

# Opal Phytoliths in Southeast Asian Flora

*Lisa Kealhofer  
and Dolores R. Piperno*



SMITHSONIAN INSTITUTION PRESS

Washington, D.C.

1998

## ABSTRACT

Kealhofer, Lisa, and Dolores R. Piperno. *Opal Phytoliths in Southeast Asian Flora. Smithsonian Contributions to Botany*, number 88, 39 pages, 49 figures, 5 tables. 1998.—One of the major uses of phytolith analysis is the reconstruction of regional environmental histories. As a relatively new subset of paleoecology, reference collections and studies of phytolith distributions and morphology are still relatively few. This article summarizes a study of phytolith form and distribution across a broad spectrum of 77 families of both monocotyledons and dicotyledons. A total of 800 samples from different plant parts of 377 species were analyzed, with diagnostic phytoliths occurring in nine monocotyledon and 26 dicotyledon families. These diagnostic types are described and illustrated herein. Poaceae phytoliths were not included in this review because they warrant more detailed and systematic description. The wide distribution of diagnostic phytoliths across all basic habitats described for Thailand, demonstrated herein, indicates that phytolith analysis has great potential for paleoecological reconstruction.

OFFICIAL PUBLICATION DATE is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, *Annals of the Smithsonian Institution*. SERIES COVER DESIGN: Leaf clearing from the katsura tree *Cercidiphyllum japonicum* Siebold and Zuccarini.

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### Library of Congress Cataloging-in-Publication Data

Kealhofer, Lisa.

Opal phytoliths in Southeast Asian flora / Lisa Kealhofer and Dolores R. Piperno.

p. cm. — (Smithsonian contributions to botany ; no. 88)

Includes bibliographical references.

1. Angiosperms—Cytotaxonomy—Thailand. 2. Angiosperms—Cytotaxonomy—Asia, South-eastern. 3. Phytoliths—Thailand. 4. Phytoliths—Asia, Southeastern. I. Piperno, Dolores R. II. Title. III. Series.

QK364.K435 1998

571.6'82'0959—dc21

98-38793

CIP

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## Introduction

Phytolith analysis was first used in archaeology in the early 1970s and came of age in the 1980s in New World archaeology (Rovner, 1971; Piperno, 1988; Pearsall, 1989). Phytolith analysts working in other parts of the world have contributed important but often isolated studies of specific families or issues (e.g., Fujiwara et al., 1985; Rosen, 1989). Recently, we have begun to build a comparative phytolith collection for Southeast Asian flora. Much of the phytolith work to date focuses on the reconstruction of prehistoric agricultural systems; however, phytolith studies are becoming increasingly important for issues in geology, paleoecology, and paleontology (Piperno, 1988; Piperno and Ciochon, 1990; Piperno and Pearsall, 1994; Kamanina, 1997; Madella, 1997; Pinilla et al., 1997).

The comparative collection reviewed herein was created to study environmental change and the development of land use in Southeast Asia (e.g., Kealhofer and Piperno, 1994; Kealhofer, 1996a, 1996b; Kealhofer and Penny, in press). Phytolith analysis, only recently applied in Old World tropical studies, is one of the primary means of palaeoecological and human ecological analysis (e.g., Mercader et al., in press; Runge and Runge, 1997). In this paper, we present the initial results of an investigation of phytolith production and morphology in Southeast Asian flora, focusing in particular on Thai flora. We also assess the utility of phytolith analysis for the reconstruction of vegetation patterns and plant use in this critical region.

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*Reviewers: Arlene Miller-Rosen, Department of Archaeology, Ben Gurion University, P.O. Box 653, Beer Sheva, 84 105 Israel; Deborah Pearsall, Department of Anthropology-American Archaeology, University of Missouri, Columbia, 103 Swallow Hall, Columbia, Missouri 65211, United States.*

**METHODS.**—Three hundred seventy-seven species from 77 families were analyzed for opal phytoliths. The species analyzed were chosen on the basis of three criteria: (1) known phytolith production in related genera or families from other regions of the world (Piperno, 1988); (2) known economic uses (Yen, 1982; Jacquat, 1990; Harlan, 1992); and (3) the species' specificity of habitat, and therefore its potential as an environmental indicator (Craib, 1912, 1913; Ogawa et al., 1961; Smitinand, 1968; Kuchler and Sawyer, 1967; Stott, 1986; Maloney, 1992).

The 377 species represent 17 monocotyledon families (11 orders, four subclasses) and 59 dicotyledon families (27 orders, five subclasses). Samples were taken from specimens at the United States National Herbarium (USNH) or were field-collected in northeastern Thailand (J.C. White, private collection (JCW)). Herbarium samples were from Thai plants when possible, but when a Thai sample was unavailable, samples from other East and Southeast Asian locales were used. USNH vouchers are identified by herbarium sheet number.

The species were subsampled by leaf, inflorescence, fruit, and root when possible. Piperno (1988) showed that size and form differences often distinguish phytoliths from different plant parts, and these can have taxonomic and economic significance. Standard phytolith extraction techniques (wet ashing), as described by Piperno (1988) and Kealhofer (1996b), were followed. Samples were mounted on slides, and the slides were scanned three times using a light microscope, 50 mm per scan, at  $\times 400$ , to count and identify assemblages of phytolith forms. Diagnostic phytolith types were photographed at  $\times 100$ – $\times 400$ . (Figures 1–48 herein were reduced 11%.)

The basic phytolith forms (i.e., silicified tissues) identified by Piperno (1985, 1988) also were found in this assemblage, including epidermis cells, hair-base cells, hair cells, stomata, mesophyll cells, sclerenchyma cells, and vascular tissue. The forms identified and discussed herein are based on these previous descriptions, with added distinctions as appropriate.

**ACKNOWLEDGMENTS.**—This research was made possible by a grant from the Andrew W. Mellon Foundation to the Smithsonian Tropical Research Institute, Paleocology Sec-

tion. The National Science Foundation also partially supported the collection and analysis of material for this study. We would particularly like to thank Vince Pigott for his generous assistance. Guiselle Mora and Roque Viera provided valuable technical support for this project. The Thai Fine Arts Department, the people of Huai Pong, Thailand, Joyce White, and the staff at both the United States National Herbarium and the Smithsonian Tropical Research Institute (STRI) also contributed significantly to this undertaking. Particular thanks are due to the Photographic Services Department at STRI.

### Results of Phytolith Analysis

Eight hundred samples were analyzed from 377 species. Of these, 154 samples (47 monocotyledons, 107 dicotyledons) contained diagnostic phytolith forms, representing nine monocotyledon and 26 dicotyledon families. This distribution reinforces the utility of phytoliths as significant indicators of many types of vegetation, not only as indicators of grasses.

The diversity of phytolith types present in grass species warrants a separate presentation; therefore, the grass species included in this project are not discussed herein but will be discussed in a subsequent publication on Southeast Asian Poaceae. When the Gramineae (Poaceae) are excluded, 29 monocotyledon species with diagnostic phytoliths remain. Only those species with diagnostic phytolith forms are discussed below; species studied that had no phytoliths or had nondiagnostic phytoliths are summarized in Table 5. Results are presented by taxon. Table 1 summarizes the families in which diagnostic phytoliths occur.

Economic and ecological information is discussed, where pertinent and available, based on general botanical reviews (Mabberly, 1987; Heywood, 1993) and specific discussions of Thai flora (Craib, 1912, 1913; Ogawa et al., 1961; Küchler and Sawyer, 1967; Smitinand, 1968; Smitinand and Larsen, 1972, 1975; Maxwell, 1975; Ogino, 1976; Bunyavejchewin, 1983; Stott, 1984, 1986; Maloney, 1992). Table 2 presents the primary habitats of the genera and families with diagnostic phytoliths.

#### MONOCOTYLEDONS

Eleven of 19 orders in four of five subclasses of monocotyledons were studied: Alismatales, Arales, Arecales, Cyperales, Eriocaulales, Liliales, Najadales, Orchidales, Poales, Typhales, and Zingiberales. Nine families in these orders have diagnostic phytoliths (Table 3). As noted above, phytoliths in Poaceae will be described elsewhere. No diagnostic phytoliths were found in Arales (Araceae), Eriocaulales (Eriocaulaceae), Typhales (*Typha*), or *Najas* sp. of Najadales (Table 5). The diagnostic forms are described below.

#### Order ALISMATALES

The species of family Alismataceae are of particular interest for environmental reconstruction because they are common in

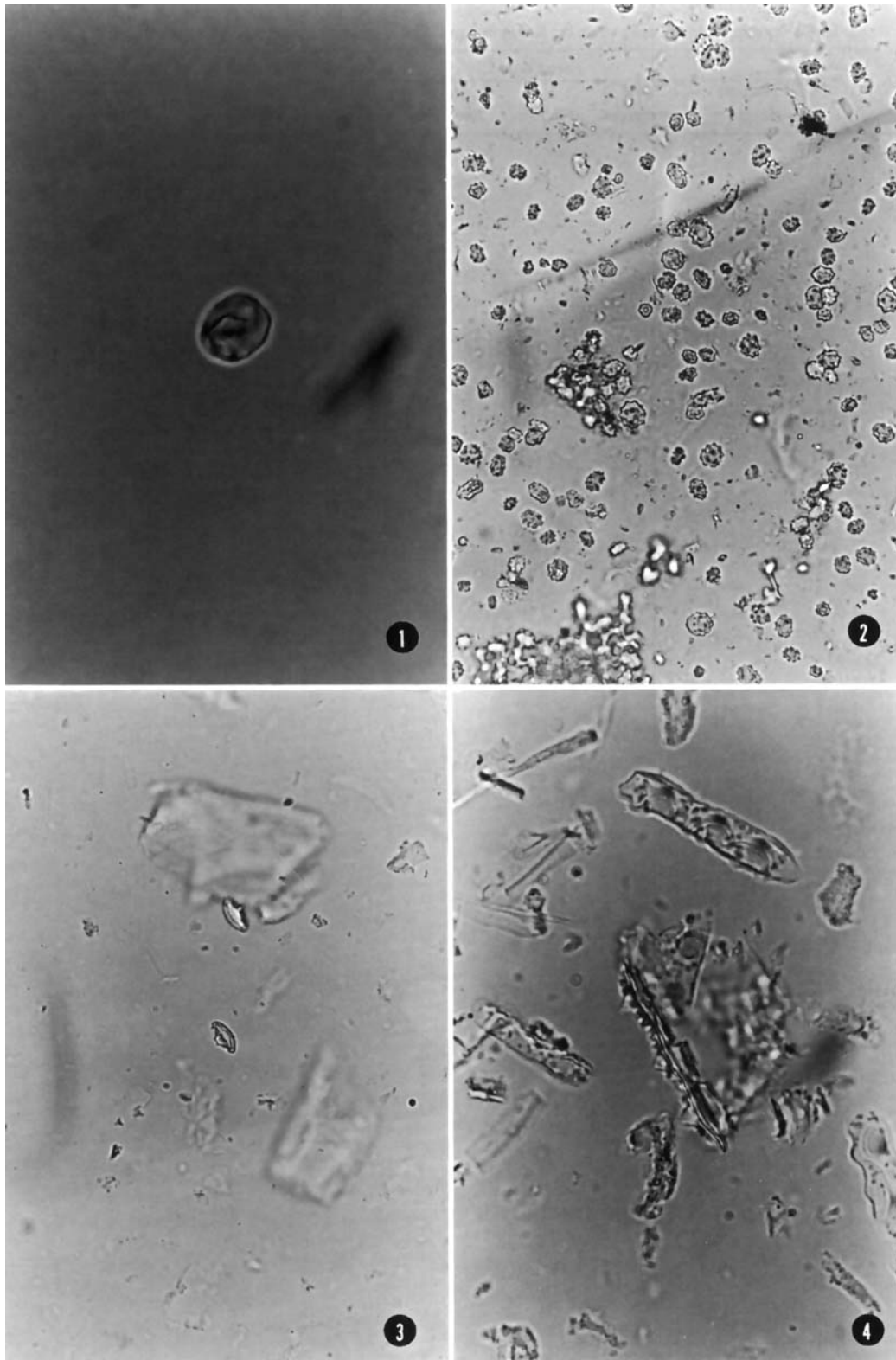
TABLE 1.—Families with diagnostic phytoliths.

Monocotyledons	Dicotyledons
ALISMATACEAE	ANACARDIACEAE
CYPERACEAE	ANNONACEAE
DIOSCOREACEAE	BORAGINACEAE
GRAMINEAE (POACEAE)	BURSERACEAE
MARANTACEAE	CHRYSOBALANACEAE
MUSACEAE	CLUSIACEAE (GUTTIFERAE)
ORCHIDACEAE	CONNARACEAE
PALMAE	CUCURBITACEAE
ZINGIBERACEAE	DILLENIIACEAE
	DIPTEROCARPACEAE
	EBENACEAE
	EUPHORBIIACEAE
	FABACEAE (LEGUMINOSAE)
	FAGACEAE
	FLACOURTIACEAE
	LORANTHACEAE
	MAGNOLIACEAE
	MELIACEAE
	MORACEAE
	MORINGACEAE
	MYRTACEAE
	OLEACEAE
	RHIZOPHORACEAE
	SCROPHULARIACEAE
	STERCULIACEAE
	ULMACEAE

freshwater-swamp habitats. The two species analyzed each contain two types of spheres. Both species have folded spheres; additionally, *Caldesia* has a sphere 8  $\mu\text{m}$  in diameter, with pentagonal facets, and *Ranalisma* has dimpled spheres (Figure 1), ranging from 10  $\mu\text{m}$  to 20  $\mu\text{m}$  in diameter.

#### Order ARECALES

Family Palmae was studied in this order, with species chosen from seven of the eight Palmae subfamilies found in the Old World. Phytoliths are common to abundant in Palmae species. Palm phytoliths commonly are distinctive spinulose to tabular spheres (Figure 2), but some subfamilies have conical to hat-shaped phytoliths (e.g., *Caryota* and *Nypa*; Table 3, Figure 3). Except for these more diagnostic genera, the spinulose spheres vary little in shape from genus to genus, although sphere diameter varies between leaves and inflorescences in a few cases (e.g., *Borassus* and *Calamus*). Subfamilies also seem to produce spheres in overlapping but different size ranges (Table 3). For example, *Borassus* spheres were the largest phytoliths encountered, with inflorescence spheres ranging from 20  $\mu\text{m}$  to 27  $\mu\text{m}$  in diameter. Phoenicoideae spheres were the smallest phytoliths seen, ranging from 4  $\mu\text{m}$  to 6  $\mu\text{m}$  in diameter. Without study of more Palmae species no definite subfamily characterizations can be made; however, these data suggest a further study could reveal more diagnostic Palmae characteristics.



FIGURES 1-4 ( $\times 356$ ).—1, *Ranalisma rostratum* (Alismataceae): dimpled sphere from leaf sample, USNH 1425829. 2, *Areca catechu* (Palmae): spinulose spheres from fruit sample, USNH 2455123. 3, *Caryota mitis* (Palmae): conical phytoliths from leaf and inflorescence samples, USNH 2107771. 4, *Cyperus corymbosus* (Cyperaceae): regular, sharp peaks on leaf epidermis sample, JCW 285.

TABLE 2.—Environment-specific genera and families with diagnostic phytoliths in Southeast Asia. Presence at the family level is indicated only when the family is associated in general with the given habitat.

Taxon	Forest type					Other habitats			
	Tropical evergreen	Dry evergreen	Scrub	Mixed deciduous	Dry deciduous	Hill/Montane	Grassy/Disturbed	Swamp/Wet	Coast
MONOCOTYLEDONS									
[POACEAE]	-	-	x	-	-	-	x	-	x
ALISMATACEAE	-	-	-	-	-	-	-	x	-
PALMAE									
<i>Areca</i>	-	x	-	-	-	-	-	-	-
<i>Calamus</i>	x	x	-	-	-	-	-	-	-
<i>Cocos</i>	-	-	-	-	-	-	-	-	x
<i>Corypha</i>	-	x	-	-	-	-	-	-	-
<i>Livistona</i>	-	x	-	-	-	-	-	-	-
<i>Nypa</i>	-	-	-	-	-	-	-	-	x
<i>Phoenix</i>	-	-	-	x	x	-	-	x	-
<i>Rhapis</i>	-	x	-	-	-	-	-	-	-
CYPERACEAE	-	-	-	-	-	-	-	x	-
MARANTACEAE									
<i>Phrynium</i>	x	x	-	-	-	x	-	x	-
MUSACEAE	-	x	-	-	-	x	x	-	-
ZINGIBERACEAE									
<i>Costus</i>	x	-	-	-	-	-	-	-	-
<i>Curcuma</i>	-	x	-	-	x	x	-	-	-
<i>Zingiber</i>	x	-	-	-	-	-	-	-	-
DIOSCOREACEAE	-	-	-	x	-	-	-	-	-
ORCHIDACEAE									
<i>Aerides</i>	-	-	-	x	-	-	-	-	-
<i>Coelogyne</i>	x	-	-	-	-	-	-	-	-
<i>Dendrobium</i>	x	-	-	-	-	-	-	-	-
DICOTYLEDONS									
BORAGINACEAE	x	-	-	-	-	-	-	-	-
OLEACEAE									
<i>Ligustrum</i>	-	-	-	-	-	x	-	-	-
SCROPHULARIACEAE									
<i>Centranthera</i>	-	-	-	-	x	-	-	-	-
MORINGACEAE									
<i>Moringa</i>	-	-	-	x	x	-	-	-	-
DILLENACEAE									
<i>Dillenia</i>	-	x	-	x	x	-	-	-	-
EBENACEAE									
<i>Diospyros</i>	-	-	-	x	x	-	-	-	-
STERCULIACEAE	x	-	-	-	-	-	-	-	-
CLUSIACEAE									
<i>Calophyllum</i>	x	-	-	-	-	x	-	-	-
DIPTEROCARPACEAE									
<i>Hopea</i>	-	x	-	-	-	-	-	-	-
<i>Shorea</i>	-	-	-	-	x	-	-	-	-
CUCURBITACEAE									
<i>Momordica</i>	-	-	x	-	-	-	x	-	-
<i>Trichosanthes</i>	x	-	-	-	-	-	-	-	-
FLACOURTIACEAE									
<i>Casearia</i>	-	-	-	x	x	-	-	-	-
<i>Flacourtia</i>	-	-	-	x	x	-	-	-	-
<i>Hydnocarpus</i>	x	x	-	-	-	-	-	x	-
FAGACEAE									
<i>Lithocarpus</i>	-	-	-	-	-	x	-	-	-
<i>Quercus</i>	-	-	-	-	x	x	-	-	-
MORACEAE									
<i>Artocarpus</i>	x	-	-	-	-	-	-	-	-
<i>Broussonetia</i>	x	-	-	-	-	-	-	-	-
<i>Ficus</i>	x	x	-	x	-	x	-	-	-
<i>Streblus</i>	-	-	-	-	x	-	x	-	-



TABLE 2.—Continued.

Taxon	Forest type					Other habitats			
	Tropical evergreen	Dry evergreen	Scrub	Mixed deciduous	Dry deciduous	Hill/Montane	Grassy/Disturbed	Swamp/Wet	Coast
ULMACEAE									
<i>Celtis</i>	—	—	×	—	—	—	—	—	—
<i>Trema</i>	×	—	—	—	—	—	—	—	—
ANNONACEAE									
<i>Polyalthia</i>	×	—	—	—	—	—	—	—	—
<i>Uvaria</i>	×	—	×	—	—	—	—	—	—
MAGNOLIACEAE									
<i>Manglieta</i>	—	—	—	—	—	×	—	—	—
<i>Michelia</i>	×	—	—	—	—	×	—	—	—
<i>Talauma</i>	×	—	—	—	—	×	—	—	—
EUPHORBIACEAE									
<i>Phyllanthus</i>	—	—	—	—	×	—	—	—	—
<i>Sapium</i>	×	—	—	—	—	—	—	—	—
FABACEAE									
<i>Acacia</i>	—	—	×	×	×	—	—	—	—
<i>Albizia</i>	—	—	—	×	—	—	—	×	—
<i>Mimosa</i>	—	—	—	—	×	—	×	—	—
MYRTACEAE									
<i>Syzygium</i>	—	×	—	—	—	—	—	—	—
PODOSTEMACEAE									
<i>Podostemum</i>	—	—	—	—	—	—	—	×	—
RHIZOPHORACEAE									
<i>Podostemum</i>	—	—	—	—	—	—	—	×	×
CHRYSOBALANACEAE									
<i>Parinari</i>	—	—	—	×	—	—	—	—	—
LORANTHACEAE									
<i>Elytranthe</i>	×	—	—	—	—	—	—	—	—
ANACARDIACEAE									
<i>Mangifera</i>	×	—	—	—	—	—	—	—	—
BURSERACEAE									
<i>Canarium</i>	—	—	—	×	×	—	—	—	—
<i>Garuga</i>	—	—	—	×	—	—	—	—	—
<i>Scutinanthe</i>	×	—	—	—	—	—	—	—	—
MELIACEAE									
<i>Melia</i>	×	—	—	—	—	—	—	—	—

The typical *Palmae* habitat is the understory of tropical rain forests; however, individual species often have more specific habitats. For example, *Nypa* is found in mangrove habitats. *Phoenix* species occur in dry seasonal forests, swamp habitats, and mixed forests. *Calamus*, a climbing palm, is characteristically found in tropical rain forests but also is found in tall evergreen forests in northern Thailand. In the dry evergreen forest, *Areca*, *Calamus*, *Corypha*, *Livistona*, and *Rhapis* live near stream banks.

#### Order CYPERALES

Leaf and inflorescence samples of five species of Cyperaceae were studied (Table 3). Cyperaceae achenes (seeds) were not sampled; however, they often produce the most diagnostic phytolith forms. Except for *Scirpus petelotii*, phytoliths were common to abundant in both leaf and inflorescence samples. Although various forms are present in these species (see Table

3), the diagnostic Cyperaceae phytolith is known as a “hat” or cone. Ollendorf (1992) discussed the typology of hat forms found in Cyperaceae but did not distinguish achene forms. The criteria described shape (top view), number of apices, sculpturing, presence of satellites, and cone occurrence either individually or on a platelet (Ollendorf, 1992:102). The leaf and inflorescence forms of the five species studied are distinguishable based on hat diameter (at base) or maximum width and on the shape of the hat (circular or square). Both *Scirpus* and *Eleocharis* species have square and round hat shapes, whereas *Cyperus* hats are round. *Cyperus* commonly has numerous satellites, either around the perimeter or distributed evenly across the cone. The epidermal tissue of *Cyperus* also has some diagnostic characteristics, with regular, sharp peaks on flat tissue (Figure 4).

Cyperaceae species are herbaceous perennials, mainly found in marshes and swamps and disturbed, damp to wet habitats (Table 2). *Cyperus* in northern Thailand also occurs on

damp, marshy ground in evergreen forests and is occasionally associated with rice fields.

#### Order ZINGIBERALES

Ten species from three families of Zingiberales, Marantaceae, Musaceae, and Zingiberaceae, were analyzed (Table 3).

In Marantaceae, distinctive folded and nodular spheres were found in leaf samples. Phytoliths are abundant in this family. Spheres are commonly 10–12  $\mu\text{m}$  in diameter, but one species also has spheres of 5  $\mu\text{m}$  (Figure 5). Inflorescence samples, on the other hand, had both hollow and infilled conical shapes. Diameters of these varied from 14  $\mu\text{m}$  to 22  $\mu\text{m}$ . Anticlinal-epidermis forms also are characteristic of the genus *Phrynium*.

The Marantaceae are most common in the New World, but two genera, *Phrynium* and *Cucurlogo*, are common in Thai dry evergreen forests. *Phrynium* is well represented in the herbaceous layer of evergreen forests. *Phrynium parviflorum* also is a forb in higher-elevation tall evergreen forests in northern Thailand (Table 2).

Musaceae phytoliths are notable for their highly diagnostic trough shapes (Figure 9). These shapes are abundant in leaves of *Musa* sp., but no diagnostic forms were found in the inflorescence samples. One sample also had multifaceted-polyhedral shapes.

The Musaceae are known as “jungle weeds” and are characteristic of disturbed habitats in forests from India to Malesia. *Musa* is found in lowland dry evergreen forests. *Musa acuminata* also often grows in ravines in montane evergreen forests (Table 2).

In Zingiberaceae, the most common phytolith form is a folded, decorated sphere. Size ranges vary by species (Figures 6, 7), but without further analysis it is unclear if size is species or genus diagnostic. Sphere diameters are often quite uniform within species, varying by only 1–2  $\mu\text{m}$ . The intensity of folding makes these spheres quite distinctive. Other nondiagnostic phytolith forms, particularly tracheids, are common. Large multifaceted polyhedrals occur in *Zingiber* sp. and *Curcuma* sp. Inflorescences of *Zingiber* sp. also have unusual, decorated ovoids (Figure 8).

Zingiberales species in general are found in lowland tropical habitats. Zingiberaceae are perennial aromatic plants with multiple economic uses, including spices, medicines, and dyes. *Curcuma* is found from evergreen to deciduous forests in northern Thailand, whereas *Zingiber* primarily grows in damp evergreen forests. *Costus* is often a forb in tall evergreen forests.

#### Order LILIALES

Although phytoliths are rare in Dioscoreaceae, a family known for its economic species of yams (*Dioscorea* spp.), leaves in one species, *Dioscorea membranacea*, has small (5–6  $\mu\text{m}$  in diameter), tabular spheres (Figure 10). These could be

confused with the small, ovoid, rough palm or orchid phytoliths because their diminutive size makes their decoration difficult to discern. Palm species, however, also have more diagnostic spinulose forms that allow them to be definitely identified. Two other Liliales families, Pontederiaceae and Taccaceae, either do not have phytoliths or have nondiagnostic phytoliths (Table 5).

Dioscoreaceae species are herbaceous climbers in tropical forests, although temperate species do occur. Many *Dioscorea* species are climbers in hillside seasonal forests. *Dioscorea membranacea* is found in lowland mixed forests in Thailand (Table 2).

#### Order ORCHIDALES

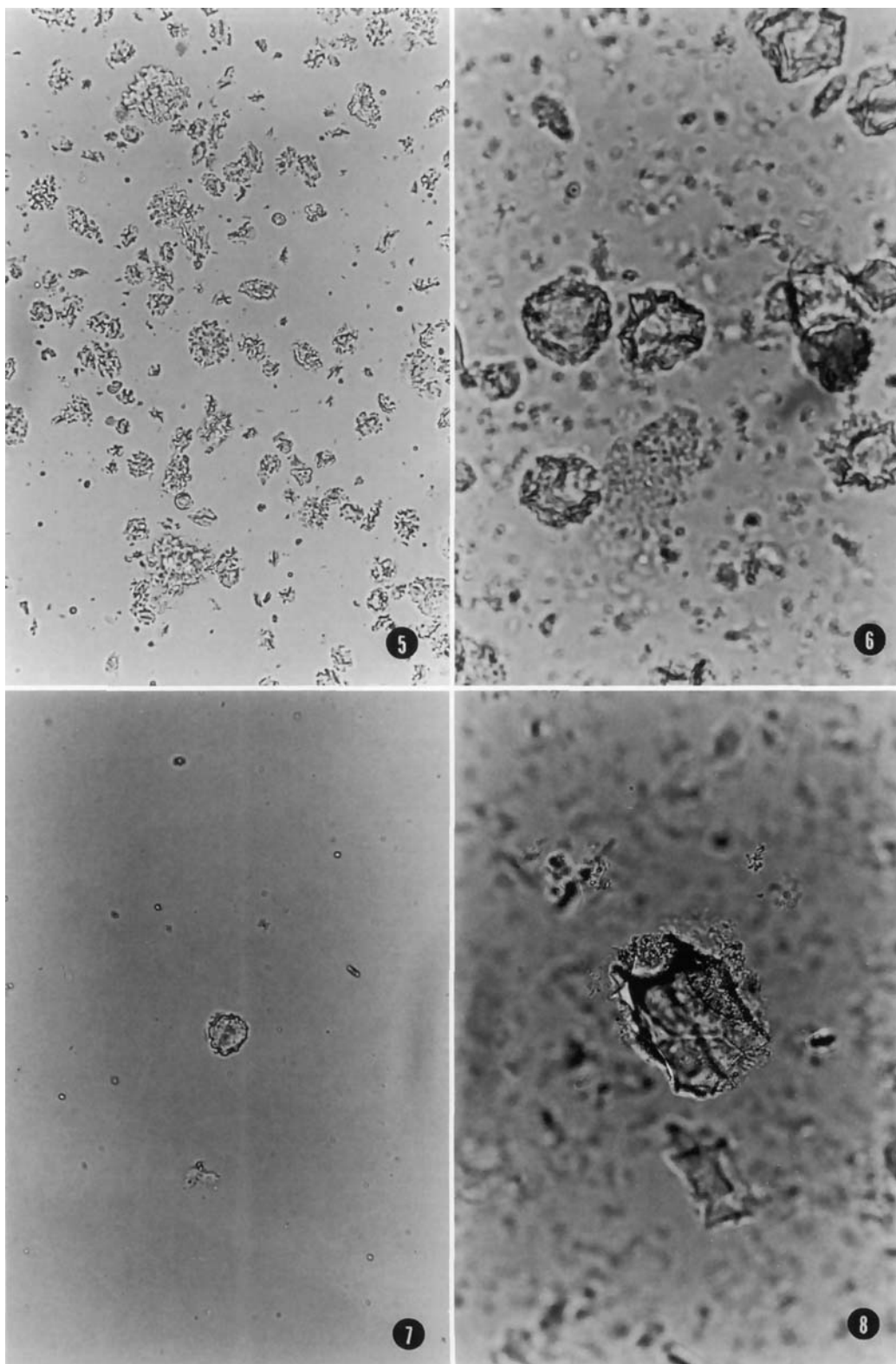
Orchidaceae species produce small, rugulose, spherical and conical phytoliths (Table 3). Three species studied herein produce spheres in unique size ranges (4–6  $\mu\text{m}$ , 8–10  $\mu\text{m}$ , 10–14  $\mu\text{m}$  in diameter; Figure 11). There also are size differences between leaf and inflorescence spheres in *Aerides*. One species, *Coelogyne fleuryi*, has distinctive truncated cones (8–10  $\mu\text{m}$  in diameter at base; Figure 12). Other than a silicified epidermis, few additional phytolith forms were found in these species. Two species, in *Eria* and *Vanilla*, do not have phytoliths.

As with the Palmae, this family warrants more detailed investigation of phytolith variability among genera and species. Although Orchidaceae is a cosmopolitan family, the distribution of individual species is often ecologically constrained (see Table 2).

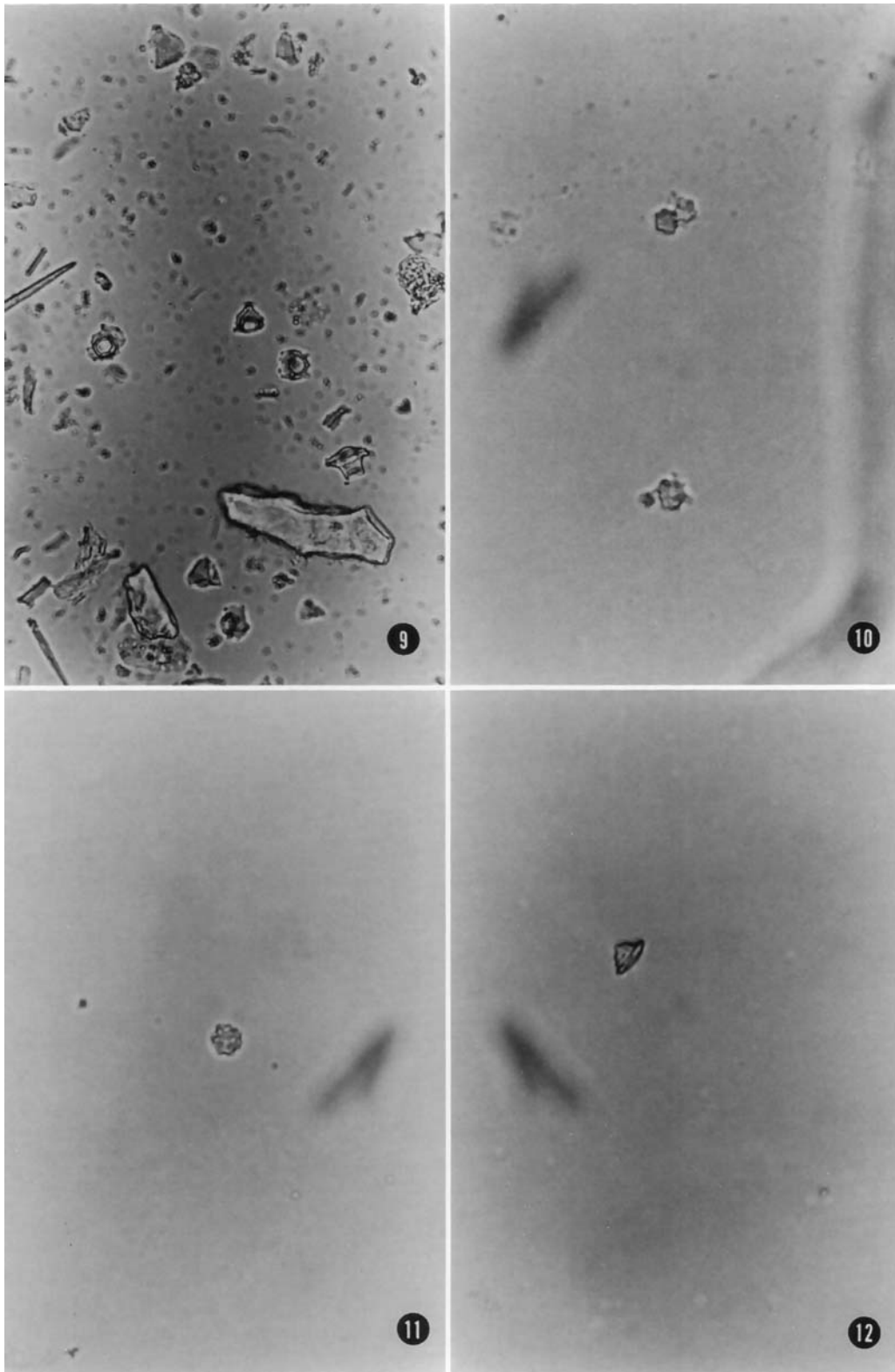
#### MONOCOTYLEDONS SUMMARY

The monocotyledon families studied herein can be identified using one or two of their diagnostic phytolith forms. Most commonly these forms are spherical or conical and show considerable potential to be diagnostic at least to genus. All monocotyledon families need detailed definition of phytolith variability within and between subfamilies, tribes, and species. This is particularly important for environmental reconstruction because a phytolith identified to genus in a sediment sequence provides more detailed environmental information than does family attribution.

Although the diversity and abundance of silica present in a plant varies in relation to soil characteristics and plant senescence (Jones and Handreck, 1967; Iler, 1979; McNaughton et al., 1985), this rarely affects the presence of diagnostic phytolith forms. Even without considering the Poaceae, phytoliths from diagnostic monocotyledon genera can be used to distinguish a diverse set of specific habitats, as shown in Table 2. Orchidaceae and Zingiberaceae phytoliths have already aided in the identification of lowland forests, and phytoliths from Cyperaceae and Palmae genera have been used to identify coastal and swamp habitats in central Thailand (Kealhofer and Piperno, 1994; Kealhofer, in press).



FIGURES 5-8.—5, *Phrynium parviflorum* (Marantaceae) ( $\times 178$ ): folded, rugulose, conical phytoliths from inflorescence sample, USNH 2411368. 6, *Costus speciosus* (Zingiberaceae) ( $\times 356$ ): folded, decorated sphere from leaf sample, USNH 2395216. 7, *Elettaria cardamomum* (Zingiberaceae) ( $\times 356$ ): folded, decorated sphere from bract sample, USNH 206300. 8, *Zingiber* sp. (Zingiberaceae) ( $\times 356$ ): decorated ovoids from inflorescence sample, USNH 2395209.



FIGURES 9-12 ( $\times 356$ ).—9, *Musa* sp. (Musaceae): trough shapes from leaf sample, USNH 1512179. 10, *Dioscorea membranacea* (Dioscoreaceae): tabular spheres, 5-6  $\mu\text{m}$  in diameter, from leaf sample, USNH 1701266. 11, *Dendrobium crumenatum* (Orchidaceae): rugulose spheres from leaf sample, USNH 2211836. 12, *Coelogyne fleuryi* (Orchidaceae): rugulose, conical phytoliths from leaf sample, USNH 2532095.

## DICOTYLEDONS

Five of the six subclasses of dicotyledons studied herein have diagnostic phytoliths: Asteridae, Dilleniidae, Hamamelidae, Magnoliidae, and Rosidae (Table 4). Dicotyledon phytolith forms most commonly include hair cells or associated cells (e.g., hair-base cells and cystoliths); tissues related to respiration, such as stomata, tracheids, sclereids, and multifaceted polyhedrals; and spheres, often from epidermal and subepidermal tissue. The sclereids, hair forms, multifaceted polyhedrals, and spheres have thus far proved to be the most diagnostic of the phytolith forms identified.

## Subclass ASTERIDAE

Boraginaceae species (Lamiales) have short, armed hair cells and spheroids (Figure 13). The hair cells found in *Cordia* are of medium length, heavily armed, and side attached, lying flush with the epidermis. The spheres in *Ehretia* are very smooth and are associated with epidermal cells. Their size range is highly variable, from 6  $\mu\text{m}$  to 22  $\mu\text{m}$  in diameter, although most are 10–12  $\mu\text{m}$ .

This family is most common in temperate regions; however, Southeast Asian genera are predominantly tropical trees.

Lamiaceae and Verbenaceae species (Lamiales) either did not produce phytoliths or contained a few rare, nondiagnostic forms (see Table 5).

*Ligustrum* (Scrophulariales: Oleaceae) contained an unusual hemispherical clump of subepidermal cells that may be diagnostic (Figure 14).

This shrubby genus has a disjunct distribution in Europe and Asia/Indomalaysia. In Thailand, *Ligustrum* is found in higher elevation evergreen forests.

The leaves of one genus of Scrophulariaceae, *Centranthera*, also have diagnostic armed-hair phytoliths. This species was collected in deciduous tropical forests. Another Scrophulariales family, Lentibulariaceae, does not produce phytoliths.

The species in other orders of Asteridae sampled, Gentianales (Apocynaceae and Asclepiadaceae), Rubiales (Rubiaceae), and Solanales (Convolvulaceae and Solanaceae), did not yield diagnostic phytoliths (Table 5).

## Subclass CARYOPHYLLIDAE

In the two families sampled, Amaranthaceae and Basellaceae, phytoliths were not found in leaves or in fruits (Table 5).

## Subclass DILLENIIDAE

In Dilleniidae, diagnostic phytoliths were identified in six orders: Capparidales, Dilleniales, Ebenales, Malvales, Theales, and Violales (Table 4). Thus far, families in Violales, specifically Cucurbitaceae and Flacourtiaceae, have yielded the most species with diagnostic phytolith forms. Several families

within the Malvales, Theales, and Violales do not produce diagnostic phytoliths.

Phytolith production in Capparidales is not consistent. *Cleome* (Capparidaceae) does not produce phytoliths, but *Moringa* (Moringaceae) inflorescences have very distinctive armed hair cells, similar to those of *Streblus* (Moraceae).

Among the Dilleniales, *Dillenia* has unusual hair cells and hair bases. Both *D. ovata* and *D. robusta* have hair cells with either square distal or square proximal ends (see Figure 16). *Dillenia robusta* has an additional hair-cell type with a proximal end shaped like an arrow point (Figure 17). Both species have angular, fused hair-base cells that may be diagnostic as well (Figure 18).

*Dillenia* species are tropical trees and are most common from China to Australia. In Southeast Asia they are found in evergreen to mixed deciduous forests, and certain species are persistent in degraded dry dipterocarp (seasonal) forests (Blasco, 1983).

Both *Diospyros* (Ebenaceae) and *Madhuca* (Sapotaceae) in Ebenales produce phytoliths. *Diospyros ebenum* has large (19–20  $\mu\text{m}$  in diameter) and small (7–9  $\mu\text{m}$  in diameter) spheres both in leaf and seed samples. *Madhuca* phytoliths are predominantly found in vascular tissue, including sclereids and tracheids. Some epidermal tissue also is silicified.

*Madhuca* and *Diospyros* species are both used for timber and fruit. *Diospyros* is often found in mixed deciduous and semievergreen forests. *Diospyros siamensis* was identified in a disturbed, open seasonal forest in northern Thailand.

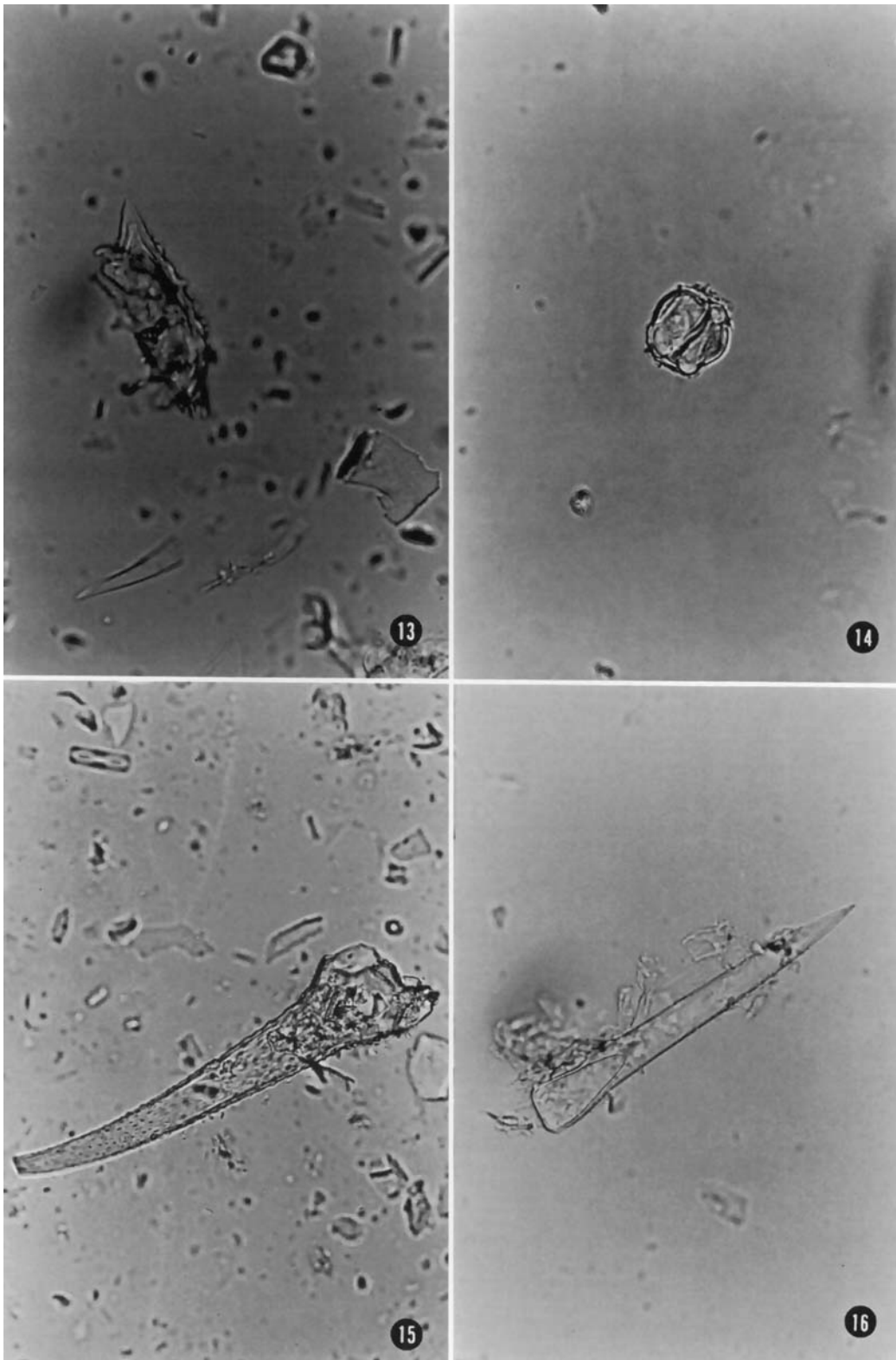
In Malvales few families produce phytoliths. A few species of Sterculiaceae have rare, diagnostic types. *Eriolaena* has a rugulose sphere 15  $\mu\text{m}$  in diameter, *Pterospermum* and *Sterculia* species both produce sclereids, and *Sterculia* has other vascular- and hair-related forms. *Melochia* has a rare, unusual form of linked spheres (Figure 19).

The species sampled from other Malvales families, Bombacaceae, Malvaceae, and Tiliaceae, produce phytoliths only rarely, and none are diagnostic (Table 5).

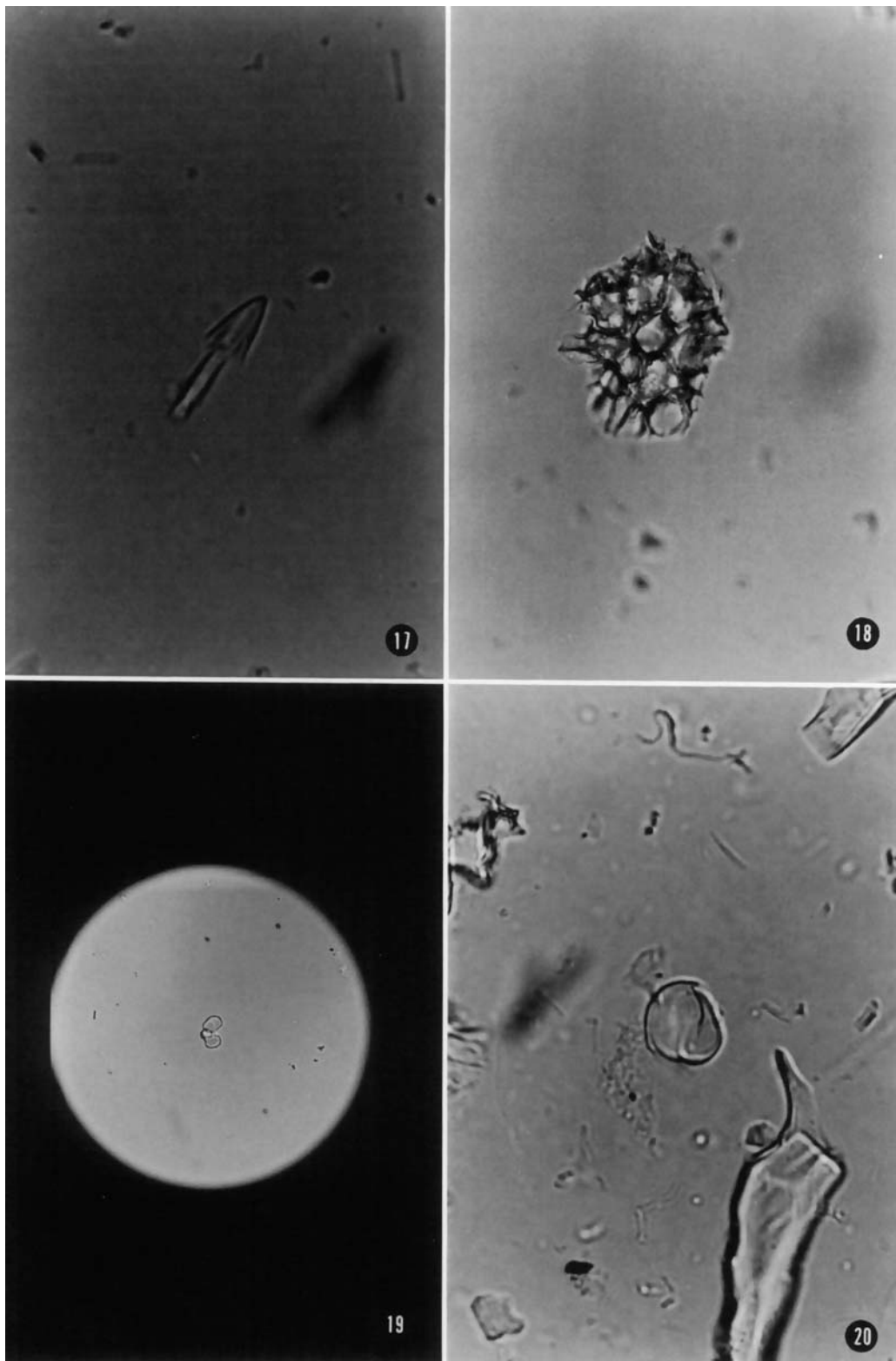
In Theales, the genus *Calophyllum* in Clusiaceae (Guttiferae) has abundant phytoliths. A spherical form, shaped somewhat like a seed, is the most distinctive shape (Figure 20). Another diagnostic, slightly spinulose, elongate epidermal form also is common and has an unusual spike on one of its longer sides (Figure 21). In six other genera of Clusiaceae, phytoliths are absent or are not diagnostic (Table 5); however, *Mammea* produces tiny (4  $\mu\text{m}$  in diameter) spheres, and *Ochrocarpus* has tiny sclereids.

Species of *Calophyllum*, like those of *Dillenia*, are predominantly tropical trees, the timber of which is useful for its durability and ease of working. The species analyzed herein are most common in hill evergreen forests.

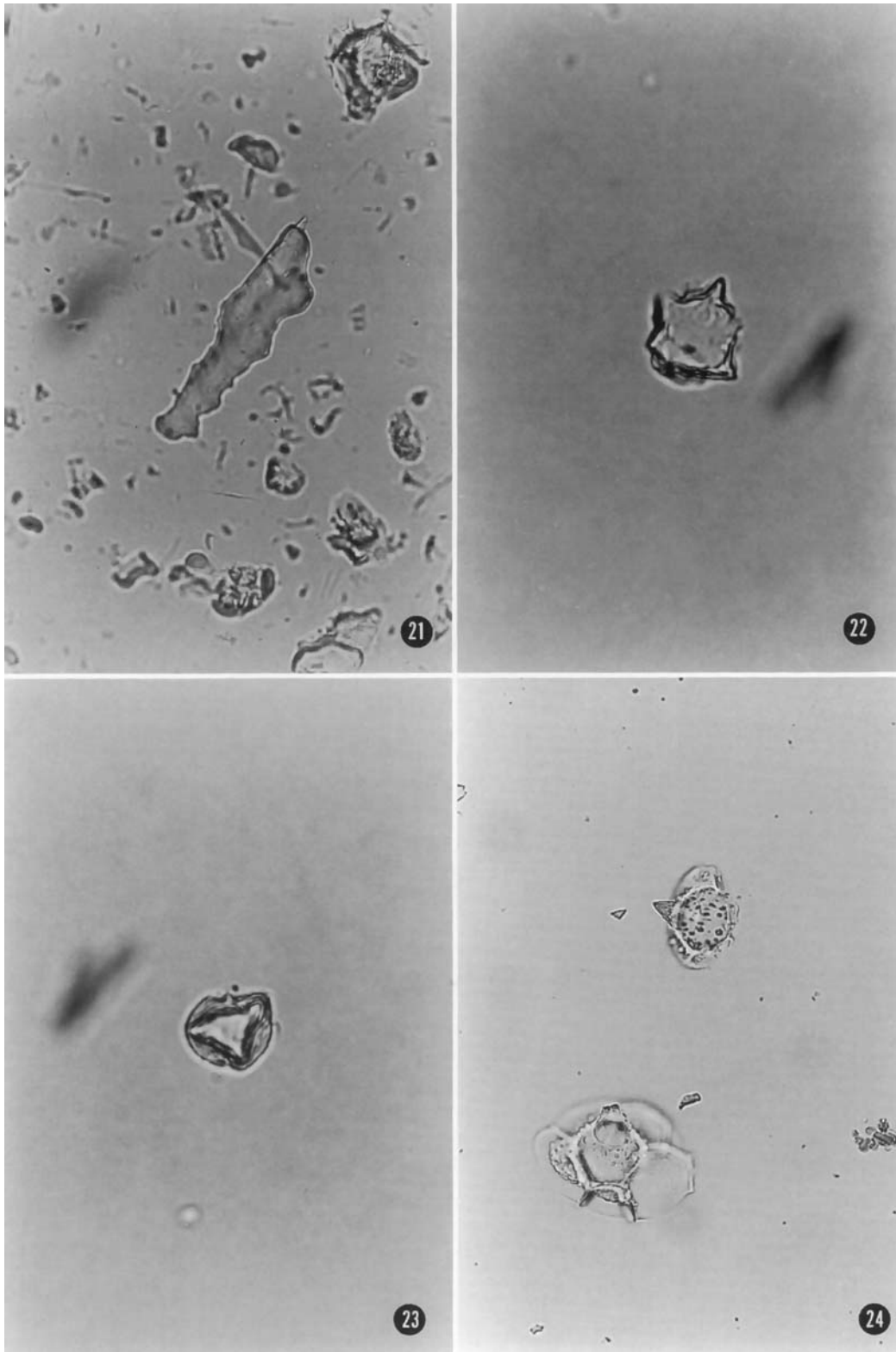
The family Dipterocarpaceae (Theales), known for habitat-specific tropical trees, yielded few diagnostic phytoliths. Leaves from two genera, *Shorea* and *Hopea*, however, did have rare, decorated, spherical phytolith forms that are at least



FIGURES 13–16.—13, *Cordia grandis* (Boraginaceae) ( $\times 178$ ): short, armed hair cells from leaf sample, USNH 1213307. 14, *Ligustrum robustus* (Oleaceae) ( $\times 356$ ): subepidermal hemispherical clump from leaf sample, USNH 1214625. 15, *Centranthera hispida* (Scrophulariaceae) ( $\times 178$ ): armed hair from leaf sample, USNH 2941665. 16, *Dillenia ovata* (Dilleniaceae) ( $\times 178$ ): square proximal hair cells from leaf sample, USNH 1700567.



FIGURES 17-20.—17, *Dillenia robusta* (Dilleniaceae) ( $\times 356$ ): proximal end of arrow-point hair cell from leaf sample, USNH 1700660. 18, *Dillenia ovata* (Dilleniaceae) ( $\times 178$ ): angular, fused hair-base cells from leaf sample, USNH 1700567. 19, *Melochia umbellata* (Sterculiaceae) ( $\times 178$ ): stalk-linked spheres from leaf sample, USNH 3083385. 20, *Calophyllum burmanii* (Clusiaceae) ( $\times 356$ ): seed-like sphere from leaf sample, USNH 1668055.



FIGURES 21-24.—21, *Calophyllum burmanii* (Clusiaceae) ( $\times 178$ ): spinulose phytolith (spike end) from leaf sample, USNH 1668055. 22, *Hopea odorata* (Dipterocarpaceae) ( $\times 356$ ): decorated sphere from leaf sample, USNH 1701199. 23, *Shorea obtusa* (Dipterocarpaceae) ( $\times 356$ ): decorated sphere from fruit sample, USNH 2211819. 24, *Solena heterophylla* (Cucurbitaceae) ( $\times 178$ ): armed hair cells from leaf sample, USNH 2553066.



genus-specific (Figures 22, 23) and have been found in sediments (Kealhofer, 1996b). The *Vatica* and *Dipterocarpus* species investigated, however, did not have diagnostic phytolith forms.

Dipterocarp species, most abundant in Malesia, also are widespread in Thailand (dipterocarp species comprise 45% of Thai forest species). The culturally modified dry dipterocarp forest type is defined by a few dominant Dipterocarpaceae species (*Pentacme siamensis*, *Shorea obtusa*, *Dipterocarpus tuberculatus*, *D. obtusifolius*). Ogawa and coworkers (1961) identified two dipterocarp forest subhabitats: *Pentacme-Shorea* (drier) and *Dipterocarpus tuberculatus-Dipterocarpus obtusifolius* (wetter). In general, the *Pentacme-Shorea* habitat is species poor, including only a few grass species (such as *Arundinaria* spp.), *Cycas siamensis*, *Phoenix humilis*, *P. acaulis*, and relatively infrequent arboreal species. Composition varies regionally. Different Dipterocarpaceae (particularly *Dipterocarpus* spp.) are found in mixed and evergreen forests, but their relative abundance is much lower as species diversity increases (Ogawa et al., 1961:67). *Hopea odorata* is common in dry evergreen forests.

Elatinaceae species (Theales) do not produce diagnostic phytoliths.

By far the most abundant and distinctive phytoliths of the Dilleniidae are found in the Violales, particularly in Cucurbitaceae and Flacourtiaceae (Table 4). The Cucurbitaceae are known for their segmented hair cells, some of which are armed. Eight genera of Cucurbitaceae from two subfamilies were analyzed. Only *Momordica* did not produce armed or segmented hair cells in their leaves. None of the inflorescences produced diagnostic phytoliths. No fruits were analyzed, but distinctive, faceted spheres have been identified with certain parts of the fruit (Bozarth, 1986).

*Citrullus*, *Cucumis*, *Gymnopetalum*, *Luffa*, and *Trichosanthes* all have distinctive segmented hair cells of various sizes, whereas *Solena* and *Mukia* have armed hair cells (Figures 24, 25). Other diagnostic features include curved hair tips (*Gymnopetalum*) and unique hair bases (*Citrullus*, *Cucumis*). *Momordica* contains cystoliths, often seen linked at the top to form a tripod arrangement (Figure 26). In only one genus, *Solena*, were two species examined, and these appeared to have species-specific forms. Further analyses within these genera may yield more phytolith forms diagnostic at the species level.

These Cucurbitaceae genera are all from the Asian tropics and are most commonly lianas, or climbing vines. They are often weeds in disturbed habitats. Members of this family were some of the earliest species domesticated.

Samples from members of Flacourtiaceae (Violales) only sporadically produced phytoliths. Nondiagnostic phytoliths are common in Flacourtiaceae leaves, and diagnostic forms are relatively rare. The fruits of several species contain spherical shapes, possibly associated with epidermal cells. These spheres are 10–14  $\mu\text{m}$  in diameter, with a dimple (*Casearia*) or with flat tissue attached (*Hydnocarpus*). *Scolopia* flowers have a

rare, spheroid, kidney-bean-shaped phytolith. In leaves, epidermal forms also are diagnostic in a few cases, particularly for *Hydnocarpus* (Figure 27). *Idesia* has an unusual, multifaceted-polyhedral form (Figure 28).

The Flacourtiaceae are fairly cosmopolitan trees and shrubs with wide distribution in the tropics and subtropics. *Casearia* and *Flacourtia* are both found in dry mixed forests and occasionally in dry deciduous forests. *Hydnocarpus* is a common shrub in tropical evergreen to dry evergreen forests. Only a few species, namely *Scolopia* and *Casearia* (useful timber) and *Flacourtia* (edible fruit), have economic uses.

Samples from species in two other families in the Violales, Caricaceae and Passifloraceae, did not yield diagnostic phytoliths (Table 5).

#### Subclass HAMAMELIDAE

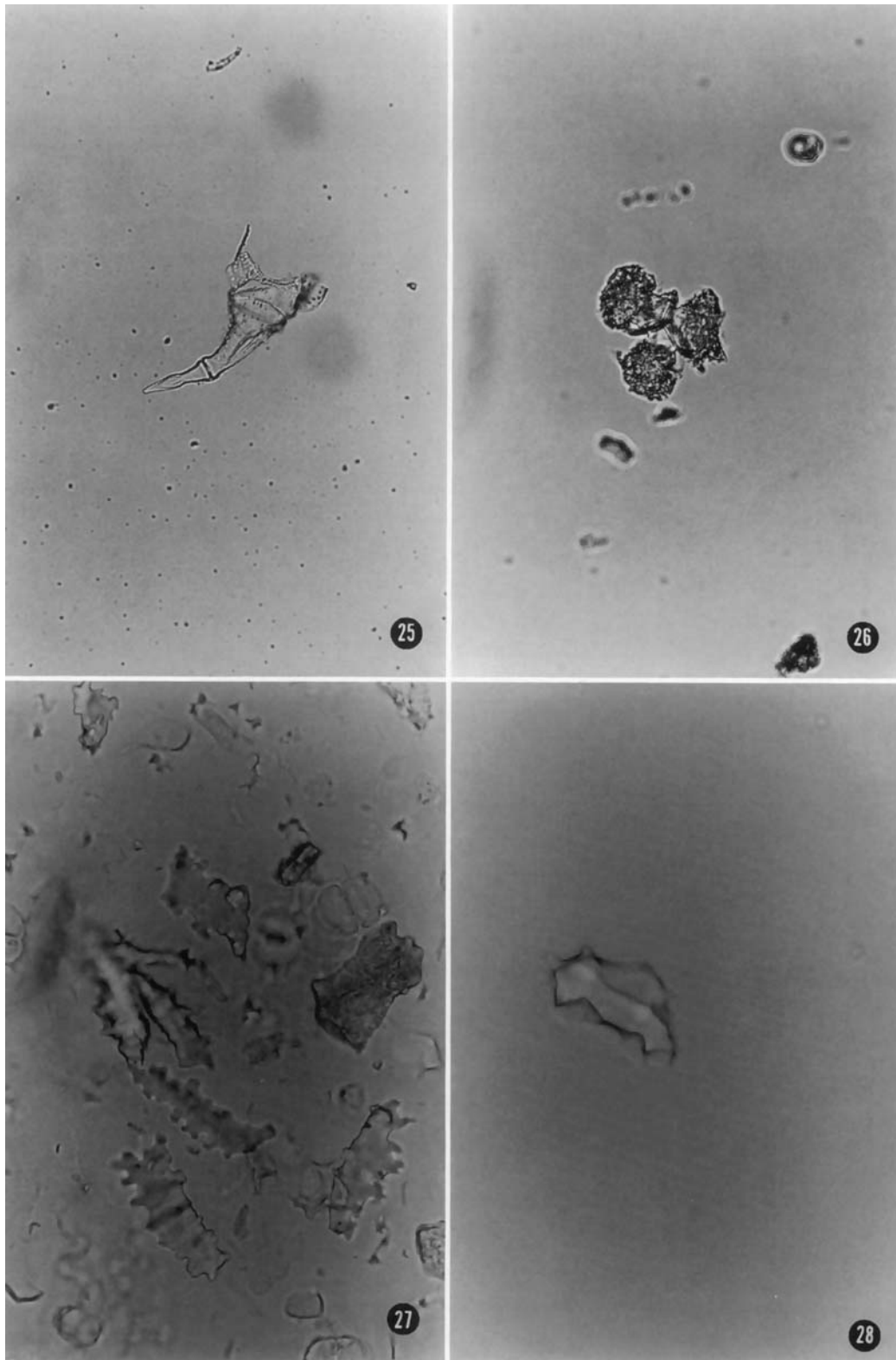
Three of the four Hamamelidae families analyzed revealed characteristic phytoliths: Fagaceae (Fagales) and Moraceae and Ulmaceae (Urticales) (Table 4). The one Juglandaceae species tested did not produce diagnostic phytoliths (Juglandales; Table 5).

In Fagaceae (Fagales), the leaves of *Lithocarpus* have distinctive, faceted, spherical polyhedrals (Figure 29) and spheres. *Quercus* samples produced spheres from the nut-shell.

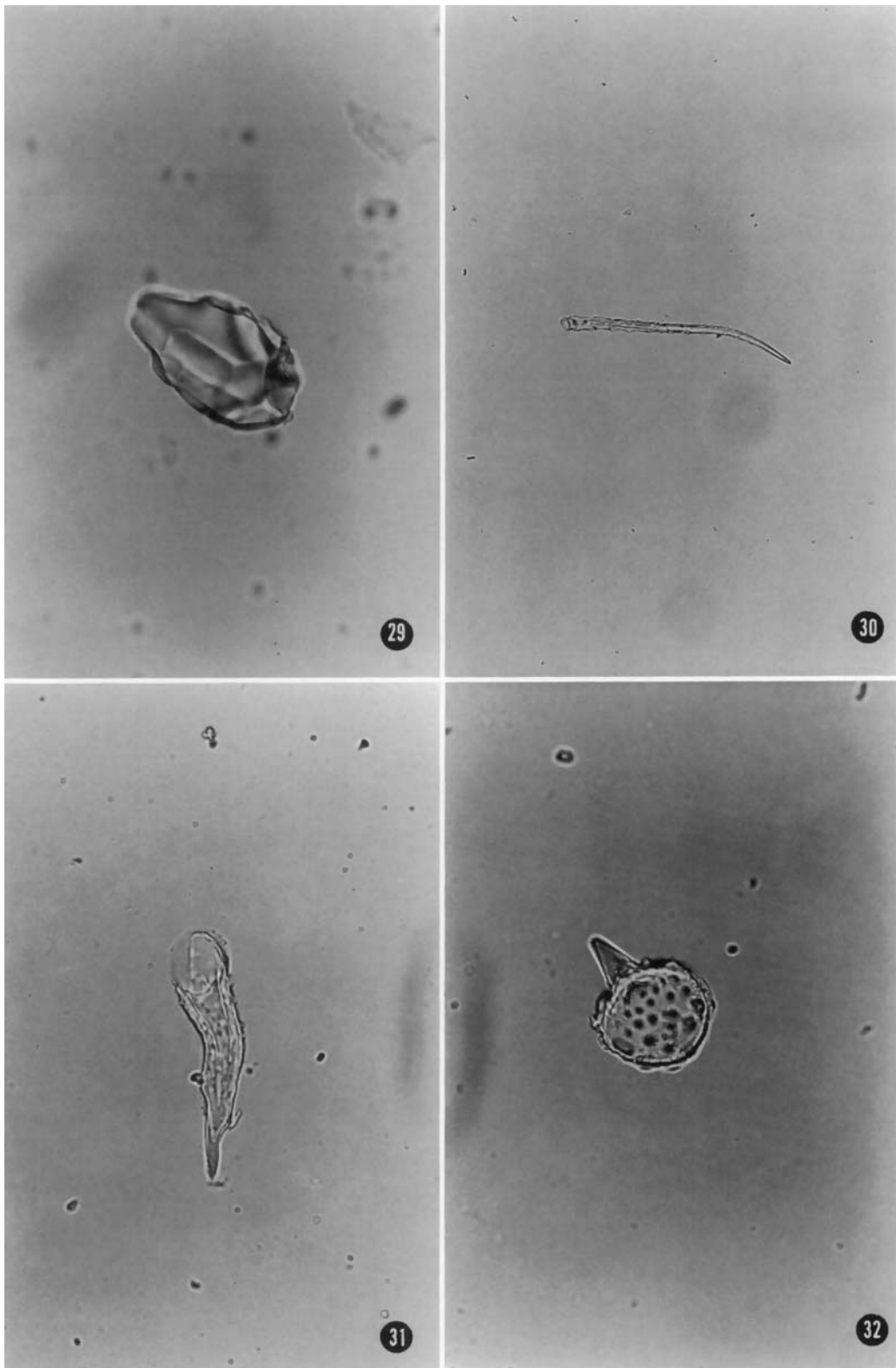
The Fagaceae are, in general, a temperate family (oaks), but in the tropics they appear in montane evergreen forests. Three *Quercus* species and one *Lithocarpus* species have been identified as particularly common on the higher slopes of montane forests in northern Thailand (Küchler and Sawyer, 1967). Other *Quercus* species, such as *Q. mespiliifoliodes* and *Q. kerrii*, however, are found in dry dipterocarp forest understory.

The order Urticales was more intensively investigated because it is more extensively represented in the tropics. Two families, Moraceae and Ulmaceae, demonstrated a wide variety of phytoliths. In both families, hair cells and cystoliths are the most diagnostic forms.

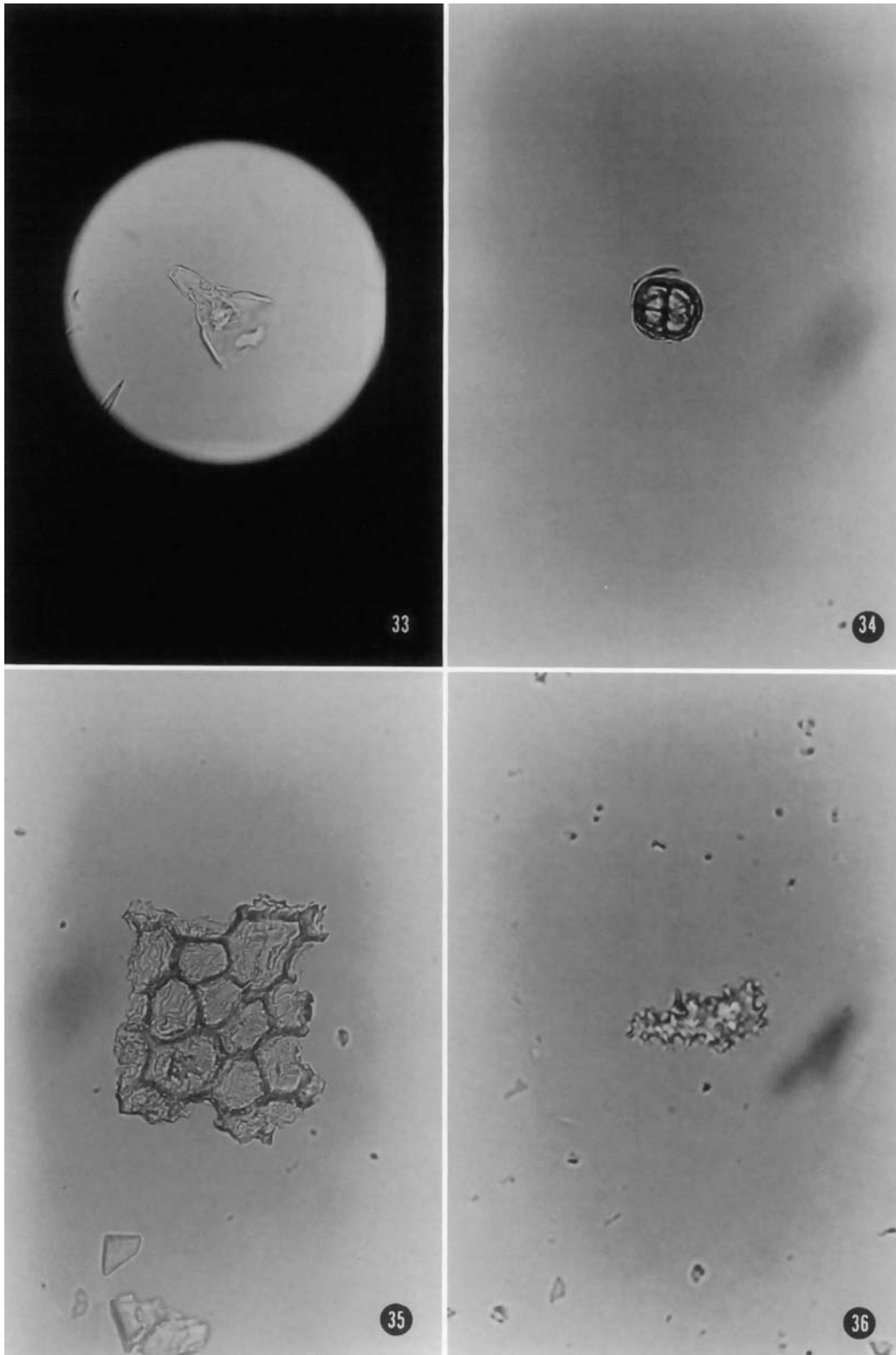
Among the Moraceae, three *Artocarpus* species were studied. Leaves of all species of *Artocarpus* revealed armed hair cells (Figure 30). One species of *Ficus* and one species of *Streblus* also have diagnostic armed hair cells, and these are the only two genera with diagnostic phytoliths in either fruit or inflorescence parts. *Streblus* has various armed and unarmed hair cells (Figures 31, 32). *Broussonetia* and *Malaisia* hair cells also are distinctive but are not armed (Figure 33). Some species contain up to five different types of hair-cell phytoliths, with characteristic attachment locations, curvature, striations, and other features. Other genera, such as *Taxotrophis*, have simpler but still diagnostic hair cells. *Ficus annulata*, *Broussonetia kasinoki*, *Artocarpus elasticus*, and *Morus alba* leaves all contain cystoliths as well (e.g., Figure 34). *Ficus hispida* epidermis has unusual hexagonal epidermal(?) cells, and *F. annulata* fruit epidermal cells have a wrinkled surface (Figure 35).



FIGURES 25–28.—25, *Mukia maderaspatana* (Cucurbitaceae) ( $\times 178$ ): armed hair cells from leaf sample, USNH 2039897. 26, *Momordica charantia* (Cucurbitaceae) ( $\times 178$ ): top-linked cystoliths from leaf sample, USNH 2039869. 27, *Hydnocarpus anthelmintheca* (Flacourtiaceae) ( $\times 356$ ): epidermal phytoliths from leaf sample, USNH 1427948. 28, *Idesia polycarpa* (Flacourtiaceae) ( $\times 356$ ): multifaceted polyhedral from leaf sample, USNH 2986601.



FIGURES 29–32.—29, *Lithocarpus acuminatissima* (Fagaceae) ( $\times 356$ ): multifaceted polyhedral from leaf sample, USNH 1701025. 30, *Artocarpus elasticus* (Moraceae) ( $\times 178$ ): armed hair cells from leaf sample, USNH 2939150. 31, *Streblus asper* (Moraceae) ( $\times 356$ ): armed hair cells from leaf sample, USNH 2064818. 32, *Streblus asper* (Moraceae) ( $\times 356$ ): armed hair cell from leaf sample, USNH 2064818.



FIGURES 33–36.—33, *Broussonetia kasinoki* (Moraceae) ( $\times 178$ ): unarmed hair cells from leaf sample, USNH 1597387. 34, *Artocarpus elasticus* (Moraceae) ( $\times 178$ ): cystolith from leaf sample, USNH 2939150. 35, *Ficus annulata* (Moraceae) ( $\times 178$ ): wrinkled epidermal cells from leaf sample, USNH 2602693. 36, *Celtis cinnamomea* (Ulmaceae) ( $\times 356$ ): unusual cystoliths from leaf sample, USNH 1212982.

Silicified epidermal cells, hair bases, stomata, tracheids, mesophyll, and nondiagnostic hair cells are common in this family.

Members of the Moraceae, and particularly *Ficus* species, are widespread but are often associated with river or stream habitats in gallery forests. Moraceae species include a variety of economically important tropical plants. Both *Artocarpus* and *Ficus* species grow in evergreen to semievergreen forests as well as often being found in middle and higher elevations. *Ficus* is a huge genus, with a broad variety of trees, shrubs, and lianas. *Broussonetia* is often in the shrub understory of evergreen forests, and *Streblus* has been identified in open disturbed seasonal forests in northern Thailand.

Many characteristics of the Moraceae also were found in the Ulmaceae. Hair-cell, hair-base, and cystolith forms are common in both leaves and fruit (Table 4). *Gironniera* has armed hair cells, and the two species of *Celtis* have unusual cystoliths (Figure 36). A spiny, irregular phytolith form was found in *Celtis*. Two *Trema* species have distinctive, small, anticlinal epidermal cells (Figure 37). *Trema orientalis* also revealed an unusual, pitted, striated phytolith form (Figure 38). *Gironniera* leaf epidermis is distinctive. No phytoliths were found in *Holoptelea* leaves.

The tropical and subtropical tribe Celtideae of Ulmaceae is composed predominantly of trees, with some shrubs. Many of these genera produce decay-resistant timber. *Celtis* is common in scrub forests, whereas species of *Trema* are often found in evergreen forests.

#### Subclass MAGNOLIIDAE

Six of the eight orders of Magnoliidae were sampled, but only one, Magnoliales (31 species), produced diagnostic phytoliths (Table 4). No phytoliths were found in Aristolochiales. Some samples from the families Illiciales, Laurales, Piperales, and Ranunculales did produce phytoliths, but they were rare to uncommon.

Among the Magnoliales, only three families are present in Thailand. Two of these families, Magnoliaceae and Annonaceae, contain characteristic phytoliths. Species sampled from the third family, Myristicaceae, did not produce silica bodies.

In Annonaceae, the characteristic phytoliths are relatively large, multifaceted polyhedrals (Figure 39). *Artabotrys* has multifaceted spheres, and other multifaceted polyhedrals were found in *Polyalthia* species and in *Sageraea elliptica*. *Sageraea* phytolith forms are unique in having tiny spinulose protrusions as decoration. Sclereid forms are present in Annonaceae, and diagnostic phytoliths occur in leaves of *Goniothalamus*, *Sageraea*, and *Uvaria* (Figure 40). *Uvaria* fruit has large, irregular spheroids (18  $\mu\text{m}$  in diameter). Vascular-tissue and stomata forms also are well represented in these species.

Annonaceae species include both trees and shrubs, several of which produce important edible fruit. All species studied herein are most common in tropical, lowland evergreen forests and

often occur in mixed deciduous forests. *Polyalthia* grows in tropical evergreen forests. *Uvaria* was identified in scrub forests, but it also is found in evergreen forests.

Magnoliaceae species also have multifaceted bodies, particularly *Michelia*. Distinctive decorated and faceted epidermal phytolith forms were found in *Talauma* and *Manglieta* (Figure 41). Phytolith production, however, seems to vary by species because no diagnostic phytoliths were found in *Michelia floribunda*.

The Magnoliaceae are most abundant in southeast Asia, and certain species are used for timber. Genera analyzed include trees of evergreen forests; *Michelia* is often found at the edge of lowland forests as well as in (mossy) montane evergreen forests, whereas *Talauma* is associated with streams or hills, and *Manglieta* is typical in the diverse, higher-slope forests of northern Thailand.

#### Subclass ROSIDAE

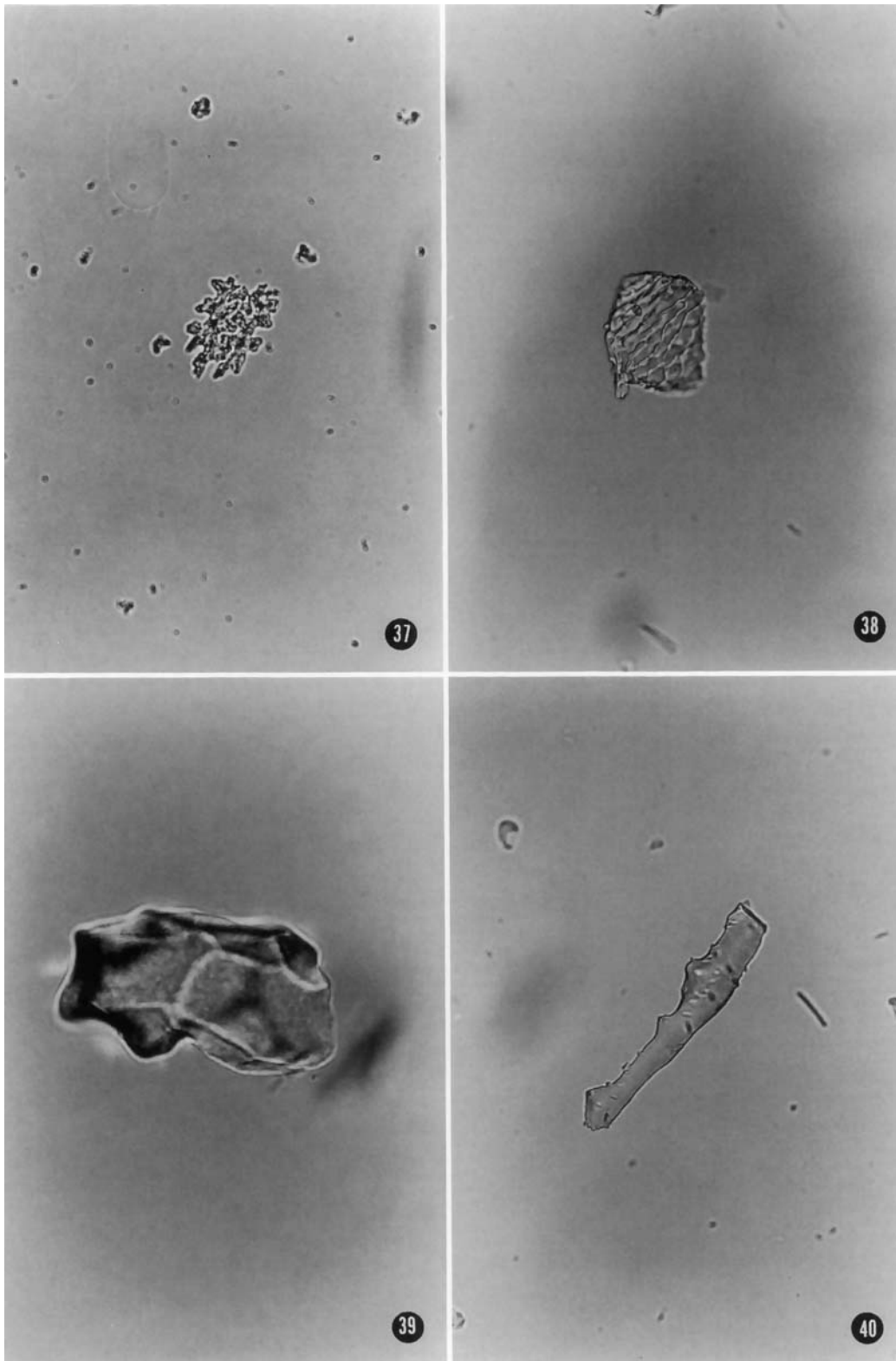
The last subclass studied, Rosidae, comprises 18 orders, 11 of which were sampled. Species in four of these orders do not produce diagnostic phytoliths: Apiales, Celastrales, Podostemales (see below), and Rhamnales (Table 5). Phytolith production is not consistent in those orders that do produce phytoliths. For example, in Santalales, some families have phytoliths, and others do not.

In the Euphorbiaceae family (Euphorbiales), phytoliths were common in three of the four genera sampled, *Sapium*, *Phyllanthus*, and *Manihot*. In *Manihot esculenta* leaves, slightly irregular spheres, 6–10  $\mu\text{m}$  in diameter, were common (Figure 42). Fruit samples of *Phyllanthus* also produced spheres, but these are nodular and 6–15  $\mu\text{m}$  in diameter. The epidermal cells of *Sapium* also are diagnostic, with an irregular, rough surface decoration (Figure 43).

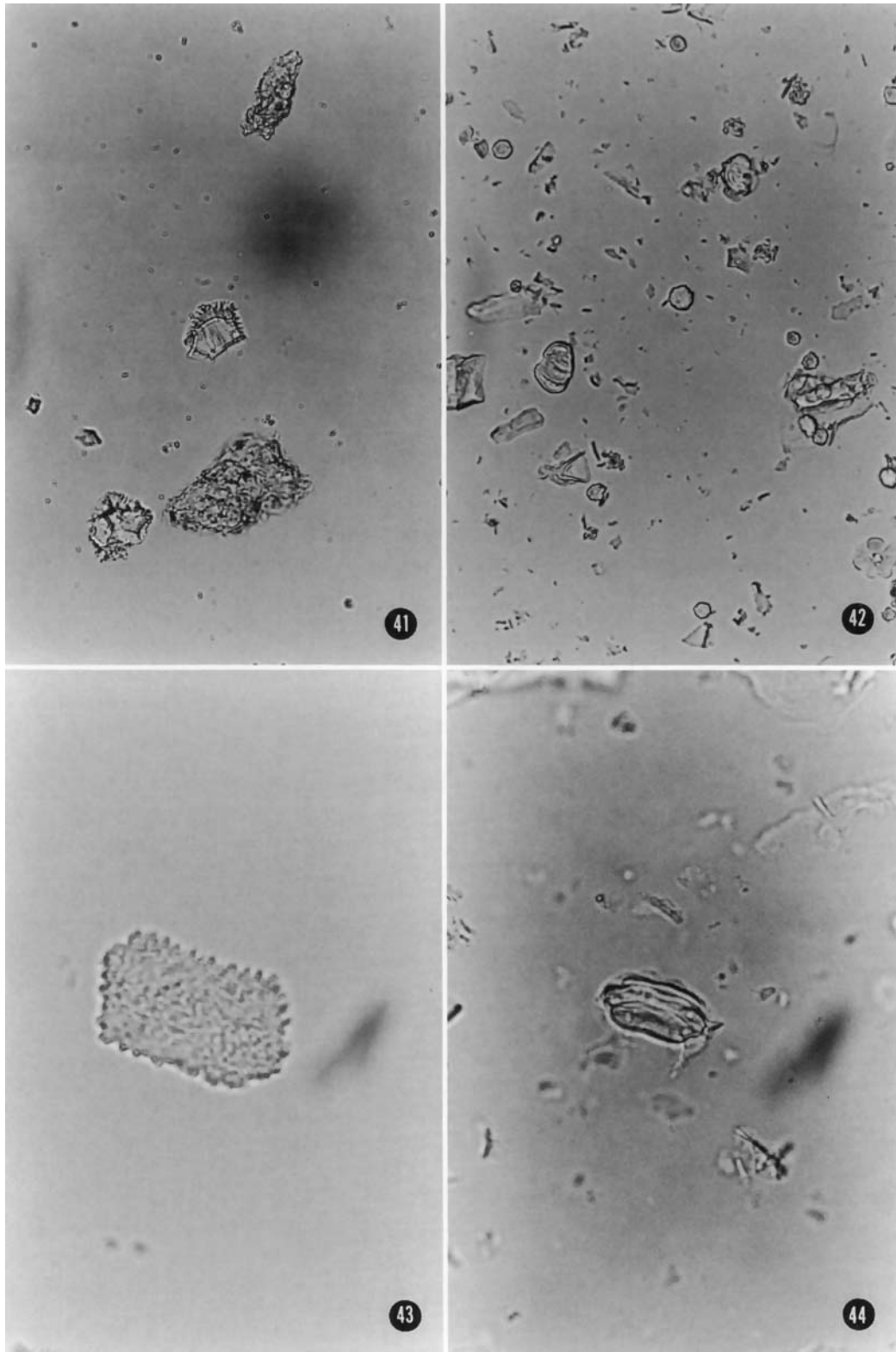
Euphorbiaceae is a large and cosmopolitan family, but its richest concentration of genera is in Indomalaysia. Two of the genera with diagnostic phytoliths are economically useful, particularly *Manihot esculenta* (cassava, a New World species), an important edible root crop, and *Phyllanthus*, used medicinally and for dyes. *Sapium* is most common in tall broadleaf evergreen forests.

In the Fabales, many species of Leguminosae (Fabaceae) produce abundant phytoliths, but few forms are diagnostic (Tables 4, 5). Three subfamilies of Fabaceae were analyzed: Caesalpinoideae, Mimosoideae, and Papilionoideae. None of the species tested in Caesalpinoideae produced diagnostic phytoliths.

In the Mimosoideae, the stomata may need further investigation because they seem to take some unusual shapes (*Albizia*, *Pithecellobium*; Figure 44). *Acacia* also may have diagnostic hair cells and hair-base cells. The epidermis in many species, particularly in subfamily Papilionoideae, also is distinctive. Tracheid or hair-base-cell forms are common to all subfamilies in which silica is present (~50% of those sampled).



FIGURES 37-40.—37, *Trema cannabina* (Ulmaceae) ( $\times 356$ ): anticlinal epidermal cells from fruit sample, USNH 2880555. 38, *Trema orientalis* (Ulmaceae) ( $\times 89$ ): pitted, striated epidermis from leaf sample, USNH 2769297. 39, *Polyalthia suberosa* (Annonaceae) ( $\times 356$ ): large, multifaceted polyhedrals from leaf sample, USNH 1171291. 40, *Goniothalamus marcani* (Annonaceae) ( $\times 178$ ): sclereid from leaf sample, USNH 1700786.



FIGURES 41-44 ( $\times 356$ ).—41, *Talauma longifolia* (Magnoliaceae): decorated, faceted phytolith from leaf sample, USNH 2407533. 42, *Manihot esculenta* (Euphorbiaceae): nodular spheres, 6-10  $\mu\text{m}$  in diameter, from leaf sample, USNH 2395207. 43, *Sapium indicum* (Euphorbiaceae): rough surface decoration on fruit epidermis sample, USNH 1701697. 44, *Pithecellobium dulce* (Fabaceae: Mimosoideae): stomata from leaf sample, USNH 2423177.

Fabaceae is a very large family and is distributed in a wide range of habitats. The subfamilies of Fabaceae have more restricted distributions, however, and Mimosoideae and Caesalpinoideae include tropical to subtropical trees and shrubs. Particular species are of enormous economic importance, especially in the Papilionoideae. The species analyzed are common in scrub and evergreen forests. *Acacia catechu* and *Albizia* are frequent in mixed deciduous forests. Vines of *Acacia* and *Mimosa* inhabit the scrub understory of disturbed, open, seasonal forests.

In Myrtales, two of the nine families present in Southeast Asia were investigated: Combretaceae and Myrtaceae. No diagnostic phytoliths were found in the three Combretaceae species studied, although phytoliths were present (Table 5). Of the two species of *Syzygium* (Myrtaceae) tested, one, *S. ipeanthia*, has an unusual, very tall stomata phytolith form.

This family is predominantly tropical and is composed mostly of large shrubs and trees. *Syzygium* is commonly found in dry evergreen forests on hillsides in Thailand and has a broader distribution elsewhere.

Podostemales are known to produce phytoliths; however, the species studied herein, *Podostemum subulatus*, does not (Piperno, 1988). Species in this order are found in flowing, fresh-water environments.

Three species in the family Rhizophoraceae were sampled. Phytoliths were not common in any of these. Sphere forms are present in all three species, although sphere size and surface decoration vary by species (Table 4).

Rhizophoraceae species are most common in coastal mangrove forests in Thailand. Many taxa are used economically for timber or charcoal.

Two of the six families of Rosales present in Thailand, Rosaceae and Chrysobalanaceae, were tested; Rosaceae did not have diagnostic phytoliths (Table 5). In Chrysobalanaceae one species, *Parinari annamense*, incorporates irregular but smooth spheres of 6–12  $\mu\text{m}$  diameter in the leaves and 6–10  $\mu\text{m}$  diameter in the inflorescence. The fruit has very large spheres (20–85  $\mu\text{m}$  in diameter).

Chrysobalanaceae species, trees and shrubs, are found in the lowland tropics (mostly in the New World), and *Parinari* includes important fruit and timber trees. This genus ranges in habitat from deciduous to evergreen forests, but in Thailand it seems to be most common in mixed deciduous forests.

One sample tested seems to be from the Connaraceae (labeled "Connarc?" in the United States National Herbarium), and it also has diagnostic epidermal forms, suggesting that this family warrants further investigation.

In Santalales, two of the four families present in Thailand were investigated. No phytoliths were found in the Olacaceae species tested. In Loranthaceae, only leaves produced phytoliths. Two distinctive stomata forms were found in *Elytranthe*, a set of elongated/palisaded cells and a set of subepidermal spherical cells in a clump (Figure 45). Unusual epidermal-cell forms also were found in this genus.

Loranthaceae includes shrubby tropical parasites. *Elytranthe* is found in evergreen forests and often impedes the regrowth of hardwood trees.

Five of the 10 families of Sapindales present in Thailand were sampled, and species in two of the families, Anacardiaceae and Burseraceae, have diagnostic phytoliths. All of the other families (Meliaceae, Rutaceae, and Sapindaceae) are phytolith producers, but the forms are rare or nondiagnostic (Table 5). Vascular tissue in both Rutaceae and Sapindaceae, particularly tracheids and adjoining tissue, occasionally includes unusual spiny forms.

Three Anacardiaceae species were tested, and the leaves of all three produced phytoliths; however, those in *Spondias pinnata* are not diagnostic (Table 5). *Mangifera indica* (mango) and *Rhus* sp. both have unique folded spheres (Figure 46).

*Mangifera* species are common in upland and lowland evergreen forests.

Burseraceae species show a wide range of unique phytoliths. Epidermal phytoliths from both fruit and leaves are the most distinctive. Silicified anticlinal and polyhedral epidermal cell shapes are both represented. *Canarium*, *Commiphora*, *Dacryodes*, *Garuga*, and *Scutinathe* species all have thick, decorated epidermal cells (Figure 47). Commonly, one surface is smooth and the opposite surface is spikey. *Canarium* fruits often have unusual, very smooth, large spheroid shapes as well (Figure 48). One *Canarium* species has a distinctive acorn-shaped hair cell (Figure 49); a related form was found in *Garuga*. Silicified stomata, tracheids, hair cells, and hair-base cells are common to abundant in Burseraceae.

Burseraceae is a tropical family of trees and shrubs. It forms a common constituent of lowland deciduous and dipterocarp forests in southeast Asia. *Canarium*, *Dacryodes*, and *Garuga* are the three Burseraceae genera most common in this lowland habitat, and all have tree species with useful timber. *Garuga pinnata* has been identified in mixed deciduous forests. *Canarium kerrii* and *C. subulatum* are common constituents of the dry dipterocarp forest. *Protium* has been identified in deciduous, closed-canopy forests in northern Thailand.

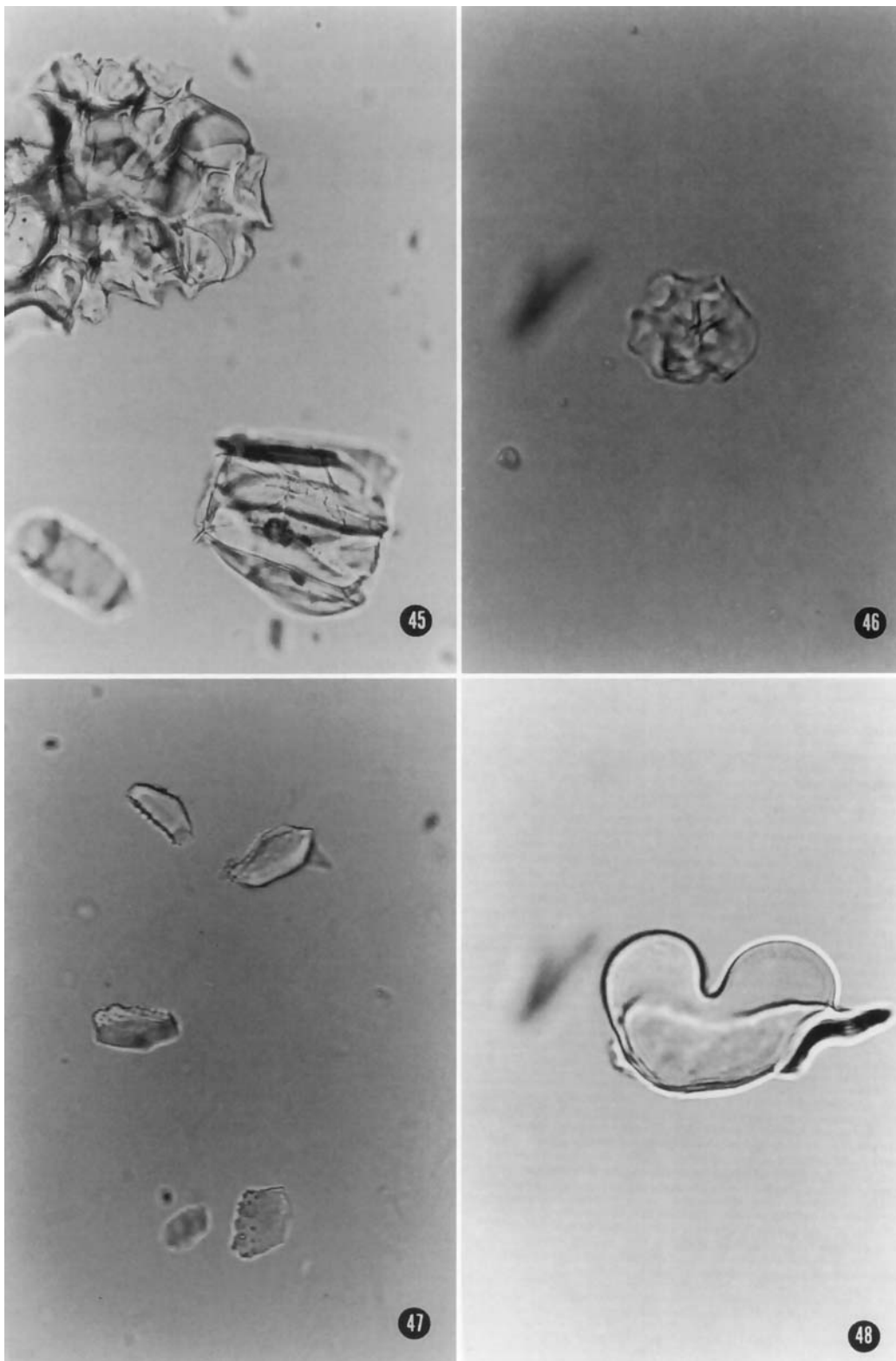
Meliaceae species only rarely produce phytoliths, but *Melia* inflorescences have rare, small spheres (5–7  $\mu\text{m}$  in diameter).

Species in this family are known for producing good timber, such as mahogany, in lowland tropical forests.

#### DICOTYLEDONS SUMMARY

The most common of the distinctive dicotyledon phytolith types are spheres (including spheroids), armed and segmented hair cells, faceted polyhedrals, and decorated epidermal cells. The variability seen in dicotyledons differs from that seen in monocotyledon families. Phytolith presence is not as predictable, and orders commonly have families and species both with and without phytoliths. A more limited range of phytolith forms also is represented, with greater frequency of vascular





FIGURES 45-48 ( $\times 356$ ).—45, *Elytranthe ampullaceae* (Loranthaceae): stomata from leaf sample, USNH 1700671. 46, *Mangifera indica* (Anacardiaceae): folded spheres from leaf sample, USNH 595090. 47, *Commiphora caudata* (Burseraceae): thick, decorated epidermis from fruit sample, USNH 2805849. 48, *Canarium kerrii* (Burseraceae): large, smooth spheroids from fruit sample, USNH 2436020.

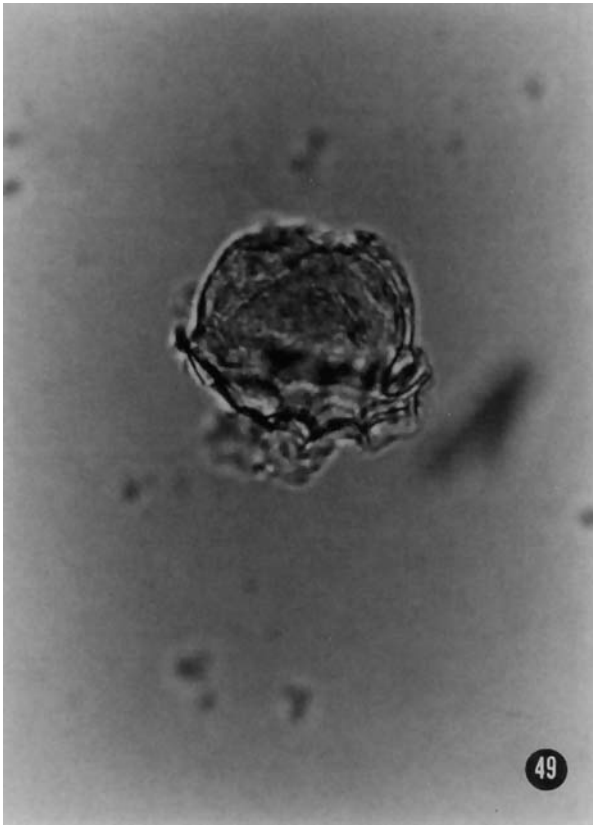


FIGURE 49.—*Canarium kerrii* (Burseraceae) ( $\times 400$ ): acorn-shaped hair cell from leaf sample, USNH 2436020.

forms (e.g., sclereids) than in monocotyledons. Short cells are not represented, nor are the distinctive tabular spheres and

cones of the monocotyledons. Dicotyledon sphere types, however, appear to be good indicators of trees in various forested habitats. The genera and families with diagnostic phytoliths include a wide range of habitats but dominate the lowland evergreen, mixed deciduous, and dry deciduous forests. Specific habitats are discernable based on the unique complement of genera identified in soil samples.

### Conclusion

The results presented herein demonstrate the abundance and diversity of diagnostic phytoliths in Old World tropical flora. These phytoliths are consistent with those described by Piperno (1985, 1989) in New World taxa, confirming the uniformity of phytolith forms among taxa with Old and New World distributions.

Based on the habitat distribution of their parent plants, phytoliths can be correlated with a wide range of specific environments. Plant age, soil chemistry, and other environmental factors may influence phytolith abundance and the diversity of forms present in a given plant; however, diagnostic forms are produced despite variable conditions. This is clearly seen when the patterns of production and morphology presented herein are compared with New World taxa (Piperno, 1988, 1989). These results further demonstrate that different kinds of habitats and economic patterns are identifiable in soil phytolith sequences. The increasing definition of diagnostic phytolith types enhances the value of phytolith sediment sequences for complementing and expanding the reconstruction of paleo-environments, and the human interactions with these environments, currently available from pollen and geomorphological analyses.







TABLE 4.—Continued.

Taxon	Phytolith abundance	Intra-/intercellular forms	Hair base	Cystolith	Stoma	Tracheid	Sclereid	Epidermal forms		Meso-phyll	MFP	Other/Comments
								elongate	antical polyhedral			
<i>Dillenia robusta</i> leaf	uncommon	-	2 fused	-	x	-	x	x	-	-	-	-
EBENALES EBENACEAE <i>Diospyros ebenum</i> Koenig leaf	uncommon	20 µm, 7 µm	-	-	-	-	-	-	-	-	-	-
seed	uncommon	19 µm, 9 µm	-	-	-	-	-	-	-	-	-	-
<i>Madhuca</i> sp. leaf	uncommon	-	-	-	-	x	x	-	ge	-	-	-
MALVALES STERCULIACEAE <i>Eriolaena caudollei</i> Wall. fruit	rare	rg, 15 µm	-	-	-	-	-	-	-	-	-	-
<i>Melochia umbellata</i> (Houtt.) Stapf leaf	rare	clump	-	-	-	-	-	-	-	-	-	connected by stalk
<i>Pterospermum semisagittifolium</i> Ham. leaf	common	-	-	-	-	x	x	-	-	-	-	-
<i>Sterculia foetida</i> L. leaf	uncommon	-	-	-	x	x	x	-	-	-	-	-
<i>Sterculia pexa</i> Pierre leaf	common	-	-	x	x	x	x	-	ge	-	-	-
THEALES CLUSIACEAE (GUTTIFERAE) <i>Calophyllum burmannii</i> Wight leaf	abundant	20-24 µm puffy	-	-	x	x	-	x	-	x	-	sk, sp elongates
DIPTEROCARPACEAE <i>Hopea odorata</i> Roxb. leaf	common	dc, 20-24 µm	-	x	x	-	-	-	-	-	-	sg sphere
<i>Shorea obtusa</i> Wall. fruit	very rare	fd, 18-21 µm	-	-	-	-	-	-	-	-	-	-
VIOLALES CUCURBITACEAE <i>Citrullus vulgaris</i> Eckl. & Zeyh. leaf	common	-	sg	x	-	x	-	-	x	-	-	double hair-base cell
<i>Cucumis trigonis</i> Roxb. leaf	uncommon	-	sg	x	-	-	-	-	-	-	-	3-cell hair base
<i>Gymnopetalum cochinchinensis</i> (Lour.) Merr. leaf	common	-	sg	x	-	-	-	x	nuclease	-	-	curved hair tip
leaf	rare	-	sg	-	-	-	-	-	-	-	-	curved hair tip
<i>Luffa cylindrica</i> (L.) M. Roem. leaf	common	-	sg	x	-	x	-	-	-	-	-	ovoid epidermal cells
<i>Momordica charantia</i> L. leaf	rare	-	-	-	x	-	-	-	-	-	-	-
<i>Mukia maderaspatana</i> (L.) M. Roem. leaf	common	-	armed	-	-	-	-	-	-	-	-	very large hairs
<i>Solena amplexicaulis</i> (Lam.) Gandhi leaf	abundant	-	armed	x	-	-	-	-	x	-	-	st, sg hairs

TABLE 4.—Continued.

Taxon	Phytolith abundance	Intra-/Inter-cellular forms	Hair	Hair base	Cysto-lith	Stoma	Tracheid	Sclereid	Epidermal forms	Meso-phyll	MFP	Other/Comments
		sphere	elongate		base				antifinal	polyhedral		
<i>Solena heterophylla</i> Lour. leaf	uncommon	—	—	armed	—	—	—	—	—	—	—	—
<i>Trichosanthes anaimalaiensis</i> Bedd. leaf	abundant	—	—	sg	x	—	x	—	—	x	—	—
FLACOURTIACEAE												
<i>Casuaria virescens</i> Jacq. fruit	very rare	dm, 10–14 µm	—	x	—	—	—	—	x	—	—	—
<i>Filacourtia jangonias</i> (Lour.) Steud. fruit	very rare	fd	—	—	—	—	—	—	—	—	—	—
<i>Hydrocarpus anthelminthea</i> Laness. leaf	abundant	—	narrow	—	—	x	x	—	x	—	—	—
<i>Hydrocarpus ilicifolius</i> SK fruit	uncommon	flat	—	—	—	—	—	—	—	—	—	—
<i>Idesia polycarpa</i> Max. leaf	abundant	—	sk	—	—	x	x	—	x	x	—	—
<i>Scolopia acuminata</i> Clos. leaf	uncommon	x	—	—	x	—	x	—	—	—	x	polyhedrals
<i>Scolopia acuminata</i> Clos. fruit	very rare	—	—	—	—	—	—	—	—	—	x	—
<i>Scolopia acuminata</i> Clos. flower	very rare	—	—	—	—	—	—	—	—	—	—	rg. bean-shaped
HAMAMELIDAE												
FAGALES												
FAGACEAE												
<i>Lithocarpus acuminatissima</i> (Bl.) Rehder leaf	uncommon	x	—	—	—	—	—	—	—	—	x	faceted spheroids
inflorescence	uncommon	6–16 µm	—	—	—	—	—	—	—	—	—	—
<i>Quercus dumosa</i> Nutt. exocarp	uncommon	4–10 µm	—	—	—	—	x	—	—	—	—	—
URTICALES												
MORACEAE												
<i>Artocarpus dadah</i> Miq. leaf	rare	—	—	armed	—	—	—	—	—	—	—	—
<i>Artocarpus elasticus</i> Reinw. ex Blume leaf	rare	—	—	armed	—	x	—	—	—	—	—	side-attached hair
<i>Artocarpus nitidus</i> Trec. leaf	rare	—	—	armed	—	x	x	—	—	bumpy	—	—
<i>Broussonetia kassinoki</i> Siebold & Zucc. leaf	common	—	—	various	x	—	—	—	—	—	—	—
<i>Ficus annulata</i> Bl. leaf	common	—	—	—	x	x	—	—	—	x	—	—
fruit	rare	—	—	—	—	—	x	—	—	wrinkled	—	—
<i>Ficus hispida</i> L. f. leaf	abundant	—	—	armed	x	x	—	—	—	hexagon	—	st hairs
seed	abundant	—	—	armed	—	—	x	—	—	hexagon	—	—
<i>Malaisia scandens</i> (Lour.) Planch. leaf	abundant	—	dc	sf	x?	x	x	—	—	x	—	curved hairs









TABLE 5.—Species without phytoliths or with nondiagnostic phytoliths. Measurements are of diameter.

Taxon	Plant part	Present(P)/ absent(A)	Phytolith forms present
<b>MONOCOTYLEDONS</b>			
<b>ALISMATIDAE</b>			
ALISMATALES: ALISMATACEAE			
<i>Caldesia ologococea</i>	seed	A	
NAJADALES: NAJADACEAE			
<i>Najas</i> sp.	leaf	P	irregular, rugulose spheroid
NAJADALES: POTAMOGETONACEAE			
<i>Potamogeton lucens</i> L.	leaf, seed	A	
<b>ARECIDAE</b>			
ARALES: ARACEAE			
<i>Alocasia macrorrhiza</i> (L.) G. Don f.	leaf	P	curved, short unsegmented hair cells; tracheids
<i>Amorphophallus corrugatus</i> Decne	leaf	A	
<i>Colocasia esculenta</i> Schott	leaf	A	
<i>Cyrtosperma johnstonii</i> Griffith	leaf	A	
<b>COMMELINIDAE</b>			
ERIOCAULALES: ERIOCAULACEAE			
<i>Eriocaulon luzulaefolium</i> L.	leaf, inflorescence	A	
<i>Eriocaulon siamense</i> L.	inflorescence	P	long, thin epidermal polyhedrals with central spikes
<i>Eriocaulon siamense</i>	seed	A	
TYPHALES: TYPHACEAE			
<i>Typha angustifolia</i> L.	reed, seed	A	
<b>ZIGIBERIDAE</b>			
ZINGIBERALES: MUSACEAE			
<i>Musa</i> sp.	inflorescence	A	
ZINGIBERALES: ZINGIBERACEAE			
<i>Curcuma</i> sp.	inflorescence	A	
<i>Elettaria cardamomum</i> (L.) Maton	inflorescence	A	
<i>Hedychium ellipticum</i> J. Koenig	leaf, inflorescence	A	
<i>Kaempferia pulchra</i> L.	leaf	A	
<b>LILIIDAE</b>			
LILIALES: DIOSCOREACEAE			
<i>Dioscorea alata</i> L.	leaf, seed	A	
<i>Dioscorea collinsae</i> L.	leaf, inflorescence, seed	A	
<i>Dioscorea membranacea</i> Pierre	inflorescence	A	
<i>Dioscorea</i> sp.	root	A	
LILIALES: PONTEDERIACEAE			
<i>Eichhornia crassipa</i> Solms	leaf, root	A	
<i>Monochoria vaginalis</i> Presl.	leaf	P	cupped cell (intrusives)
<i>Monochoria vaginalis</i>	inflorescence	P?	8–15 µm spheres, could be intrusive
LILIALES: TACCACEAE			
<i>Tacca</i> sp.	leaf, inflorescence	A	lots of intrusives
ORCHIDALES: ORCHIDACEAE			
<i>Coelogyne fleuryi</i> Torrey	root	P	rugulose, globular, irregular body
<i>Eria dasyphylla</i> Lindley	leaf, root	A	
<i>Vanilla griffithii</i> Miller	leaf	A	
<b>DICOTYLEDONS</b>			
<b>ASTERIDAE</b>			
GENTIANALES: APOCYNACEAE			
<i>Aganioneron polymorphum</i> Spire	leaf	P	hair-base cells? segments, sphere (10 µm), hexagonal bodies, anticlinal epidermis
<i>Alstonia scholaris</i> R. Br.	leaf	P	epidermis, stomata
<i>Rauvolfia verticillata</i> L.	leaf	P	sphere (10 µm), tracheid
GENTIANALES: ASCLEPIADACEAE			
<i>Atherolepis pierrei</i> Cost.	leaf	A	
<i>Telosma minor</i> Craib	leaf	P	tracheids
LAMIALES: BORAGINACEAE			
<i>Cordia grandis</i> Cham.	inflorescence	A	
<i>Ehretia</i> sp.	fruit	A	
LAMIALES: LABIATEAE (LAMIACEAE)			
<i>Perilla frutescens</i> L.	leaf, inflorescence	A	

TABLE 5.—Continued.

Taxon	Plant part	Present(P)/ absent(A)	Phytolith forms present
<i>Pogostemon glaber</i> Desf.	leaf	P	cupped epidermal cells, anticlinal epidermis, hair cells
<i>Pogostemon glaber</i>	inflorescence	A	
LAMIALES: VERBENACEAE			
<i>Callicarpa arborea</i> L.	leaf, inflorescence	A	epidermis with hemispherical bumps; short, unsegmented hairs; cell clumps
<i>Tectona grandis</i> L.f.	leaf, inflorescence	P	
RUBIALES: RUBIACEAE			
<i>Paedena foetida</i> L.	leaf, inflorescence	A	
SCROPHULARIALES: LENTIBULARIACEAE			
<i>Utricularia aurea</i> Lour.	leaf	A	
SCROPHULARIALES: OLEACEAE			
<i>Jasminum nervosum</i> L.	leaf	P	long, thin epidermal polyhedrals; tracheids; spiny, sock-shaped tracheids
<i>Jasminum nervosum</i>	inflorescence	P	
<i>Jasminum sambac</i> Aiton	leaf	A	
<i>Ligustrum robustum</i> L.	fruit, branch	A	
SOLANALES: CONVULVACEAE			
<i>Ipomoea batatas</i> (L.) Lam.	leaf	A	
<i>Ipomoea pes-caprae</i> (L.) R. Br.	leaf	A	
SOLANALES: SOLANACEAE			
<i>Capsicum frutescens</i> L.	leaf, inflorescence, fruit	A	
<i>Solanum album</i> L.	leaf	A	
CARYOPHYLLIDAE			
CARYOPHYLLALES: AMARANTHACEAE			
<i>Aerva scandens</i> Forssk.	leaf, seed	A	
CARYOPHYLLALES: BASELLACEAE			
<i>Basella alba</i> L.	leaf, fruit	A	
DILLENIIDAE			
CAPPARIDALES: CAPPARIDACEAE			
<i>Cleome gynandra</i> L.	leaf, pod	A	
DILLENIALES: DILLENIACEAE			
<i>Dillenia ovata</i> L.	inflorescence	A	
<i>Dillenia robusta</i> L.	inflorescence	A	
EBENALES: EBENACEAE			
<i>Diospyros kaki</i> L.f.	leaf	P	tracheids, long, thin epidermal polyhedrals tracheids, epidermal cells
<i>Madhuca</i> sp.	fruit	P	
MALVALES: BOMBACACEAE			
<i>Bombax ceiba</i> L.	inflorescence, seed, pod	A	
<i>Bombax valentoni</i> L.	leaf	A	
<i>Durio zibethinus</i> Murray	leaf	P	hair cell bases? segments
<i>Durio zibethinus</i>	inflorescence	P	epidermal cells, small spheres
<i>Ochroma pyramidale</i> Sw.	leaf	A	
MALVALES: MALVACEAE			
<i>Gossypium arboreum</i> L.	leaf, bract	A	
<i>Gossypium herbaceum</i> L.	leaf	A	
<i>Hibiscus sabdariffa</i> L.	leaf, inflorescence	A	
MALVALES: STERCULIACEAE			
<i>Ambroma augusta</i> L.f.	leaf, seed	A	
<i>Byttneria pilosa</i> Roxb.	leaf	P	irregular epidermal cells, tracheids
<i>Byttneria pilosa</i> Roxb.	inflorescence	A	
<i>Commersonia bartramia</i> (L.) Merr.	leaf, inflorescence	A	
<i>Eriolaena caudollei</i> Wall.	leaf	P	epidermal cells, mesophyll, tracheids, stomata
<i>Helicteres elongata</i> Wall.	leaf, inflorescence	A	
<i>Helicteres isora</i> L.	leaf	P	tracheids
<i>Helicteres isora</i>	inflorescence	A	
<i>Heritiera littoralis</i> Dryand	leaf	A	
<i>Melochia umbellata</i>	leaf, inflorescence	A	
<i>Pterospermum diversifolium</i>	leaf, inflorescence	A	
<i>Pterospermum semisagittifolium</i> Ham.	leaf	P	tracheids, sclereids
<i>Sterculia pexa</i> Pierre	inflorescence	A	

TABLE 5.—Continued.

Taxon	Plant part	Present(P)/ absent(A)	Phytolith forms present
MALVALES: TILIACEAE			
<i>Berrya mollis</i> Roxb.	leaf	P	stomata, tracheids, epidermal cells, cell clumps
<i>Berrya mollis</i>	inflorescence	A	
<i>Colona flagrocarpa</i> Cav.	leaf	P	long hair cells, spherical epidermal cells
<i>Grewia acuminata</i> L.	leaf	P	spherical epidermal cells
<i>Grewia acuminata</i>	seeds	A	
<i>Grewia confortata</i> L.	inflorescence	P	tracheids, barely silicified stomata
<i>Grewia confortata</i>	leaf	A	
<i>Triumfetta rhomboidea</i> L.	leaf, inflorescence	A	
THEALES: CLUSIACEAE (Guttiferae)			
<i>Calophyllum burmanii</i> Wight	fruit	P	tracheids, rugulose spheres
<i>Calophyllum thorelli</i> Pierre	leaf	P	tracheids
<i>Calophyllum thorelli</i>	inflorescence	A	
<i>Clusia rosea</i> L.	leaf, inflorescence	A	
<i>Cratoxylon polyanthum</i> Blume	leaf, fruit	A	
<i>Garcinia gracilis</i> Pierre	leaf	P	tracheids
<i>Garcinia gracilis</i>	inflorescence	A	
<i>Garcinia mangostana</i> L.	leaf	A	
<i>Garcinia xanthochymus</i> T. Anderson	leaf, fruit	A	
<i>Hypericum japonicum</i> Thunb.	leaf, inflorescence	A	
<i>Mammea siamensis</i> L.	leaf	A	
<i>Mammea siamensis</i>	fruit	P	tiny spheres (4 µm)
<i>Ochrocarpus siamensis</i> L.	leaf	P	tiny sclereids? same as <i>Mammea</i> ?
<i>Ochrocarpus siamensis</i>	inflorescence, fruit	A	
THEALES: DIPTEROCARPACEAE			
<i>Dipterocarpus obtusifolius</i> Miq.	leaf	P	epidermal cells, stomata, hair-base cells
<i>Dipterocarpus obtusifolius</i>	fruit	A	
<i>Hopea odorata</i> Roxb.	inflorescence	P	tracheids (fat)
<i>Shorea henryi</i> Roxb. ex Gaertner	leaf	P	tracheids (fat), hair-base cells
<i>Shorea henryi</i>	inflorescence	A	
<i>Shorea siamensis</i> Roxb. ex Gaertner	leaf, inflorescence	A	
<i>Shorea obtusa</i> Wall.	leaf	A	
<i>Vatica cinerea</i> L.	leaf	P	stomata, epidermal cells, hair-base cells
<i>Vatica cinerea</i>	inflorescence	A	
<i>Vatica</i> sp.	leaf, inflorescence	P	unsegmented V-shaped hair cells, stomata, hair-base cells
THEALES: ELATINACEAE			
<i>Bergia ammanioides</i> L.	inflorescence, root	A	
<i>Bergia ammanioides</i>	leaf, stem	P	epidermal cells, spheres
VIOLALES: CARICACEAE			
<i>Carica papaya</i> L.	leaf	A	
VIOLALES: CUCURBITACEAE			
<i>Citrullus vulgaris</i> Shard.	inflorescence	P	hair-cell fragments
<i>Coccinia cordifolia</i> L. Cogn.	leaf, inflorescence	A	
<i>Gynostemma</i> sp.	leaf	P	hair-base cell clumps
<i>Hodgsonia heteroclita</i> Hook.f. & Thomson	leaf	A	
<i>Lagenaria siceraria</i> Ser.	leaf	A	
<i>Luffa cylindrica</i> (L.) M. Roem.	seeds, pod	A	
<i>Momordica charantia</i> L.	inflorescence	A	
<i>Trichosanthes anaimalaiensis</i> Bedd.	inflorescence	P	segmented hair cells
VIOLALES: FLACOURTIACEAE			
<i>Casearia grewiaefolia</i> Vent.	fruit	A	
<i>Casearia grewiaefolia</i>	leaf	P	tracheids, dendritic forms
<i>Casearia virescens</i> Pierre	leaf	A	
<i>Erythrospermum zeylanicum</i> (Gaertner) Alston	leaf, fruit	P	tracheids, stomata
<i>Flacourtia indica</i> (Burm. f.) Merr.	leaf	P	tracheids
<i>Flacourtia indica</i>	fruit/bract	A	
<i>Flacourtia jangonias</i>	leaf	P	tracheids, grainy elongates
<i>Flacourtia sepiaria</i> Roxb.	leaf, inflorescence	A	
<i>Homalium damrongianum</i> Craib	leaf, inflorescence	P	tracheids, hair cells
<i>Homalium tomentosum</i> Benth.	leaf, inflorescence	A	

TABLE 5.—Continued.

Taxon	Plant part	Present(P)/ absent(A)	Phytolith forms present
<i>Hydnocarpus ilicifolius</i> King	fruit	A	
<i>Itoa orientalis</i> Hemsl.	leaf	P	unsegmented hair cells, grainy elongates
<i>Ryparosa javanica</i> Merr.	leaf	P	grainy elongates, tracheids, stomata, polyhedral epidermal cells
<i>Ryparosa javanica</i>	fruit	A	
<i>Scolopia acuminata</i> Clos.	leaf	A	
<i>Scolopia spinosa</i> (Roxb.) Warb.	leaf, inflorescence	A	
<i>Trichadenia zeylanica</i> Thw.	leaf	A	
<i>Xylosma</i> sp.	leaf, flower	A	
VIOLALES: PASSIFLORACEAE			
<i>Passiflora biflora</i> L.	leaf	P	stomata, epidermal cells with central sphere
<i>Passiflora biflora</i>	inflorescence	A	
HAMAMELIDAE			
FAGALES: FAGACEAE			
<i>Castanopsis diversifolia</i> (D. Don) Spach.	leaf	P	stomata, hair-base cells, epidermal cells
<i>Quercus lobata</i> Neé	leaf	A	
<i>Quercus dumosa</i> L.	leaf, nut	A	
JUGLANDALES: JUGLANDACEAE			
<i>Engelhardia serrata</i> Blume	leaf	P	anticlinal epidermis
<i>Engelhardia serrata</i>	seed	A	
URTICALES: MORACEAE			
<i>Allaeanthus kwizii</i> Standley	leaf	P	tracheids, anticlinal epidermis
<i>Artocarpus dadah</i> Miq.	fruit	P	V-shaped small hair cells
<i>Artocarpus nitidus</i> Trec.	fruit	P	epidermis
<i>Broussonetia kasinoki</i> Seibold & Zucc.	inflorescence	P	unsegmented hair cells of variable size
<i>Broussonetia papyrifera</i> Vent.	leaf	P	long, curved fiber-like hair cells and hair-base cells
<i>Broussonetia papyrifera</i>	fruit	P	small hair cells with cystoliths
<i>Cudrania poilanei</i> Gagnep.	leaf	P	epidermis, stomata
<i>Cudrania poilanei</i>	fruit	P	tiny hair cells, tracheids, hair-base cells
<i>Cudrania cochinchinensis</i> Lour.	leaf	P	stomata, tracheids, polyhedral epidermal cells, fused hair-base cells?
<i>Cudrania cochinchinensis</i>	fruit	P	small, unsegmented hair cells; hair-base cells
<i>Ficus</i> sp.	leaf	P	pronged hair cells; armed, unsegmented hair cells; tracheids; unsegmented hair cells
<i>Ficus</i> sp.	fruit	A	
<i>Malaisia scandens</i> (Lour.) Planch.	inflorescence	P	funnel-shaped, unsegmented hair cells of variable length
<i>Morus alba</i> L.	inflorescence	P	tracheids, 2 types of unsegmented hairs with cystoliths
<i>Morus</i> sp.	leaf	P	long, curved, armed and short hair cells; tracheids; cystoliths
<i>Taxotrophis macrophylla</i> (Bl.) Merr.	inflorescence	A	
URTICALES: ULMACEAE			
<i>Holoptelea integifolia</i> (Roxb.) Pl.	leaf	A	
<i>Trema cannabina</i> Lour.	leaf	A	
MAGNOLIIDAE			
ARISTOLOCHIALES: ARISTOLOCHIACEAE			
<i>Aristolochia pothieri</i> L.	leaf, fruit	A	
ILLICIALES: ILLICIACEAE			
<i>Illicium</i> sp.	leaf	P	stomata, MFPS, tracheids
<i>Illicium</i> sp.	fruit	A	
ILLICIALES: SCHISANDRACEAE			
<i>Kadsura chinensis</i> Juss.	leaf, fruit	A	
<i>Schisandra perulata</i> Michaux	leaf	A	
<i>Schisandra perulata</i>	inflorescence	P	long, thin epidermal polyhedrals
LAURALES: LAURACEAE			
<i>Beilschmiedia glauca</i> Nees	leaf, fruit	A	
<i>Beilschmiedia glomerata</i> Nees	fruit	A	
<i>Cinnamomum iners</i> Schaeffer	leaf, inflorescence	A	
<i>Endiandra macrophylla</i> R. Br.	leaf	P	epidermal cells?
<i>Endiandra macrophylla</i>	inflorescence	A	
<i>Litsea panamanja</i> Lam.	leaf	P	tracheids
<i>Litsea panamanja</i>	inflorescence	A	

TABLE 5.—Continued.

Taxon	Plant part	Present(P)/ absent(A)	Phytolith forms present
MAGNOLIALES: ANNONACEAE			
<i>Anomianthus heterocarpus</i> Zoll.	leaf, fruit	A	
<i>Artabotrys siamensis</i> Miq.	inflorescence	P	epidermal cells
<i>Cananga</i> sp.	leaf	P	tracheids, polyhedral epidermal cells
<i>Cananga</i> sp.	fruit	A	
<i>Mitrephora collinsae</i> Craib	inflorescence	P	tracheids
<i>Orophea polycarpa</i> A. DC.	leaf	A	
<i>Polyalthia suberosa</i> (Roxb.) Thwaites	fruit	A	
<i>Popowia fomentosa</i> Endl.	leaf	A	
<i>Unona?</i> <i>chinensis</i>	leaf	P	tracheids, stomata
<i>Unona chinensis</i>	fruit	A	
MAGNOLIALES: MAGNOLIACEAE			
<i>Manglietia garrettii</i> Craib	fruit	A	
<i>Michelia champaca</i> L.	leaf	P	tracheids; stomata; barely silicified, polyhedral epidermal cells; elongated, multifaceted bodies with tracheid impressions
<i>Michelia champaca</i>	fruit	A	
<i>Michelia floribunda</i> Finet & Gagnep.	leaf, fruit	P	stomata
MAGNOLIALES: MYRISTICACEAE			
<i>Myristica fragrans</i> Houtt.	leaf, inflorescence	A	
PIPERALES: PIPERACEAE			
<i>Piper longum</i> L.	leaf	P	small, irregular MFPs; epidermal cells
<i>Piper longum</i>	inflorescence	P	geometric epidermal cells; curved, irregular MFPs; dome-shaped cells?
<i>Piper sarmentosum</i> Roxb.	leaf	P	short, unsegmented, fat hairs; geometric epidermal cells; cells with spheres
RANUNCULALES: MENISPERMACEAE			
<i>Tiliacora triandra</i> Diels	leaf	P	tissue with embedded spheres
ROSIDAE			
APIALES: APIACEAE (Umbelliferae)			
<i>Coriandrum sativum</i> L.	leaf, inflorescence	A	
<i>Eryngium foetidum</i> L.	leaf	P	tracheids
<i>Eryngium foetidum</i>	inflorescence	A	
<i>Foeniculum vulgare</i> Miller	leaf	A	
<i>Foeniculum vulgare</i>	inflorescence	P	anticlinal epidermis
<i>Pimpinella wallichiana</i> L.	leaf, inflorescence	A	
CELASTRALES: AQUIFOLIACEAE			
<i>Ilex triflora</i> L.	leaf	A	
EUPHORBIALES: EUPHORBIACEAE			
<i>Cladogynos orientalis</i> Zipp. ex Span.	leaf, inflorescence, seed	A	
<i>Manihot esculenta</i> Crantz.	seed	P	subrectangular bodies, epidermal cells
<i>Phyllanthus acidus</i> Skeels	leaf	A	
<i>Phyllanthus emblica</i> L.	leaf	P	spherical epidermal cells, grainy elongates, cupped cells
<i>Phyllanthus emblica</i>	fruit	A	
<i>Sapium baccatum</i> P. Browne	leaf, inflorescence	P	stomata
FABALES: FABACEAE (Leguminosae)			
CAESALPINOIDEAE			
<i>Bauhinia bracteata</i> L.	leaf, inflorescence	P	tracheids
<i>Cassia occidentalis</i> L.	leaf, inflorescence, fruit	A	
<i>Cassia tora</i> L.	leaf	A	
<i>Crudia caudata</i> Schreber	leaf	P	spikey epidermal cells, stomata, folded spheres, rugulose spheres
<i>Tamarindus indica</i> L.	leaf	P	epidermal cells, stomata
<i>Tamarindus indica</i>	inflorescence	A	
MIMOSOIDEAE			
<i>Acacia catechu</i> Willd.	leaf	P	tracheids, unsegmented hairs, cupped cells
<i>Acacia catechu</i>	inflorescence	A	
<i>Acacia farnesiana</i> (L.) Willd.	leaf	A	
<i>Acacia rugata</i> Voight	inflorescence	A	
<i>Acacia tomentosa</i> Willd.	leaf	P	fat tracheids, stomata, knobby epidermal cells, hair-base cells, square-base hair cells

TABLE 5.—Continued.

Taxon	Plant part	Present(P)/ absent(A)	Phytolith forms present
<i>Adenanthera pavonina</i> L.	leaf, pod	A	
<i>Albizia garretti</i> F. Nielsen	fruit	P	subepidermal cells
<i>Albizia lucidior</i> Durazz.	leaf	P	tracheids, square-base hair cells, stomata, cupped cells
<i>Albizia lucidior</i>	seed	A	
<i>Albizia vialleana</i> Pierre	leaf	P	grainy elongates
<i>Leucaena glauca</i> Benth.	leaf, fruit	A	
<i>Mimosa pudica</i> L.	leaf	A	
<i>Neptunia oleracea</i> Lour.	leaf	P	anticlinal epidermis
<i>Neptunia oleracea</i>	leaf	A	
<i>Prosopis juliflora</i> (SW.) DC.	leaf	P	tracheids, anticlinal epidermis, stomata
<i>Xylia dolabriformis</i> Benth.	pod	A	
<i>Xylia dolabriformis</i>	leaf	P	tracheids
PAPILIONOIDEAE			
<i>Arachis hypogaea</i> L.	shell, nut	A	
<i>Cajanus cajan</i> (L.) Huth.	inflorescence	P	long hair cells
<i>Cajanus cajan</i>	pod with seeds	A	
<i>Cajanus cajan</i>	leaf	P	hair cells, stomata, mesophyll, concave cells
<i>Canavalia ensiformis</i> (L.) DC.	leaf	P	epidermal cells, tracheids
<i>Dalbergia dongnaensis</i> L.f.	leaf	A	
<i>Glycine max</i> Merr.	leaf	P	circular striated cells, tracheids
<i>Indigofera galeoides</i> L.	leaf, inflorescence	A	
<i>Lablab purpureus</i> (L.) Sweet	leaf	P	hair cells, mesophyll, stomata, hair-base cells
<i>Lablab purpureus</i>	Pods	P	unsegmented hair cells, epidermal cells with central protrusion
<i>Lablab purpureus</i>	flower	A	
<i>Lathyrus sativa</i> L.	leaf	A	
<i>Milletia pendula</i> Brown	seed	P	irregular rugulose spheres
<i>Milletia pendula</i>	pod	P	tiny spikey spheres
<i>Phaseolus</i> sp.	leaf	P	long hair cells with arrow tip, anticlinal epidermis, tracheids, hair-base cells
<i>Phaseolus</i> sp.	pod	A	
<i>Pterocarpus indicus</i> Willd.	leaf	A	
<i>Pterocarpus indicus</i>	inflorescence	P	amorphous silica bodies
<i>Sesbania grandiflora</i> Desv.	leaf, inflorescence	A	
<i>Vicia sativa</i> L.	leaf	A	
<i>Vicia sativa</i>	seeds	P	tracheids
MYRTALES: COMBRETACEAE			
<i>Combretum griffithii</i> Loefl.	leaf	P	tracheids, angular epidermal cells, stomata, cupped cells
<i>Combretum griffithii</i>	inflorescence	P	long, unsegmented hairs; tracheids; long, thin epidermal polyhedrals
<i>Lumnitzera racemosa</i> Willd.	leaf	A	
<i>Lumnitzera racemosa</i>	inflorescence	P	epidermal cells with spheroids attached
<i>Terminalia bellerica</i> (Gaertner) Roxb.	leaf, inflorescence	A	
MYRTALES: MYRTACEAE			
<i>Syzygium ieptantha</i> Gaertner	inflorescence	P	hair-base cells? mesophyll?
<i>Syzygium aromaticum</i> (L.) Merr. & Perry	leaf	A	
PODOSTEMALES: PODOSTEMACEAE			
<i>Podostemum subulatus</i> Michaux	plant	A	
RHAMNALES: RHAMNACEAE			
<i>Colubrina longipes</i> Back.	leaf	A	
<i>Ziziphus jujuba</i> Miller	leaf, seed	A	
RHIZOPHORALES: RHIZOPHORACEAE			
<i>Bruguiera cylindrica</i> Lam.	leaf	P	tracheids, epidermal cells
<i>Ceriops tagal</i> (Perrottet) C. Robinson	inflorescence	A	
<i>Rhizophora apiculata</i> L.	inflorescence	A	
ROSALES: ROSACEAE			
<i>Agrimonia eupatoria</i> L.	leaf	A	
<i>Eriobotrya tenyuehensis</i> Lindley	leaf, inflorescence	A	
<i>Potentilla fulgens</i> Wall.	leaf, inflorescence	A	
<i>Potentilla kleiniana</i> Wight	leaf	P	hair cells



TABLE 5.—Continued.

Taxon	Plant part	Present(P)/ absent(A)	Phytolith forms present
<i>Prunus arborea</i> L.	leaf, fruit	A	
<i>Prunus hirsutus</i> L.	inflorescence	A	
<i>Pyracantha angustifolia</i> (Franch.) Schneid.	leaf, inflorescence	A	
<i>Raphiolepis indica</i> (L.) Lindl.	leaf, fruit	A	
<i>Rubus ellipticus</i> Sm.	leaf, inflorescence	A	
<i>Rubus efferatus</i> Craib	leaf, inflorescence	A	
<i>Spiraea cantonensis</i> L.	leaf, inflorescence	A	
SANTALALES: LORANTHACEAE			
<i>Loranthus pentapetalus</i> Jacq.	leaf	P	hair-base cells, spheres? (rare)
<i>Loranthus pentapetalus</i>	inflorescence	A	
<i>Elytranthe ampullaceae</i> (Blume) Blume	fruit	A	
SANTALALES: OLACACEAE			
<i>Otax scandens</i> L.	leaf, inflorescence, fruit	A	
<i>Scorodocarpus borneensis</i> (Baillon) Becc.	leaf	A	
SAPINDALES: ANACARDIACEAE			
<i>Mangifera indica</i> L.	inflorescence	A	
<i>Rhus</i> sp.	fruit	A	
<i>Spondias pinnata</i> Kurz.	leaf	P	stomata, geometric epidermal cells, tracheids, cell clumps with spheres
SAPINDALES: BURSERACEAE			
<i>Canarium album</i> Raeuschel	leaf, inflorescence	P	hair cells; hair-base cells; stomata; tracheids; long, thin epidermal polyhedrals
<i>Canarium commune</i> L.	leaf, inflorescence	P	hair cells, stomata, hair-base cells
<i>Canarium kerrii</i> L.	leaf	P	hair cells; hair-base cells; stomata; MFPs, 1 side spiculate; epidermal cells
<i>Canarium littorale</i> Bl.	fruit	P	mesophyll; armed, unsegmented hair cells; conical cells (see Table 4)
<i>Canarium nigrum</i> L.	leaf	P	stomata, tracheids
<i>Canarium pimela</i> Koen	leaf	P	stomata, hair cells, hair-base cells
<i>Canarium pimela</i>	inflorescence	P	hair cells
<i>Canarium subulatum</i> Guillaum	leaf, inflorescence	P	stomata, tracheids, hair cells, hair-base cells, epidermal cells
<i>Canarium sumatranum</i> Benth.	leaf, inflorescence	P	stomata, tracheids, MFPs, hair cells, hair-base cells
<i>Canarium zeylanicum</i> L.	inflorescence	P	hair cells, tracheids, stomata, hair-base cells
<i>Commiphora caudata</i> (Wight & Arn.) Engl.	leaf	P	tracheids, stomata
<i>Garuga pinnata</i> Roxb.	leaf	P	unsegmented hair cells (size variable), stomata, tracheids
<i>Garuga pinnata</i>	leaf, inflorescence	P	curved, unsegmented hair cells; tracheids; cystoliths; hair-base cells; stomata
<i>Santiria apiculata</i> A.W. Benn	leaf, inflorescence	P	stomata, tracheids, hats (round crown), knobby epidermal cells
<i>Santiria laevigata</i> Blume	leaf, inflorescence	P	grainy, irregular epidermal cells; tracheids; hair cells; hair-base cells; stomata
<i>Scutinathe brunnea</i> Thw.	fruit	P	stomata, tracheids, hair-base cells
SAPINDALES: MELIACEAE			
<i>Aglaia chandocensis</i> Lour.	leaf	P	tracheids, cell clumps (stomata?)
<i>Aglaia chandocensis</i>	inflorescence	A	
<i>Azadirachta indica</i> Juss.	leaf, inflorescence	A	
<i>Dysoxylum cochinchinensis</i> Blume	leaf	P	tracheids; long, thin epidermal polyhedrals; cupped cells
<i>Dysoxylum cochinchinensis</i>	inflorescence	A	
<i>Melia azedarach</i> L.	leaf	P	epidermal cells
SAPINDALES: RUTACEAE			
<i>Clausena excavata</i> Burm.f.	leaf	P	stomata, tracheids, epidermal cells, cupped cells
<i>Clausena excavata</i>	inflorescence	P	tracheids
SAPINDALES: SAPINDACEAE			
<i>Allophylus cobbe</i> (L.) Rausch.	leaf	P	stomata, tracheids, epidermal cells, mesophyll, spheres
<i>Nephelium hypoleucum</i> L.	leaf	P	tracheids, vascular forms?, stomata, cupped cells
<i>Nephelium hypoleucum</i>	fruit	A	

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