

Phytoliths from Woody Plants: A Review

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Abstract: Phytoliths are efficient proxies in archaeology, plant taxonomy, palaeoenvironment, and palaeoecology reconstruction, the research of which has been developing rapidly in recent years. Phytolith morphology is the basis of phytolith research. The morphological identification and classification of grass phytoliths are clear and detailed enough for application. However, the morphology of phytoliths from woody plants is ambiguous and unsystematic because of the relatively rare research on modern phytoliths and consequently seldom used in archaeology and palaeoenvironment reconstruction. This paper summarizes and concludes the research of woody phytolith morphology in the past decades. Previous studies show that palms and conifers produce some diagnostic phytoliths for identification and classification. There is progress in micromorphology, morphometry, and taxonomic identification of palms and conifers phytoliths. The phytolith morphology of broad-leaved trees is summarized according to produced parts of phytoliths in plants. The potential of further classification for broad-leaved phytoliths was discussed.

Keywords: phytolith; morphology; woody plants



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1. Introduction

Phytoliths are silica bodies composed of soluble silica ($\text{SiO}_2 \cdot n\text{H}_2\text{O}$) that is absorbed by plant roots/rootlets from soils, transported by their vascular system, and deposited in the cell walls, cell cavities, and intercellular spaces [1]. Although phytoliths are produced in a variety of plants, their morphology might vary greatly among plants as well as in different parts of the same plant [2,3]. Interestingly, they are usually preserved well in soils and sediments after plants decayed and in many different climatic and environmental conditions for millions of years [4]. They are found in most plant communities and also in atmospheric dust and marine sediments. Phytoliths are widely used in palaeoecology, palaeoclimatology, archaeology, geology, soil science, and so on [5–7], and in the last decade, the number of research papers based on phytolith analyses has increased exponentially [6,7].

Morphological and geochemical characteristics are the main bases for phytolith research [8,9]. Phytoliths found in soil can reflect the composition of historical vegetation and can be used to reconstruct certain environmental parameters, such as forest coverage [10], vegetation landscape change [11], and environmental climate factors [12], among others.

Grass phytolith morphology was extensively investigated in the past, especially its morphological classification [6]. However, phytolith morphology of woody plants is scarcely known, mostly because the production of phytoliths in many woody plants is still poorly studied. Many morphotypes still do not have definitive characters that allow their classifications. Undoubtedly, there is a need for a comprehensive study of the phytolith morphology of modern woody plants. In an attempt to improve the use of phytolith analyses in palaeoecology and archaeology, we provide a review of woody phytolith research and discuss their value in research endeavours.

2. Morphology of Woody Plant Phytoliths

During 1955–1975, most phytolith studies were about their botanical value [13,14], and unfortunately, there was little attention to their morphologies. Rovner [15] discussed the phytolith potential value in palaeoecological reconstruction which attracted extensive attention from researchers interested in archaeological and palaeoenvironmental studies [13,14]. Phytoliths provide the possibility for distinguishing dicotyledons from monocotyledons, woody plants from grasses, and Gramineae subfamilies, thus opening a new way for the study and interpreting past vegetations.

Early studies on phytoliths from woody plants explored several aspects such as their main morphological types, degree of silicification, which plant organs produced them, etc. Those studies recognized not only that dicotyledons and monocotyledons produce different types of phytoliths but also that phytoliths from woody plants are very similar and only a few genera and species produce special morphotypes with identification significance [15–19]. Subsequent scholars studied a wider range of genera and species with more comprehensive and detailed results [13,14,20–25], while Wang and Lu [26] and Kondo [27] systematically summarized their morphological classification.

After the publication of ICPN 1.0 [28], in a further effort to standardize their nomenclature, the International Committee for Phytolith Taxonomy (ICPT) formulated a modified nomenclature code—ICPN 2.0 [29], focused on a more standardized systematic classification. Based on ICPN 1.0 and ICPN 2.0, studies on the morphology of woody phytolith can be divided into:

- (1) Those that surveyed phytoliths from a variety of plants and established database for phytoliths [23,30–46].
- (2) Those that studied the differences in phytolith morphology and assemblages among some families and genera [19,20,47–51].
- (3) Those that investigated the ability of shared morphologies to further differentiate plants by detailed character differences [37,45,47,48,51–56].
- (4) Those that studied the forming mechanism and influence factors of phytolith morphology and microstructure [57–63].

Here, we review and discuss seed plant phytoliths with the main goal of providing information on the different morphotypes among phytoliths produced by gymnosperms, monocotyledons, and dicotyledons.

2.1. Gymnosperms

Living gymnosperms comprise four subclasses, Pinidae (~600 species), Cycadidae (~300 species), Gnetidae (~100 species), and Ginkgoideae [64]; however, phytolith research has only focused on Pinidae (conifers). Only a few studies are about other gymnosperms and show some indistinctive morphotypes [14,65,66].

In conifers, common silica bodies are found mostly in the needles, while other parts, such as branches [25,35,46], barks [46], and reproductive structures [65] can also produce phytoliths. Element analyses of needles showed that there are at least two modes of silicification: one is concentrated in the transfusion tissue (e.g., Eastern white pine with long thick needle) whereas the other occurs near the epidermis (e.g., European larch with short thin needle) [59,67,68].

It is important to mention that almost all cells in needles can be silicified. The most common silicified cells are those cells of the vascular tissue (mostly transfusion tissue and endodermis), epidermal and hypodermal cells while fibres, mesophyll, and stomata are only occasionally silicified [19,20,25,50]. In general, conifers do not produce annulate\helical vessels (except for Gnetopsids) or tracheid phytoliths, which can be utilized to distinguish conifers from dicotyledons [40]. In addition, coniferous phytoliths often have natural pits and cavities on their surfaces which distinguish them from similar graminaceous (monocot) morphologies, such as elongate and block phytoliths [44,51]. Up to now, the phytoliths from the families Pinaceae, Cupressaceae, and Araucariaceae are the most studied. Regrettably, the rest of gymnosperms are, so far, poorly studied [66].

2.1.1. Pinaceae

The production of needle phytoliths is quite variable among members of Pinaceae. *Larix* and *Picea* needles produce a large number of phytoliths while *Pinus*, *Abies*, and *Tsuga* have a lower amount of phytoliths [50,69,70].

Silicified epidermal cells (Figure 1a) are tabular or elongate, with entire, sinuate, or crenate margins, similar to the elongate phytoliths from those of Gramineae [27,51]. Under the epidermis, there may exist several layers of sclerenchymatous cells that constitute the hypodermis. Silicified hypodermis (Figure 1b) cells are elongate or ellipsoid with a baculate surface [27,50]. The mesophyll cells are rarely silicified and considered non-diagnostic [19,50]. Endodermal and transfusion tissue cells produce irregular blocky phytoliths (Figure 1c) with psilate or granulate surfaces, some of which are cubes or cuboids or similar shapes [51,59]. These block phytoliths are similar to the grass bulliform cells [51,71]; however, conifer blocks have sharp edges and clear ridges [27,51,59], features not observed at bulliform cells. Because transfusion tracheids in Pinaceae species have mostly the secondary walls with bordered pits [72], blocky phytoliths (Figure 1d) produced by them usually have bordered pits on surface as well [50,52]. Remarkably, near the vascular bundles, they are narrower and longer, but close to the endodermis, they are much wider, shorter, and more irregular [72,73]. Hair and stomata phytoliths (Figure 1e) usually are considered non-diagnostic [25,40,50].

Researchers have found differences among Pinaceae genera. Cuneiform phytoliths (Figure 1f), which may be derived from intercellular silicified fragments, are the dominating and typical phytoliths in *Larix*, followed by epidermal elongate phytoliths while other morphotypes are rarely found [27,30,40,50].

In the needles of the *Picea*, *Pinus*, and *Abies*, the predominant phytoliths are blocks. The highest percentage of phytoliths in *Pinus* and *Picea* are found in transfusion tracheids, while endodermic or transfusion parenchymal phytoliths are dominant in *Abies* [19,25,50,51]. Kondo et al. [52] effectively distinguish the phytoliths from *Picea*, *Pinus*, and *Abies* by the size of the surface bordered pits of the transfusion tracheids. However, their study was limited to a small sampling from Japan, and the general applicability of their results remains to be verified.

In addition, Bozarth [69] reported in *Picea glauca* a distinct epidermal plate with wavy margins on all sides and silicified spiny bodies in *Pinus banksiana*. Kern [74] and Blinnikov [30] described spiny irregular bodies in *Pinus ponderosa* which were diagnostic to the genus. The astrosclereid phytoliths (Figure 1p) from needles of *Pseudotsuga menziesii* (Douglas-fir) may have significance for species classification [19,27,35,50,75]. Additionally, McCune and Pellatt [35] have found the presence of this astrosclereid phytoliths can be used to reliably distinguish between Douglas-fir forest and Garry oak (*Quercus garryana*) savannah habitats.

Phytoliths are rarely produced in the bark or branches of Pinaceae [25,35,44,46,65,76]. But according to Carnelli et al. [25], all the branches they processed for their study, produced phytoliths, although most of them were non-diagnostic blocks. Stromberg [65] also examined the reproductive parts of conifers and found spheroid and tracheid types, as well as some elongate and tabular types.

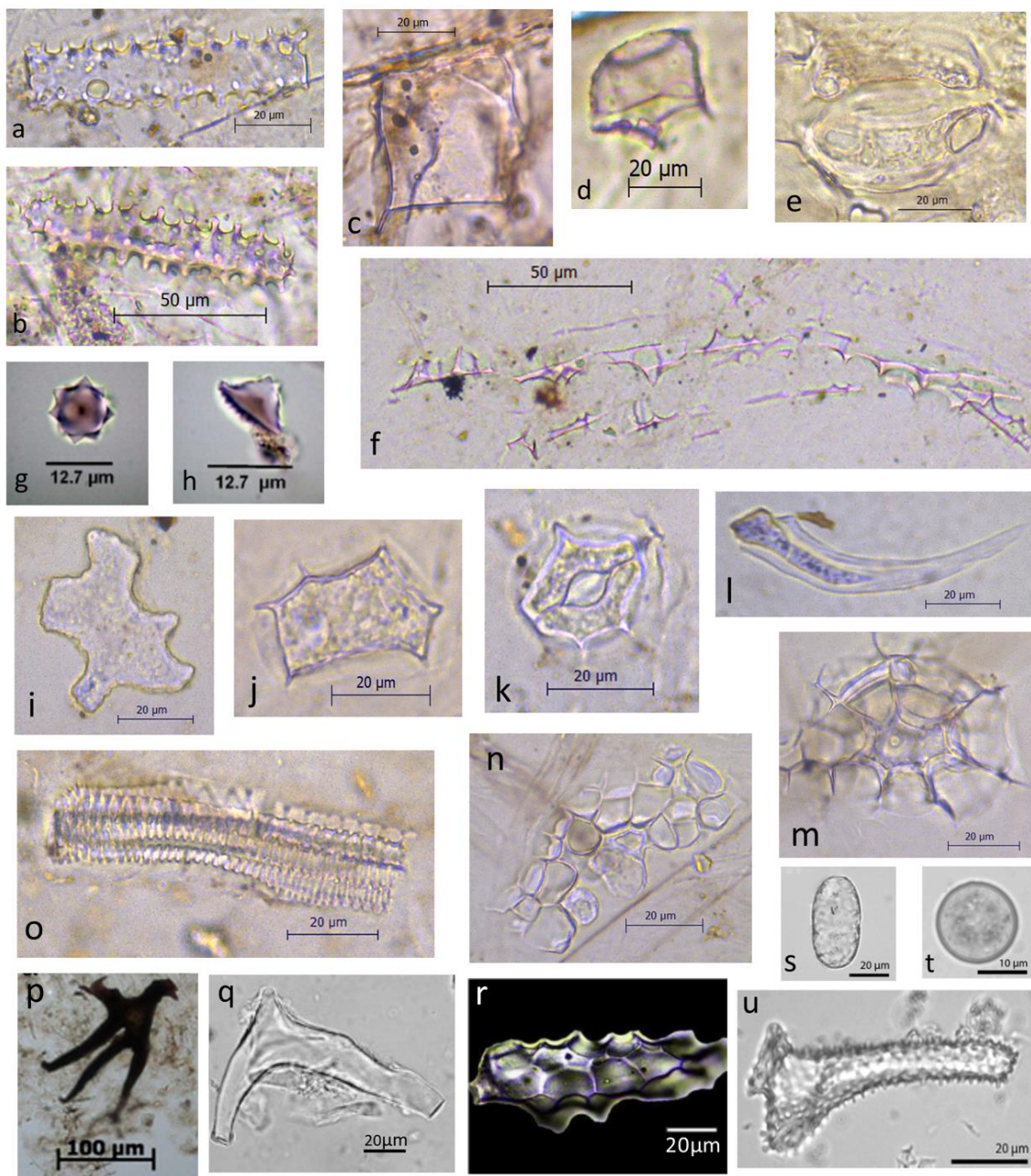


Figure 1. Phytolith morphotypes in woody plants: (a) Epidermal phytolith, *Picea asperata* (N); (b) Hypodermis, *Picea asperata* (N); (c) Block, *Pinus bungeana* (N); (d) Transfusion tracheid, *Abies georgei* (N); (e) Stoma, *Abies georgei* (N); (f) Cuneiform, *Larix principis-rupprechtii* (N); (g) Spheroid echinate, *Ammandra decasperma* (L); (h) Conical, *Bactris sphaerocarpa* (L); (i) Jigsaw, *Berberis thunbergii* (L); (j) Polygonal, *Quercus mongolica* (L); (k) Stomata, *Betula platyphylla* (L); (l) Hair, *Quercus mongolica* (L); (m) Hair base, *Acer pilosum* var. *stenolobum* (L); (n) Honeycomb assemblage, *Acer pilosum* var. *stenolobum* (L); (o) Tracheary, *Berberis thunbergii* (L); (p) Asterosclereid, *Pseudotsuga menziesii* (N); (q) Y-shaped Sclereid, *Erythroxylum mucronatum* (L); (r) Facetate, *Pittosporum truncatum* (L); (s) Ellipsoid, *Lannea acida* (W); (t) Spheroid psilate, *Malacantha alnifolia* (W); (u) Sclereid pitted, *Klainedoxa gabonensis* (B); (B) = Bark, (L) = Leaf, (N) = needle, (W) = Wood. (g,h) reprinted with permission from Morcote-Ríos et al., 2016, Oxford University Press. (r) reprinted with permission from Ge et al., 2020, CC BY license. (s–u) reprinted with permission from Collura, L.V. and Neumann, K., 2017, Elsevier. (p) reprinted with permission from McCune, J.L. and Pellatt, M.G., 2013, Elsevier. (q) reprinted with permission from Watling, J. and Iriarte, J., 2013, Elsevier.

2.1.2. Araucariaceae

Parr and Watson [48] studied six species of two genera of Araucariaceae to investigate the genetic affiliation of *Wollemia nobilis* by phytoliths analysis. The results showed that the crater-shape and elongate phytoliths from the epidermis are the common types in *Araucaria* and that these types are lacking in *Agathis*. On the other hand, there are abundant epidermal irregular nodules and oblong phytoliths in *Agathis* but not in *Araucaria*. Silicified stomata were also found in all the samples.

Kondo [27] also found that Araucariaceae produce tracheid phytoliths.

2.1.3. Cupressaceae

In the needles of the Cupressaceae, the most common phytoliths are blocks, which are rarely cubes [20,26,27]. Bozarth [69] found that silicified transfusion tracheids also occur in *Chamaecyparis* and *Sequoiadendron*. Blinnikov [30] reported tracheid phytoliths in *Juniperus occidentalis*, and Mazumdar [77] found that spiny bodies occur in *Cupressus goveniana*. Gao et al. [40] studied three species of Cupressaceae and found that the needles produce blocky, epidermal elongate, and tracheid phytoliths.

Nevertheless, other studies of a few species of Cupressaceae have found lack of phytoliths [33,35,44,46,51,76].

For other families of gymnosperms, such as Cycadaceae, Zamiaceae and Podocarpaceae [77], Taxaceae [46,78], Taxodiaceae [78], phytolith research data are very limited. Only a few species and genera have been studied, showing little taxonomic significance [20,44,46,65,77,78].

Gymnosperms evolve slowly, and *Picea*, *Pinus*, and *Abies*, which are closely genetically related to each other [79], have different silicification patterns from *Larix*. The reason for this phenomenon is still unknown and may be related to needle size [67] or the control of the endodermis over material transport [80–82]. Further and comprehensive studies on gymnosperm phytoliths are necessary to explore their internal mechanism of silicification, to clarify their characters, and to improve the precision of palaeoenvironment reconstruction based on phytoliths.

2.2. Monocotyledonous Woody Plants

The high phytolith producers among monocotyledons mainly belong to the comelinids with Orchidaceae as the only exception [83,84]. Plants have a close pattern of silicification, either concentrated near the epidermis of leaf and stem or concentrated in the stegmata cells near the vascular bundle sheath [84]. Arecaceae and Pandanaceae are the main woody families of monocotyledons, but Pandanaceae do not yield phytoliths [23,84].

Arecaceae

Arecaceae is one of the representative families in tropical and subtropical regions of the world; comprising about 190 genera and 2600 species mainly distributed in tropical America, tropical Asia, some Pacific islands, and a small amount in tropical Africa [85]. Most Arecaceae produce phytoliths in abundance [86]. The most prominent phytolith morphology in this family is the spheroid echinate (Figure 1g), basically a solid sphere with conical projections on the surface [86]. The second type is the conical or hat-shaped (Figure 1h) with acute projections at the top or bottom [47,86]. There are also variants of these two types based on the differences in the overall shape and surface ornamentation [87].

It is generally believed that spheroid echinate and hat-shaped echinate morphology are characteristics of Arecaceae. Both types can occur in all parts of the plant, although they occur most commonly in leaves [63,87]. The size and number of phytoliths may vary significantly in different parts of the plants [22,88,89]. Some uncommon morphologies, such as tracheid, stomata, and elongate, are of little classification significance for the family [22,43,54].

Spheroid echinate and conical echinate phytoliths originate from the small cells called “stegmata” [62,90]. The earliest study of silica in palm was by Tomlinson [90], who conducted the first comprehensive anatomical study of palm trees, describing the types and

distribution of silica bodies in the plants. Tomlinson [90] found that in leaves, stems, and roots, stegmata cells are adjacent to fibrous sheaths or isolated fibrous bundles of vascular tissue and distributed along the axial direction of the fibres and that silicate bodies inside the cells were spherical or conical with decorated surface, mostly representing small echinates or nodules. This finding has been verified by later studies [27,62,86,89,91].

Lins et al. [57] analysed the leaves of *Syagrus coronata* and confirmed the presence of sphere echinate in the hypodermis and amorphous small, silicified particles (mean diameter 300 nm) in the vacuoles of palisade cells. Schmitt et al. [92] conducted an anatomical study on the stem of *Calamus axillaris*, revealing that silica-bodies form and develop gradually in the stegmata cell vacuoles. Bokor et al. [62] explored the presence of phytoliths in Arecaceae and studied in detail the absorption, accumulation, and distribution of silicon in *Phoenix dactylifera* (date palm).

It is worth noting that only a few Arecaceae plants have both spheroid echinate and conical echinate phytoliths [22,47,54,86]. The above phenomena are particularly rare when only referring to the phytoliths in leaves, although there are a handful of exceptions [14,36].

Archaeologists and palaeoclimatologists are more interested in the role of phytoliths in plant identification and classification, but there are some issues when identifying Arecaceae phytoliths and those of some members of Zingiberales. Spheroid echinates are also found in abundance in Bromeliaceae while conical echinates are recognized in Marantaceae and Orchidaceae, among which the conical echinates are difficult to distinguish [27,54].

Morphometrics is a good method for further identification of characteristic palm phytoliths [47,53,54,89,93]. Using some phytolith parameters such as diameter, sphericity, number of spines, and length of the spines, Arecaceae can be distinguished from other families, especially from Bromeliaceae as Arecaceae spheroid echinate phytoliths have longer and more spines than those of Bromeliaceae [54].

Morphological measurements of the spheroid echinate from different genera or different parts of one plant have shown statistical differences as well [53,89,93], but there are very few morphometric studies on the conical echinate ones. Benvenuto et al. [54] measured the length and height of conical echinate phytoliths from several Arecaceae, Marantaceae, and Orchidaceae but found no differences.

Other attempts were made to build a better detailed morphological classification of palm phytoliths. Using information from 29 palm species, Bowdery [94] proposed a classification method for spheroid echinate (using three-dimensional overall shape, surface ornament, spine density and number) and successfully identified six palm species from sediments. Morcote-Ríos et al. [86] and Huisman et al. [87] further developed the morphological classification of Arecaceae phytoliths, which improved the level of taxonomic resolution in palms by phytoliths

Spheroid echinate and conical echinate phytoliths produced by Zingiberales are sometimes indistinguishable from those of Arecaceae [54,95]; nevertheless, because of the restricted geographical distribution of Zingiberales (Pantropical plants) today in tropical forests with high temperature and humidity, they can be used as indicators of environmental factors [96] when found in sediments.

2.3. Broad-Leaf Trees

According to the APG IV [83] classification system, angiosperms are classified into 416 families within the magnoliids, monocots, eudicots, and basal angiosperms clades. In this contribution, we refer as dicotyledons or dicots to all angiosperms except for the monocots. “Broad-leaf tree” is defined as the woody plants within the dicots.

The phytolith production by dicots is lower than that of monocotyledons, but a few families are high-productive, such as Magnoliaceae, Moraceae, Ulmaceae, and Fagaceae [21,24,97].

Most phytoliths produced by dicots have limited characters and can only be identified as belonging to dicotyledons, and in most cases, they cannot even be used to differentiate dicotyledonous herbs from broad-leaf trees [98]. Even families and genera of dicotyledons with high phytolith production are rarely studied. Therefore, in the majority of

the palaeoenvironmental reconstructions, all phytoliths from dicotyledonous plants or broad-leaf trees are classified singly as “dicots”, with few further classifications.

The major phytolith-producing organ of broad-leaf trees are the leaves. Evergreen trees are more siliceous than deciduous ones, and the older the leaves in the same tree, the more silicon particles they have [18]. Phytoliths are also produced in other parts of the plants [99], such as in bark [38]. The following summarizes the phytolith production based on the plant parts of broadleaf trees.

2.3.1. Leaves of Broad-Leaf Trees

The cells in leaves producing phytoliths include epidermal cells, vascular tissues cells (vessels and tracheids), hairs and hair bases, stomata, mesophyll cells (palisade cells or spongy cells), sclerenchyma, etc. [22,26,27,40].

The epidermal cells (Figure 1i,j) in the leaves of dicots are different from those of Cyperaceae and Poaceae [100]. Phytoliths derived from epidermal cells are usually poorly silicified and tend to be tabular polygonal or tabular/irregular sinuate (jigsaw) [27]. These types, while common in dicots, are also found in monocots [36], gymnosperms [25], and pteridophytes [44,101], which requires a careful and comprehensive investigation of local plants when using these phytoliths as vegetation indicators. However, the jigsaw epidermal cells have shown significant morphological differences among some species [65,98,102].

The phytoliths from stomata (Figure 1k) are usually a combination shape of the two occlusive cells. Carnelli et al. [25] have described stomatal phytoliths from Ericaceae, conifers, Cyperaceae, and Gramineae. Stromberg [65] has distinguished stomatal phytoliths among dicotyledons, monocotyledons, conifers, and Equisetum. Gao et al. [40] provided further classification and description of stomatal phytoliths in dicotyledons. In general, the stomatal phytoliths with ciliate ornamentation at the stomatal margins only occur in dicots, and therefore, they indicate the presence of dicots [40,65,102].

Silicified hair cells (Figure 1l) are very common and diverse phytolith morphologies frequently observed [22,24,27,36,76]. According to ICPN 2.0 [29], phytoliths of these hair types are altogether called Acute Bulbosus. Silicified hair cells vary greatly in size and shape, and Piperno [14] considered this type to be of considerable taxonomic significance. However, Watling and Iriarte [36] found that most species from the French Guiana flora produce similar silicified hair cells, and their sizes vary greatly within and among species; consequently, they have very limited diagnostic significance. McNamee [76] classified hair cells into 13 subtypes. Other similar work has been carried out [25,40,44,65]. Lepsch et al. [103] and Tsutsui et al. [58] studied the morphology and distribution of phytoliths (mainly trichomes) on the leaf surface attempting to reveal the silicification of hair cells. The newly defined Solid Globular Phytolith in Piperno and McMichael [45] is probably a globular glandular trichome from the epidermis. However, it is difficult to preserve intact hair cells in soils and sediments [104], which reduces the potential of using hair cell phytoliths in soils and sediments studies.

The hair base (Figure 1m) is the connector between hair cells and leaf epidermis, in the centre of which there is a concave area formed by the base of the hair cell that is surrounded by silicified epidermis cells. Although this type of phytolith is found in many families such as Dilleniaceae, Moraceae, and Cannabaceae [36], it lacks taxonomic significance [22,32,33].

The mesophyll is usually divided into palisade and spongy tissue. Phytoliths derived from these cells are poorly silicified and are referred to as palisade or honeycomb aggregation (Figure 1n), which are usually found in dicotyledons, but are considered of little taxonomic value as well [36,65,98].

The tracheary cells (Figure 1o) from the xylem of vascular tissue are divided into vessels and tracheids. Silicified vessels and tracheids resemble the shape and wall structure of the source cells. Although several types of them can be found in sediments [96,105], these morphotypes in broad-leaved trees have rarely been studied in detail [40,44,65]. It is believed that its distinguishing potential is inadequate possibly due to the scarce variation and limited classification ability of tracheary cells.

Silicified fibres are uncommon and usually in the form of fibrous elongate [19]. Sclereids are more common in bark, fruits, and seeds than in leaves and xylem [106–108]. Leaf sclereids are usually astrosclereids (Figure 1q), which give rise to Y-shaped or brachiate phytoliths [14,21]. However, some Brassicaceae [33] (mostly herbaceous) also have brachiate epidermal hairs that needs to be carefully distinguished from of those astrosclereids. Sclereid phytoliths have been observed in broad-leaf trees [22,27,31,34,36,76] and show low production in other plants; hence, they are used as a proxy for broad-leaf trees in vegetation reconstructions [109].

The spheroid phytoliths (Figure 1s,t) with psilate, verrucate, or granulate surfaces are also a common morphology in leaves and branches of broad-leaf trees, occurring in many dicots [65] and in some monocots [14], and are considered to originate from the leaf epidermis or subepidermal tissues [22]. Lepsch et al. [103] found a large number of small spheroidal phytoliths in leaf epidermal cells of *Curatella americana*. Some research on tropical vegetation suggested using these spheroids (<15 µm in diameter) to indicate broad-leaf trees [4,31,56]; however, a comprehensive survey of local plants is needed to clarify representativeness [45,56].

Facetate phytoliths (Figure 1r), probably formed by terminal tracheid by the extrusion of surrounding cells [110], are commonly found in dicots, especially in magnoliids [14,27,36,45,102]. Annulate/helical bodies found in the broadleaf tree are thought to be formed by terminal tracheid as well [21]. Both types are considered good indicators for broadleaf trees [14,21,27,102].

The less common morphotypes may have good classification purposes and require further investigation. Therefore, we summarize the data of some special phytoliths found in leaves by predecessors in Table 1.

Table 1. Specific phytoliths produced in leaves of broad-leaf trees.

Morphotype	Description	Family (Genus)	Reference
Specific epidermal phytoliths	Large (>50 µm) Attached to the periphery of hair bases	Dichapetalaceae	(Piperno and McMichael 2020)
	Tabular to blocky and half-decorated with a papillate texture	Chrysobalanaceae	(Watling et al., 2020)
	Shape square to rectangular epidermal cell) with round/spherical bulb or projection in centre of one flattened side. All surfaces smooth, but surface of rectangle and edges are upturned and undulating.	Fabaceae	http://phytolith.missouri.edu (accessed on 22 January 2022)
		Magnoliaceae Hamamelidaceae	(Kondo and Peason 1981) (Kondo 2010)
Y-shaped or brachiate Sclereids	Usually irregular elongate, branched, and may have psilate or fluted surfaces. Sizes are 50 to >90 µm in length.	Fagaceae	(Kondo and Peason 1981) (Piperno and McMichael 2020)
		Annonaceae	(Kealhofer and Piperno 1998) (Watling and Iriarte 2013)
		Thymelaeaceae	(Iriarte and Paz 2009)
		Sterculiaceae Dipterocarpaceae Sapindaceae Lauraceae	(Kondo 2010)
		Anacardiaceae Erythroxylaceae Myrtaceae	(Watling and Iriarte 2013)
		Picrodendraceae	(Piperno and McMichael 2020)
		Papilionaceae	(Lentfer 2003)
		Bombacaceae Ericaceae Ebenaceae Dichapetalaceae	http://phytolith.missouri.edu (accessed on 22 January 2022)

Table 1. Cont.

Morphotype	Description	Family (Genus)	Reference
Acute Bulbosus (Specific hairs)	Elongated cones with tuberculate or echinate ornamentation	Cannabaceae Loganiaceae Orobanchaceae	(Wallis 2003)
		Moraceae	(Wallis 2003) (Levin 2019) (Ge et al., 2020)
		Boraginaceae Urticaceae (<i>Pipturus</i>)	(Levin 2019)
	Squat cones with tuberculate or echinate ornamentation	Ulmaceae	(Wallis 2003) (Morris et al., 2009)
		Urticaceae (<i>Pipturus</i>) Moraceae	(Levin 2019)
		Cannabaceae	(Watling and Iriarte 2013)
	Segmented acicular hair	Asteraceae	(Bozarth 1992) (Lentfer 2003) (Iriarte and Paz 2009)
		Euphorbiaceae Piperaceae	http://phytolith.missouri.edu (accessed on 22 January 2022)
Facetate phytoliths	Spheroidal, elongate, or irregular body Large (usually >50 µm) The facetate surface may be formed by the squeeze of surrounding cells	Annonaceae	(Kealhofer and Piperno 1998) (Watling and Iriarte 2013) (Piperno and McMichael 2020)
		Flacourtiaceae	(Kealhofer and Piperno 1998)
		Fagaceae	(Kondo and Peason 1981) (Kealhofer and Piperno 1998) (Kondo 2010) (Watling and Iriarte 2013)
		Lauraceae	(Kondo and Peason 1981) (Kondo 2010) (Ge et al., 2020)
		Cunoniaceae Magnoliaceae Sapindaceae	(Kondo and Peason 1981) (Kondo 2010)
		Chrysobalanaceae Dilleniaceae Elaeocarpaceae	(Watling and Iriarte 2013)
		Pittosporaceae	(Ge et al., 2020)
		Ebenaceae	http://phytolith.missouri.edu (accessed on 22 January 2022)
		Piperaceae Sapotaceae	(Lentfer 2003)
		Adoxaceae (<i>Viburnum</i>)	(Kondo and Peason 1981)
Annulate/helical bodies	Usually, irregular elongate solid body Large (>50 µm) Originate from silicified tracheid tissues	Lauraceae	(Kondo and Peason 1981) (Kondo 2010) (Ge et al., 2020)
		Cunoniaceae Fagaceae Sapindaceae	(Kondo 2010)
		Malvaceae	(McNamee 2013)
		Magnoliaceae Pittosporaceae	(Ge et al., 2020)
		Flacourtiaceae	http://phytolith.missouri.edu (accessed on 22 January 2022)
		Spheroid folded	Anacardiaceae (Kealhofer and Piperno 1998)
Specific Spheroids	Spheroid bisected	Solanaceae (<i>Solanum</i>)	(Mercader et al., 2009) (Ge et al., 2020)
	Single rounded projection or “hat” on one side	Lauraceae	http://phytolith.missouri.edu (accessed on 22 January 2022)
	Fracture marks on the other side		

Table 1. Cont.

Morphotype	Description	Family (Genus)	Reference
Cystoliths	spheroidal phytoliths with contiguous verrucate sculpturing and stalk-like projections	Ulmaceae	(Kealhofer and Piperno 1998)
		Moraceae	(Bozarth 1992) (Kealhofer and Piperno 1998) (Watling and Iriarte 2013)
		Cannabaceae	(Bozarth 1992) (Watling and Iriarte 2013)
		Urticaceae	(Bozarth 1992)
		Boraginaceae (<i>Cordia</i>)	(Ricardo et al., 2018)
		Bombacaceae	http://phytolith.missouri.edu (accessed on 22 January 2022)
		Campanulaceae	(Lentfer 2003)
Papillae	Similar to sedge, but non-ornamented silicified papillae-like cells	Proteaceae	(Novello et al., 2018)
Baculate Elongates	baculate irregular bodies (named as boney bodies) The phytoliths have elaborated terminals that consist of a bunch of irregular protrusions on one end and one flatter end that is greater in diameter than the cylindrical stem	Burseraceae	(Watling and Iriarte 2013) (Piperno and McMichael 2020)
	baculate irregular bodies without elaborated terminals	Achariaceae Burseraceae Chrysobalanaceae Dichapetalaceae Moraceae Sapindaceae	(Piperno and McMichael 2020)
	baculate rectangular	Achariaceae Chrysobalanaceae Dichapetalaceae Euphorbiaceae Moraceae Phyllanthaceae Urticaceae	(Piperno and McMichael 2020)

2.3.2. Bark, Wood, and Other Parts

There are few studies regarding phytoliths in bark [38,39,43,45,46,76], as phytoliths in bark have received little attention and are often sampled and analysed indiscriminately on branches or trunks. Collura and Neumann [38] conducted a systematic study in taxa from West Africa and reported that more than 90% of bark samples produced phytoliths suggesting that silica production is concentrated in bark more than in wood and that there are morphological differences between bark and wood phytoliths. There are a large number of irregular blocks and silica particles/aggregations in the bark. These two types have non-specific character. Some of the irregular blocks look like frayed minerals whereas bark samples are very easily contaminated, and it is necessary to identify the source. Many morphological types that reflect the anatomical structure of the bark, such as fibres, sclereids (Figure 1u), cork, parenchyma, and aerenchyma, are absent from the wood.

Liu et al. [46] studied barks of 57 species of woody plants from the warm temperature humid region in the Southern Liaoning Province, China. Only two species of Magnoliaceae and Eucommiaceae produce phytoliths in bark. Spheroid psilate, Spheroid granulate, tabular granulate, elongates, and amoeboid occurred in bark samples.

The typical sclereids in the bark may be good indicators for broad-leaf trees, since they are rarely found in other plants [14]. At present, the phytolith data of bark are limited, and further comparative studies are needed for the use in palaeoenvironmental reconstructions.

Current studies indicate that only about 10% of woody plants produce phytoliths in their wood [38,49,111,112]. However, temperate trees and shrubs produce much less silica in their wood and bark than tropical species [38,46]. Environmental factors are probably the main reason for this difference. Phytoliths in wood are mainly spheroids and aggregations, while other types rarely appear. They are not specific to wood, also occurring in other dicot

organs as well as in monocots. Aggregations may be characteristic of wood, but they occur only in a few taxa [38].

Phytoliths are also produced in the reproductive structures of broad-leaved trees, such as inflorescences, flowers, fruits, and seeds, but the number of phytoliths is much lower than in monocots [22,27,31,33–36,88]. The fruits and seeds of Cannabaceae [31,36,98], Moraceae [88], Ulmaceae [88], Urticaceae [88], Euphorbiaceae [22], Burseraceae [36,88], Acanthaceae [88], Chloranthaceae [113], and Lauraceae [113] (<http://phytolith.missouri.edu>; accessed on 22 January 2022) are known to produce specific morphotypes.

Piperno [14] concluded that angiosperms with weaker silicification of vegetative tissue usually produce fewer reproductive phytoliths. In addition, phytoliths from reproductive structures are probably underrepresented in soils but can still play a role in archaeological studies if they are collected and preserved [45]. Few studies have focused on phytoliths produced in roots [114]; one study showed that blocky phytoliths are produced in the aerial roots of mangroves [37].

The current phytolith data are too limited to distinguish the largely diverse dicotyledons. This review suggests classifying phytoliths according to the taxonomic classification and gradually enriching phytolith data for each part of the plant. Some families and genera, e.g., Magnoliids, Ulmaceae, Moraceae, and Fagaceae, which are known to have high phytolith production, need further systematic study. Some phytolith types, such as hair cells, sclereids, polyhedral, etc., need to be further explored for identification and classification. Further work needs to be carried out to distinguish broad-leaved trees from other plants.

3. Conclusions

In summary, because phytoliths can be applied in palaeovegetation, palaeoenvironment, and palaeoclimate studies, it is necessary to have a clear systematic and taxonomic classification of them. This paper summarizes woody phytolith morphology and describes the silicification patterns of various woody plants, provides original locations in plant and their identification significance. Unfortunately, data from woody plants are still scarce and need to be extended.

Additionally, identifying the relationship between phytolith and gene and comparing the results to those about ancient plants could help to explain phytolith fossils in more historical sediments.

Exploring the relationship between phytolith morphology and environmental factors is helpful to improve and develop a phytolith index that can definitely improve detailed interpretations of the palaeoenvironment in which plants grew; furthermore, correct characterization of phytoliths is helpful to enhance their classification and to accurately interpret phytolith assemblages in sediments and soils. In a few words, phytolith analysis can become a powerful tool to reveal palaeoecological and archaeological information.

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