

A Review on Diagnostic Phytoliths for the Application in Paleovegetation Reconstruction and Environmental Archaeology in East Asia

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Abstract

Phytoliths are extensively utilized as an archaeobotanical indicator in paleovegetation reconstruction and environmental archaeology. Over the past two decades, numerous phytolith morphotypes, particularly those exhibiting diagnostic morphological features and over representative of source plants at the genus and species levels, were discovered and reported. These advancements have significantly contributed to phytolith-based vegetation reconstruction on different timescales, enhanced our understanding of prehistoric plant utilization, and elucidated cultivation and domestication processes of key crops in ancient agriculture. However, there are still inconsistencies and misunderstandings regarding the morphological characteristics of diagnostic phytoliths in various plant groups. This review highlighted the standardization in the classification and description of phytolith morphotypes, and summarized the advancements in phytolith morphology research over the past two decades. Morphological illustrations of diagnostic phytoliths from various plant groups, particularly key crops and their relatives from dryland and rice agriculture in East Asia, were presented as references for phytolith identification and application. Finally, this review proposes future directions for phytolith morphological studies, emphasizing the comprehensive consideration of anatomical structure and morphometric parameters, as well as the need for extensive research on modern plant phytoliths and control experiments on phytolith growth.

Keywords

Diagnostic Phytolith, Paleovegetation Reconstruction, Environmental Archaeology

1. Introduction

Phytoliths are amorphous silica gel concretions (opal) formed in the cells and intercellular spaces of plant tissues such as stems, leaves, seeds and fruits [1] [2]. Their grain size is mostly around 20 - 200 μm , with a large specific gravity of 2.1 - 2.3 [2]. Phytoliths have characteristics of corrosion resistance and *in-situ* deposition [2]. Phytoliths can directly inherit the morphology of source plant cells (e.g., epidermal cell, bulliform cell, hair cell) and intercellular spaces. Consequently, they have strong taxonomic significance for identification of source plant groups [1]. In some cases, phytolith types of diagnostic features can be classified into plant genera or even species [1] [2] [3] [4] [5]. Therefore, phytoliths are widely utilized to reconstruct paleovegetation changes [6] [7] [8] [9], early plant use in the Neolithic and Paleolithic Periods [1] [10] [11] [12] [13], prehistoric crop cultivation and domestication [14] [15] [16] [17], plant diet of ancient animal [18], ^{14}C dating in the Late Quaternary [19] [20], and estimation of carbon sink potential [21] [22], etc.

Phytolith morphology research is an important basis for application of phytolith analysis [1]. Up to now, there are about 260 types of phytolith morphological types that can be distinguished by their morphological characteristics, among which about 110 types come from grasses, and more than 50 types from angiosperm woody taxa and ferns [23]. Generally, common phytolith morphotypes are those widely existing in plants of different taxonomic groups, such as Rodel and Acute [1] [2]. Diagnostic phytolith morphotypes are those with specific features and over representative of source families, genera or species [24], such as Saddle of Bambusoideae [25], *Stipa* Bilobate [26], Saddle of Chloridoideae [27], Spheroid echinate of Arecaceae [28], as well as those with unique features from some key crops and their relatives (e.g., millets crops [5], wild and cultivated rice [29]) in ancient dryland and rice agriculture that have been intensively studied in East Asia [3] [4] [5] [12] [29]-[35]. Along with the development of phytolith analysis, the standardization of phytolith morphology nomenclature and description became increasingly important. In 2005, the International Phytolith Society (IPS) guided the release of the first version of the International Code for Phytolith Nomenclature (ICPN 1.0) [24], which made a primary attempt to standardize phytolith nomenclature and terminology [36] [37]. And then, the International Committee for Phytolith Taxonomy officially released the second version ICPN 2.0 in the year 2019 [38].

In the last 20 years, numerous phytolith morphotypes from various plant taxa have been reported, based on a large number of modern phytolith investigations [3] [5] [25]-[35] [39]-[46]. However, there are still great inconsistency in the naming and classification of phytolith morphology, and difficulties and disagreements in the identification of diagnostic phytolith morphotypes [24] [36]. This review briefly outlines the updated scheme in the ICPN 2.0, and presents illustrative plates of diagnostic phytolith morphotypes, particularly focusing on those in East Asia. The aims of this review are to provide illustrated material for

identification and application of diagnostic phytolith morphotypes in vegetation reconstruction and environmental archaeology.

2. Progress in Phytolith Nomenclature Scheme

The standardization of morphotype nomenclature and description for phytoliths plays an important role in phytolith research [38]. The ICPN 1.0 suggested that the nomenclature of phytolith types should follow the sequence of shape (three- and two-dimensional descriptor), texture and/or ornamentation, and anatomical origin, and use standard morphological descriptors [24]. Subsequently, ICPN 2.0 revised phytolith nomenclature and morphological description [38]. The ICPN 2.0 scheme specifies 7 principles for the morphological nomenclature of phytolith types in detail, including unique and concise phytolith naming, hierarchical naming order from taxonomic to anatomical to morphological (with an exception of short cell phytoliths from grass), using standard descriptors in the given glossary, use of combined name for closely related morphotypes, capitalizing only the first descriptor, an unique code for each morphotype, and rationale for a new name or retained one [38].

Here, comparison of ICPN schemes and former used names were made for reference (Table 1). Following the above guidelines, ICPN 2.0 scheme retained names with clear and unique characteristics, such as Papillate, Saddle, Bilobate, Polylobate, Cross, Rondel and so on [24] [38]. Phytolith types that were difficult to distinguish by morphological characteristics, should be classified according to the principles [38]. For example, Spheroid phytoliths could be divided into Spheroid psilate, Spheroid echinate and Spheroid ornate [38]. Elongate long cells could be classified into Elongate entire, Elongate sinuate, Elongate dentate and Elongate dendritic [38]. Those of bulliform cells could be divided into Blocky and Bulliform flabellate (referring to curved edge on one side) [38]. Some morphotypes with similar feature under the microscope and few taxonomic significance were merged. For example, Acicular hair cells and Unciform hair cells were combined into Acute bulbosus [38].

Compared with former schemes, the description glossary of shape, texture and ornamentation were revised in the ICPN 2.0 [38]. For example, the changes in shape descriptors included new descriptors of amoeboid (*i.e.*, an irregular plate shape with several small rounded projections), bulbous and prismatic, and substitution of globular with spheroidal and fan-shaped with flabellate, and combination of descriptors lanceolate and unciform, and so on [38]. Terms of velloate and dentate were added into the margin descriptors [38]. Besides, ICPN 2.0 classified meanings of rugulate into descriptors plicate and rugose, and combined cavate and lacunose into descriptor scrobiculate [38].

3. Typical Illustrations of Diagnostic Phytoliths

Based on a wide range of investigations on modern phytolith morphology, many advances were achieved in phytolith morphotypes, particularly in the field of

Table 1. Comparison of different schemes for phytolith naming.

ICPN 2.0 [38]	Code [38]	ICPN 1.0 [24]	Former name [1] [2] [24]
Spheroid psilate	SPH_PSI	Globular psilate	Spherical smooth
Spheroid echinate	SPH_ECH	Globular echinate	Spherical crenate
Spheroid ornate	SPH_ORN	Globular granulate	Spherical rugose
Acute bulbosus	ACU_BUL	Acicular hair cell/Unciform hair cell	Point-shaped
Blocky	BLO	Parallelepipedal bulliform	Bulliform/Square/Rectangle
Bulliform flabellate	BUL_FLA	Cuneiform bulliform cell	Bulliform/Fan-shaped
Elongate entire	ELO_ENT	Elongate psilate	Smooth elongate
Elongate sinuate	ELO_SIN	/	/
Elongate dentate	ELO_DET	Elongate echinate long cell	Elongate spiny/Elongate sinuous
Elongate dendritic	ELO_DEN	Dendritic/Dentritic	Dendriform
Papillate	PAP	Papillate	Papillate
Stomata	STO	Stomata	Stomata
Tracheary	TRA	Cylindric sulcate tracheid	Tracheid
Saddle	SAD	Saddle	Saddle
Bilobate	BIL	Bilobate short cell	Dumbbell/Bilobate
Polylobate	POL	Cylindrical polylobate	Polylobate/Multilobate
Cross	CRO	Cross	Cross
Crenate	CRE	Trapeziform polylobate /Trapeziform sinuate	Wavy trapezoid/Tooth
Rondel	RON	Rondel	Hat-shaped/Tower-shaped
Trapezoid	TRZ	Trapeziform short cell	/

diagnostic phytolith morphotypes and their taxonomic significance of different plant groups [1] [2] [3] [4] [5] [25]-[35] [39]-[47]. However, there are still some confusions in the definition and description of diagnostic phytolith morphotypes [40] [47]. Here, research progress and typical morphological illustrations of diagnostic phytolith morphotypes in the past 20 years were sorted out, focusing on the region of East Asia. The following naming and description of phytoliths refer to the ICPN 2.0 [38].

3.1. Diagnostic Phytoliths in Grasses

Compared with traditional palaeoecological indicators such as pollen and spores, the herbaceous diagnostic phytolith morphotypes have more explicit representations for many plant groups, particularly for those in Poaceae including Bambusoideae, Oryzoideae, Arundiacae, Chloridoideae and Panicoideae, and Cyperaceae [48], etc. This advantage of herbaceous phytoliths has been widely applied to the reconstruction of grassland vegetation, and recovered details about the changes in vegetation composition and plant diversity of grassland at different geological time scales [6] [8].

Phytolith types from Bambusoideae included Saddle, Bulliform flabellate, Blocky, Rondel, Stomata, Acute bulbosus, Tracheary, etc., among which Saddle (length/width ratio > 1) (**Figure 1(a)**) and Bulliform flabellate (clavate margin) (**Figure 1(b)**) were diagnostic morphotypes of Bambusoideae [2] [25]. Phytoliths from Oryzoideae included Bilobate, Bulliform flabellate, Rodel, Elongate sinuate, Acute bulbosus, Double-peaked glume, etc., among which Bulliform flabellate with scale-decoration (**Figure 1(c)**) and Double-peaked glume (**Figure 1(d)**) were diagnostic morphotypes [31] [49]-[53]. Phytolith from Arundiaceae included Saddle, Bulliform flabellate, Elongate sinuate, Trapezoid, Acute bulbosus, etc., among which Saddle (length/width ratio \approx 1) (**Figure 1(e)**) and Bulliform flabellate (shield margin) (**Figure 1(f)**) were diagnostic [2] [27] [41]. Phytoliths from plants of Chloridoideae included Saddle, Bilobate, Elongate sinuate, Acute bulbosus, Bulliform flabellate, Tracheary, etc., among which Saddle with a length/width ratio < 1 (**Figure 1(g)**) was the diagnostic morphotype [2] [21]. Phytolith from Pooideae included Bilobate, Elongate dentate, Rodel, Acute bulbosus, blocky, Tracheary, etc., among which Bilobate trapeziform (**Figure 1(h)**) and Elongate dentate (**Figure 1(i)**) were diagnostic morphotypes [2] [26]. Phytolith from Panicoideae included Bilobate (including Cross), Polylobate, Blocky, Elongate sinuate/Elongate dendritic, Bulliform flabellate, Rodel, Acute bulbosus, Tracheary, etc., among which Bilobate (**Figure 1(j)**), Polylobate (**Figure 1(k)**) [2] [54] and Elongate sinuate of lemma (**Figure 1(l)**) [3] [4] [5] were diagnostic morphotypes. Cyperaceae phytoliths included Polygonal granulate (**Figure 1(m)**), Papillate (**Figure 1(n)**), Acute bulbosus, Elongate, Stomata, Tracheary, etc., among which the first two were the diagnostic morphotypes [2] [42] [55]. In addition, there were some other phytolith producers in herbaceous plants (e.g., Zingiberaceae [39], Commelinaceae [56]).

3.2. Diagnostic Phytoliths in Woody Plants and Ferns

In recent years, phytolith morphological studies of woody plants have gradually established diagnostic phytolith morphotypes for the groups of broadleaved trees and conifer trees, which exhibit significant potential in the reconstruction of forest and woodland environment [28] [40] [44] [46] [47]. It was found that phytolith types in broadleaved trees included Stomata stellate, Elongate brachiate geniculate, Irregular sinuate, Polygonal tabular, Trichome irregular tubercule, Trichome bulbous irregular, Elongate facetate, Tracheary annulate/facetate geniculate, Tracheary annulate/facetate claviform, Tracheary helical, Spheroid favose, Elongate entire, Spheroid hollow, Irregular articulated granulate and so on [44]. Among these types, Elongate brachiate geniculate (**Figure 2(a)**), Polygonal tabular (**Figure 2(b)**), Elongate facetate (**Figure 2(c)**), Tracheary annulate/facetate claviform (**Figure 2(d)**) and Tracheary annulate/facetate geniculate (**Figure 2(e)**) could be used as diagnostic phytolith morphotypes for broadleaved trees [44]. Besides, Spheroid echinate (**Figure 2(f)**) was a diagnostic phytolith morphotype for Arecaceae [28] [39] [46], whose diameter (6 - 25 μm) could be used

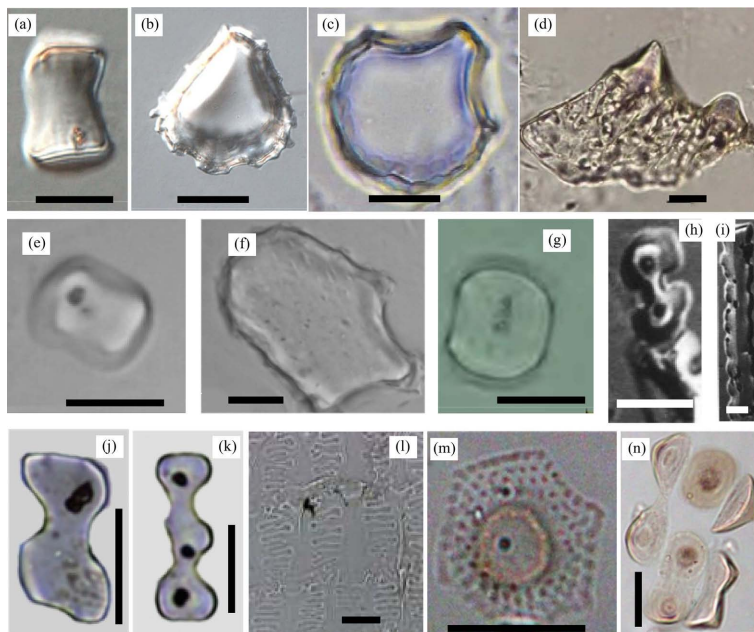


Figure 1. Illustrations of diagnostic phytolith morphotypes from grasses. (a) Bambusoideae Saddle [25], (b) Bulliform flabellate clavate [25], (c) Bulliform flabellate with scale-decoration [43], (d) Double-peaked glume [53], (e) Arundinaceae Saddle [41], (f) Bulliform flabellate [41] (g) Chloridoideae Saddle [27], (h) Bilobate trapeziform [26], (i) Elongate dentate [26], (j) Bilobate [23], (k) Polylobate [23], (l) lemma Elongate dendritic [5], (m) Polygonal granulate [55], (n) Papillate [55]. Scale = 10 μm .

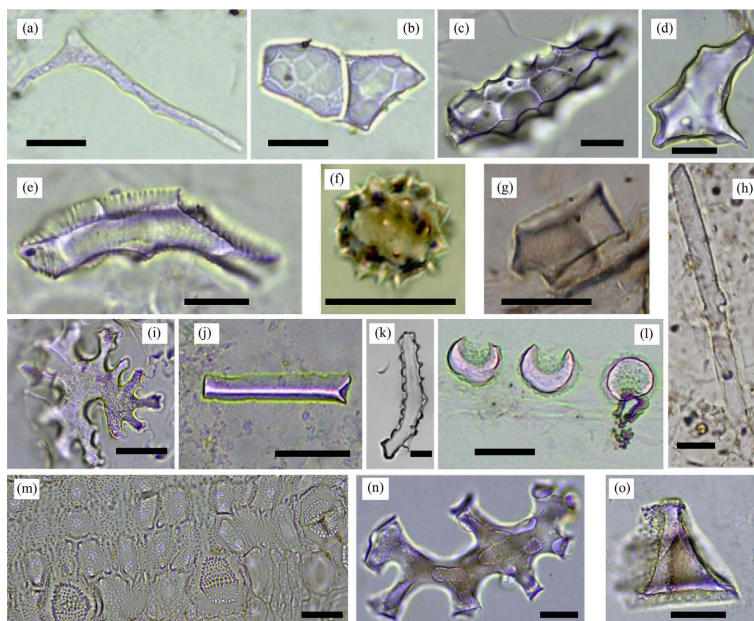


Figure 2. Illustrations of diagnostic phytolith morphotypes from woody plants and ferns. (a) Elongate brachiate geniculate [44], (b) Polygonal tabular [44], (c) Elongate facetate [44], (d) Tracheary annulate/facetate claviform [44], (e) Tracheary annulate/facetate geniculate [44], (f) Spheroid echinate [46], (g) Blocky polyhedral [40], (h) Elongate tabular cavate [40], (i) Irregular anticlinal [45], (j) Prismatic elongate [45], (k) Elongate sinuate [57], (l) Spheroidal cavate granulate [45], (m) Silicified epidermis granulate [45], (n) Amoeboid branchiate [45], (o) Prismatic cubic [45]. Scale = 20 μm .

to distinguish it from Spheroid echinate of Bromeliaceae (<2 to 10 μm) [39] [46]. The morphotypes of conifer phytoliths included Blocky polyhedral, Elongate tabular cavate, Elongate echinate, Elongate entire, Stomata, etc., among which Blocky polyhedral (**Figure 2(g)**) and Elongate tabular cavate (**Figure 2(h)**) were diagnostic morphotypes [40] [47].

In addition, studies on modern fern phytoliths have shown that there are mainly 12 types of fern phytoliths, including Acicular, Amoeboid branchiate, Elongate echinate, Elongate sinuate, Irregular anticlinal, Prismatic elongate, Prismatic cubic, Stomata, Spheroidal cavate granulate, Silicified epidermis granulate, Tracheary elongate, and Silicified epidermis/hypodermis [45] [57]. Among them, Irregular anticlinal (**Figure 2(i)**), Prismatic elongate (**Figure 2(j)**), Elongate sinuate (**Figure 2(k)**), Spheroidal cavate granulate (**Figure 2(l)**), Silicified epidermis granulate (**Figure 2(m)**), Amoeboid branchiate (**Figure 2(n)**) and Prismatic cubic (**Figure 2(o)**) were diagnostic morphotypes for ferns [45].

3.3. Diagnostic Phytoliths in Key Crops and Their Relatives in East Asia

Researches in environmental archaeology have promoted investigation and application of diagnostic phytoliths of crops and their relatives [2] [3] [4] [5] [10]-[15] [53]. Some phytolith morphotypes have the potential of identification precision and accuracy to genus or species [3] [4]. Therefore, they have been widely utilized in the study of domesticated and cultivated processes of key crops in dryland and rice agriculture in East Asia, such as rice, various types of millets and their relative plants [4] [12] [14] [15] [16].

Morphological studies of maize (*Zea mays* L.) phytolith confirmed that Cross (**Figure 3(a)**) was the diagnostic morphotype, whose size and basal features could be used to distinguish it from other grasses [1] [13] [58] [59]. The diagnostic phytolith morphotype of cereals were Epidermis elongate dendritic and Papillate (**Figure 3(b)**), whose size and margin shape could be used for identification of wheat and barley remains [17] [60].

Rice (*Oryza sativa*) is one of the most important crops in East Asia [49]. Rice phytolith of Double-peaked glume (**Figure 1(d)**) and its morphological parameters could be used to distinguish between wild and domesticated rice [31]. The number of fish-scaled decoration on Bulliform flabellate (**Figure 1(c)**) could also effectively distinguish between wild and domesticated rice [50]. The percentage of Bulliform flabellate with ≥ 9 scale decorations among all Bulliform flabellate phytoliths could be used as an indicator to evaluate whether ancient rice had developed domestication properties [49] [50] [51] [52] [53], based on the finding that the lowest value of Bulliform flabellate with ≥ 9 scale decorations was $\sim 40\%$ in domesticated rice [50].

The glumes phytoliths of millets, typical crops of dryland agriculture in China, had important significance in identification of ancient millet plants [12]. The Ω -type (**Figure 3(c)**) and η -type (**Figure 3(d)**) margin shapes of Epidermis elongate dendritic on the outer and inner glumes were the most important

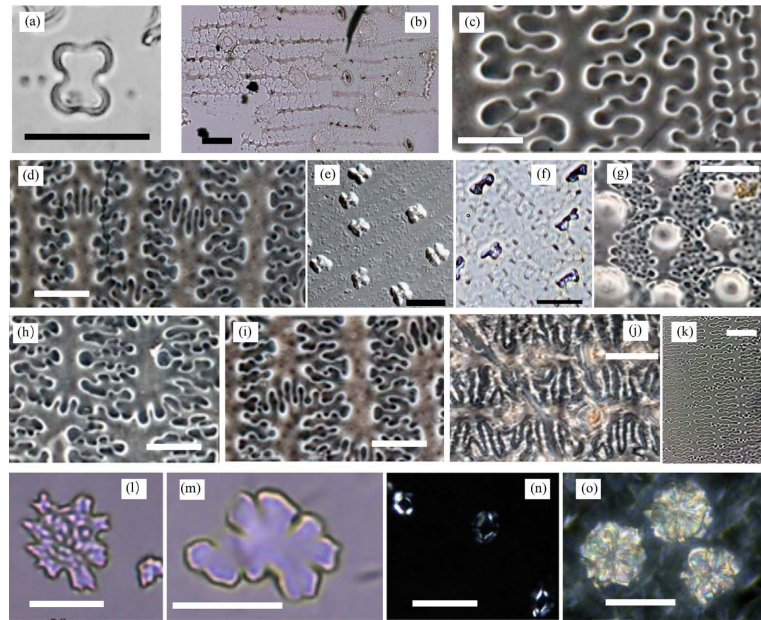


Figure 3. Illustrations of diagnostic phytolith morphotypes from key crops and related plants. (a) maize Cross [58], (b) cereal Epidermis elongate dendritic and Papillate [17], (c) Ω -type Epidermis elongate dendritic [3], (d) η -type Epidermis elongate dendritic [3], (e) foxtail millet Cross [3], (f) common millet Bilobate [3], (g) foxtail millet Papillate [3], (h) cross-wavy ends of epidermal long cells from foxtail millet [3], (i) cross-finger ends of epidermal long cells from common millet [3], (j) silicon surface ridgy line sculpture in Ω -type Elongate dendritic from foxtail millet [3], (k) β -type epidermis elongate dendritic from barnyard millet [33], (l) Tabular sinuate verrucate [35], (m) Tabular sinuate psilate [35], (n) Trichome base calcium phytolith with regular cracks [61], (o) Druse calcium phytolith [61]. Scale = 20 μm .

features for identifying common millet and foxtail millet, respectively [12]. Furthermore, Lu *et al.* [3] demonstrated five identification criteria of diagnostic morphological features for these two groups: 1) foxtail millet had Cross phytolith (Figure 3(e)) in glumes and lower lemma, while common millet had Bilobate (Figure 3(f)); 2) only foxtail millet had Papillae in upper lemma and palea (Figure 3(g)); 3) Elongate dendritic in upper lemma and palea of foxtail millet had Ω -type margins, while that of common millet had η -type margins, and these two margin types could be subdivided into three subtypes; 4) the ends of epidermal long cells of foxtail millet and common millet were cross-wavy type (Figure 3(h)) and cross-finger type (Figure 3(i)), respectively; 5) rippling feature developed on the surface keratose layer and long cells of the upper lemma in foxtail millet (Figure 3(j)). Moreover, Zhang *et al.* [30] [34] found that morphological parameters of Elongate dendritic of Ω III margin on inner and outer glume could discriminate between foxtail millet and green foxtail. Ge *et al.* [33] found that the diagnostic phytolith morphotype of barnyard grass was Elongate dendritic with β -type margins (Figure 3(k)).

In addition, Wang *et al.* [35] found that Tabular sinuate verrucate (Figure 3(l)) and Tabular sinuate psilate (Figure 3(m)) were the diagnostic phytoliths in bastfiber crops. Recently, a new kind of calcium phytoliths, with similar ana-

tomical origin to silicified phytoliths, were successfully applied in the identification of ancient tea residues [61]-[63]. The diagnostic morphotypes of tea calcium phytoliths in *Camellia sinensis* L. were Trichome base calcium phytolith with regular cracks (Figure 3(n)) and Druse calcium phytolith (Figure 3(o)) [61] [62].

4. Conclusions and Prospects

Significant progress has been made in the study of phytolith morphology in recent 20 years. The morphotype nomenclature and description for phytoliths have been gradually standardized. Numerous diagnostic phytolith morphotypes, especially those with over-representative to plant groups, have been discovered and reported. Based on the ICPN 2.0 scheme, this review briefly summarized the research progress of diagnostic phytoliths of plants of grasses, woody plants, key crops and relatives in dryland agriculture and rice agriculture in East Asia, and presented typical illustrations as a reference for phytolith analysis in vegetation reconstruction and environmental archaeology. The prospects for phytolith morphology research could be that:

- 1) Phytolith analysis should strictly follow the ICPN 2.0, and take comprehensive consideration of diagnostic morphotypes and their geometric parameters in identification process.
- 2) Extensive analysis on the morphology of modern plants, especially woody plants, can improve the representative of phytolith and enhance the reliability and plant diversity of paleovegetation reconstruction.
- 3) Control experiments of phytolith growth and morphological change under different environmental conditions and interventions will provide important modern evidences for the mechanism interpretation in the phytolith-based paleoenvironment reconstruction and understanding of management strategies in ancient crop domestication.

Conflicts of Interest

The author declares no conflicts of interest regarding the publication of this paper.

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