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Phytoliths in modern plants from amazonia and the neotropics at large: Implications for vegetation history reconstruction

Dolores R. Piperno [a,b,*], Crystal McMichael [c]

[a] Department of Anthropology, Smithsonian National Museum of Natural History, Washington, D.C., USA
[b] Smithsonian Tropical Research Institute, Panama
[c] Department of Ecosystem and Landscape Dynamics, Institute for Biodiversity & Ecosystem Dynamics (IBED), University of Amsterdam, Netherlands

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ABSTRACT

Phytolith analysis is increasingly being applied in studies of Neotropical forest history and associated pre-Columbian human influences, especially in the Amazon Basin. In order to enlarge modern reference collections that are integral to these efforts, we analyzed phytoliths from 360 species of mainly eudicotyledons from 80 different families and 10 Arecaceae species. Many are native to Amazonia and have not been studied previously. Production and morphological characteristics of the phytoliths were assessed along with their survivability in ancient soils and sediments. Our analysis affirmed the validity of family- and genus-level diagnostic phytoliths from arboreal and other woody growth taxa uncovered in previous research. It also revealed new diagnostic phytoliths from both well- and little-studied families of importance in the Amazonian forest, and affirmed the utility of other types such as spheroids and sclereids for documenting arboreal/woody growth more generally in paleoecological research. Although where pollen is recovered it will continue to document a greater number of arboreal/woody species, phytoliths can identify a diversity of those taxa in the Amazonian and Neotropical forest at large–including when pollen does not– with family, genus, and possibly even species-level diagnostics.

1. Introduction

During the past few decades, paleoecological and archaeobotanical research in Amazonia and the Neotropics at large have dramatically increased knowledge of Late Pleistocene through Holocene environmental history, along with pre-Columbian cultural interactions with the native flora that included the domestication of many annual and perennial species and active management of an unknown number of others (e.g., Hodell, et al., 2008; Fedick, 2010; Clement et al., 2010; McNeil et al., 2010; Piperno, 2011a,b; Whitney et al., 2011; Dickau et al., 2012; Ford and Nigh, 2015; Carson et al., 2014; Flatua et al., 2016; Kelly et al., 2018; Lombardo et al., 2019; Plumpton et al., 2019a; Gomes et al., 2020a). Phytolith analysis has taken its place alongside palynology, fire history studies, and geological research as an important contributor to these allied topics. Phytoliths are employed in lake sediments as indicators of past vegetation and climate, and prehistoric human influences on them (e.g., Piperno, 2011a; Carson et al., 2015; Brugger et al., 2016; Maezumi et al., 2018; Huisman et al., 2019; Plumpton et al., 2019a). In tandem with palynology, phytolith analysis provides data on vegetation composition and fossil source area, including on aspects that each analysis alone does less well, leading to more robust data sets (e.g., Piperno, 2006; Iriarte et al., 2012; Plumpton et al., 2019b, 2020). Moreover, unlike pollen, phytoliths survive well in terrestrial soils, providing data from specific, well-defined tracts of landscapes, minimizing complicating influences from factors such as long-distance transport that occurs in lake records, and refining studies of phytolith over- and under-representation (e.g., McMichael et al., 2012a, b; Dickau et al., 2013; Whitney et al., 2014; Piperno et al., 2015, 2019; Watling et al., 2017, 2018; Capriles et al., 2019).

As with any methodology concerned with documenting a highly diverse flora, large phytolith reference collections are essential. A considerable amount of work has been carried out on phytolith production and taxonomic significance in New and Old World tropical plants, together with preservation once deposited into soil/sediment contexts (e.g., Piperno, 1988, 2006; Kealhofer and Piperno, 1998; Runge, 1999; Lentfer, 2003; Mercader et al., 2009; Mazumdar, 2011; Dickau et al., 2013; Watling and Iriarte, 2013, Watling et al., 2016, 2020;Morcote et al., 2016; Collura and Newmann, 2017). This study further extends knowledge of phytolith characteristics in the Neotropical flora with an emphasis on the Amazon Basin, where phytolith along

* Corresponding author. Department of Anthropology, Smithsonian National Museum of Natural History, Washington, D.C., USA.
E-mail addresses: Pipernod@si.edu (D.R. Piperno), C.N.H.McMichael@uva.nl (C. McMichael).

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with other studies are addressing significant questions regarding vegetation history and pre-Columbian human influences on the forests and their biodiversity (e.g., Erickson, 2008; McMichael et al., 2012a,b; Denevan, 2011; Scoles and Gribel, 2011; Levis et al., 2012, 2017; Balée, 2013; Clement et al., 2015; Piperno et al., 2015, 2019; Watling et al., 2017).

2. Material and methods

We analyzed 360 species of mainly eudicotyledons from 80 families and 10 species of the Arecaceae. Many genera and species are native to the lowland forests of Amazonia, while others are native to the Neotropics more broadly including its arid and highland regions. A large number to our knowledge were not previously investigated. A few species are temperate zone or tropical Old World and were included to investigate phytolith occurrence in unstudied families and/or those with Neotropical representatives (e.g., in Achariaceae, Francoaceae, Garryaceae, Viburnaceae). Plants were sampled at the herbaria of the Missouri Botanical Garden, St. Louis; Smithsonian National Museum of Natural History, Washington, DC; National Herbarium of the Netherlands, Leiden, NL; and the palaeoecology laboratory at the Florida Institute of Technology, Melbourne, Florida. Tropical forests are not made of trees alone; there are numerous lianas, vines, shrubs, subshrubs, and eudicotyledonous herbs, whose phytolith attributes are little studied. To provide the most in-depth appraisal of phytoliths as repositories of vegetational history, we studied the widest sample of this Amazonian flora as possible, whether frequent in vegetation and of considerable economic use, or not. We primarily used ter Steege et al. (2013)and Cardoso et al. (2017) for lists of species and growth habits. 97 of the 464 regional and Amazonian-wide hyperdominant tree species that together account for over half of the trees in the Amazonian forest (ter Steege et al., 2013) were studied in this and Piperno's previous work (Piperno, 1988, 2006). Species belonging to an additional 38 hyperdominant genera were analyzed (in the Appendix A and Tables 2–5 hyperdominant species and genera are bold printed).

As our focus was on arboreal and other woody taxa, with the exception of the Arecaceae we did not include well-investigated monocotyledonous families (Poaceae, Cannaceae, Commelinaceae, Marantaceae, Zingiberaceae, Strelitziaceae), relying instead on previous detailed work on them (Piperno, 1988; 2006; Piperno and Pearsall, 1998; Prychid et al., 2003;Pearsall et al., 2011; Chen and Smith, 2013; ICPN 2.0, 2019). While our focus was placed on leaves where phytolith production is typically highest, we included when possible fruits, seeds, flowers, twigs, and trunk wood, often from the same species. We reviewed Piperno's existing modern Neotropical phytolith reference collection, including by revisiting species notes and curated microscope slides, and re-processing plant material of some species.

Phytoliths were extracted using the wet oxidation technique with Schultze's solution (a combination of nitric acid and potassium chlorate) (Piperno, 2006), then mounted on slides with permount and viewed with a Zeiss microscope at 200x or 400x. Phytolith morphotypes were photographed and saved on associated computer software for image curation and publication. Unless otherwise noted, phytoliths were described following nomenclature in the most recent version of the International Code for Phytolith Nomenclature (ICPN 2.0, 2019).

3. Results

3.1. Overall phytolith production and taxonomic patterns

Production and morphological patterns in new taxa studied here usually conformed to previous results from Amazonia and the Neotropics at large (Table 1 and Appendix A) (e.g., Piperno, 2006, Table 1.1; Dickau et al., 2013; Watling and Iriarte, 2013; Watling et al., 2020). Most families and genera previously reported to be high phytolith producers with a significant number of family- or genus-specific types continued to be in this category (Table 1). An exception was the Acanthaceae in which production in 17 new species analyzed here was rare or absent in most and with no additional family-or genus-level discriminations in any. Families and genera previously found to be infrequent, rare, or non-producers, and with limited (occurring in a significant number of unrelated taxa) or no taxonomic utility followed those patterns. Among these, we were able to sample many species of such families as Apocynaceae, Euphorbiaceae, and Sapindaceae, further strengthening this evidence among all their growth habits. The Fabaceae and Malvaceae were previously classified as variable phytolith producers (Table 1.1 in Piperno, 2006); however, analysis of dozens more species here shows them to be mostly rare to non-producers across all their sub-families and growth habits (Appendix A).

In most families not previously or little studied, such as the Bonnetiaceae, Callophylaceae, Cardiopteridaceae, Cyrillaceae, Garryaceae, Gentianaceae, Gunneraceae, Humiriaceae, Icacinaceae, Phyllanthaceae, Picrodendraceae, Rapateaceae, and Tetrameristaceae, phytolith production was absent or rare, and when present it was of no taxonomic importance. (We note that ter Welle, 1976 found appreciable amounts of

Table 1
Patterns of phytolith production and taxonomic significance in neotropical plants.

I. Families where production is usually high and phytoliths specific to family, sub-family, and genera occur, sometimes widely in the family	
Pteridophytes:	Cyatheaceae, Hymenophyllaceae, Selaginellaceae
Basal Angiosperms:	Annonaceae, Magnoliaceae
Monocotyledons:	Arecaceae*, Bromeliaceae, Commelinaceae, Costaceae, Cyperaceae*, Heliconiaceae*^, Marantaceae*^, Orchidaceae, Poaceae*, Zingiberaceae*
Eudicotyledons:	Asteraceae*, Boraginaceae, Burseraceae*, Cannabaceae*, Chrysobalanaceae*, Cucurbitaceae*, Dichapetalaceae, Dilleniaceae, Moraceae, Podostemaceae, Ulmaceae*, Urticaceae*
II. Families where production is rare or absent in many species studied, but where family- or genus-specific forms occur	
Pteridophytes:	Polypodiaceae
Eudicots:	Acanthaceae (*Mendoncia**)
III. Families where production may be common to abundant, but where taxonomically significant phytoliths will be limited in number	
Basal Angiosperms:	Aristolochiaceae, Chloranthaceae, Piperaceae (production high in the genera *Piper* and Pothomorphe; phytoliths absent in four *Peperomia* species analyzed)
Eudicots:	Combretaceae, Loranthaceae, Sapotaceae, Verbenaceae
IV. Families where phytoliths have not been observed, or where production is often uncommon to rare and is usually of limited or no taxonomic significance	
Gymnosperms:	Gnetaceae, Podocarpaceae
Basal Angiosperms:	Myristicaceae, Nymphaeaceae, Winteraceae
Monocotyledons:	Agavaceae, Alismataceae, Amaryllidaceae, Araceae, Burmanniaceae, Cyclanthaceae, Dioscoreaceae, Eriocaulaceae, Hydrocharitaceae, Iridaceae, Mayacaceae, Pontederiaceae, Smilacaceae, Typhaceae, Xyridaceae
Eudicotyledons:	Acanthaceae, Amaranthaceae, Apiaceae, Apocynaceae, Araliaceae, Asclepiadaceae, Bignoniaceae, Bixaceae, Bombacaeae, Bonnetiaceae, Cactaceae, Callophyllaceae, Campanulaceae, Caricaceae, Chenopodiaceae, Clusiaceae, Convolvulaceae, Ericaceae, Euphorbiaceae, Fabaceae, Guttiferae, Lacistemnaceae, Lauraceae, Lecythidaceae, Loganiaceae, Malphigiaceae, Malvaceae, Mayacaceae, Melastomataceae, Meliaceae, Myrtaceae, Myrsinaceae, Olacaceae, Polygonaceae, Primulaceae, Proteaceae, Rhamnaceae, Rosaceae, Rubiaceae, Rutaceae, Salicaceae, Sapindaceae, Saxifragaceae, Solanaceae, Tiliaceae, Vitaceae, Violaceae, Zygophyllaceae

*Reproductive structures (fruits and seeds) may produce high amounts of phytoliths often diagnostic of family, genus, and in some cases possibly species, or growth habits.
^Underground organs also produce high amounts of diagnostic phytoliths.
Notes: Information based on studies in Piperno (1988), 1989, 2006, Piperno and Pearsall (1998); Prychid et al. (2003);Pearsall et al. (2011), Chen and Smith (2013); Watling et al. (2020).

Table 2
List of Taxa with Rugose, Psilate, and Ornate Spheroids.

Family	Species	Herbarium	Accession #	Habit and Plant Part	Rugose	Psilate	Ornate
Acanthaceae	*Aphelandra sinclairiana* Nees	MoBot	2619486	Shrub, small tree	x (Large)		
Acanthaceae	*Mendoncia retusa* Turril	STRI	4339	Liana			x^
Acanthaceae	*Ruellia nudiflora* (Engelm. & A. Gray) Urb.	MoBot	6200972	Herb			X
Acanthaceae	*Ruellia pedunculata* Torr. ex A. Gray	MoBot	5700934	Herb		x	X
Annonaceae	***Guatteria*** *amplifolia* Triana & Planch.	STRI	N.A	Tree		x	
Annonaceae	***Guatteria*** *dumetorum* R.E. Fr.	STRI	9279	Tree		x	
Apocynaceae	***Aspidosperma excelsum*** **Benth.**	NHN	187	Tree	x (Large)		X
Apocynaceae	***Geissospermum*** *reticulatum* A.H. Gentry	NHN	246	Tree			X
Boraginaceae	***Cordia*** *alliodora* (Ruiz & Pav.) Oken	STRI	4799	Tree		x	
Brunelliaceae	*Brunellia stuebelii* Hieron.	ANS	7472	Tree		x	
Burseraceae	*Bursera aptera* Ramírez	MoBot	5837191	Tree		x	X
Burseraceae	*Bursera leptophloeos* Mart.	NMNH	3042516	Tree		x	
Burseraceae	*Bursera orinocensis* Engl.	NMNH	3023330	Tree		x	
Burseraceae	***Protium decandrum*** **(Aubl.) Marchand**	NMNH	3170546	Tree		x	
Burseraceae	*Protium goudotianum* (Tul.) Byng & Christenh.	NMNH	3143154	Tree		x	X
Burseraceae	***Protium*** *prancei* (Daly) Byng & Christenh.	NMNH	370	Tree			X
Burseraceae	***Protium rhoifolium*** **(Benth.) Byng & Christenh.**	NMNH	3098836	Tree	x (Large)	x	X
Burseraceae	***Protium heptaphyllum*** **(Aubl.) Marchand**	NMNH	3170541	Tree		x	
Burseraceae	***Protium tenuifolium*** **(Engl.) Engl.**	STRI	6233	Tree		x	X
Chrysobalanaceae	*Acioa longipendula* (Pilg.) Sothers & Prance	MoBot	4320394	Tree (Twig)	x		
Chrysobalanaceae	*Chrysobalanus icaco* L.	STRI	1399	Tree (Fruit)	x	x	
Chrysobalanaceae	*Couepia bracteosa* Benth.	MoBot	5945479	Tree (Twig)	x	x	
Chrysobalanaceae	***Couepia paraensis*** **(Mart. & Zucc.) Benth. ex Hook. f.**	ANS	2676	Tree	x	x	
Chrysobalanaceae	*Couepia polyandra* (Kunth) Rose	ANS	6198	Tree	x	x	
Chrysobalanaceae	*Exellodendron cordatum* (Hook. f.) Prance	MoBot	5049557	Tree	x	x	
Chrysobalanaceae	***Hirtella racemosa*** **Lam.**	STRI	4860	Tree (Seed)	x	x	
Chrysobalanaceae	*Hirtella triandra* Sw.	STRI	4644	Tree (Fruit)	x	x	
Chrysobalanaceae	***Licania*** *arborea* Seem.	ANS	10015	Tree (Fruit)	x	x	
Chrysobalanaceae	***Licania*** *guianensis* (Aubl.) Griseb.	ANS	4591	Tree	x	x	
Chrysobalanaceae	***Licania*** *jefensis* Prance	ANS	4591	Tree	x (Large)	x (Large)	
Chrysobalanaceae	***Licania*** *latifolia* Benth. ex Hook. f.	ANS	2574	Tree (Leaf, Fruit)		x (Fruit)	
Chrysobalanaceae	***Licania*** *morii* Prance	STRI	N.A.	Tree	x	x	
Euphorbiaceae	*Acalypha macrostachya* Jacq.	STRI	N.A.	Shrub, tree	x	x	
Euphorbiaceae	***Hevea brasiliensis*** **(**Willd. ex A. Juss.) Müll. Arg.	MoBot	4836037	Tree (Root)			x
Fabaceae	*Calapogonium caeruleum* (Benth.) C. Wright)	Mobot	5621490	Woody Vine		x(Large)	
Hypericaceae	*Vismia bassifera* L.) Triana & Planch.	STRI	B1	Tree (Bark, Wood)	x(Large)		x
Lecythidaceae	***Eschweilera*** *chartacea* (O. Berg) Eyma	NHN	291	Tree	x	x (Large)	x
Lecythidaceae	***Eschweilera coriacea*** (DC.) S.A. Mori	NHN	N.A.	Tree	x	x	x
Lecythidaceae	***Eschweilera sagotiana*** Miers	NHN	13	Tree	x	x	x
Lecythidaceae	***Eschweilera*** *turbinata* (O. Berg) Nied.	NHN	300	Tree	x	x	
Malvaceae	*Bombacopsis sessillis* (Benth.) Pittier	STRI	8654	Tree		x	
Malvaceae	***Matisia*** *alata* Little	MoBot	NNN.A.	Tree			x
Malvaceae	***Matisia*** *longipes* Little	MoBot	3892025	Tree	x		x
Malvaceae	***Pseudobombax*** *marginatum* (A. St.-Hil., Juss. & Cambess.) A. Robyns	NMA	411	Tree	x	x	
Malvaceae	***Pseudobombax*** *septenatum* (Jacq.) Dugand	STRI	N.A.	Tree			x
Moraceae	***Brosimum guianense*** (Aubl.) Huber	NMNH	N.A.	Tree	x		x
Moraceae	***Castilla*** *elastica* Sessé ex Cerv.	STRI	5335	Tree (Fruit)			x
Moraceae	*Chlorophora tinctoria* (L.) Gaud.	MoBot	2247651	Tree		x	
Moraceae	***Pseudolmedia*** *spuria* (Sw.) Griseb.	STRI	601	Tree	x		
Moraceae	***Sorocea*** *guilleminiana* Gaudich.	NMNH	2278140	Tree	x (Large)*	x	x
Peraceae	*Pera schomburgkiana* (Klotzsch) Müll. Arg.	MoBot	5991317	Tree	x		
Podocarpaceae	*Retrophyllum rospigliosii* (Pilg.) C.N. Page	Mobot	6155769	Tree (Leaf + Twig)	x		
Proteaceae	***Roupala montana*** **Aubl.**	STRI	N.A.	Tree	x	x	
Proteaceae	***Roupala*** *sp.*	STRI	N.A.	Tree	x	x	
Putranjivaceae	***Drypetes*** *brownii* Standl.	MoBot	5867242	Tree		x	
Rapateaceae	*Spathanthus unilateralis* (Rudge) Desv.	MoBot	4362430	Herb			x
Rutaceae	*Pilocarpus racemosus* Vahl	MoBot	6132232	Tree	x		
Rutaceae	*Rauia resinosa* Nees & Mart.	MoBot	5999657	Shrub, tree (Twig)	x	x	
Salicaceae	*Hasseltia floribunda* Kunth	STRI	4602	Shrub, tree		x+	
Sapindaceae	***Talisia*** *hexaphylla* Vahl	MoBot	6028939	Tree		x	
Violaceae	***Rinoreocarpus ulei*** **(Melch.) Ducke**	MoBot	4318836	Tree		x	X
Vochysiaceae	***Qualea*** *polychroma* Stafleu	MoBot	3714864	Tree			X
Xyridaceae	*Xyris ambigua* Beyr. ex Kunth	NHN	158	Herb	x	x	
Zygophyllaceae	*Larrea nitida* Cav.	MoBot	2325397	Shrub, small tree	x		

Unless noted specimens are leaves. N.A. = Accession number is not presently available.
Large phytoliths are >20 μm in maximum diameter.
*Rugose spheroids in *Sorocea guilleminiana* and *Licania jefensis* can have undulating and bulging surfaces, and large rugose ellipsoidal phytoliths occur in *S. guilleminiana*.
+Phytoliths have a small cavity. ^also has small rectanguloid to ellipsoidal to irregular ornate forms.
Bold printed taxa are hyperdominant species or genera that contain hyperdominant species in Amazonia (ter Steege et al., 2013).
Herbarium Names: MoBot, Missouri Botanical Garden, St. Louis; NMNH, Smithsonian National Museum of Natural History, Washington DC; STRI, Smithsonian Tropical Research Institute, Panama; ANS, Herbarium of the Arnold Arboretum, Harvard University; NHN, National Herbarium of the Netherlands, Harteveldweg in Leiden.

It was not possible to review all of the basal angiosperms and eudicotyledons in Piperno's reference collections made before this study was undertaken, but this table contains a large and representative sample of the distribution of spheroid forms in those taxa in it.

Table 3
GESP phytolith size in modern palms.

Species	Mean Size GESP µm	Range	n
Chelyocarpus dianeurus (Burret) H.E. Moore	9.4	6–12	20
Chelyocarpus repens F.Kahn & K.Mejia	10.8	7–15	20
Chelyocarpus ulei Dammer	8.3	6-11, 14	20
Euterpe oleracea Mart.	8.8	5-24, 34	20
Euterpe precatoria var. precatoria Mart.	9.2	5–38	20
Manicaria saccifera Gaertn.	6.9	3–9	20
Oenocarpus bacaba Mart.	14.2	7-33, 38	20
Oenocarpus bataua Mart.	16.6	8-31, 32	20
Oenocarpus mapora H.Karst.	8.8	7–17	20
Oenocarpus *minor* Mart.	10.8	6-14, 18	20
Prestoea ensiformis (Ruiz & Pav.) H.E. Moore	8.5	7–12	20
Prestoea schultzeana (Burret) H.E.Moore	7.3	5–10	20
Prestoea tenuiramosa (Dammer) H.E. Moore	6.7	5–10	20
Syagrus botryophora (C. Martius) C. Martius	9.2	7–13	20
Syagrus comosa (Mart.) Mart.	7.1	5–13	20
Syagrus coronata (Mart.) Becc.	8.6	7-10, 14	20
Syagrus inajai (SPRUCE) Becc. Leaf	11.2	6–17	20
Syagrus inajai, fruit	–	5–10	>150
Syagrus sancona H. Karst.	7.1	3–9	20

Notes: All specimens analyzed are leaves, unless noted, sampled from vouchered specimens housed at the herbaria of the Missouri Botanical Garden, St. Louis and Smithsonian National Museum of Natural History, Washington, D.C. Bold printed taxa are hyperdominant species or genera that contain hyperdominant species in Amazonia (ter Steege et al., 2013). The number for Range after the comma indicates the largest phytolith observed on extended scanning of the slide. Some data were originally published in Piperno et al. (2019).

phytoliths in the wood of certain Bonnetiaceae and Humiriaceae). However, two genera, *Tapura* and *Stephanopodium*, in the little-studied Dichapetalaceae, a small family of trees and lianas that are nonetheless well-distributed in Amazonian forest (Cardoso et al., 2017), produced high numbers of diagnostic leaf phytoliths, described below.

With regard to different plant structures, taxa that do not produce leaf phytoliths also showed an absence in fruits and seeds, taxa of some families with leaf phytoliths produced no fruit or seed phytoliths, and flowers were non-producers regardless of which taxon they represent. This is in accordance with previous information. Woods (trunks and twigs) studied showed variable phytolith production across taxa, as has been evidenced from other studies (e.g.,Ter Welle, 1976). Present data then indicate that of the ten most speciose families of trees in Amazonia; namely, Fabaceae (1042 species), Lauraceae (400), Myrtaceae (393), Annonaceae (388), Rubiaceae (338), Melastomataceae (263), Chrysobalanaceae (256), Sapotaceae (244), Malvaceae (214), and Ochnaceae (166) (Cardoso et al., 2017), two families, Annonaceae and Chrysobalanaceae, will leave behind significant numbers of phytoliths in soils/sediments. As discussed in detail below, those two families also produce phytoliths of diagnostic importance. In addition to infrequent phytolith formation, the eight others produce few diagnostic forms (Table 1, Appendix A and below).

This picture of taxonomic significance in eudicotyledon representatives of Amazonian and other Neotropical forest improves when high phytolith-producing families such as the Boraginaceae, Burseraceae, Cannabaceae, Dilleniaceae, Moraceae, Ulmaceae, and Urticaceae are considered. Although not among the most speciose families in tropical flora, they are nonetheless well-represented in the vegetation and produce diagnostic forms of value in paleo-ecological reconstruction, discussed below. Also, a few genera and species in what are mostly non-informative families have diagnostic forms. With regards to growth habit, it appears from this and previous studies that most lianas and vines as well as herbaceous eudicotyledons have no to limited production and will not be identifiable in soil and sediment phytolith assemblages (Appendix A).

3.2. Phytolith morphology, categories, and taxonomic utility

In this section we describe in detail and review what appear to be the most diagnostic phytolith types in Neotropical flora revealed by this study or previous research, whether confined to a particular family, genus, or species, or appearing to be limited in distribution to a narrow range of taxa. It is well-understood that plants globally produce some types of phytoliths of largely no taxonomic value derived from silicification of the polyhedral and jigsaw-shaped epidermal cells proper (that form a continuous layer over the surface of the plant), hair cells (trichomes) and hair bases, stomata, mesophyll, and tracheids. The Neotropics are no exception. Those types of little taxonomic value are not discussed further and are noted as "None" in the Appendix A are of these types.

3.3. Rugose, ornate, and psilate spheroids

Solid spheroids encompassing spherical, slightly ellipsoid, or largely irregular shapes and having varied surface decorations exclusive of echinate types typical of palms and granulate forms described here from wood (discussed later) are documented in a number of monocotyledons and eudicotyledons (e.g., Kealhofer and Piperno, 1998; Piperno, 1988; 2006; Iriarte and Paz, 2009;Pearsall et al., 2011; Chen and Smith, 2013; Watling and Iriarte, 2013; Watling et al., 2020; ICPN 2.0, 2019). They usually range from 3 to 20 µm in diameter. Where identified within tissue they are often formed in epidermal and sub-epidermal cells depending on the taxon, are produced most commonly in leaves, and may also be found in twigs, stems, seeds, and fruits. Different descriptors have been given to the surface ornamentations of these spheroids found in plants and soils around the globe (ICPN 2.0, 2019). We group them here into three types; psilate, ornate, and rugose. The latter refer to surface decorations called rugulose in Piperno (1988) and verrucate in Piperno (2006), while ornate decorations refer to a variety of patterns we have decided to group together. In this study and taxa studied previously by Piperno, the three forms occur in a wide variety of unrelated eudicotyledons, but in a limited number of species investigated, with the great majority formed in woody eudicots (Appendix A, Table 2; note, Tables 2–5 include a survey of the taxa previously studied in Piperno's research). Psilate and rugose, and psilate and ornate types often occur in the same taxon, whereas rugose and ornate forms often do not (Table 2).

Rugose spheroids (with a rough, irregular surface texture and few to no defined protuberances) have been isolated from a few woody tropical taxa as well as monocotyledonous herbs from the Cannaceae, Marantaceae, and Heliconiaceae (e.g., Kealhofer and Piperno, 1998; Piperno, 2006; Iriarte and Paz, 2009;Pearsall et al., 2011; Chen and Smith, 2013; ICPN 2.0, 2019) (Fig. 1 here and also see Fig. 1B in ICPN 2.0, 2019). Here they were found in 13 eudicot families encompassing 18 species outside of the Chrysobalanaceae, a well-known heavy producer of them (Table 2). All but one, *Xyris ambigua* not reported from Amazonia, are trees and shrubs, and most are trees. Their plant-to-plant production is far higher in Chrysobalanaceae species than in others. The phytoliths commonly range from about 5 to 12 µm in size, reaching 25 µm in a few species (with notations of "Large" in Table 2), and 35 µm in

Table 4
List of Taxa with Elongate Phytoliths.

Family	Species	Herbarium	Accession Number	Part	Habit	Curved	Tapered	Striate	Baculate Decoration		Rounded Ends	Serrate
									Rectangular, Short Rect, Rounded Ends	Irregular		
Acanthaceae	*Fittonia albivenis (Lindl. ex Veitch) Brummitt*	MoBot	7779208	Stem	Herb		x, (B)					
Acanthaceae	*Geissomeria pubescens* Nees	MoBot	4910159	T	Shrub	x						
Acanthaceae	*Mendoncia lindavii* Rusby	STRI	S16519	Leaf	Vine	x, thin	x (B)	x				
Acariaceae	*Hydnocarpus castanea* Hook.f. & Thomson	MoBot	3945502	Leaf, T	Tree				x, Rect	x		
Aquifoliaceae	***Ilex*** *cassine* L.	MoBot	3393581	Leaf	Tree	x, thin						
Burseraceae	*Protium copal* (Schltdl. & Cham.) Engl.	MoBot	4756470	Leaf + T	Tree					x		
Burseraceae	*Protium costaricense* (Rose) Engl.	STRI	6295	Leaf	Tree		x (B)					
Burseraceae	*Protium glabrum* (Rose) Engl.	STRI	7339	Leaf	Tree		x					
Burseraceae	*Protium goudotianum* (Tul.) Byng & Christenh.	NMNH	3143154	Leaf	Tree							x
Burseraceae	***Protium nodulosum*** Swart	MoBot	3711682	Leaf + T	Tree				x. Rect	x		
Burseraceae	*Tetragastris unifoliolata* (Engl.) Cuatrec.	NMNH	2685053	Leaf	Tree					x*		
Calophyllaceae	*Marila pluricostata* Standl. & L.O. Williams	MoBot	4650845	Leaf	Tree							
Chysobalanaceae	*Exellodendron cordatum + gardneri* (Hook. f.) Prance	MoBot	5049557	Leaf + Pet	Tree				x, Rect			
Chysobalanaceae	*Hirtella americana* L.	STRI	6541	Leaf	Tree	x	x		x, Rect, RE	x	x*	
Chysobalanaceae	***Hirtella gracilipes*** (Hook. f.) Prance	MoBot	3477206	Leaf	Shrub, tree				x,Rect, RE, Sq	x	x*	
Chysobalanaceae	***Hirtella racemosa*** Lam.	STRI	4860	Leaf	Tree		x		x,Rect, SR			
Chysobalanaceae	*Hirtella triandra* Sw.	STRI	4644	Leaf	Tree		x (B)					
Chysobalanaceae	***Licania hypoleuca*** Benth.	STRI	5393	Leaf	Tree		x (B)		x, Rect			
Connaraceae	*Rourea glabra* Kunth	STRI	13153	Leaf	Liana	x					x*	
Dichapetalaceae	*Stephanopodium angulatum* (Little) Prance	MoBot	2225548	Leaf	Tree	x, thin			x, Rect			
Dichapetalaceae	***Tapura*** *guianensis* Aubl.	MoBot	4995808	Leaf	Tree	x, thin				x		
Dichapetalaceae	***Tapura*** *juruana* (Ule) Rizzini	MoBot	6134146	Leaf	Tree	x						
Dilleniaceae	*Davilla nitida* (Vahl) Kubitzki	STRI	8210	Leaf	Liana		x (B					
Dilleniaceae	*Tetracera portobellensis* Beurl.	STRI	7846	Leaf	Liana	x	x				x	
Dilleniaceae	*Tetracera volubilis* L.	STRI	N.A.	Leaf	Liana		x					
Euphorbiaceae	***Mabea*** *occidentalis* Benth.	STRI	N.A.	Leaf	Tree		x (B)	x	x, Rect			
Fabaceae	***Cynometra*** *bauhiniifolia* Benth.	MoBot	2063083	Leaf	Tree		x					
Moraceae	*Brosimum bernadettea* Woodson	STRI	10306	Leaf	Tree	x						
Moraceae	***Brosimum utile*** (Kunth) Oken	NMNH	2199338	Leaf	Tree				x, Rect, RE, SR	x		

(*continued on next page*)

Table 4 (*continued*)

Family	Species	Herbarium	Accession Number	Part	Habit	Curved	Tapered	Striate	Baculate Decoration		Rounded Ends	Serrate
									Rectangular, Short Rect, Rounded Ends	Irregular		
Moraceae	*Brosimum* sp.	STRI	N.A.	Leaf	Tree	x						
Moraceae	***Clarisia racemosa*** Ruiz & Pav	NMNH	283764	Leaf	Tree				x, Rect			
Moraceae	***Castilla*** *tunu* Hemsl.	MoBot	2247652	Leaf	Tree	x, can be thin	x, can be thin		x, SR			
Moraceae	***Sorocea*** *affinis* Hemsl.	STRI	4106	Leaf	Tree	x						
Peraceae	*Pera schomburgkiana* (Klotzsch) Müll. Arg.	MoBot	5991317	Leaf	Tree			x				
Phyllanthaceae	*Amanoa almerindae* Leal	MoBot	3648347	Leaf	Tree				x, Rect			
Picrodendraceae	***Piranhea logipedunculata*** Jabl.	MoBot	3519365	Leaf	Tree	x, thin						
Sapindaceae	***Talisia*** *nervosa* Radlk.	STRI	6498	Leaf	Shrub					x		
Urticaceae	*Coussapoa ovalifola* Trécul	STRI	N.A.	Leaf	Tree				x, Rect			

N.A. = accession number not presently available.

Notes: Pet = petiole; T = twig; Elon = elongate; Irr = irregular; Rect = rectangular; SR = short, rectangular; RE = rounded ends; Elongate, tapered (B) includes with a broken appearance at the tapered end. *Appear at the present time to be genus-diagnostic. Bold printed taxa are hyperdominant species or genera that contain hyperdominant species in Amazonia.

It was not possible to review all of the species in Piperno's reference collections made before this study, but this table is a large and representative example of the distribution of elongate forms in it.

one species examined, *Sorocea guillemiana* (Moraceae). In monocots rugose spheroids usually range from 9 to 30 μm (Piperno, 2006). Therefore, as has been assumed in the literature, a soil/sediment phytolith assemblage dominated by rugose spheroids of a size 5–12 μm can be interpreted to reflect significant arboreal cover.

Furthermore, monocots that produce rugose spheroids usually make other types of phytoliths such as druses and with troughs that should reveal their presence (e.g., Piperno, 2006;Pearsall et al., 2011; Chen and Smith, 2013). We note also that rugose spheroids commonly produced in Zingiberaceae seeds have marked concavities that separate them from other taxa (Piperno, 2006). Some distinctive morphological variation is also apparent in rugose spheroids in woody taxa, as those in two species, *Sorocea guillemiana* and *Licania jefensis* (Chrysobalanaceae), a Central American taxon, exhibit undulating or bulging surface textures not seen in other species and also distinguishable from the large monocotyledon spheroids (Fig. 1).

Spheroids with varying surface decorations that we have grouped into an ornate category have been reported in the leaves and less often twigs, stems, and fruits of a small number of tree species from the Old and New World (Kondo and Peason, 1981; Kealhofer and Piperno, 1998; Lentfer, 2003; Piperno, 2006; Barboni et al., 2007; Iriarte and Paz, 2009; Pearsall et al., 2011). The surface decorations are described by different authors as granulate, tabular, verrucate, tuberculate, decorated, and dimpled (Fig. 2). They have often been combined with rugose forms in counts from soils/sediments. In this study they were found in 22 species from 11 different families (Table 2; Figs. 3–5). Most contributors are trees with occurrences also in three herbs and a liana; three of the latter four are Acanthaceae species. Surface decorations and shape may vary within and across taxa. Size is small in most species, ranging from about 3 to 15 μm in diameter with many ≤12 μm. They often occur in rare frequencies with the exception of *Hevea brasiliensis* where they were common in the roots (Fig. 6). This was a surprising finding, as root phytoliths are reported from a very few eudicotyledons and are best known in Poaceae and a few other monocots (e.g., Sangster and Hodson, 1992; Chandler-Ezell et al., 2006; Piperno, 2006). This may indicate a lack of focused work on eudicots.

The *Hevea* root phytoliths may be distinguishable from other ornate types considered here and appear similar to those in roots from the Poaceae associated with silicification of the inner tangential cell walls of the endodermis (e.g., Sangster, 1978; Lux et al., 2020). This opens a possibility of identifying root vs. leaf, twig, or fruit decay, but much exploratory work needs to be carried out on the Neotropical woody/arboreal flora to ascertain root phytolith presence and morphology. It appears that most taxa where ornate spheroids occur would not be expected to make large contributions to soils/sediments, leaving open the question of root decay. We note that some hyperdominant tree species in otherwise phytolith-poor families such as *Aspidosperma excelsum* and *Geissospermum reticulatum* (Apocynaceae) and *Eschweilera sagotiana* (Lecythidaceae) contribute them, probably improving their phytolith representation in soils/sediments. It appears that some taxa considered here may be differentiable from others; additional work is required with a larger sample of species and different plant structures (e.g., stems) to examine this question more robustly. As has been assumed in the literature, they mainly denote woody/arboreal growth when found in soils/sediments. Also, small, unique rectanguloid to ellipsoidal to irregular ornates occurred commonly in the fruit exocarp of *Mendoncia retusa* (Acanthaceae) (Fig. 7).

Psilate spheroids have been found in more species than rugose and ornate forms, and to have the widest taxonomic distribution. These points are reinforced in this work (Table 2). Among eudicots studied here they occurred nearly exclusively in trees and shrubs supporting their usage as indicators of woody/arboreal growth if monocotyledonous herbs that produce them can be taken into account.

Data from this and other Neotropical research are then consistent that the great majority of spheroids in eudicotyledons derive from arboreal/woody growth with most coming from trees, and that they occur in a fairly limited number of taxa (e.g., Iriarte and Paz, 2009; Pearsall et al., 2011; Watling et al., 2013, 2020). The Chrysobalanaceae are especially rich producers of rugose and psilate spheroids. One may expect this family, one of the 10 most speciose families in the Amazon with 256 species including eleven hyperdominants in the genera *Licania* and *Couepia* (Cardoso et al., 2017;ter Steege et al., 2013), to have often

Table 5
Phytolith Potential and Predicted Potential in Some Major Economic non-Arecaceae Trees.

Family	Species	Phytolith Production	Taxonomic Value
Anacardiaceae	*Anacardium occidentale* L.	R	None
Anacardiaceae	***Spondias mombin* L.**	C (L), Absent (S)	None
Annonaceae	*Annona glabra* L.	Absent	
Annonaceae	*Annona montana* Macfad.	Probably Absent to R	Probably None
Annonaceae	*Annona muricata* Linn	Absent (L and Stem)	None
Annonaceae	*Annona mucosa* Jacq.	Probably Absent to R	Probably None
Annonaceae	*Annona squamosa* L.	Absent (L, S)	None
Bignoniaceae	*Crescentia cujete* L.	R	None
Bixaceae	*Bixa orellana* L.	NC	None
Chrysobalanaceae	***Couepia guienensis*** Aubl.	Probably C to Abun.	Family to a small number of families
Euphorbiaceae	***Hevea brasiliensis*** Müll.Arg.	R	None
Fabaceae	***Inga edulis*** Mart.	C to R	Probably None
Lecythidaceae	***Bertholletia excelsa*** Bonpl.	Probably Absent to R	Probably None
Malvaceae	***Theobroma cacao*** L.	R	None
Malvaceae	*Theobroma bicolor* Humb. & Bonpl.	R	None
Malvaceae	***Theobroma subincanum*** Mart.	Absent (W)	
Malvaceae	***Theobroma speciosum*** Willd. ex Spreng.	Probably Absent to R	Probably None
Myrtaceae	*Psidium guajava* L.	Absent (L,F,S)	
Rubiaceae	*Genipa americana* L.	Absent	

Notes: Abun = phytoliths abundant, C = common, NC = not common R = Rare. L = leaf analyzed,
F= Fruit, S = seed, W=Wood; unless otherwise noted leaves were analyzed.
Bold printed taxa are hyperdominant species or genera that contain hyperdominant species in Amazonia (ter Steege et al., 2013).

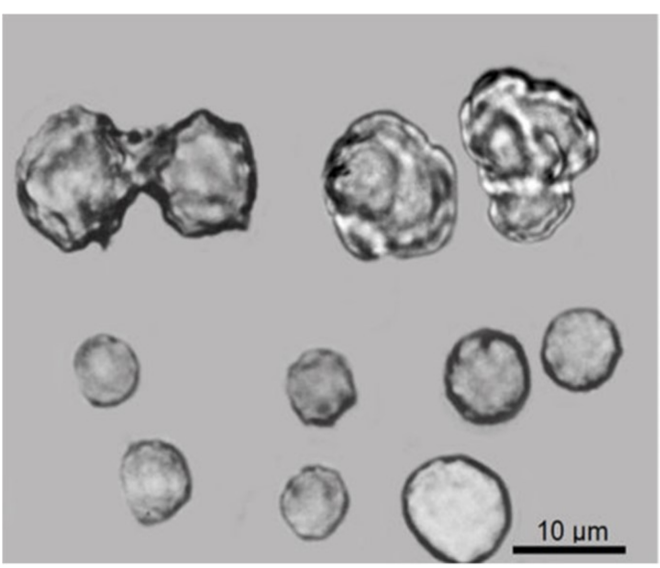

Fig. 1. Bottom group, three psilate spheroids from the seeds of *Hirtella triandra* (Burseraceae); middle group, left, another psilate spheroid, and center and right, three rugose spheroids from *H. triandra* seeds. At the top left are two larger rugose spheroids from the monocotyledon *Canna indica*. The two phytoliths at the top right are a different type of rugose spheroid with undulating and bulging surfaces from *Sorocea guilleminiana* (Moraceae) that have been found only in this species and *Licania jefensis* (Chrysobalanaceae). Reprinted from Piperno (2006).

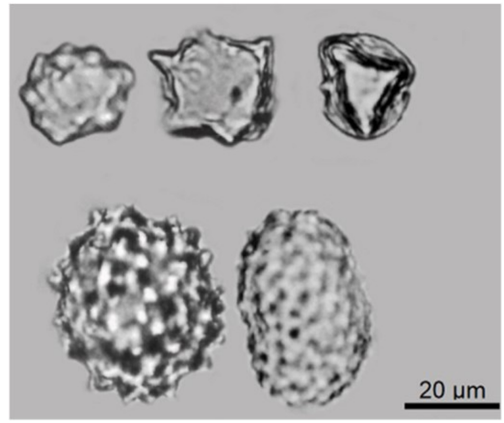

Fig. 2. Top left and center, ornate spheroids from the twig of *Sebastiana brasiliensis* (Euphorbiaceae), and top right from the fruit of *Shorea obtusa* (Dipterocarpaceae). On the bottom are two ornate spheroids from modern soils underneath tropical African forest. Reprinted from Piperno (2006).

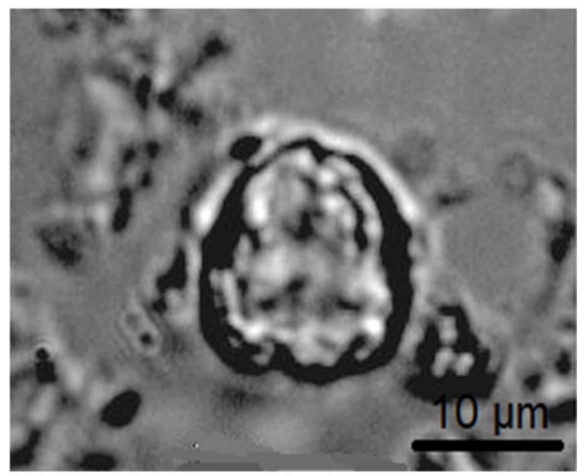

Fig. 3. An ornate spheroid from the leaf *Matisia longipes* (Malvaceae). It has small rounded protuberances distributed unevenly on the surface.

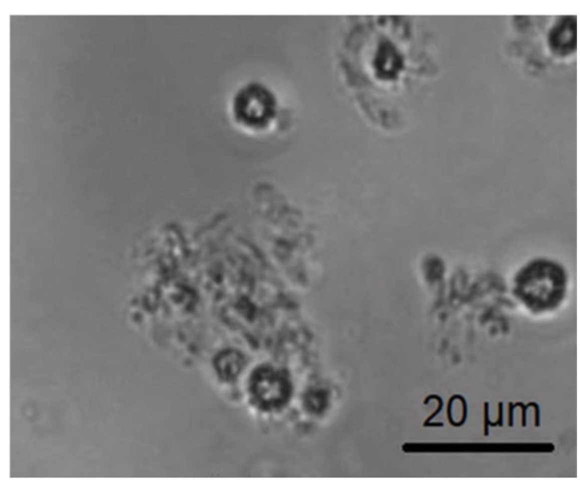

Fig. 4. Ornate spheroids from the leaf of *Spanthanthus unilateralis* (Rapateaceae). They have spiky protuberances on the phytolith edge.

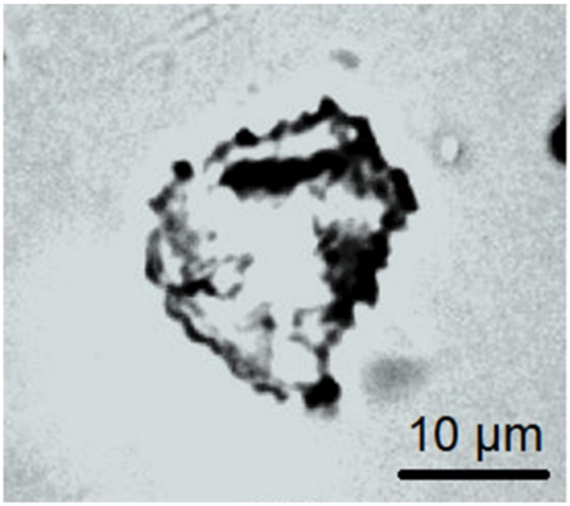

Fig. 5. An ornate spheroid from the leaf of *Pseudobombax septenatum* (Malvaceae).

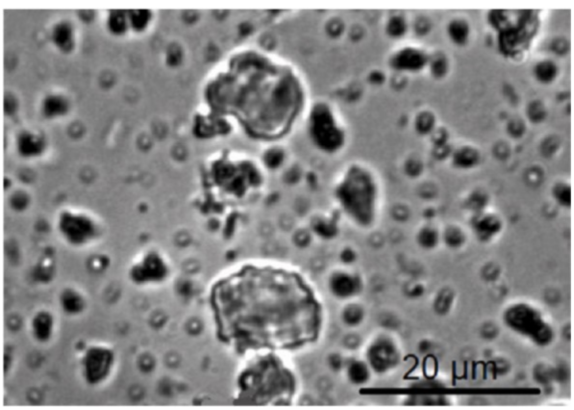

Fig. 6. Ornate spheroids from the root of *Hevea brasiliensis* (Euphorbiaceae). They arevariable in surface decoration and shape.

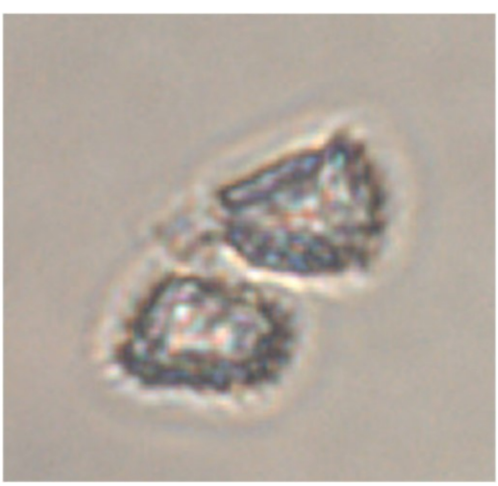

Fig. 7. Unique rectanguloid and irregular ornates from the fruit exocarp of *Mendoncia retusa*. They are 10 μm in maximum length.

contributed the majority of these spheres when they dominate Amazonian and perhaps other Neotropical soil/sediment assemblages (e.g., McMichael et al., 2012a; Heijink et al., 2020).

3.4. Spheroids from wood and phytoliths from bark

It is estimated that only 10% of woody species globally silicify their woods (ICPN 2.0, 2019). The phytoliths, which accumulate in the ray and parenchyma cells–mostly the former– have been described from a diverse array of taxa (Amos, 1952;Ter Welle, 1976; Collura and Neumann, 2017). A large study of Neotropical taxa especially from Surinam revealed phytoliths in 300 species from 32 families and 90 genera (Ter Welle, 1976). We studied trunk wood and twigs from 96 species in 32 families, finding phytoliths in 15 species and 10 families (Appendix A). Our sample size is smaller than in Ter Welle's analysis, but there is generally good correspondence in phytolith production among taxa analyzed in both studies; for example, absence in Bignoniaceae, Boraginaceae (*Cordia* spp.), and most Euphorbiaceae and Fabaceae, and presence in some Burseraceae and Chrysobalanaceae. Silicification of woods can be quite variable among different species of the same genera and among genera in a family, as we and Ter Welle (1976) found. We are assuming twigs are comparable to trunks in silicification patterns.

Shapes of phytoliths we studied in both trunk wood and twigs are spheroidal, ellipsoid, or irregular, and when rotated one somewhat concave face is often seen. Sizes range from about 6 to 25μ m with most not exceeding 20 μm. Surface decorations are often composed of tiny granules that are frequently densely distributed (Figs. 8–10). On a minority of phytoliths the granules are less clearly defined and the decorations would be classified as rugose. Rare psilate phytoliths occurred in some species, and in two, *Perebea guianensis* and *Poulsenia armata* (Moraceae), phytoliths basically lacked surface decorations. The size distributions, shapes, and tiny granule decorations correspond to those studied by Ter Welle (1976), who described them as globular to oblong with a granular surface. Spheroids with this surface decoration are mainly confined to the woody structures of taxa. A very few species, such as in the Chrysobalanaceae, Acanthaceae, and Malvaceae exhibit them infrequently in their leaves as well (Appendix A). In those phytoliths the concave face seen in wood may not be as apparent. Phytoliths with a surface decoration similar to those from wood but without the shape concavity were also surprisingly found in a fruit of a palm species, below.

Wood phytoliths we describe here can be very similar from taxon to taxon. Spheroids may be more irregular in outline in some species than in others, but it appears from this and other studies that differentiation will be largely limited. Nonetheless, the phytoliths are typically produced in high numbers and can point to tree and shrub decay in soils/sediments. We did not see types of wood silicification observed in other

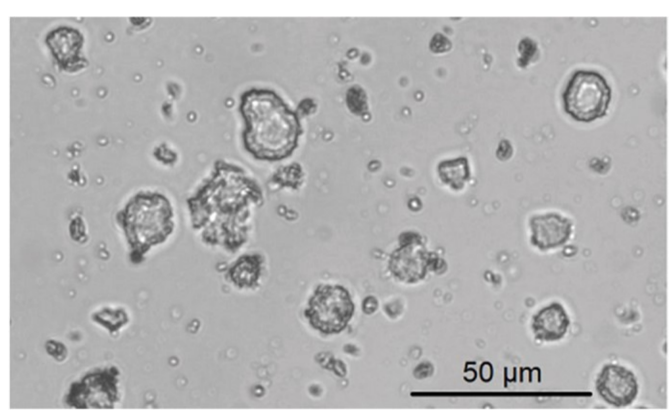

Fig. 8. Spheroids from the wood of *Chrysophyllum oppositum* (Sapotaceae). The surface decoration has tiny granules.

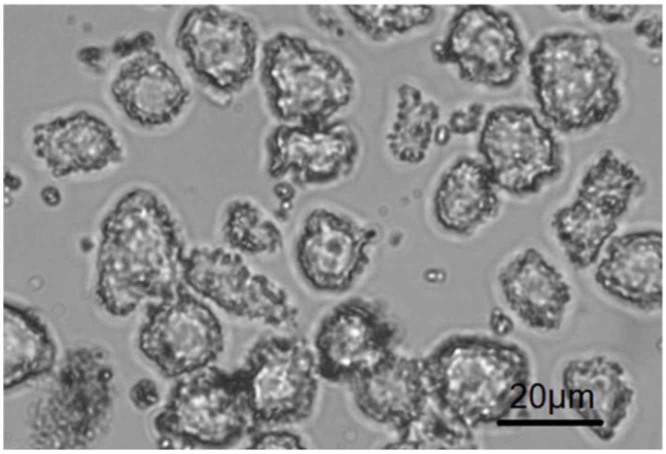

Fig. 9. Spheroids from the wood of a *Pouteria* sp. (Sapotaceae) with the surface decoration of tiny granules.

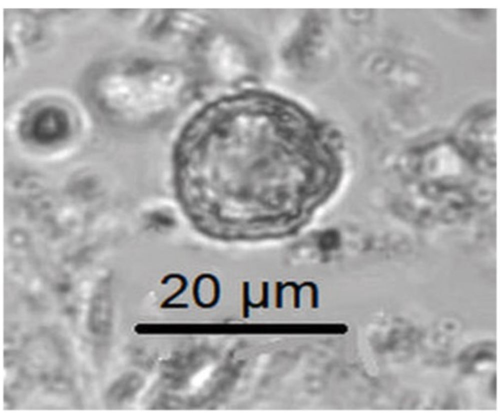

Fig. 10. A spheroid from the twig of *Castela erecta* (Simarobaceae) with the surface decoration of tiny granules.

studies resulting, for example, in what are called aggregate grains (Kondo et al., 1994), or large irregular phytoliths with surface decorations of a type we describe below as baculate (Lentfer, 2003). Additional Neotropical study would likely reveal phytoliths of these types.

We include bark in this section. We were able to study bark from nine species, including a *Brosimum* sp., two *Theobroma* species, *Trema micrantha*, and *Annona muricata*. None produced phytoliths. Of significant note is that because *Trema micrantha* lacked phytoliths in its bark we can probably eliminate that species from consideration in our Amazonian terrestrial soil studies carried out to date, where in Piperno (et al., 2019) they were listed as potentially occurring in the sand fraction at some sites on the basis of comparisons of bark phytoliths isolated by Collura and Neumann (2017) from African *Trema* species. Like for wood, phytolith production in barks may vary from species to species in a genus.

3.5. Arecaceae echinate spheroids and conicals

We studied here 10 new species or structures (fruits) of palms from eight genera (Appendix A). They produced the expected basic phytolith types that define palm assemblages—echinate spheroidal or conical often about 5–20 in size–(Tomlinson, 1961; Piperno, 2006;Morcote Rios et al., 2016), along with some unexpected variations in shapes and surface decorations, and an apparent diagnostic form not previously recorded. Recent descriptions and classifications by Morcote Rios et al. (2016) and Huisman et al. (2018) discriminate, respectively, lowland Amazonian and Andean taxa at lower taxonomic levels than previously and provide detailed information on distributions of phytolith sub-types across sub-families and tribes. For example, Morcote-Rios et al. (2016) defined a sub-type in Amazonian palms called globular (here called spheroidal) echinate with short acute projections (GESP) only in the genera *Chelyocarpus*, *Prestoea*, *Manicaria*, *Syagrus*, *Euterpe*, and *Oenocarpus*, with those in the latter two found to be larger than in the others. Our analysis of additional Amazonian palm species confirmed again these patterns and differences (see also Piperno et al., 2019), including by showing that fruit-derived phytoliths do not introduce confusion with separation of *Euterpe* and *Oenocarpus* from other GESP-producing palms (Appendix A and Table 3). Importantly, these two genera contain major economic species. Based on present information, GESP phytoliths with both an average size of 14–16 μm and higher, and maximum diameters of >20 μm are likely to be *Oenocarpus bacaba* or *O. bataua* (Table 3). Questions concerning the palms' prehistoric distributions and usages along with possible human influences on their modern abundances are thus amenable to study with phytolith records (see Piperno et al., 2019 for an example).

We isolated a previously undescribed phytolith from *Prestoea schultzeana* that appears unique to genus or species. It is a large spheroid 26–40 μm in diameter with a surface decoration of densely clustered, rounded projections (Fig. 11). These phytoliths occur much less commonly in the assemblage than GESPs but appear to be highly diagnostic. Also, leaves of *Chelyocarpus chuco* unlike other species in the genus did not produce GESPs, but rather spheroids with only slightly echinate decorations or few decorations at all. Phytoliths in its fruit are also atypical of palms. They are spheroids with densely distributed tiny granules that appear more pointed than those in some eudicot wood phytoliths and more densely distributed than in others (Fig. 12). Fruits from other members of the genus should be analyzed.

Huisman et al. (2018) identified new subtypes of spheroid echinate and conical forms in mid-elevation Andean palms, based on DIC microscopy using 630x magnification, which was necessary to confidently identify some of these more subtle forms. They also documented considerable size differences between some taxa with varying ecological preferences that will be useful in their discrimination. This type of work will be of high utility in paleoecological reconstructions of the Andean mountain chain flora and climate, and potentially in the Amazonian lowlands and other Neotropical systems.

3.6. Complete and ½ and ¾ globular phytoliths

We defined a class of solid globular phytoliths apart from spheroidal forms for a number of reasons. They are often more circular in circumference than spheroids that can be more irregularly spherical; tend to be considerably larger than those we classify as spheroids; are mostly psilate but can have different surface decorations than any spheroid; and occur in a limited number of woody taxa. Their origin in tissue is unclear, but likely epidermal. They were all identified from the

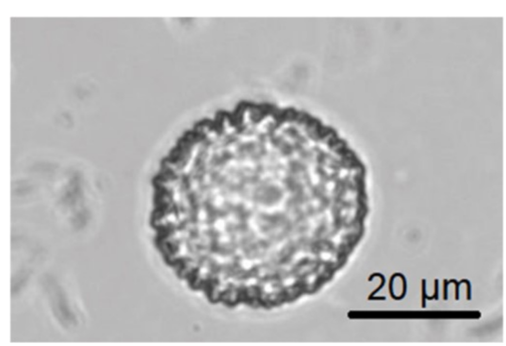

Fig. 11. A phytolith from a leaf of *Prestoea schultzeana* (Arecaceae). It is large in size and with densely clustered rounded projections on its surface.

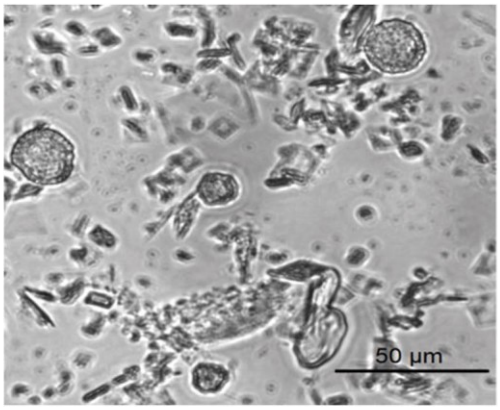

Fig. 12. Phytoliths from a fruit of *Chelyocarpus chuco* (Arecaceae). It has densely distributed surface granules that may be more pointed than in eudicot woods.

review undertaken of Piperno's existing reference collection and to our knowledge have not been previously described from plants. Four species from two genera in two families produced them; *Aphelandra sinclairiana* (Acanthaceae) and *Protium goudotianum*, *P. prancei*, and *P. rhoifolium* (Burseraceae, all ex. *Crepidospermum*). *A. sinclairiana* is a shrub native to Central America while the three *Protium* species are trees that are frequent components of, and widespread in the Amazonian forest.

Some of these phytoliths form in globular shapes with fracture lines apparent (a result of processing?). They would likely fracture in soils/ sediments and create what we term one-half and three-quarter globular shapes (Fig. 13). Others more clearly originate as usually two, or rarely more, joined siliceous bodies, fracturing at times to create one-half to three quarter globular forms (Figs. 14, 15). Others are complete or nearly so globular shapes (Fig. 16). Surface decorations are present on some and largely confined to the edge of an otherwise psilate phytolith (Figs. 17, 18). *Protium* and *Aphelandra* edge decorations can be similar. In *A. sinclairiana* decorations can extend over the entire phytolith (Fig. 19).

Ellipsoidal shapes are also produced in both *A. sinclairiana* and the *Protium* species that initially form attached to another much smaller phytolith (Fig. 20). Both globular and ellipsoidal forms survive well over time; based on information here, some are what Piperno et al. (2019) described as Forest E phytoliths in the sand fractions of Amazonian terrestrial soils.

3.7. Irregular phytoliths derived from the periphery of hair bases; the Dichapetalaceae

The Dichapetalaceae are a small family with three genera of trees and lianas that are nonetheless well-distributed across Amazonian forest (e.g., Cardoso et al., 2017). Four species of trees in the genera *Tapura* and *Stephanopodium* were studied here (Appendix A). They produced high numbers of large (>50 μm), solidly silicified diagnostic forms derived from cells that are attached to the periphery of hair bases (Figs. 21, 22). Often the end(s) that attached to the hair base are evident. The phytoliths provide informative data on forest composition; we now know that in Piperno et al. (2019) they routinely occurred in the Forest B category of the terrestrial soil sand fractions.

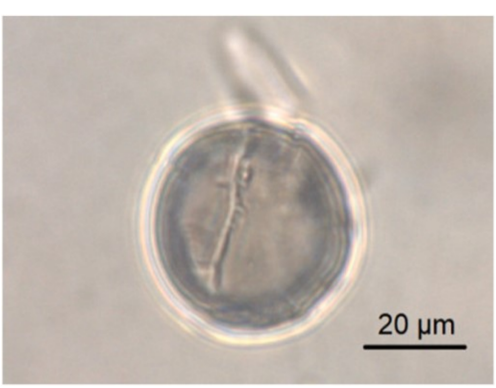

Fig. 13. A globular psilate phytolith from a leaf of *Aphelandra sinclairiana* (Acanthaceae) with a fracture line.

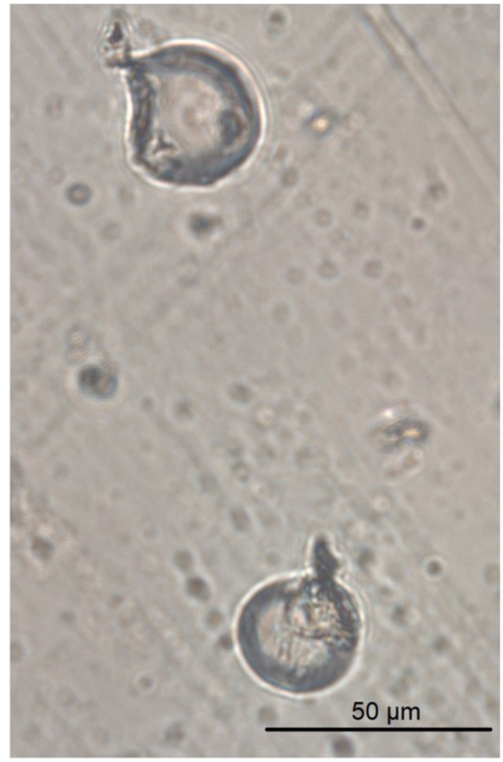

Fig. 14. Top, a three-quarters globular psilate phytolith from a leaf of *Protium prancei*. The bottom phytolith is a complete globular form.

Fig. 15. What would be described as a three-quarters globular psilate phytolith from a leaf of *Protium rhoifolium*.

3.8. Elongate phytoliths

Grasses are well-known for their types of elongate phytoliths. Some Neotropical trees, lianas, shrubs, and rarely vines produce a number of types not reported to our knowledge in Neotropical Poaceae and other

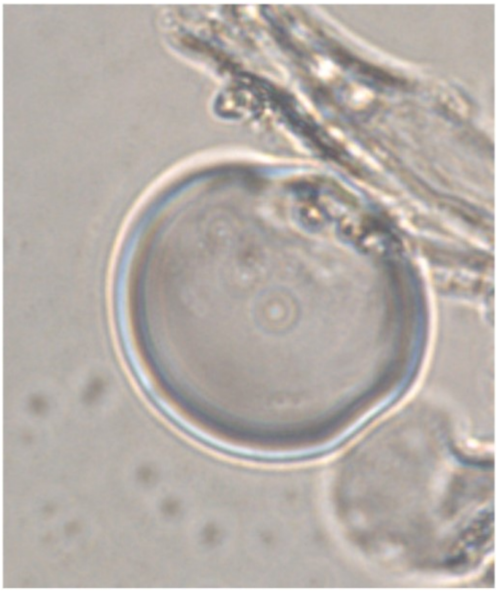

Fig. 16. A globular psilate phytolith from *Protium goudatianum*. It is 42 μm in maximum dimension.

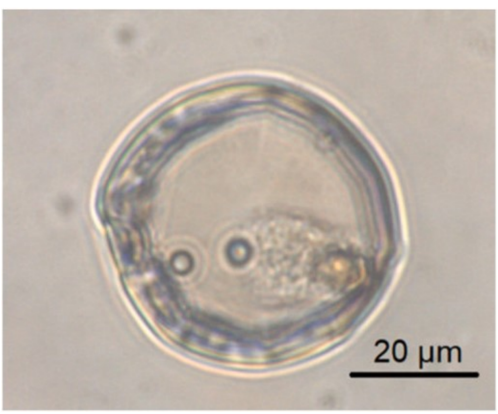

Fig. 17. A globular psilate phytolith with decorated edges from *Aphelandra sinclairiana*.

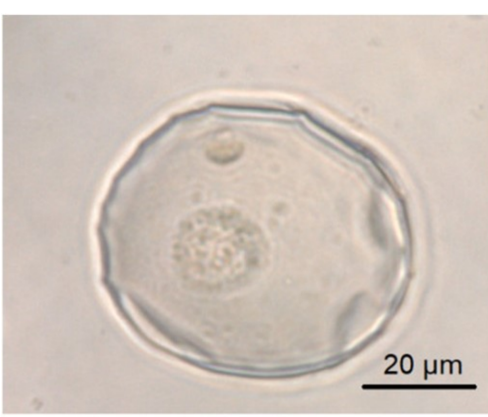

Fig. 18. A globular psilate phytolith with decorated edges from *Aphelandra sinclairiana*.

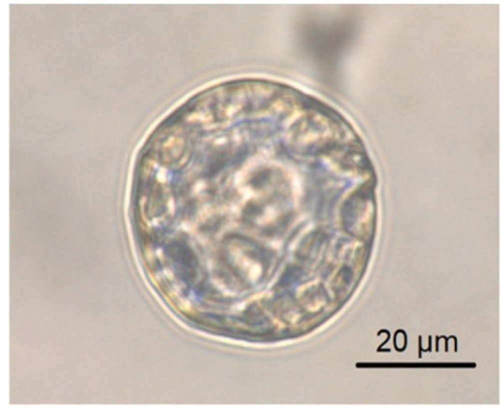

Fig. 19. A globular phytolith from *Aphelandra sinclairiana* with a completely decorated surface.

Fig. 20. An ellipsoidal psilate phytolith from *Protium prancei.*

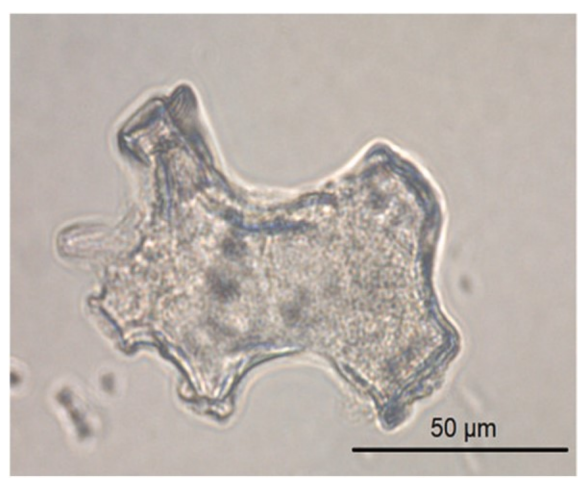

Fig. 21. A family-specific phytolith from a leaf of *Tapura guianensis.* It is also produced in *Stephanopodium* sp. Places where it attached to a hair base can be seen on the right side of the phytolith.

monocotyledons, and that within the general category elongate we placed into six shape categories; curved, tapered, rectangular, short rectangular, irregular, and with rounded ends) (Appendix A and Table 4). The phytoliths mostly occur in leaves, with some in a few species possibly from twigs. The rectangular, short rectangular, and

Fig. 22. Family-specific phytoliths from a leaf of *Stephanopodium angulatum*. They are also produced in *Tapura* sp.

irregular forms have surface and/or edge decorations termed here baculate, serrate, or striate that distinguish them from other elongates. All of these elongate types are known to survive in soils. For example, before the availability of data in this study they were described either as Forest B, arboreal elongate, or stipulate (here baculate) in Piperno et al. (2019). Each type has a limited distribution among taxa studied.

Curved or undulating forms, as their shape denotes, aren't straight-sided (Fig. 23). They were found in 14 species from eight families (Table 4). Some of these forms such as thin examples are likely sclereids, while for others derivation from tissue is unclear (Fig. 24). The thin forms (< about 10 μm wide) also typically have a greater degree of edge undulation (Fig. 24). Some curved elongates have tapered ends (Fig. 25). *Marila pluricostata* (Calophyllaceae) contributed a unique hyper-curved shape (Fig. 26). Watling et al. (2020) recorded what we term elongate curved phytoliths in the leaves of *Dodecastigma amazonicum*

Fig. 23. Elongate curved phytolith from a leaf of *Mendoncia lindavii* (Acanthaceae).

Fig. 24. Left, an elongate curved and thin phytolith from a leaf of *Tapura guianensis*. The elongate phytolith on the right is thin, slightly curved, and tapered (explanation of tapered in text).

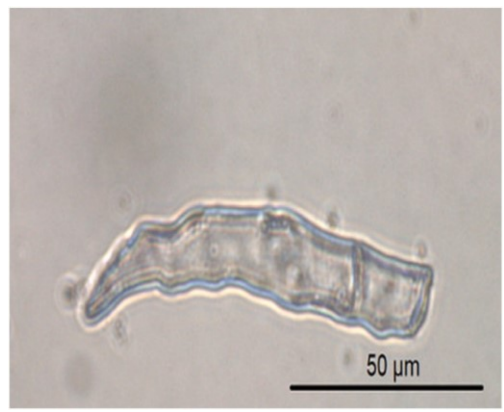

Fig. 25. Elongate curved phytolith from a leaf of *Brosimum utile*. It is also tapered, has a somewhat decorated surface, and is segmented near the right end.

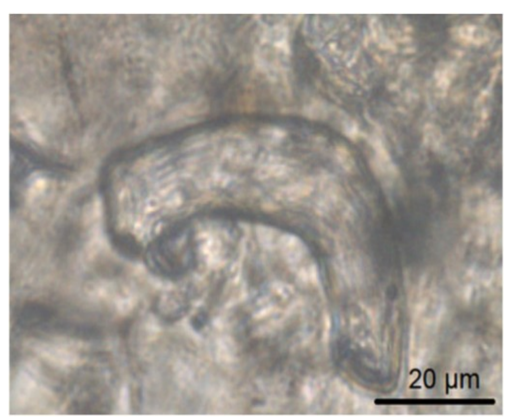

Fig. 26. A hyper-curved elongate from a leaf of *Marila pluricostata* (Calophyllaceae).

(Euphorbiaceae), a tree.

Tapered elongates have one tapered end (Figs. 27, 28). They were found in 14 species from seven families. In some taxa denoted with a (B) in Table 4, the tapered end has an appearance that a part of it has broken off, but these appear to be completely formed phytoliths (Figs. 29, 30). Variations of curved and tapered forms occur with some showing attributes of both. Another type of elongate having rounded ends was

Fig. 27. Center, right, elongate phytolith with tapered end from a leaf of *Hirtella americana* (Chrysobalanaceae). Center, left is an elongate with rounded ends discussed later.

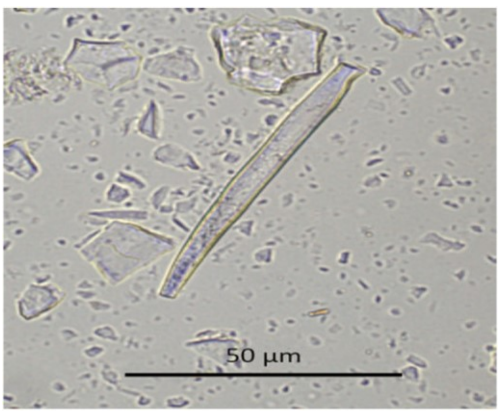

Fig. 28. Elongate phytolith with tapered end from a leaf of *Mendoncia lindavii*.

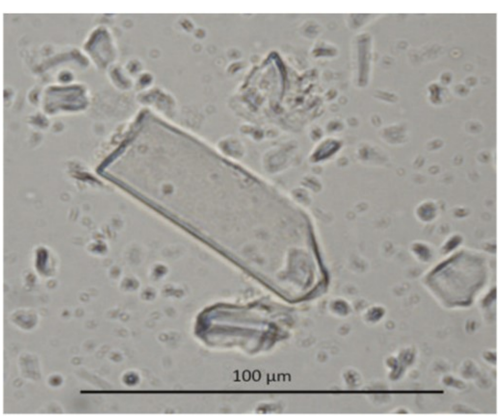

Fig. 29. Elongate tapered phytolith with a broken appearance at its end from a leaf of *Mendoncia lindavii*.

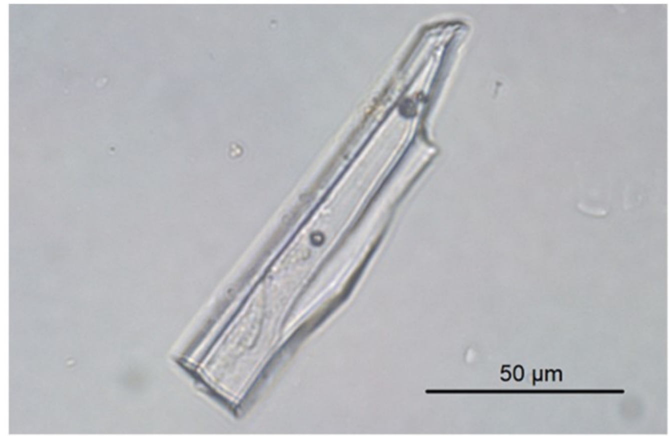

Fig. 30. Elongate tapered phytolith with a broken appearance from the stem of *Fittonia albivenis* (Acanthaceae).

Fig. 31. Phytolith with rounded ends from a leaf of *Rourea glabra* (Connaraceae). It has edge curvatures.

Fig. 32. Phytolith with rounded ends from a leaf of *Hirtella americana*.

found in a few species (Table 4) (Fig. 27 center, left, and 31, 32). Those in *Hirtella americana* and *Rourea glabra* appear distinctive to genus, with those in the latter having curvatures and indentations (Fig. 31), and the former torpedo-like or plump shapes and entire margins (Figs. 27 and 32).

Baculate surface decorations characterize shapes that we refer to as rectangular/oid, short rectangular, irregular, and with rounded ends. Collectively, the phytoliths were found in 17 species from seven families, and some, such as the short, rectangular and rounded end types, occur in a very few taxa, all of them arboreal (Table 4). In some taxa the decoration may range from baculate to clavate to tuberculate. Rectangular/oid forms may be hundreds of microns in length, some having tapered ends, while the short rectangulars are regular rectangular shapes and do not exceed about 50–70 μm in length (Figs. 33–39). The irregular forms take on a large variety of shapes, some of which after additional studies may prove to be taxon-specific (Figs. 40–44). Some of these phytoliths derive from tracheids or sclereids and with some derivation is unclear. Dickau et al. (2013) described baculate phytoliths from NE Bolivian Amazonian soils, terming them echinate tracheids. Similar forms have been found in bark of various Old and New World tropical taxa where they were described as pitted sclereids (Collura and

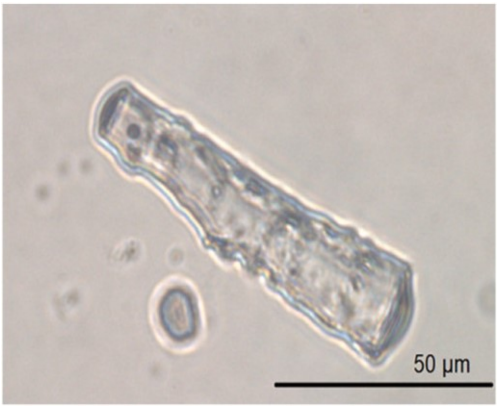

Fig. 33. Baculate rectangular phytolith from a leaf of *Brosimum utile*.

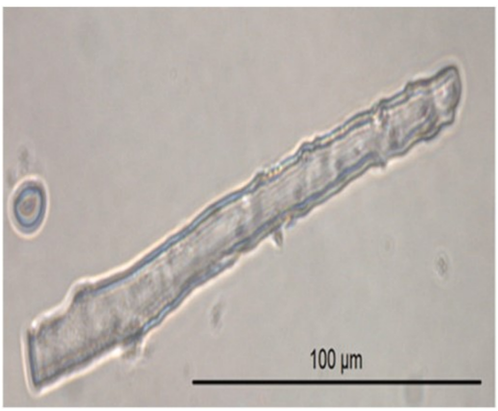

Fig. 34. Baculate rectangular phytolith from a leaf of *Brosimum utile*.

Fig. 35. Baculate rectanguloid phytolith from a leaf of *Hirtella racemosa*.

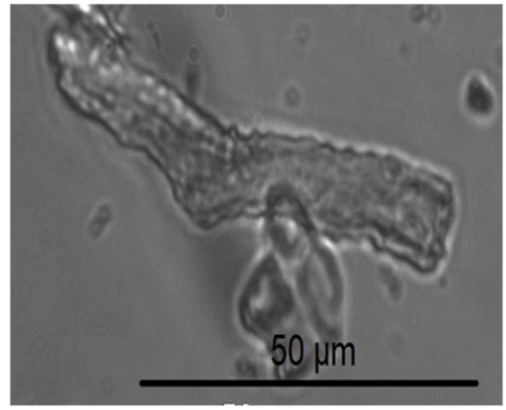

Fig. 36. Baculate rectangular phytolith from *Almanoa almerindae*.

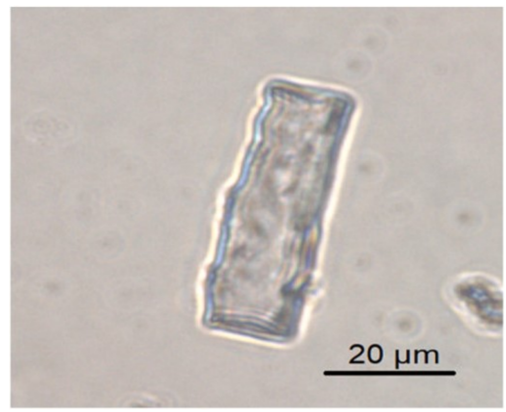

Fig. 37. Baculate short rectangular phytolith from *Brosimum utile*.

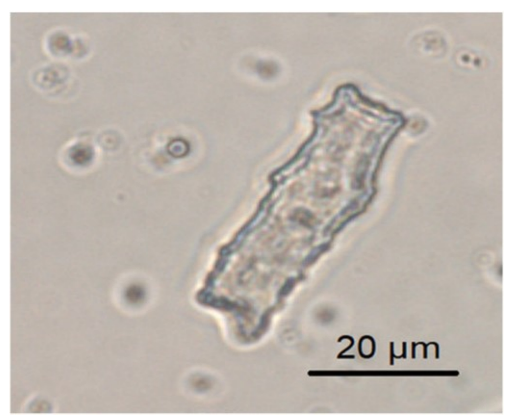

Fig. 38. Baculate short rectangular phytolith from *Hirtella racemosa*.

Neumann, 2017; Watling et al., 2020).

The baculate decoration is also found on a square-shaped phytolith we recorded only in *Hirtella gracilipes* (Chrysobalanaceae) (Fig. 45) and this species also contributed a tabular to blocky form half-decorated with a baculate pattern reported also by Watling et al. (2020) in *Hirtella racemosa*. Phytoliths with different decorations yet that we termed striate and serrate are found as well in a very few taxa with the latter isolated only from *Protium goudotianum* (Table 4) (Figs. 46, 47). It appears the various elongates described here are highly useful indicators of woody/arboreal growth, that some may be distinctive to the genus level, and others can serve to rule in or out species representations in soil/sediment contexts. The preservation of all types is good as they were consistently recorded in Amazonian terrestrial soil cores before their presence and distributions in plants were known (Piperno et al., 2019).

3.9. Facetate phytoliths

Distinctive large phytoliths of different shapes with facetate surface decorations are well-known from the leaves of the Annonaceae and the forms commonly appear in Neotropical soils/sediments (e.g., Piperno, 1988; 2006 et al., 2015, 2019; Dickau et al., 2013; Watling and Iriarte, 2013; Watling et al., 2020). We continue to differentiate three shape categories for facetates; spheroidal (formerly spherical to aspherical), elongate, and irregular (Piperno, 2006). We have isolated spheroidals

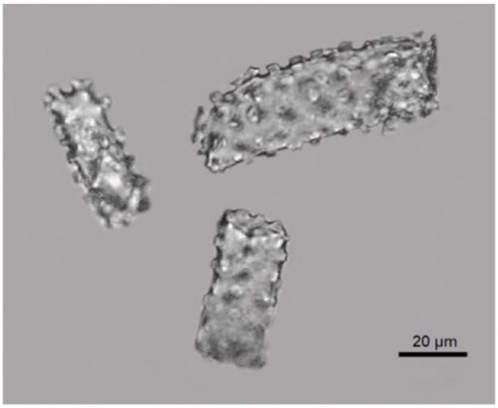

Fig. 39. Baculate phytoliths from *Castilla tunu*. Left and bottom, short rectangular; upper right, rectangular. Reprinted from Piperno (2006).

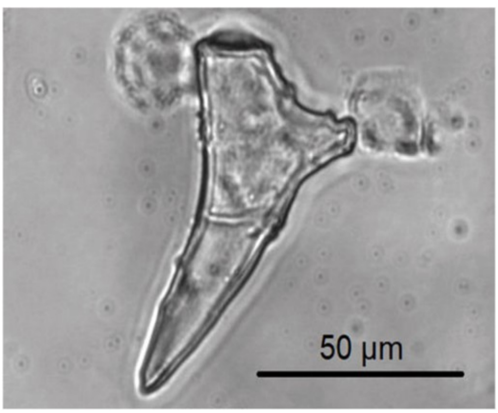

Fig. 40. A baculate irregular phytolith from *Brosimum utile*.

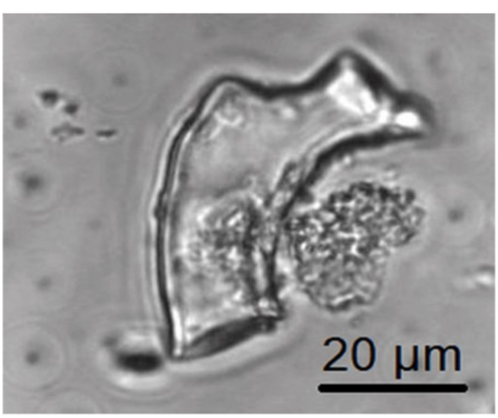

Fig. 41. A baculate irregular phytolith from *Brosimum utile*.

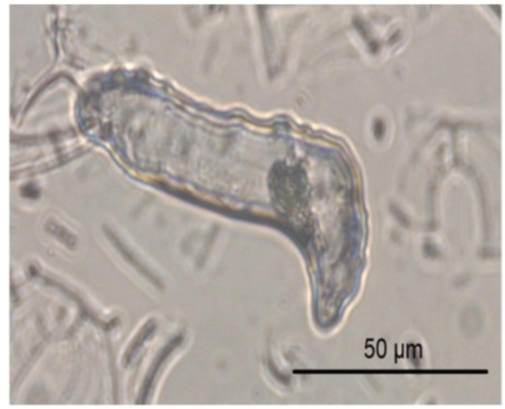

Fig. 42. A baculate irregular phytolith from a leaf of *Stephanododium angulatum*.

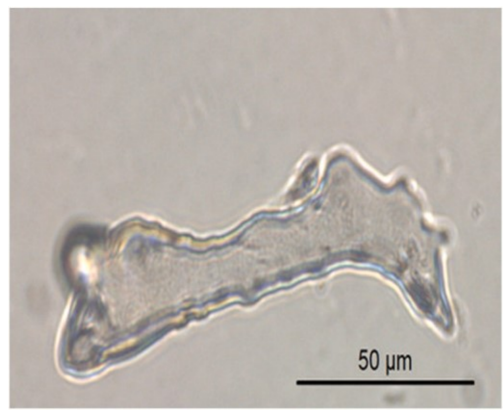

Fig. 43. A baculate irregular phytolith from a leaf of *Tapura guianensis*.

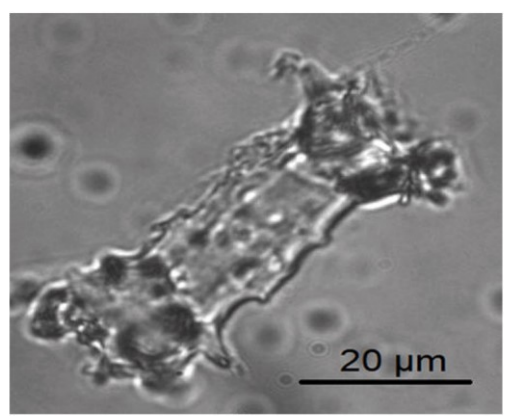

Fig. 44. A baculate irregular phytolith from a leaf of *Tetragastris unifoliata*.

from the genera *Oxandra* and *Unonopsis*; elongates in *Guatteria* and *Oxandra*; and irregulars in *Guatteria* and *Oxandra* (Figs. 48–50). In a study of *Annona*, *Anaxagorea*, and *Dugetia*, Ramirez (2018) recorded elongated facetates only in *Anaxagorea*, while Watling and Iriarte (2013) found irregular facetates in *Guatteria guianensis* (a widespread species in the Amazon), and spheroidal facetates in *Unonopsis stipitata*. Watling et al. (2020) found more or less spheroidal facetates in *Bocageopsis*. Additional comparisons will determine if they are distinguishable from those in *Oxandra* and *Unonopsis.*

We define here a presently unique type of facetate elongate with markedly tapered ends in *Guatteria amplexifolia* (Fig. 51). In the leaves and wood of three Annonaceae genera studied here, *Annona*, *Bocagea*, and *Duguetia* spp., we found no facetates or other phytoliths of taxonomic importance, and no phytoliths confusable with Annonaceae facetates occurred in other families (Appendix A). No facetates and often no phytolith formation occurred in several species of *Annona*, *Bocagea*, *Desmopsis*, *Rollinia*, and *Xylopia* studied by Piperno previously.

The Annonaceae are one of the ten most speciose families of trees in Amazonia, and from several studies we have now a significant amount of data regarding which genera of the family produce the faceted forms, and in which shapes. Taxa of considerable dietary importance in the family such as *Annona* spp. lack facetates or other phytoliths of useful

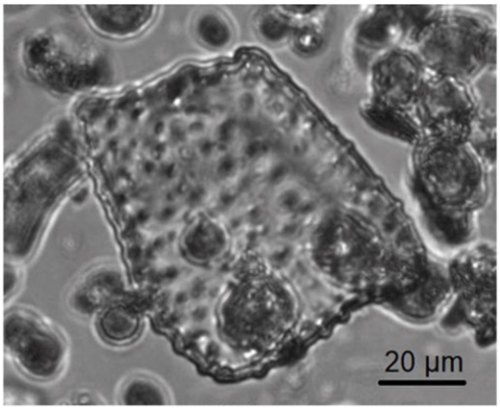

Fig. 45. A baculate square phytolith from terrestrial soil from Site 127, 0–20 cm level, in a transect sampled from Porto Velho to Manaus, Brazil (Piperno et al., 2019). It was not identified to a taxon in that publication and is likely to be from *Hirtella*.

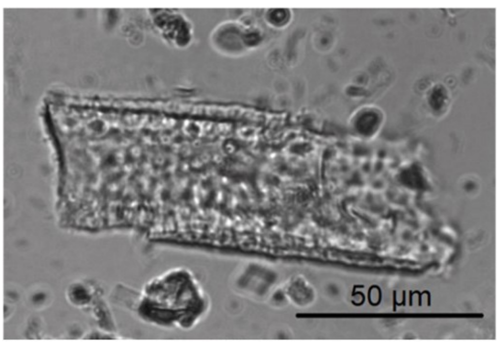

Fig. 46. An elongated phytolith with a serrated edge from *Protium gaudatianum*.

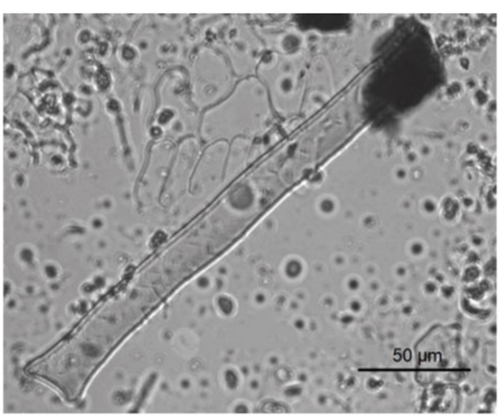

Fig. 47. An elongated phytolith with a striate surface from *Mabea occidentalis* (Euphorbiaceae).

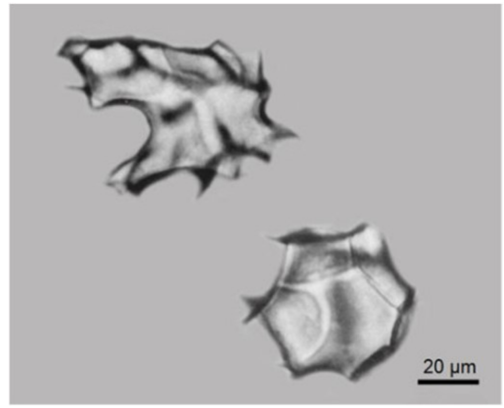

Fig. 48. Facetate phytoliths from *Guatteria dumetorum*, upper left and *Unonopsis pittieri*, lower right, both Annonaceae. Reprinted from Piperno (2006).

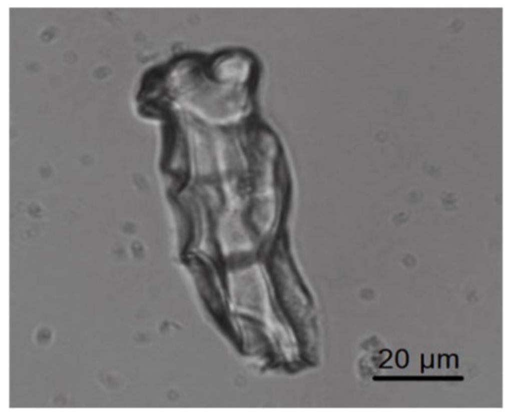

Fig. 49. A facetate elongated phytolith from *Oxandra longipetala*.

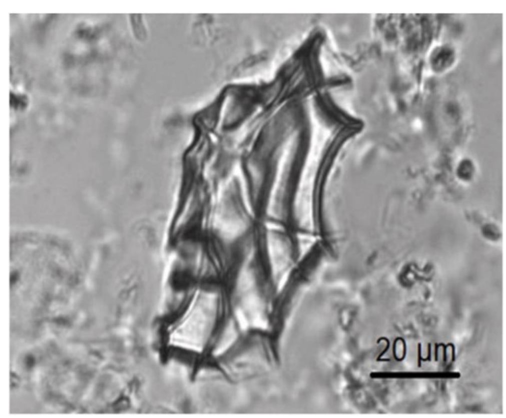

Fig. 50. A facetate irregular phytolith from *Oxandra panamensis*.

morphology (Table 5). However, *Anaxagorea*, *Bocageopsis*, *Guatteria*, *Oxandra*, and *Unonopsis* spp. are frequent forest components and all five genera have hyperdominant species (ter Steege et al., 2013). It is clear the facetates survive well in soils/sediments, providing valuable information on forest composition and change in Amazonian and other Neotropical contexts (e.g., Dickau et al., 2013; Piperno et al., 2019).

3.10. Phytoliths derived from fruits and seeds

Phytoliths formed in the epidermis of fruits and seeds from Neotropical monocotyledons, basal angiosperms, and eudicotyledons have been well-described (e.g., Piperno, 1988, 1989, 2006; Chen and Smith, 2013). They are often diagnostic to the family or genus, and in some cases as in domesticated plants and possibly other species, to the species level (Table 1). In eudicotyledons the Acanthaceae vine/liana genus *Mendoncia* and trees from the Burseraceae (*Bursera*, *Protium*, *Tetragastris*, *Trattinickia*), and Cannabaceae (*Celtis*) are among those with family- and genus-level diagnostics (Figs. 52–55) (Piperno, 1988, 2006; Watling et al., 2020). Watling et al. (2020) suggested from their analysis of *Protium* and *Tetragastris* spp. fruits that overlap between the two specimens was sufficient to consider the phytoliths family- and not

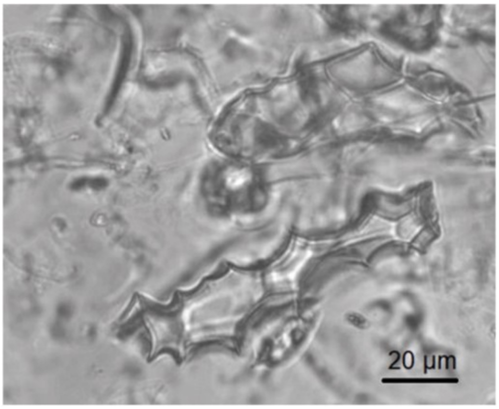

Fig. 51. Two facetate elongates from *Guatteria amplexifolia*. The bottom phytolith has a markedly tapered end.

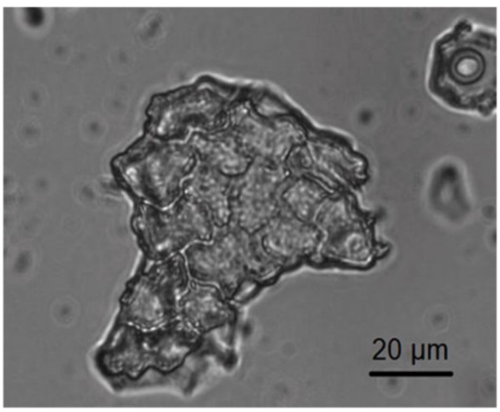

Fig. 52. Articulated phytoliths from a seed of *Celtis schippi* (Cannabaceae) with the distinctive *Celtis* surface decoration.

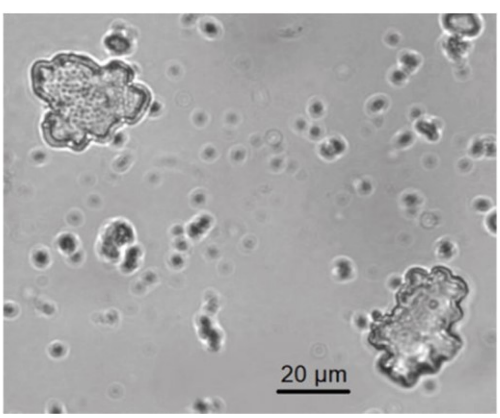

Fig. 53. Phytoliths from a seed of *Celtis spinosa*. Shape differences probably allow differentiation of the taxa.

genus-specific. We believe, judging from the images they displayed, that in edge and surface attributes the phytoliths do bear characteristics of each respective genus (phytolith margin sloping characteristics that also inform genus discrimination are not visible in the images). Additional work will clarify this issue.

Outside of the Arecaceae, phytoliths were rare or absent in fruits/seeds of species studied here and no diagnostics or forms overlapping diagnostics described from other families occurred (Appendix A). As in previous studies, few to no seed/fruit phytoliths occurred in taxa where

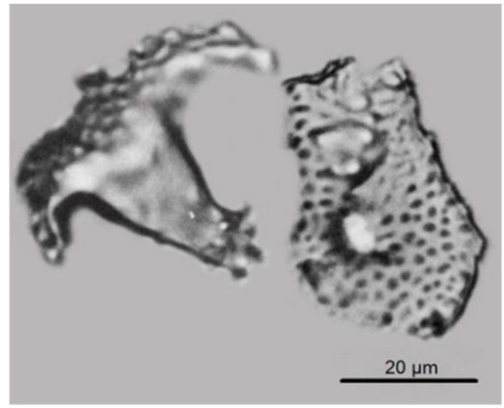

Fig. 54. Fruit phytoliths from *Tetragastris panamensis* (Burseraceae). Right phytolith is a surface view and left phytolith a side view. Reprinted from Piperno (2006).

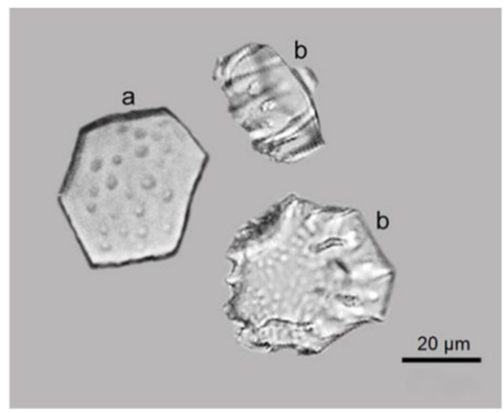

Fig. 55. Seed phytoliths from *Bursera simaruba* (a) and Protium panamense (b). The latter are in two different orientations. Reprinted from Piperno (2006).

leaves are not considerable accumulators, while in some taxa the converse is true. Phytoliths occurred in all palm fruits tested, for example. Although many phytoliths from eudicotyledon fruits and seeds are solidly silicified, those diagnostic to family and genus so far appear to be under-represented in soils and sediments (Dickau et al., 2013; Watling et al., 2016, 2020; Piperno et al., 2015, 2019). This is likely because their per/plant phytolith production is considerably lower than for leaves and other structures.

3.11. Hair cells and hair bases

Many eudicotyledons are well-known to silicify their hair cells (trichomes) and hair bases, and the phytoliths are often widely redundant among taxa. There are, however, forms found to be more limited in distribution with some appearing to be distinctive to genus and species (e.g., some Aristolochiaceae, Burseraceae, Cannaceae, Cucurbitaceae, Dilleniaceae; see Piperno, 1988, 2006). Six species in this study and one in Watling et al. (2020) produced hair cell or base phytoliths and all found here (in *Justicia*, *Aristolochia*, *Centrosema*, *Gunnera*, and *Pleurisanthes* spp.) (Appendix A) were of no taxonomic value. Therefore, previous information on the diagnostic potential of certain others, above, does not change. However, a factor that appears to hamper their utility in vegetational reconstruction is their survivability, as many are not solidly silicified. With the exception of a few taxa such as *Trema micrantha* (Cannabaceae) and *Curatella americana* (Dilleniaceae) (e.g., Piperno, 1985, 1988; Piperno and Jones, 2003; Piperno unpublished data) (Fig. 56), they are not being recovered with any frequency from

Fig. 56. A hair cell phytolith from the leaf of *Trema micrantha*. It is solidly silicified, curved, and stubby at the half closest to the base. The phytolith is 60 μm long.

soils and sediments. Nonetheless, those taxa are of considerable ecological importance, *T. micrantha* being a frequent shrub/tree of early secondary growth, including swidden fallows (Gomes et al., 2020b), and *C. americana* a common savanna shrub/tree.

3.12. Sclereid phytoliths

Sclereid phytoliths derive from schlerenchyma cells that function in plants for mechanical support. They are usually associated with vascular tissue and may occur in leaves or fruits. In the tropical flora they are not produced in many phytolith-accumulating taxa and have been found to occur in widely unrelated woody/arboreal taxa, but no monocotyledons (e.g., Piperno, 1988, 2006; Kealhofer and Piperno, 1998; Watling et al., 2020). In shape, sclereids are usually irregularly elongated, sometimes branched, and may have psilate or fluted surfaces (Fig. 57) (Piperno, 2006). In new plants studied here sclereids of these shapes and surface patterns occurred in two *Dussia* species (Fabaceae), and the unrelated *Piranhea longipedunculata* (Picrodendraceae), all of which are trees (Appendix A). Sclereid phytoliths survive well in soils/sediments and the accumulated data attest they are useful indicators of woody, especially arboreal growth.

3.13. Cystoliths

Cystoliths, formed as outgrowths of specialized epidermal cells and here mainly composed of silicon dioxide, occur in some Neotropical Acanthaceae, Boraginaceae, Moraceae, and Urticaceae (Piperno, 1988, 2006). They are large, well-known phytoliths with verrucate, echinate,

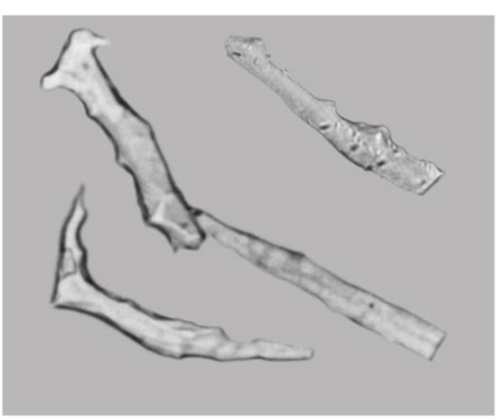

Fig. 57. Sclereid phytoliths from *Hirtella triandra* (group of three on the left) and *Goniothalamus marcani* (SE Asia Annonaceae) at the top, right. Sizes of these types typically range from 50 to >90 μm in length. Reprinted from Piperno (2006).

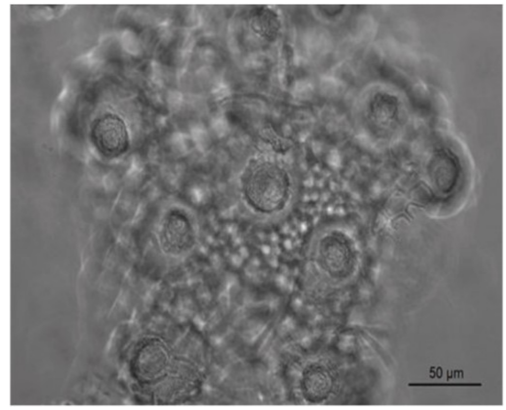

Fig. 58. Spheroidal cystoliths from *Cordia alliodora* embedded in epidermal tissue.

granulate, or tuberculate surface decorations, and spheroidal, ellipsoidal or irregular shapes depending on the particular taxon producing them (Fig. 58, see Piperno, 2006, Fig. 2.12). Some appear diagnostic to genus or family (Piperno, 1988, 2006). None were observed in the new species studied here (Appendix A), further informing their distributions and taxonomic significance in the Neotropical flora. However, their utility in Neotropical vegetational reconstruction may be hampered by their survivability, as they have been infrequently recovered from modern (surficial) and ancient soils and sediments (e.g., Dickau et al., 2013; McMichael et al., 2012a,b; Piperno et al., 2019; Watling et al., 2016, 2020).

4. Discussion

The Neotropical flora is recently estimated to harbor between 18,000 and 25,000 tree species (Slik et al., 2015), the Amazonian forest flora about 14,000 seed plants and 6700 trees (Cardoso et al., 2017). This at first look could make the task of building reference collections that confidently identify ancient representatives seem unending. However, a considerable amount of research, starting with foundational studies carried out many years ago on numerous families including many eudicotyledons (e.g., Crűger, 1857;Debary, 1884; Mobius, 1908; Solereder, 1908; Netolitzky, 1929; Frey-Wyssling, 1930–here sub-tropical and tropical plants were noted as particularly good phytolith producers; Bigalke, 1933;Tomlinson, 1961,1969) shows that production and morphological patterns of many phytoliths are consistent across flora. Significant variability in intra-specific production appears largely to do with silicification of foliage tissue such as the surface epidermis (polyhedral and jigsaw shapes) and types of vascular elements that can be dependent on the environmental conditions of growth, and in any case are mostly un-useful taxonomically. Also, mature specimens of any plant organ should be analyzed to ensure the most representative results.

With the addition here of many eudicotyledon species including from unstudied families and genera, we found no morphological overlap with diagnostic forms previously documented from other Neotropical taxa. A detailed review of Piperno's existing reference collection defined additional phytolith types useful for documenting arboreal/woody growth that occur in a limited number of families and genera (e.g., elongates, globulars). Phytoliths document a diversity of arboreal/woody taxa along with ferns and monocotyledon understory herbs in Neotropical contexts, with family, genus, and possibly even species-level diagnostics. Future research will likely reveal cases where types of phytoliths that occur in a number of unrelated taxa and achieve good representation in soils/sediments, such as rugose and ornate spheroids, and elongates and globulars, are more widely produced. The present evidence indicates they should be found in a relatively limited number of additional taxa and retain their stature as useful indicators of woody/arboreal growth.

With relation to different structures of plants, future sampling of fruits and seeds will most profitably focus on families and genera with appreciable amounts of leaf phytoliths, as others are unlikely to yield productive data. Neotropical barks, roots, and stems need considerably more research. Collura and Neumann's (2019) extensive study of bark phytoliths in African plants reveals a number of taxonomically useful forms that may bode well for future Neotropical work. Phytoliths in roots are currently best studied in the Poaceae and a few other monocotyledons. Interestingly Lux et al. (2020) describe spheroidal phytoliths in date palm roots that appear the same or nearly so as echinates in aerial parts of palms. Information in eudicotyledons is sparse and future studies will reveal whether root phytoliths are truly rare in eudicots, or instead may provide another line of evidence.

An important debate is taking place over the scale and intensity of pre-Columbian modifications of the Amazonian forest, including by tree species management and enrichment (e.g., Erickson, 2008; Scoles and Gribel, 2011; McMichael et al., 2012a,b; Levis et al., 2012, 2017; Balée, 2013; Heckenberger, 2013; Clement et al., 2015a,b; McMichael et al., 2015; Piperno et al., 2015, 2019; Watling et al., 2017; Ferreira et al., 2019). Phytolith data are informing the issues and with improvements in reference collections will increasingly do so. Apparent new family- and genus-diagnostic phytoliths uncovered here that will help speak to past Amazonian forest structure/diversity and human influences on them include from the Arecaceae (*Prestoea schultzeana*, perhaps species-specific), Chrysobalanaceae (*Hirtella*), and Dichapetalaceae (*Stephanopodium*, *Tapura*). With regard to the phytolith morphologies that have limited distributions among different taxa, modern vegetation surveys that have been carried out in many regions may sometimes aid in resolving phytolith overlap by pointing to the relevant species' presence or absence in a study area. For example, large rugose spheroids with undulating or bulging surface textures are presently documented in two tree species, *Sorocea guilleminiana* and *Licania jefensis* (Table 2). The latter is native to Central America, opening the possibility that the former can be identified in some Amazonian contexts. At the least, these and other phytoliths can be employed to rule in or out representation of a taxon and follow its possible changes in abundance through time.

Although many major economic tree species don't produce phytoliths of diagnostic utility (Table 5), important exceptions occur. For example, palm phytoliths are among the most prolifically produced, preserved, and diagnostic. Major economic species such as *Oenocarpus bataua*, *O. bacaba*, *Euterpe oleraceae*, and *E. precatoria*, all hyperdominants today, can be discriminated on the basis of size from the small number of other palms producing the same phytolith type (Table 3) (see also Marcote Rios et al., 2016; Piperno et al., 2019; Watling et al., 2020). In this study the *Oenocarpus* species also have considerably larger mean sizes than *Euterpe* species. It will be possible to study the scale and degree of pre-Columbian influence on them and elucidate questions concerning the reasons for their present distributions and abundances (see Piperno et al., 2019). As palm phytoliths continue to be more intensively studied other genus-level diagnostics may arise.

Hevea brasiliensis is another tree of considerable economic importance, and presence of a type of ornate phytolith in its roots was unexpected. Considerable work is required on arboreal/woody root phytoliths, but the potential now exists to at least rule in or out *Hevea* presence in soils/sediments and possibly follow changes in its abundance through time. We note also that *Brosimum utile*, another major economic and hyperdominant taxon with a widespread distribution in Amazonia today (Cardoso et al., 2017), is among the three species in our study with the baculate short, rectangular phytolith (Table 4). The tree is thus amenable to analysis of its past distribution and abundance, including by using modern tree survey data as discussed above.

5. Conclusions

This work considerably expands modern Neotropical phytolith reference collections of eudicotyledon species including with increased attention to non-arboreal members of tropical forest. The strengths and weaknesses of phytolith production and taxonomic specificity in paleoecological reconstruction are better understood, along with how they complement and improve pollen-based interpretations. How, when, and to what extent pre-Columbian populations modified the Amazonian forest and influenced its species diversity and abundances have been enduring questions. They again are under considerable debate and we expect this study will contribute significantly to informing the issues.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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