

## Phytolith Production in the Malvales

(Bixaceae, Bombacaceae, Malvaceae, Sterculiaceae, Tiliaceae)

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Note on the text: This overview was written in 2008 as a sample chapter for a planned book on the *Phytoliths in the Flora of Ecuador Project*. During the project the MU lab tested plant groups (families, genera, and species) not previously studied for production of phytoliths, examined Ecuadorian representatives of previously studied plant groups, and examined replicate samples of important economic and indicator species. Phytolith production/non-production patterns by botanical orders and families for plants studied during the project can be compared to data from other studies, to investigate the level at which distinctive phytoliths are “universally” diagnostic (Pearsall 2000).

### BIXACEAE

This family is included in the Flacourtiaceae (Violales) by some authors. The Bixaceae is a family of three genera and 16 species, indigenous in the tropics (Mabberley 1997). Three genera and six species occur in Ecuador (Jørgensen and León-Yáñez 1999). *Bixa orellana* L., the spice and dye *achiote*, was studied (Table 1; standard phytolith abundance codes used in the text and tables are: VR, very rare; R, rare; M, moderate; C, common; A, abundant; VA, very abundant.). It is native and cultivated in Ecuador, and occurs as a shrub, treelet, or tree from 0-1500 m in coastal, Andean, and Amazonian settings. It was selected for study because of its utility, and occurrence in the archaeological record in Ecuador (Pearsall 2004). Research conducted prior to this project found *Bixa* to be a non-producer of phytoliths (Piperno 1988).

Fruit specimen 2638 did not yield extract; the others produced low quantities of silica. Some silicification of tissues occurs in the fruit, including both quadrilateral and non-quadrilateral epidermal cells. An irregularly 3-D non-quadrilateral with rugulose surfaces (22IBd, VR-R) is being explored as a generalized fruit/seed indicator (Plate 1, a). Straight (140II, M) and undulating (140I, VR) transport elements are also silicified. Undulating transport elements are commonly produced in some fruit and seeds, and may serve as a generalized indicator of those tissues (Chandler-Ezell et al. 2006). An ashed fruit specimen (2904) produced very abundant yellowish small smooth spheres that appear to be oil droplets. Achiote seeds, both chemically oxidized and ashed, also produced apparent oil droplets along with silicified undulating transport elements (140I, VA) and small diameter bundled fibers (150I, M), which are a generalized fruit and seed indicator (Plate 1, b).

There are small smooth spheres in achiote that appear silicified (i.e., are not yellow in appearance, but light purple and opaque, 80IAa1, VR-M) (Plate 1, c). This is likely the round to sub-round planar psilate silica phytolith described by Korstanje and Babot (2007) for achiote seed. The diagnostic value of this type is limited; small smooth opaque spheres occur in the Chrysobalanaceae (e.g., in *Hirtella triandra*, Piperno 1988) and somewhat larger ones in the Cannaceae (MU database, discussed with Zingiberales), for example. Imperfect, transparent spheres (i.e., less well-silicified; 80IAb, c) have a wide distribution, and are not a useful type.

## BOMBACACEAE

There are 15 genera and 47 species of the Bombacaceae in Ecuador (Jørgensen and León-Yáñez 1999). The Bombacaceae is a tropical family of large trees, often with soft light wood and thickened trunks (Mabberley 1997). Four of the principle genera of the family, *Ceiba*, *Matisia*,

*Pachira*, and *Quarariba*, occur in Ecuador. Seven genera were studied: one species each of *Ceiba*, *Huberodendron*, *Ochroma*, *Pachira*, *Pseudobombax*, and *Quarariba*, and four species of *Matisia* (Table 2). Prior to the beginning of this project, four genera that occur in Ecuador had been tested (*Bombacopsis*, *Cavanillesia*, *Ceiba*, and *Ochroma*) (Piperno 1988; Runge 1996; Kealhofer and Piperno 1998).

### *Ceiba*

Four species of *Ceiba* occur in Ecuador; *C. pentandra* (L.) Gaertn., the common coastal species that also occurs in the Amazon (Jørgensen and León-Yáñez 1999), was studied. It is likely that the wood specimen (2866) is also this species.

Neither the leaf nor inflorescence of *Ceiba pentandra* produced silica (no extract recovered). Piperno (1988) also found *Ceiba pentandra* to be a non-producer, but Runge (1996) recovered calcium oxalate druses and silicified epidermis (polyhedral-shaped) with thickened cell walls and a stippled surface from an African specimen of this species.

The *Ceiba* wood specimen produced tabular crystals with granular surfaces (100Va, VA) (Plate 2, a), probably composed of calcium carbonate, and also spherical cystoliths (100IA, VA) of various sizes (Plate 2, b). Cystoliths are considered generalized arboreal indicators (Piperno 1988); the status of tabular crystals remains to be determined.

### *Huberodendron*

*H. patinoi* Cuatrec., a tree native to the coast, is the single representative of the genus in Ecuador (Jørgensen and León-Yáñez 1999). *Huberodendron* had not been studied prior to this project. No diagnostic phytoliths were produced in the inflorescence except cystoliths (100Cb,

elongated, VR), which are generalized arboreal indicators. Silicification was higher in the leaf, in which a genus-level diagnostic phytolith was identified, a hairbase composed of rounded cells with a large, rounded central cell (40IVBa201c, M) (Plate 2, c). Sclereids (110), which are generalized arboreal indicators, were also present (Plate 2, d). A variety of non-diagnostic phytoliths were produced (Table 2).

### *Matisia*

*Matisia* had not been studied prior to this project. There are 18 tree species in Ecuador (Jørgensen and León-Yáñez 1999).

*Matisia cf. alata* Little, a tree endemic to the Ecuadorian coast, produced only non-diagnostic phytoliths in the leaf. Spherical yellowish bodies that appeared to be oil droplets were very abundant. Phytoliths with some diagnostic value, small nodular spheres (80ICa1, M, 8-16 microns), occur in the inflorescence (Plate 2, e). Nodular spheres were first described in the Marantaceae by Piperno (1988, e.g., *Maranta arundinacea*, *Stomathe lutea*) and later by Kealhofer and Piperno (1998) and Runge (1999, *Halopegia azurea*), and are now documented in the Bombacaceae.

*Matisia coloradorum* Benoist, another tree endemic to the Ecuadorian coast, produced no diagnostic phytoliths in the leaf, except for polyhedral non-quadrilateral epidermis (20IBa, R), which is a generalized dicot indicator (e.g., Piperno 1988). The inflorescence produced no diagnostic phytoliths.

*Matisia cordata* Bonpl. is a tree native and cultivated in the Ecuadorian coast, Andes, and Amazon. A family-level diagnostic occurs in this species, 120IIA (R), stomata with four large, turgid subsidiary cells (Plate 2, f). A generalized dicot indicator (polyhedral non-quadrilateral

epidermis, 20IBa, M) and an arboreal indicator (sclereid, 110, R-A) are also present. A second phytolith type first identified in the Marantaceae by Piperno (1988) was found in *M. cordata*, nodular conical bodies (80IIIB, R) (Plate 2, g). Small nodular spheres were also present. Irregular rugulose epidermis (22IBd, R) was documented.

*Matisia longipes* Little, native to the Ecuadorian coast, produced only a trace of extract in the inflorescence. Rugulose non-quadrilateral epidermis (22IBd, C) and a family-level diagnostic, stomata 120IIA (VR), were present. The leaf was highly silicified. One interesting form observed was a facetate hemisphere (80IFb202, R), first identified in *Pseudobombax millei* (see below), and now determined to be a family-level diagnostic (Plate 2, h). Similar, but distinguishable hemispherical to elliptical facetate phytoliths occur in the New World Burseraceae and Ebenaceae (MU Phytolith Database; also Piperno 1988, *Protium panamense*, Burseraceae), and more irregular forms are documented in the Annonaceae (e.g., Piperno 1988). Two smooth hairs appear to be species-level diagnostics: short conical hair (40IIIAa202Ba2, R) and long, thin hair (40IIIAb200Ab2, C) (Plate 2, i, j). Other distinctive forms include sclereids (110, VR).

### *Ochroma*

*Ochroma pyramidalis* (Cav. ex Lam.) Urb. is the single Ecuadorian species in the genus (Jørgensen and León-Yáñez 1999). This tree is native and cultivated on the coast and in the Amazon. *Ochroma pyramidale* Sw. was studied by Kealhofer and Piperno (1998), and found to be a non-producer of phytoliths.

The inflorescence produced very rare small nodular spheres (80ICa1), as well as non-diagnostic phytoliths. The leaf produced sclereids (110, R, generalized arboreal indicators).

## *Pachira*

*Pachira aquatica* Aubl. is one of three Ecuadorian species in this genus, and is native to the Amazon (Jørgensen and León-Yáñez 1999). *Pachira* had not been studied prior to this project. The inflorescence produced only non-diagnostic phytoliths. The leaf produced some interesting forms. Hair base 40IVAA300 (R) is a genus-level diagnostic (Plate 2, k). It has short, regular appendages from a solid, angular rim. The center is a smooth rounded concavity. Distinctive stomata with four subsidiary cells outside the guard cells (120IIA, M-A) were silicified in the leaf. These were also observed in *Matisia longipes*, and are a family-level diagnostic. Broken examples (20VD, C, pieces of 120IIA) were also present (Plate 2, l). Sclereids (110, C) occur in the leaf.

## *Pseudobombax*

*Pseudobombax* had not been studied prior to this project. There are three Ecuadorian species, all native to the coast (Jørgensen and León-Yáñez 1999). *Pseudobombax millei* (Standl.) A. Robyns was studied. Leaf and inflorescence produce similar phytoliths, but silicification is higher in the leaf. Facetate hemispheres (80IFb202) are common in the leaf and moderate in the inflorescence. These are diagnostic at the family level since they also occur, rarely, in *Matisia longipes*. Ruminant nodular spheres (80ICc) are very abundant in the leaf and abundant in the inflorescence (Plate 2, m). The same kinds of spheres are produced in *Costus guaniensis*, in the Zingiberaceae, leaving this a mixed Bombacaceae/Zingiberaceae type. Cystoliths, including bulbous (100ID) are very abundant in the leaf and rare in the inflorescence. These are generalized arboreal indicators, as are sclereids (110). In addition, the leaf only produces single-outline trichomes with an enclosed verrucose cystolith (40IIBc3, C) (Plate 2, n), which are a

genus level diagnostic, and small smooth nodular spheres (80ICa1, VA; mixed Marantaceae/Bombacaceae type).

### *Quararibea*

Four species of *Quararibea* are native to Ecuador, either on the coast or in the Amazon (Jørgensen and León-Yáñez 1999). The specimen studied was collected by Pearsall in Manabí Province, Ecuador (E1079) and identified by P. Bech and B. Ollgaard as *Quararibea* cf. *grandifolia* Little. *Q. grandifolia* is considered synonymous to *Matisia grandifolia* Little by Jørgensen and León-Yáñez (1999), and is not one of the four *Quararibea* species listed for the country.

Whether considered *Quararibea* sp. or *Matisia grandifolia*, specimen E1079 produced a diagnostic hair base (40IVAA201Aa, M), as well as a diagnostic segmented hair (40IIIBa203A, M) (Plate 2, o, p). Sclereids (110, C) and spherical cystoliths (100IA, VA), both generalized arboreal indicators, were present, along with epidermal non-quadrilateral 20IAa (M) or anticlinal epidermis, a dicot indicator.

### Family Summary and Discussion

The Bombacaceae, a tropical family of large trees, produces the following diagnostic phytoliths:

**40IIBc3** non-armed trichome with spherical verrucose cystolith as base. *Pseudobombax millei* leaf. Genus-level diagnostic

**40IIIAa202Ba2** medium unicellular hair, curved, with smooth surface and bulbous base. *Matisia longipes* leaf. Species-level diagnostic

**40IIIAb200Ab2** long unicellular hair, non-armed, no interior space. *Matisia longipes* leaf. Species-level diagnostic

**40IIIBa203A** segmented hair, non-armed, with a broad tip. *Quariba* cf. *grandifolia*/M. *grandifolia* leaf. Genus- or species-level diagnostic

**40IVAa201Aa** hairbase with discernable center and long radiating appendages. *Quariba* cf. *grandifolia*/M. *grandifolia* leaf. Genus- or species-level diagnostic

**40IVAa300** hairbase with discernable center and short radiating appendages. *Pachira aquatica* leaf. Genus-level diagnostic

**40IVBa201c** hairbase comprised of rounded cells, with a single row of attached cells. *Huberodendron patinoi* leaf. Genus-level diagnostic

**80ICa1** small smooth nodular sphere. *Matisia* cf. *alata* (inflor), *M. cordata* (leaf), *Ochroma pyramidalis* (inflor), *Pseudobombax millei* (leaf). Mixed Marantaceae/Bombacaceae type.

**80ICc** ruminant nodular sphere. *Pseudobombax millei*, leaf and inflorescence. Mixed Zingiberaceae/Bombacaceae type.

**80IFb202** faceted hemisphere with irregular concavities. *Matisia longipes* leaf, *Pseudobombax millei* leaf, inflorescence. Family-level diagnostic.

**80IIIB** nodular conical. *Matisia cordata*, leaf. Mixed Marantaceae/Bombacaceae type.

**120IIA** stomata with four large turgid subsidiary cells. *Matisia cordata* (leaf), *M. longipes* (inflor), *Pachira aquatica* (leaf). Family-level diagnostic. Broken (20VD): *Pachira aquatica* (leaf).

In addition, the following more generalized indicators are present:

**20IAa** epidermal non-quadrilateral, anticlinal cells. *Quararibea* cf. *grandifolia* (leaf).

**20IBa** epidermal non-quadrilateral, polyhedral cells. *Matisia coloradorum* (leaf), *M. cordata* (leaf).

**100IA** spherical cystoliths. See table for occurrence.

**110** sclereids. See table for occurrence

As Piperno (1988, 2006) early observed, it is often hairs and hair bases that are silicified in dicotyledon taxa that silicify tissues. This is the case in the Bombacaceae. For the most part hairs and hair bases were lightly silicified in the specimens studied, and unlikely to survive in



soils. This limits their usefulness in archaeological and paleoenvironmental applications. 80IFb202, facetate hemisphere with irregular concavities, is well-silicified, however, and potentially useful as a Bombacaceae family indicator.

A striking feature of phytolith production in the Bombacaceae is the fact that three kinds of well-silicified phytoliths produced in this family also occur in families in the Zingiberales. Smooth nodular spheres (80ICa1) and conical bodies (80IIIB) were originally described by Piperno (1988) for the Marantaceae; ruminant nodular spheres (80ICc) were identified at MU in *Costus* in the Zingiberaceae as well as in the Bombacaceae. These forms are so similar to Marantaceae and Zingiberaceae examples that we have classified them under the same numbers. There are some subtle differences in the number and arrangement of nodules, however, which may allow separation if a large enough sample was present. The spheres are also produced in different abundances in the two families. These aspects of phytolith production will be discussed in more detail in the Zingiberales review.

In addition to the taxa studied during this project, two other genera with Ecuadorian representatives were studied by Piperno (1988): *Bombacopsis quinata*, *B. sessiles*, and *Cavanillesia platanifolia*. Only *B. sessiles* commonly silicified tissues (epidermis, stomata, and tracheids). *Bombax* and *Durio*, which do not occur in Ecuador, were studied by Kealhofer and Piperno (1998), who found that *Bombax* was not a phytolith producer (two species studied), while *Durio* (two species) silicified hair bases, epidermal cells, and small spheres, none of which were considered diagnostic.

## MALVACEAE

There are 31 genera of Malvaceae in Ecuador (Jørgensen and León-Yáñez 1999). Prior to this project, *Abutilon*, *Gossypium*, *Hibiscus*, *Malvastrum*, *Malvaviscus*, *Pavonia*, and *Sida* had been tested. *Abutilon* and *Malvastrum* were determined to be non-producers (Runge 1996; Piperno 1988). *Gossypium* was reported to be non-productive to not common by Piperno (1988), while Bozarth (1996) reported a rare diagnostic. The other genera produced non-diagnostic phytoliths (Piperno 1988, Runge 1996, Polcyn et al. 1997; Kealhofer and Piperno 1998). Based on this information, the Malvaceae was not given high priority for sampling. Specimens of *Bastardia*, *Gossypium*, and *Malachra* on-hand in the MU laboratory were included in the study; *Hesperia* was sampled (Table 3).

*Bastardia cf. parvifolia* H.B.K. was collected by Pearsall in Guayas Province, Ecuador, and determined by Balslev and Bech. This is not one of the two *Bastardia* species listed for Ecuador by Jørgensen and León-Yáñez (1999). This taxon is a phytolith producer, but no diagnostic types were observed except for cystoliths (100IA, VA) and rugulose epidermal (22IBd, M; diagnostic value being explored). Two hairs were present (40I/II, VR; 40IIIAb200, R), but neither could be classified completely since they were carbon-occluded due to incomplete ashing of the specimen.

### *Gossypium*

Five specimens of cotton, *Gossypium* sp., were studied. These included leaves of two wild *Gossypium* specimens collected by Pearsall in Ecuador (OS638, E1022), and fruit (2665), fiber (2666), and seeds (2667) of cultivated *G. barbadense* L. provided by K. Chandler-Ezell. Specimen OS638 was poorly processed and will not be discussed further. The other leaf specimen (E1022) produced spherical cystoliths (100IA, C), cubical crystals (100IV, C) that

appeared to be broken pieces of 100IA, and straight transport elements (140II, R). A potentially diagnostic multicellular hair, 40III Bb (M), was also present in the leaf (Plate 3, a). This radiating hair arises from a cystolith base, and also occurs as single, broken hairs (40III Ab1/2, A).

*G. barbadense* fiber produced no extract, and seeds very little silica, and nothing diagnostic. The fruit sample was more interesting in that it contained silicified secretory cells (160II, R-M) with variable centers and a distinct ring (Plate 3, b). Size ranged from 12-16 microns. These are similar, but not identical, to secretory cells produced by manioc, *Manihot esculenta* (Euphorbiaceae) (Chandler-Ezell et al 2006). This type must be tracked in other families, but may be a useful cotton diagnostic. Undulating transport tissues (140I, A) were also present.

Bozarth (1996), as part of a study of prehistoric agriculture in the lower Verde River valley of Arizona, studied phytolith production in a broad array of cultivated and useful wild plants, including cultivated *G. hirsutum* var. *hirsutum*. He found that cotton fiber occasionally formed silicified rods, both hollow and solid. Within the context of his collection, curved or branched hollow rods were unique to cotton. Piperno (1988) found, as we did, that *Gossypium barbadense* fiber did not produce silica. Kealhofer and Piperno (1998) tested *G. arboreum* L. (leaf, bract) and *G. herbaceum* L. (leaf) and found no phytolith production.

*Hesperia populnea* L. was studied; neither leaf nor inflorescence yielded silica.

*Malachra alceifolia* Jacq. is an herb or subshrub native to the coast and Amazon (Jørgensen and León-Yáñez 1999). A multicellular radiating hair (40III Bb, R) has potential diagnostic value, but was carbon-occluded and so could not be completely classified. Carbon-occluded unicellular hairs common in this sample (40III Ab2, C) are likely broken from this

radiating hair. Undulating transport elements (140I, R) and spherical cystoliths (100IA, A) were also present.

### Family Summary and Discussion

The limited sampling in the Malvaceae reported here suggests that a multicellular radiating hair with or without a cystolith base (40IIIb), as well as broken elements of this hair (40IIIAb2), may have potential as a family-level diagnostic. These hairs were observed in both *Malachra* and *Gossypium*. A potential genus-level diagnostic to be explored further is the secretory body (160II) found in *Gossypium* fruit. Generalized woody (100IA) indicators are present.

Overall, our results agree with the prior assessments of several researchers that the Malvaceae is a family with low production of useful silica bodies. An exception is the potentially diagnostic rods identified by Bozarth (1996) in *Gossypium hirsutum* fiber. Both *Malvaviscus* (Piperno 1988) and *Pavonia* (Runge 1996) silicify hairs and hair bases.

### STERCULIACEAE

There are 10 genera of Sterculiaceae in Ecuador, ranging from herbs to lianas, shrubs, and trees (Jørgensen and León-Yáñez 1999). This family has been well-studied, and a number of genera produce diagnostic phytoliths: *Eriolaena*, *Pterospermum* (not Ecuadorian), *Melochia*, and *Sterculia* (Kealhofer and Piperno 1998). Found to be non-producers or producers of non-diagnostic phytoliths: *Ambroma*, *Commersonia*, *Helicteres*, *Heritiera*, (not Ecuadorian), *Byttneria*, *Guazuma*, and *Theobroma* (Piperno 1988; Kealhofer and Piperno 1998).

*Herrania*, not studied prior to this project, was sampled, as were *Guazuma*, *Sterculia*, and *Waltheria*. *Theobroma cacao*, cacao, an important economic taxon, was also studied (Table 4).

### *Guazuma*

*Guazuma ulmifolia* Lam. is a widespread polymorphic tree species (Jørgensen and León-Yáñez 1999). All samples studied produced silica extracts.

The ashed wood specimen (2870) produced granular blocky (100VI, VA) and granular elongated tabular (100Vb, VA) crystalline bodies (probably calcium carbonate) (Plate 4, a, b). These are similar, but not identical, to the crystalline tabular bodies present in *Ceiba* sp., Bombacaceae, wood (100Va). Small opaque spheres (80IAa1), also observed in *Bixa*, Chrysobalanaceae, and *Canna*, were abundant in the sample.

The leaf specimens were well-silicified overall, with common to very abundant silicification of epidermal cells in chemically-extracted specimens, including polyhedral cells (20IBa) considered generalized dicotyledon indicators. The ashed leaf specimen had very abundant spherical cystoliths (100IA), generalized arboreal indicators. A distinctive hair base (40IVAA202) with radiating appendages and a large, open circular center was also commonly silicified in the leaf in one ashed and one chemically-extracted specimen (Plate 4, c). This is a genus-level diagnostic. Like the wood, the leaf produced small smooth spheres (80IAa1), further indicating the low diagnostic value of this type. The inflorescence also commonly silicified epidermal tissues, but no distinctive forms were produced. Piperno (1988) also found common phytolith production in *Guazuma ulmifolia*, with silicification of the epidermis, hairs, hair bases, sclereids, and rods.

A single leaf specimen identified only as *Herrania* sp. was studied. Silicification of tissues was rare, and no diagnostic forms were observed.

Five specimens of domesticated cacao, *Theobroma cacao* L. were analyzed. Unfortunately for the prospects of identifying this important domesticated plant, our results confirm earlier research in indicating little silicification of discrete tissues, and no diagnostic forms except spherical cystoliths (100IA), generalized arboreal indicators. Granular elongated tabular (100Vb, C) crystalline bodies observed in *Guazuma ulmifolia* wood were also present in one cacao stem sample. Piperno (1988) found that cacao did not commonly silicify tissues, and noted the presence of silicified stomata, scherids, and tracheids, none of which were diagnostic.

While not an Ecuadorian species, a specimen of *Wattheria americana* on hand in the lab was examined as a representative of this genus, which does occur in Ecuador (Jørgensen and León-Yáñez 1999). A long unicellular hair with an enclosed base (40IIIAb200Bd, VR, R) (Plate 4, d) was observed that has potential as a genus-level diagnostic. Both the ashed and chemically-extracted specimens contained spherical cystoliths (100IA), although these were less abundant in the chemically-extracted specimen. Piperno (1988) found that *W. indica* commonly produced silica, and noted silicification of the epidermis, hairs, hair bases, mesophyll, and tracheids.

As part of their study of phytolith production in the Southeast Asian flora, Kealhofer and Piperno (1998) studied three genera in the Sterculiaceae, *Byttneria*, *Melochia* and *Sterculia*, which have Ecuadorian representatives. Phytolith production was rare in *M. umbellata* (Houtt.) Stapf leaf, but a diagnostic form of linked spheres was produced. *S. foetida* L. and *S. pexa* Pierre leaves produced more silica (uncommon, common), including hair bases, stoma, tracheids, sclereids, and polyhedral epidermal. The hair-related forms may have diagnostic value. Silica

was absent in *S. pexa* inflorescence. *B. pilosa* Roxb. inflorescence lacked silica; the leaf silicified non-diagnostic epidermal cells and tracheids.

#### Family Summary and Discussion

Based on our research and that of others, it is clear that phytolith production is generally low in the Sterculiaceae, and when tissues are silicified, distinctive forms are rarely produced. In this the family closely parallels the Malvaceae. Exceptions include: a distinctive hair base (40IVAA202, M-A) with radiating appendages and a large, open circular center in *Guazuma ulmifolia*; a long unicellular hair with an enclosed base (40IIIAb200B, VR, R) in *Wattheria americana*; and a linked sphere (R) in *Melochia umbellata* (Houtt.) Stapf.

#### TILIACEAE

The Tiliaceae is a family of herbs, trees, and shrubs comprising 11 genera and 24 species in Ecuador (Jørgensen and León-Yáñez 1999). Prior to this project two Ecuadorian genera had been studied, *Corchorus*, with rare to non-production of silica (Polcyn et al. 1997) and *Triumfetta*, found to be non-productive (Kealhofer and Piperno 1998). Three non-Ecuadorian genera tested, *Berrya*, *Colona*, and *Grewia*, were either non-producers or produced only non-diagnostic phytoliths (Kealhofer and Piperno 1998; Runge 1996).

Given these indications of low silica accumulation, only *Apeiba*, *Heliocarpus*, and *Trichospermum* were sampled. No extract was produced (Table 5).

#### MALVALES DISCUSSION

The Bixaceae, Malvaceae, Sterculiaceae, and Tiliaceae are characterized by low phytolith production, varying from non-production to production of non-diagnostic silica or generalized

woody indicators such as cystoliths and sclereids. There are a few exceptions in which distinctive hair bases or hairs are silicified. While these lightly silicified forms are of limited use in soil or sediment work, they demonstrate that even in low silica-accumulating families distinctive phytoliths may be produced. Overall, study of Ecuadorian taxa in these families produced results consistent with prior research.

*Gossypium hirsutum* and *G. barbadense* each produced a distinctive, more well-silicified type of phytolith worth further study, given the economic importance of these species. Interestingly, these potential diagnostics are produced in distinctive tissues in these two species, and two other species are non-producers. Overall, the genus displays a consistent pattern of little to no silicification of tissues, in line with the family.

The exception to the general Malvales pattern of low phytolith production is the Bombacaceae, a family in which most taxa tested were silica-accumulators, and a number produced diagnostic phytoliths. As discussed earlier, there is one well-silicified form, the facetate hemisphere (80IFb202), which has potential as a family-level indicator, and a number of more fragile hairs and hair bases are genus or species-level diagnostics. Production of nodular spheres and conical bodies by some Bombacaceae potentially complicates use of these types for identifying taxa in the Zingiberales.

There are a number of cases in the Malvales in which the same species was studied more than once. This provides an opportunity to examine variability in phytolith patterning among replicates. In some cases there are observable differences in the extent of cell wall silicification, a common silica accumulation mechanism in dicotyledons (Piperno 1988). In *Ceiba pentandra* leaf and inflorescence, for example, New World specimens were non-producers while an African



specimen exhibited silicification in some polyhedral-shaped epidermal cells. In *Theobroma cacao*, all replicates produced silica, but the extent of cell wall silicification varied. Some variation is likely due to differences in the quantity of tissue from which silica was extracted and the manner and success of the extraction; other differences may relate to the maturity of tissues or environmental conditions.

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