicate varied depending on the surface area of the phytoliths exposed from the polishing process and the spatial accuracy of each indent. A total of 81 indents were made on the silica phytoliths.

3. Results

The hardness of silica phytoliths from the four species of grass was found to range between 51 and 211 Vickers Hardness (HV, Table 1) and was considerably softer than the dental enamel of the sheep tested, which was shown to range between 293 and 357 HV. Our hardness values for silica phytoliths were considerably less than the hardness values of silica phytoliths measured by Baker et al. (590–610 Knoop Hardness (HK), equivalent to 579–598 HV). In contrast, our hardness values for the dental enamel of sheep were consistent with the hardness values of dental enamel measured by Baker et al. [2] (270–382 HK equivalent to 257–367 HV).

Only indentations well within the boundary of the phytolith are reported. Fig. 2 is an SEM micrograph showing a silica phytolith with a small triangular indent located in the front lobe, surrounded by four larger triangular indents that have impacted the adjacent epoxy resin.

4. Discussion

Our results indicate that the silica phytoliths of the four grass species tested are considerably softer than the dental

Table 1
Hardness values for silica phytoliths from four species of grass

	HV ± SE	HV_{max}	*n*
Paspalum dilatatum	96.8 ± 27.7	163.6	8 (18)
Setaria viridis	108.7 ± 47.4	179.5	5 (14)
Arundo donax	97.6 ± 30.1	211.2	6 (24)
Phragmites australis	51.1 ± 16.9	122.9	8 (25)

HV, Vickers hardness value; HV_{max}, maximum Vickers hardness value observed; *n*, number of individual plants with total number of indents on silica phytoliths per species in parentheses.

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