SILICA GRAINS IN WOODY PLANTS OF THE NEOTROPICS, ESPECIALLY SURINAM

B. J. H. TER WELLE

Institute of Systematic Botany,
University of Utrecht, The Netherlands

Summary. Distribution patterns, frequency, size, shape, and surface texture of silica grains in the secondary xylem of neotropical taxa, especially from Surinam were studied extensively. Over 2000 samples were examined. Silica grains occur in about 300 species (32 families and about 90 genera). The grains proved to be present in many taxa so far considered as non-siliceous. They are most frequently found in the parenchymatous tissues (in 80% of siliceous material studied, grains were present in the ray cells). Their distribution is very constant, especially when they are restricted to one type of tissue, although some exceptions exist. The diagnostic value of the silica grains, often neglected, appears to be very high. The shape of the grains is usually variable though, in a few cases it is very characteristic. Various types of surface structures are recognized. Size of the grains is reported. The great variation in grain size greatly reduces its importance as a diagnostic tool.

INTRODUCTION

In 1857 Crüger for the first time described the occurrence of silica grains in the secondary xylem of some species in what is now recognized as the family of the Chrysobalanaceae. The presence of silica has since been the subject of many investigations (Küster, 1897; Petrucci, 1903; Gonggrijp, 1923, 1932; Frison, 1942; Besson, 1946; Amos, 1951, 1952; Bamber & Lanyon, 1960; Burgess, 1965; Balan Menon, 1965; Murthy, 1965; Sharma & Rao, 1970; Hirata *et al.*, 1972; Scurfield *et al.*, 1974a, 1974b). Some investigators have attempted to evaluate the taxonomical significance of the presence of silica, whereas others primarily dealt with some technical aspects such as a possible correlation between the occurrence of silica grains and the resistance of the timber to marine borers or between the presence of silica and difficulties encountered in sawing timbers.

By using saws made from special steel and sawing under wet conditions, using logs completely soaked with water, most problems caused by silica inclusions were solved. The effect of the silica grains on the resistance to marine borers is only small, as can be judged by the results of investigations carried out by Southwell & Bultman (1971) who examined over a hundred species.

The diagnostic importance of silica grains, considered by Amos (1952) as a very promising subject, is still of interest although most wood anatomists take the value of this character as about equal to that of a comparable feature like the presence of crystals. Most articles on this subject are restricted to geographical regions in Africa and Asia. Only Gonggrijp (1923) and Amos (1951) reported the occurrence of silica grains in a few neotropical species. In his worldwide survey Amos (1952) included only 44 species with silica inclusions from the neotropics, 20 species belonging to the Chrysobalanaceae. The present investigation therefore is focussed on the neotropics; especially Surinam woods were studied because of a good representation in the Utrecht collection.

MATERIALS AND METHODS

All woody species from Surinam represented in the wood collection of the Institute of Systematic Botany of the University of Utrecht were investigated. Besides, a great number of species from Guyana and French Guiana were included in the present study. When silica grains were found in a Surinam representative of a family, the other neotropical genera of that family were studied as well. Most of the families not found in the Guianas, but represented in our wood collection were also examined. About 2000 samples (*c.* 75 families, *c.* 440 genera and *c.* 1300 species) were investigated. All wood samples are backed by herbarium material, which is deposited, for the greater part, in the Institute of Systematic Botany of the University of Utrecht. In accordance with an earlier study (ter Welle, 1976) samples for sectioning were taken from a wood block of the heartwood.

To study the silica distribution, radial sections of 15 to 25 μm thick were prepared. The sectioning was done without any pre-treatment, only cold water was used. After sectioning the sections were bleached with a domestic bleaching agent for one or two minutes, then rinsed in water and heated in carbolic acid, and finally mounted in clove oil.

In addition scanning electron microscopy (SEM) was used to obtain better information about the surface of the grains.

Although various types of siliceous inclusions occur in the secondary xylem this investigation is restricted to the occurrence and distribution of silica grains only.

RESULTS

No silica grains were observed in the families and genera listed in Table 2. Species in which silica grains occur are described as follows: the data on the distribution of the grains, the locality and the source of the specimens are given in Table 1; size, shape, frequency, and additional data of a given species or genus are reported below. The families are treated in alphabetical order. Pertaining data from the literature are included. Non-siliceous genera of the families are listed at the end of each family description. The number of species investigated is given between brackets.

ANACARDIACEAE

Silica grains are present in all species of *Anacardium*. Grains globular with a smooth or a granular surface, maximum size 10 to 13 μm, one grain per cell, but there are also cells without a grain. De Paula & de Hamburgo Alves (1973) did not report anything about the presence of silica in *A. spruceanum*. In the material of *Loxopterygium sagotii* some wood specimens contain silica grains, others do not. Grains were absent in eight of fourteen samples investigated (*BBS 12*; *v. Hall 57*; *LBB 10734*; *Lindeman 5841*, *6057*, *6080*, *6194*, *6856*; *BAFOG 198 M*). They were present in the samples listed in Table 1. Grains nearly always globular with a smooth surface, size 5 to 10 μm. No silica grains were observed in *Schinus* (1), *Spondias* (1), *Tapirira* (2), and *Thyrsodium* (2).

BOMBACACEAE

The genus *Bombax* s.l. comprises both species with and species without silica grains. Grains globular with a granular surface, size normally up to 15 μm, but sometimes as large as 23 μm, one grain per cell, but not in every cell. Species without silica grains: *B. flaviflorum*, *B. globosum*, and *B. surinamense*. According to Amos (1952), who studied 5 species, *Bombax* is non-siliceous. If the classification of Robyns (1963), who split *Bombax* into several genera, is followed all genera comprise siliceous and non-siliceous species. All species of *Quararibea* contain silica grains, in the ray cells as well as in the axial parenchyma. Grains globular with a more or less smooth surface, size up to 15 μm. The grains occur more frequently in the axial parenchyma than in the ray cells. No silica grains were observed in *Catostemma* (2), *Ceiba* (1), *Matisia* (1), and *Scleronema* (1).

BONNETIACEAE

The family concept followed here is that of Maguire (1972). Silica grains occur in all samples of two genera, viz. *Archytea* and *Haploclathra*. In *Archytea* the grains are globular and sometimes they assume other shapes, the surface is smooth, size of the globular grains 3 to 15 μm, the oval/oblong ones up to 30 × 13 μm. Normally they occur in the procumbent ray cells, but sporadically also in the upright ray cells. The grains in *Haploclathra* are mostly globular and their surface is less smooth than in *Archytea*. They measure 3 to 13 μm. De Paula (1974) noticed silica in *Haploclathra* but considered its occurrence in this genus of no taxonomic value. Three specimens of *Kielmeyera* were studied. Silica grains are present in only one specimen. Two types of grains were found: (1) globular, with a smooth surface and a compact structure (size up to 8 μm); (2) irregular, the grains look like a cluster of small silica particles glued together. Baretta-Kuipers (1976) who studied the same wood samples reports differences in other anatomical characters between the sample with and the samples without silica.

No silica grains were observed in *Bonnetia* (3), *Caraipa* (3), *Mahurea* (2), *Marila* (2), and *Neblinaria* (1).

BURSERACEAE

In this family silica grains occur in the ray cells, axial parenchyma cells, fibres and/or tyloses of the vessels. Their distribution pattern is very variable. Grains in *Dacryodes* are globular, oval or oblong with a granular surface; the globular grains measure up to 17 μm, the oblong ones up to 25 × 12 μm. In *Paraprotium* the grains occur in all tissues except the vessels. Grains of various shapes, the globular ones up to 17 μm. *Protium* is a genus in which both species with and species without silica grains are represented. The non-siliceous species are: *P. alstonii*, *P. aracouchini*, *P. crassifolium*, *P. glabrescens*, *P. hostmannii*, and *P. pullei*. The grains, when present, are sometimes restricted to rays or parenchyma only; sometimes they are found in all tissues. Grains usually more or less globular, with a granular surface, size up to 18 μm, but sometimes, as in *P. insigne*, they do not exceed 5 μm. In some cases they look like a cluster of small silica particles glued together. The fourth genus containing silica is *Trattinickia*. Here, too, the distribution pattern is very variable, but in all species grains occur in the ray cells, although often restricted to the marginal ray cells (Plate 1/4). Grains more or less globular with a granular surface, size 11 to 22 μm. Webber (1941) did not record silica grains in her wood anatomical study of the Burseraceae. No silica grains were observed in *Canarium* (1), *Hemicrepidospermum* (1), and *Tetragastris* (4).

CARYOCARACEAE

Silica grains are present in all species investigated of *Anthodiscus*. Grains nearly globular, size up to 13 μm. The grains in the axial parenchyma resemble those in the rays. No silica grains were observed in *Caryocar* (6).

CHRYSOBALANACEAE

The occurrence of silica grains in the secondary xylem was reported for the first time by Crüger (1857) in some species of this family. A worldwide survey on the distribution pattern of silica grains in this family was made by ter Welle (1976). All species investigated contain silica (Plate 1/1–2). The following genera were included in the investigation: *Acioa*, *Chrysobalanus*, *Couepia*, *Exellodendron*, *Hirtella*, *Licania*, and *Parinari*.

CONNARACEAE

Silica grains occur in *Pseudoconnarus* and *Rourea*. Grains globular, with a granular surface, size up to 23 μm. The occurrence of silica grains in this family is not reported by Metcalfe & Chalk (1950), Amos (1952) nor by Dickison (1972). According to Mennega & Veenendaal (unpublished results) all samples of *Agelaea* from Cameroon show the same silica distribution pattern as *Pseudoconnarus* and *Rourea*. An african species of *Connarus*, *C. griffonianus*, unlike the neotropical species of this genus, contains silica in the ray cells. No silica grains were observed in *Cnestidium* (1) and *Connarus* (6).

ERYTHROXYLACEAE

Out of nine species of *Erythroxylon* investigated, *E. squamatum* is the only one in which no silica grains were observed. The grains are globular, oval or oblong. All shapes may occur in the same sample. Their size and shape are often determined by the size and shape of the ray cells and they may fill up the entire cell. The surface is granular, except in *E. citrifolium*; in this species grains with a granular and grains with a more or less smooth surface may occur side by side. Consequently the size is highly variable, but the grains are always large (up to 50 × 20 μm), except in *E. citrifolium* where the maximum size is 15 μm. Each of the procumbent ray cells contains one or two grains; in the upright marginal ray cells, grains may be present or absent, but there is never more than one grain per cell. In the literature the occurrence of silica grains in this family is not reported (Record & Hess, 1943; Metcalfe & Chalk, 1950; Normand, 1950; Amos, 1952; Brazier & Franklin, 1961). The presence of silica grains is perhaps restricted to the neotropical species as a sample from New Guinea (*E. ecarinatum*) studied by me, is also devoid of silica.

EUPHORBIACEAE

In three genera, *Actinostemon*, *Maprounea*, and *Senefeldera* the occurrence of silica is a constant feature. *Actinostemon* and *Senefeldera* are two allied genera which share the same characteristic silica distribution pattern. The silica grains, which often fill the entire ray cell lumen, have a granular surface and they measure up to 60 × 25 μm. The oblong grains are more frequent than the globular grains.
In *Maprounea* they are small (about 3 μm) and of various shapes. Sometimes they suggest a cluster of small silica particles glued together. Species with and species without silica grains occur in *Micrandra*. Grains globular, with a granular surface, oval or oblong, size of the globular grains up to 23 μm, size of the oblong ones up to 30 × 13 μm. In *M. elata* from Surinam the grains are very small (3 μm). In two species, *M. glabra* and *M. spru-*

ceana no silica is present. These two species, formerly included in the genus *Cunuria*, were transferred to *Micrandra* by Schultes (1952). Webster (1975) reinstated *Cunuria*. The silica distribution seems a feature in favour for keeping the two genera apart.

No silica grains were observed in *Acalypha* (1), *Alchornea* (1), *Alchorneopsis* (1), *Amanoa* (1), *Aparisthmium* (1), *Chaetocarpus* (1), *Conceveiba* (2), *Croton* (12), *Drypetes* (2), *Fluggea* (1), *Glycydendron* (1), *Hevea* (3), *Hura* (1), *Hyeronima* (1), *Jatropha* (1), *Mabea* (3), *Manihot* (1), *Margaritaria* (1), *Micrandropsis* (1), *Omphalea* (1), *Pausandra* (1), *Pera* (2), *Phyllanthus* (4), *Piranhea* (1), *Plukenetia* (1), *Sagotia* (1), and *Sapium* (2).

FLACOURTIACEAE

The wood anatomy of the Flacourtiaceae was extensively studied by Miller (1975), who reported silica grains in the ray cells of *Mayna amazonica* (size 10 to 16 μm) and *Lindackeria laurina*. All other genera from the neotropics lack silica grains. This observation is in agreement with my own investigation of species from the Guianas.

GUTTIFERAE

Only one species of *Clusia*, *C. palmicida* contains silica grains. Grains globular, small, 2 to 10 μm, mostly 2 to 5 μm; surface mostly smooth. Sometimes the grains look like a cluster of small silica particles glued together. Grains were not reported by de Paula (1974). In the sample of *Oedematopus quadratus* investigated small silica grains with a granular surface (size 3 μm) are present. An unidentified sample of the same genus did not contain silica.

In fourteen species of *Tovomita* investigated silica grains occur, whereas six other species lack silica (*T. choisyana*, *T. obovata*, *T. pittieri*, *T. plumeri*, *T. rileyi*, and *T. rubella*). Grains normally globular with a granular surface, size 3 to 15 μm, sometimes up to 25 μm, never more than one per ray cell. Probably the grains do not occur in the uniseriate rays. According to de Paula (1974) the occurrence of silica grains is a constant feature of all species of *Tovomita*. The herbarium vouchers of the non-siliceous species were checked by Mrs. A. R. A. Görts-van Rijn. There is no doubt that they belong to this genus.

No silica grains were observed in *Calophyllum* (1), *Havetia* (1), *Moronobea* (1), *Platonia* (1), *Rheedia* (3), *Symphonia* (1), and *Thysanostemon* (1).

HIPPOCRATEACEAE

The wood anatomy of this family was described by Mennega (1972). Of the twelve genera investigated the monotypic genus *Prionostemma* was the only one in which silica grains were found. They are restricted to the ray cells and mostly show a globular shape but other shapes are present as well. Their surface is granular and they measure up to 23 μm. This is one of the few lianas known sofar to possess silica grains.

No silica grains were observed in *Anthodon* (1), *Cheiloclinium* (4), *Cuervea* (1), *Elachyptera* (1), *Hemiangium* (1), *Hippocratea* (2), *Hylenea* (1), *Peritassa* (3), *Pristimera* (3), *Salacia* (9), and *Tontelea* (2).

HUMIRIACEAE

Only one species of *Sacoglottis*, *S. guianensis*, contains silica grains in both ray cells and axial parenchyma cells. No difference in silica grain distribution was noted in the formas and varieties of this species described by Cuatrecasas (1961). Grains with a granular surface, mostly globular, sometimes (*BBS 117* and *Krukoff 6653*) of other shapes; size of the globular grains 3 to 13 μm, sometimes up to 18 μm, oval ones up to 20 × 15 μm; there is never more than one grain per cell, in the axial parenchyma there are also cells without a grain. In two species (*S. amazonica* and *S. cydonioides*) no silica grains were observed. The occurrence of silica grains in this family was not reported before (Metcalfe & Chalk, 1950; Amos, 1952).

No silica grains were observed in: *Humiria* (1), *Humiriastrum* (1), *Schistostemon* (1), and *Vantanea* (2).

LAURACEAE

Silica grains occur in four neotropical genera. In *Cryptocarya* they look like a cluster of small silica particles glued together. The grains are small (ca. 5 μm). In the genus *Licaria* three species studied have silica grains; twelve species were found to be without silica grains (*L. amara*, *L. aritu*, *L. armeniacum*, *L. aurea*, *L. canella*, *L. cayennense*, *L. debilis*, *L. guianensis*, *L. martiana*, *L. multiflorum*, *L.polyphylla*, and *L. vernicosa*). Grains globular to oblong, with a granular surface, globular ones 2 to 25 μm, oblong ones up to 45 × 25 μm. In *Mezilaurus itauba* they are globular (3 to 20 μm) with a granular surface and they occur only in part of the ray cells. There is never more than one grain per cell. In some samples the grains are grouped together in subdivided procumbent ray cells (Plate 1/5). In these cell families their size is about the same although within one sample it varies much. This distribution pattern, according to Amos (1952) unique to *Mezilaurus*, was not noticed in *M. synandra*. Here the grains are globular with a more or less smooth surface and measure 3 to 13 μm. Two species of *Ocotea*, *O. glaucinia* and *O. splendens*, contain silica grains in the fibres. The fibres are septate and normally each compartment contains one grain. The grains measure 5 to 15 μm. In contrast, a further twenty-six species of *Ocotea*, are without silica.

No silica grains were observed in *Aniba* (10), *Beilschmiedia* (1), *Endlicheria* (3), *Nectandra* (4), and *Systemonodaphne* (1).

LEGUMINOSAE

Silica grains occur in the ray cells and/or axial parenchyma cells in three genera of this family. In *Dialium guianense* they are restricted to the axial parenchyma. Grains globular with a granular surface, size up to 15 μm, sometimes up to 20 μm; all parenchyma cells contain one grain each. The distribution pattern of the grains in *Dicorynia* is quite different from that in *Dialium*. Here the grains occur both in ray cells and parenchyma cells. Grains globular with a granular surface, size up to 28 μm in the rays as well as in the axial parenchyma. In the rays the grains occur only in the marginal cells. Normally there is one, but sometimes there are two or three grains per cell. Four species of *Sclerolobium* were investigated. Two of them, *S. albiflorum* and *S. guianense*, contain silica grains in the ray cells and sometimes in the axial parenchyma. Grains globular with a granular surface, size up to 15 μm in *S. albiflorum* and up to 22 μm in *S. guianense*. The two other species, without silica grains, are *S. melinonii* and *S. micropetalum*. According to Koeppen (1967) a few other genera from the neotropics contain silica, e.g. *Apuleia* and *Tachigalia*.

No silica grains were observed in *Alexa* (2), *Aldina* (1), *Anadenanthera* (1), *Andira* (6), *Bowdichia* (1), *Caesalpinia* (1), *Calliandra* (1), *Campsiandra* (1), *Cassia* (2), *Cedrelinga* (1), *Clathropis* (1), *Copaifera* (1), *Crudia* (2), *Cynometra* (2), *Dahlstedtia* (1), *Dalbergia* (5), *Derris* (4), *Dimorphandra* (2), *Diplotropis* (2), *Dipteryx* (4), *Elizabetha* (2), *Enterolobium* (2), *Eperua* (3), *Erythrina* (1), *Etaballia* (1), *Gliricidia* (1), *Heterostemon* (1), *Hymenaea* (1), *Hymenolobium* (2), *Lecointea* (1), *Lonchocarpus* (9), *Machaerium* (3), *Macrolobium* (4), *Marmaroxylon* (1), *Martiodendron* (1), *Mora* (2), *Ormosia* (5), *Palovea* (1), *Parkia* (2), *Peltogyne* (2), *Piptadenia* (2), *Piscidia* (2), *Pithecellobium* (9), *Platymiscium* (1), *Poecilanthe* (1), *Pterocarpus* (4), *Samanea* (1), *Sesbania* (1), *Stryphnodendron* (3), *Swartzia* (5), *Tephrosia* (1), *Vatairea* (1), *Vataireopsis* (1), *Vouacapoua* (1), and *Zygia* (2).

LECYTHIDACEAE

The silica grains in the Lecythidaceae show a great variation in shape, size, and frequency. They mostly occur in the rays and sporadically in the axial parenchyma and in the tyloses of the vessels. The grains are globular, oval, or oblong. Sometimes only one shape occurs in a sample, in a species or in a whole genus, but often samples appear to contain all shapes. The cells normally contain one grain, but sometimes, although sporadically, cells with two grains are seen; in addition a certain number of cells without grains are always found. The grains in *Allantoma* are globular and measure up to 8 μm. All species investigated of *Cariniana* contain silica grains in the rays and sometimes in the parenchyma. Grains mostly globular, sometimes oval or oblong, size of the globular grains up to 20 μm, size of the oblong ones up to 35 × 20 μm; in samples which contain globular grains only, the grain size is 3 to 13 μm; small grains often show a smooth surface unlike the bigger ones the surface of which is granular. The grains in the axial parenchyma of *C. pyriformis* are smaller than those in the ray cells of the same sample. In *Corythophora* the grains are globular with granular surface, and are up to 13 μm in size. The silica grains in *Couratari* are restricted to the ray cells. Their frequency is variable, sometimes they are abundant and sometimes they are sporadic. Grains mostly globular, sometimes oval or oblong, always large, size of the globular ones up to 20 μm (partly up to 30 μm), the oblong ones measure up to 30 × 15 μm or even up to 40 × 20 μm, and in *C. stellata* (*Krukoff 8893*) up to 80 × 25 μm. Generally the grains in *Couratari* are larger, more granular, more oblong and less frequent than those in *Cariniana*.

Thirty species of *Eschweilera* were analysed. In four species; *E. chartacea*, *E. congestiflora*, *E. poiteaui*, and *E. roroda* silica grains were never found. In one species, *E. simiorum*, four samples were analysed, two of which appeared to contain sporadic silica grains in the rays, whereas the other two lacked silica grains. All other species investigated of *Eschweilera*, however, show a large amount of grains in the rays. Grains globular, oval or oblong, size of the globular ones 4 to 20 μm, sometimes 25 to 30 μm, oblong grains mostly 25 × 10 μm to 30 × 20 μm, sporadically up to 40 × 15 μm or even up to 60 × 15 μm in two samples of *E. obversa*.

In *Holopyxidium jaranum* globular grains (up to 18 μm) and oblong grains (up to 50 × 20 μm) were observed, but *H. latifolium* (*IANw 3879*) on the contrary lacks silica.

Six species of *Lecythis* were investigated. Grains of sporadic occurrence (Plate 1/3) mostly oval, square or oblong and sporadically globular, always large, size of the globular ones up to 18 to 25 μm, oblong ones from 45 × 20 μm to 70 × 20 μm. The grains are usually restricted to the ray cells, but there are two exceptions: *Lecythis peruviana* contains silica grains in the ray cells and also in the parenchyma cells. Besides, these grains are much smaller than those in the other species of *Lecythis* and their occurrence is abundant, contrary to the few grains present in the other species. In *L. gigantea* (two samples) no silica grains were observed. Dr. G. T. Prance (New York Botanical Garden) studied the herbarium vouchers of these two species. In his opinion the samples are probably referable to *Eschweilera*.

No silica grains were observed in *Asteranthos* (1), *Bertholletia* (1), *Couroupita* (8), *Grias* (1), and *Gustavia* (4).

MELIACEAE

Silica grains occur in two genera of this family. Both *Guarea* and *Trichilia* comprise species with and species without silica. A total of fifteen species of *Guarea* was investigated, six of these contained silica grains in the ray cells. Grains mostly globular but other shapes are present too, size of the globular grains up to 18 μm and the size of the oblong ones up to 35 × 15 μm; the globular grains are compact while those with various shapes are more or less loosely built. According to Amos (1952) small silica inclusions occur in the ray elements of *Guarea* from Nigeria, Ivory Coast, and British Honduras. The grains in the samples investigated by me are large. In an African species like *G. laurentii* again large grains are found (up to 15 μm). Species of *Guarea* without silica grains are *G. alborosea*, *G. borisii*, *G. costata*, *G. davisii*, *G. duckei*, *G. kunthiana*, *G. pohlii*, *G. pubiflora*, and *G. rhabdotocarpa*. Only three out of nineteen species of *Trichilia* investigated are without silica grains, *T. casarettii*, *T. grandifolia*, and *T. elegans*. The grains are for the greater part globular and up to 12 μm except in *T. trinitensis* (up to 20 μm). As in *Guarea*, both compact and loosely built grains normally occur in the same sample, but, in *Trichilia*, these loosely built grains are more frequent than in *Guarea*. There is never more than one grain per cell, and grains do not occur in each cell.

The origin of the specimens of *Trichilia* investigated by Amos (1952) is not known. Two species were studied and were reported as non-siliceous. An African species, *T. lancei*, examined during the present investigation contains silica grains in the ray cells. Apparently the distribution of silica grains is not restricted to the neotropical species of *Trichilia*. According to Amos (1952) and Pennington & Styles (1975) a few other genera contain silica grains. Nothing is said by these authors about their taxonomic importance.

No silica grains were observed in *Cabralea* (2), *Carapa* (2), *Cedrela* (2), and *Swietenia* (3).

MENISPERMACEAE

The wood anatomy of this family was studied by Mennega (1977). Silica proved to be present only in two species of *Anomospermum*: *A. bolivianum* and *A. solimoesanum*. On the contrary three other species of this genus lack silica. Grains globular with a granular surface, size up to 13 μm. They occur in both rays and axial parenchyma.

Silica grains were not observed in thirteen other genera investigated by Mennega.

OLACACEAE

The occurrence of silica grains in this family is restricted to the ray cells of one genus, *Liriosma*. Grains globular and sometimes oval or oblong with a granular surface, size 10 to 28 μm. Some ray cells lack silica but contain a crystal instead. According to Amos (1952) this family is largely non-siliceous, although some species may contain small quantities of silica.

No silica grains were observed in *Chaunochiton* (2), *Heisteria* (2), *Minquartia* (1), and *Ptychopetalum* (1).

POLYGONACEAE

According to Metcalfe & Chalk (1950) and Amos (1952) this family is non-siliceous. Parente (1959–1961) for the first time reported the occurrence of silica grains in the ray cells of *Triplaris gardneriana.*

The present investigation proved the occurrence of silica grains in the ray cells of four genera. There is never more than one grain per cell and, besides grain-containing cells, there are also cells without grains, especially in *Triplaris.* The grains in *Neomillspaughia* are mostly globular and small-sized (up to 8 μm). In *Ruprechtia* they are slightly larger (up to 10 μm). In this species, besides globular ones, other shapes are sporadically present. The grains in *Symmeria* are large (up to 20 μm) and they are normally globular with a granular surface. In *Triplaris* the grains are globular with a smooth surface and they are always small (up to 5 μm), except in *T. punctata* where they measure up to 8 μm. *Triplaris peruviana* lacked silica grains, but only one sample of that species was available so further research must prove if this is a constant feature.

No silica grains were observed in *Coccoloba* (13).

PROTEACEAE

In three genera, *Euplassa*, *Panopsis*, and *Roupala*, species with silica grains in the ray cells and sometimes also in the axial parenchyma cells were observed. However, in the same genera species without silica occur too. Shape, distribution pattern, and size of the grains is very variable and there is no correlation between these characters and the delimitation of species or genera. Mostly two types of grains occur: (1) more or less globular, compact with a smooth surface; (2) grains with various shapes, like clusters of small silica particles glued together. The size of the grains in *Euplassa*, *Panopsis*, and *Roupala* is 4 to 10 μm, 5 to 10 μm and 5 to 13 μm respectively. Only in *Roupala montana* (*O.N.S. 293*) the grains are larger (globular ones up to 25 μm, oval ones up to 38 × 25 μm). The size of the grains in the ray cells is about the same as that of those in the parenchyma cells. In one sample of *Panopsis rubescens* var. *simulans* (*L. & L. 2872*) silica grains are not present. The herbarium voucher, however, leaves some doubt as to its correct identification; possibly it should be referred to another species.

Notwithstanding minor differences, these results are in agreement with those of Amos (1952) and Mennega (1966). On the contrary, Chattaway (1948) reported nothing about silica grains in this family nor did Araujo & de Mattos Filho (1974a and 1974b). According to Engler & Prantl (1889) the genera comprising species with silica grains are restricted to one tribe, Grevilleae. Another classification was proposed by Johnson & Briggs (1975). Here all genera containing silica fall within the subfamily Grevilleoideae. An exception in both classifications is one sample of *Petrophila teretifolia* in which silica grains occur in the rays and the pith, reported by Amos, 1952. Nevertheless, the occurrence of silica grains has so far been neglected in taxonomic studies on Proteaceae, but it seems to be an important character in this family.

No silica grains were observed in *Embothrium* (1).

QUIINACEAE

The wood anatomy of this family was extensively studied by Gottwald & Parameswaran (1967). Silica grains were reported for all species of *Lacunaria* investigated. Their occurrence was considered to be of taxonomic value.

No silica grains were observed in *Froesia*, *Quiina*, and *Touroulia*.

RHABDODENDRACEAE

Four samples of *Rhabdodendron amazonicum* were investigated. Silica grains occur in the ray cells and probably in the axial parenchyma cells. Grains globular to oblong, with a granular surface, size of the globular grains up to 20 μm, size of the oblong ones up to 30 × 18 μm; some of them are compact and others are loosely built; normally one grain per cell is found, sometimes two grains per cell, but ray cells without grains are present too. The grains were not observed by Prance (1968, 1972). He even stated: 'The wood of Rhabdodendron differs from that of the Chrysobalanaceae in some features, e.g. silica deposits are not present in any form'.

RUBIACEAE

The wood anatomy of this family was studied extensively by Koek-Noorman (1969a, 1969b, 1970, 1972, 1974). Except for the African genus *Mitragyna* no silica grains were observed.

RUTACEAE

Only two species from two genera contain silica grains. In *Erythrochiton brasiliense* they are mostly globular with a size of 7 to 20 μm. Those in the axial parenchyma are oval or oblong and less compact than those in the ray cells. There is never more than one grain per cell. Two samples of *Galipea* were investigated and silica occurs only in one sample. The grains are globular, with a granular surface (size up to 18 μm) and there is never more than one grain per cell.

No silica grains were observed in *Adiscanthus* (1), *Balfourodendron* (1), *Citrus* (1), *Cusparia* (1), *Esenbeckia* (2), *Fagara* (1), *Helietta* (1), *Hortia* (1), *Metrodorea* (1), *Pilocarpus* (1), *Rauia* (1), and *Ticorea* (1).

SABIACACEAE

Silica grains occur in two samples of *Meliosma sinuata* and two samples of the same genus not identified to species. In two samples the grains look like a cluster of small silica particles glued together, in the other two samples they show a compact structure. Grains mostly globular or oval, sometimes oblong, with a granular surface, size of the globular ones up to 25 μm, size of the oval/oblong grains up to 50 × 20 μm; there is never more than one grain per cell but normally most of the ray cells are without silica.

SAPINDACEAE

In this family silica grains seldom occur (Amos, 1952). There is only one genus from the neotropics, *Toulicia*, in which silica was observed. The occurrence is not constant which means that, in the same species, samples with and samples without grains can be found. The grains occur in the axial parenchyma, especially in the broad bands which are in contact with the vessels. They show various shapes and their size is about 13 μm.

No silica grains were observed in *Allophyllus* (2), *Cupania* (4), *Matayba* (3), *Pseudima* (1), *Sapindus* (1), *Serjania* (1), *Talisia* (10), and *Vouarana* (1).

SAPOTACEAE

One or more species from twenty-one genera were investigated. In one genus only, *Manilkara*, silica grains were not observed.

The genus *Chrysophyllum* comprises both species with and species without silica. In all other neotropical genera investigated silica grains are always present. According to Gonggrijp (1932), Amos (1952), Murthy (1965) and Sharma & Rao (1970) in most genera from Africa and Asia, species with and species without silica are normally present in the same genus. We thus see a marked difference between all but one genera from the neotropics and genera from the palaeotropics, as regards their silica contents, and one wonders if, perhaps, taxonomists have been more successful in the delimitation of neotropical genera than they have been with genera in the Old World. Normally there is one grain per cell but sometimes cells with two grains are present.

The grains in *Achrouteria* are sporadic but they are always large (up to 80 × 40 μm). The entire ray cell is often completely filled by the grains.

In *Calocarpum* various shapes occur, the globular ones measure up to 25 μm and the oval ones show a size of up to 30 × 18 μm. Sometimes the grains are fragmented. *Caramuri* contains silica grains in the ray cells and the axial parenchyma cells. There is no difference in shape and size (up to 15 μm). They are all globular. As mentioned before, in *Chrysophyllum* species with and species without silica are present. No grains were observed in *C. gonocarpum* and *C. viride*. According to Dr. J. C. Lindeman these species are easily separated on morphological characters from the other, silica containing, species. Grains globular, oval or oblong, with a granular surface, size of the globular ones 15 to 23 μm, size of the oblong ones up to 30 × 13 μm. In *C. marginatum* and *C. schomburgkianum* the grains in the procumbent ray cells are smaller than those in the square or upright ray cells. In *Ecclinusa* the grains are mostly globular but other shapes may be present as well. Size of the globular grains 10 to 25 μm, of the oblong ones up to 30 × 17 μm. In *E. balata* the grains in the procumbent cells are smaller than those in the square or upright ray cells. On the contrary, in *E. ramiflora* the largest grains are found in the procumbent ray cells.

Globular grains (up to 10 μm) with a granular surface occur in *Eremoluma*. In *Franchetella* the grains mostly are globular, but other shapes are present as well. Size up to 10 μm. Those in the axial parenchyma do not differ from those in the ray cells.

Only one sample of *Lucuma ephedrantha* from Amazonas was investigated. Although Gonggrijp (1932) and Amos (1952) described this genus as non-siliceous, silica grains with a globular shape are frequently present. Those in the procumbent ray cells are smaller (up to 8 μm) than those in the square or upright ray cells which measure up to 15 μm.

The grains in *Micropholis* show various shapes but most of them are globular, and measure 10 to 20 μm. Normally, they are not present in the procumbent ray cells, but, if sporadically present, then they are much smaller than those in the upright or square ray cells.

In *Nemaluma* globular grains and grains of other shapes are present. The globular grains are up to 15 μm, the oblong ones are up to 28 × 15 μm. The square or upright ray cells mostly do not contain silica grains.

In *Neopometia* grains with various shapes occur, measuring up to 15 μm. Contrary to the other genera, the occurence of silica grains in the axial parenchyma of *Neoxythece* seems to be constant. There is normally one grain per ray or parenchyma cell, but sometimes two grains per cell occur. Various shapes are present, globular grains up to 20 μm, oblong ones up to 28 × 15 μm.

Twenty species of *Pouteria* were investigated. The grains, restricted to the ray cells, are mostly globular (18 to 25 μm). The marginal ray cells in *P. caimito* sometimes lack grains. In the procumbent ray cells of four species, *P. glomerata*, *P. krukovii*, *P. mensalis*, and *P. pariry*, the grains are smaller than those in the square or upright ray cells.

The surface of the grains in *Pradosia* is sometimes smooth. They measure up to 9 μm and are mostly globular. In *Pseudocladia* and *Pseudolabatia* they are globular, with a granular surface, and measure up to 15 μm. Various shapes from globular to more or less oval occur in *Radlkoferella*. The maximum size is about 18 μm.

Only one sample of *Richardiella* was investigated. The shape shows a continuous variation from globular (up to 20 μm) to oval (up to 28 × 15 μm). Globular grains with a granular surface and up to 15 μm occur in *Sandwithiodoxa*. In *Sarcaulus* grains with various shapes are present but globular ones are most frequently found. Size up to ca. 15 μm.

No silica grains were observed in *Manilkara* (8).

SIMARUBACEAE

Silica grains occur in some species of one genus, *Simaba*. In the same sample various shapes, from globular to oblong, are present. Size of the grains in *S. multiflora*: globular ones up to 13 μm, oblong ones up to 18 × 10 μm. In *S. alata* and *S. guianensis* they are smaller (max. 8 μm). The grains were not observed by Webber (1936) in her study on the wood anatomy of the Simarubaceae.

No silica grains were observed in *Aeschrion* (1), *Picramnia* (3), *Quassia* (1), and *Simarouba* (1).

STYRACACEAE

Five species of *Styrax* were investigated and only one is without silica (*S. argenteus* from Panama). In the other species, the grains are small to very small (4 to 8 μm) and often loosely built. The shape is variable. They are mostly found in the square or upright ray cells although they sometimes occur sporadically in the procumbent ray cells. There is never more than one grain per cell. According to Amos (1952) two species from Malaya and Indonesia are without silica. In contrast, Gonggrijp (1932) reported very small grains in *S. sumatrana* from Indonesia.

THEOPHRASTACEAE

All samples investigated from the genus *Clavija* contain silica grains in the ray cells. They are mostly globular but other shapes are present as well. In *C. lancifolia* the grains reach a maximum size of 23 μm, whereas they do not exceed 10 μm, in *C. parviflora*. There is never more than one grain per cell, but they do not occur in all ray cells, particulary not in *C. parviflora*.

TILIACEAE

In one neotropical genus, *Luehea*, silica grains occur. Their presence is not constant in this genus, because *L. seemannii* from Panama (*Stern et al. 1839*) lacks silica. Grains globular with a smooth surface, size up to 7 μm, never more than one grain per cell, part of the ray cells contain crystals instead of silica grains.

No silica grains were observed in *Apeiba* (3), *Christiania* (1), *Heliocarpus* (1), *Lueheopsis* (3), and *Mollia* (2).

THEACEAE

The occurrence of silica grains in this family is restricted to the ray cells in one genus, *Ternstroemia*. Two species contain silica and 5 other species lack silica (*T. browniana*, *T. circumcissilis*, *T. delicatula*, *T. schomburgkiana*, and *T. seemannii*). Grains globular and mostly with a smooth surface, size max. 5 μm, never more than one grain per cell, but most ray cells do not contain silica.

No silica grains were observed in *Cleyera* (1), *Laplacea* (1), and *Pelliciera* (1).

VERBENACEAE

Silica grains occur in the ray cells in three species of *Vitex*. On the contrary, 8 other species lack silica (*V. amazonica*, *V. cooperi*, *V. cymosa*, *V. excelsa*, *V. krukovii*, *V. orinocensis*, *V. stahelii*, and *V. triflora*). In *V. compressa* there is one grain present in every ray cell. They are mostly globular and sometimes oblong (max. size 20 μm). One sample of *V. floridula* contains globular grains in the ray cells. Shape and distribution pattern is like that in *V. compressa*. Size of the grains up to 15 μm. In another sample of the same species silica is not present. This sample contains many septate fibres which were hardly found in the sample with silica grains. Loosely built grains of various shapes occur in the septate fibres of *V. megapotamica*. Max. size 9 μm. Their occurrence is abundant.

No silica grains were observed in *Aegiphila* (2), *Citharexylum* (3), and *Petraea* (1).

VOCHYSIACEAE

In this family the grains are restricted to the ray cells of one genus, *Qualea*. Although Amos (1952) reported that some species of this family may have small quantities of silica, Normand (1966, 1967) used this character in his key to determine the Vochysiaceae from the Guianas. The grains are most obvious in *Q. albiflora* and *Q. acuminata*. They vary in shape but they are mostly globular. Size of globular ones up to 15 μm, of oval ones up to 25 × 13 μm. In *Q. acuminata* they are most frequent near the vessels. Grains occur sporadically in the rays near the vessels in *Q. coerulea*. Grains of various shapes and as large as 10 μm. Globular grains with a smooth surface occur in *Q. ingens* var. *ingens* and *Q. rosea*. The grains are small (3 to 5 μm). Another type is found in *Q. ingens* var. *ingens* too. These grains are loosely built and show a granular surface, their shape is variable. In *Q. cordata*, *Q. cryptantha*, and *Q. dinizii* silica grains were not observed.

TABLE 1. Distribution of silica grains in the secondary xylem of neotropical taxa

Abbreviations used in Table 1:

a. Collection and locality

BAFOG	- Bureau Agricole et Forestier Guyanais, Fr. Guiana
BBS	- Bos Beheer Suriname
Br.	- Brazil
BW	- Boschwezen
Dan. & Jonk.	- Daniels & Jonker
F.D.	- Forest Department, Guyana
Flor. & Ms.	- Florschütz & Maas
LBB	- 's Lands Bos Beheer
L. & H. de H.	- Lindeman & Horreus de Haas
L. & L.	- Lanjouw & Lindeman
O.N.S.	- Oldenburger, Norde & Schulz
Pr. & Ms.	- Prance & Maas

b. Distribution of the silica grains

(f), f, ff	- fibres, respectively: probably present, present, abundant
(p), p, pp	- axial parenchyma, respectively: probably present, present, abundant
(r), r, rr	- rays, respectively: probably present, present, abundant
rr^r	- rays, silica grains restricted to the marginal ray cells
v^t	- present in the tyloses of the vessels

Species	Collection	Locality	Distribution
<u>Anacardiaceae</u>			
Anacardium giganteum Hancock	Stahel 278	Surinam	r
giganteum Hancock	O.N.S. 590	Surinam	r
occidentale L.	Stahel 268	Surinam	rr
spruceanum Benth. ex Spruce	LBB 10735	Surinam	r
tenuifolium Ducke	Krukoff 4723	Br. Amazonas	rr
Loxopterygium sagotii Hook. f.	Stahel 81	Surinam	rr
sagotii Hook. f.	BW 5780	Surinam	r
sagotii Hook. f.	de Hulster 18	Surinam	rr
sagotii Hook. f.	Lindeman 6057	Surinam	r
sagotii Hook. f.	Lindeman 6194	Surinam	rr
sagotii Hook. f.	Steyermark 89343	Brazil	rr

Table 1 (continued)

Species	Collection	Locality	Distribution
Bombacaceae			
Bombax aquaticum (Aubl.) Schum.	Stahel 301	Surinam	pp
aquaticum (Aubl.) Schum.	Maguire 51844	Br. Amapa	pp
crassum Uitt.	Schulz 8927	Surinam	p
nervosum Uitt.	L. & L. 2420	Surinam	pp
nervosum Uitt.	L. & L. 2761	Surinam	pp
nervosum Uitt.	Lindeman 3568	Surinam	pp
spectabile Ulbrich	L. & L. 1889	Surinam	pp
spectabile Ulbrich	Lindeman 6345	Surinam	pp
Quararibea duckei Huber	Krukoff 5721	Br. Amazonas	pp, rr
guianensis Aubl.	L. & L. 3241	Surinam	pp, r
guianensis Aubl.	Lindeman 6288	Surinam	pp, rr
lasiocalyx (Schum.) Vischer	Maguire 48453	Brazil	(p), r
Bonnetiaceae			
Archytea multiflora Benth.	F.D. 5143	Guyana	rr
multiflora Benth.	Maguire 17628	Guyana	rr
multiflora Benth.	Maguire 45521	Guyana	rr
multiflora Benth.	Maguire 46107	Guyana	rr
Haploclathra leiantha Benth.	Ducke 158	Br. Amazonas	r
paniculata Benth.	Ducke 306	Br. Amazonas	r
verticillata Ducke	Ducke 257	Br. Amazonas	r
Kielmeyera sp.	Pires 9182	Brazil	rr
Burseraceae			
Dacryodes cf. belemnensis Cuatr.	Stahel 308	Surinam	rr, v^t
Paraprotium firmum (Swart) W. Rodr.	Krukoff 7142	Br. Amazonas	ff, p, rr
Protium apiculatum Swart	Lindeman 4671	Surinam	ff, pp, rr
giganteum Engl.	L. & L. 2410	Surinam	rr
heptaphyllum (Aubl.) March	Stahel 180	Surinam	(f)
heptaphyllum (Aubl.) March	de Hulster 12	Surinam	ff
insigne Engl.	L. & L. 390	Surinam	f, p, r
neglectum Swart	de Hulster 23	Surinam	ff, p, (r)
neglectum Swart	Schulz 8330	Surinam	ff, pp, r
neglectum Swart var. robustum Swart	Stahel 262	Surinam	ff, p, r
neglectum Swart var. robustum Swart	Dan. & Jonk. 869	Surinam	ff, p, rr, v^t
polybotryum (Turcz.) Engl.	Lindeman 6778	Surinam	ff, (p), r
polybotryum (Turcz.) Engl.	Schulz 8332	Surinam	ff, p, r
sagotianum March	Schulz 8937	Surinam	ff, pp, rr
sagotianum March	L. & L. 693	Surinam	ff, p
sagotianum March	F.D. 2139	Guyana	ff, p

<u>Burseraceae</u>			
Trattinickia burserifolia Mart.	Stahel 40	Surinam	f, r
burserifolia Mart.	Lindeman 3954	Surinam	ff, pp, rr
burserifolia Mart.	Lindeman 4525	Surinam	f, r^r
burserifolia Mart.	Lindeman 6117	Surinam	(f), r^r
demerarae Sandw.	BBS 1041	Surinam	p, rr^r
demararae Sandw.	BBS 1042	Surinam	p, rr^r
demararae Sandw.	Schulz 8341	Surinam	rr^r
rhoifolia Willd. ssp. rhoifolia	L. & L. 1719	Surinam	r^r
rhoifolia Willd. ssp. rhoifolia	Lindeman 6168	Surinam	p, rr, v^t
<u>Caryocaraceae</u>			
Anthodiscus amazonicus Gleason & Smith	Krukoff 7017	Br. Amazonas	(p), rr
mazarunensis Gilly	Maguire 24576	Surinam	p, rr
trifoliatus G.F.W. Meyer	F.D. 2991	Guyana	r
<u>Connaraceae</u>			
Pseudoconnarus sp.	van Donselaar 3077	Surinam	rr
sp.	Krukoff 8304	Br. Amazonas	rr
Rourea cf. cuspidata Benth.	Lindeman 5227	Surinam	rr
cf. cuspidata Benth.	van Donselaar 2377	Surinam	rr
pubescens (DC.) Radlk. var. spadicea (Radlk.) Forero	van Donselaar 3065	Surinam	rr
pubescens (DC.) Radlk. var. spadicea (Radlk.) Forero	van Donselaar 3753	Surinam	rr
rectinerva A.C. Smith	Krukoff 6795	Br. Amazonas	rr
surinamensis Miq.	Lindeman 6857	Surinam	rr
surinamensis Miq.	van Donselaar 3794	Surinam	rr
<u>Erythroxylaceae</u>			
Erythroxylon amazonicum Peyr.	Schulz 7356	Surinam	rr
amazonicum Peyr.	Krukoff 6851	Br. Amazonas	rr
amplum Benth.	L. & L. 2561	Surinam	rr
citrifolium St. Hil.	Heyligers 596	Surinam	rr
citrifolium St. Hil.	Stahel/Gong. 238	Surinam	rr
macrophyllum Cav.	Lindeman 4909	Surinam	rr
macrophyllum Cav.	L. & L. 1573	Surinam	rr
micranthum Bongard	L. & L. 2694	Surinam	rr
nitidum Mart.	Lindeman 6163	Surinam	rr
paraense Peyr.	Krukoff 9014	Br. Amazonas	rr

Table 1 (continued)

Species	Collection	Locality	Distribution
Euphorbiaceae			
Actinostemon amazonicus Pax et Hoffm.	Pr. & Ms. 13992	Br. Amazonas	rr
concolor (Spreng.) Muell. Arg.	Reitz 22181	Br. Sta. Catarina	rr
lanceolatus Saldanha	Krukoff 5551	Br. Amazonas	rr
schomburgkii (Klotzsch) Pax	Schulz 10061	Surinam	rr
Maprounea guianensis Aubl.	Stahel 27	Surinam	r
guianensis Aubl.	Schulz 7365	Surinam	rr
guianensis Aubl.	Maguire 51745	Br. Amapa	rr
Micrandra elata (Didrichs.) Muell. Arg.	L. & L. 1869	Surinam	r
elata (Didrichs.) Muell. Arg.	Lindeman 6997	Surinam	(r)
elata (Didrichs.) Muell. Arg.	MADw 24279	Peru	rr
siphonioides Benth.	Pires 51922	Br. Amazonas	rr
Senefeldera karsteniana Pax et Hoffm.	USw 8193	Brazil	rr
macrophylla Ducke	Krukoff 6922	Br. Amazonas	rr
macrophylla Ducke	Krukoff 7171	Br. Amazonas	rr
macrophylla Ducke	USw 8050	Brazil	rr
nitida Croizat	Krukoff 7126	Br. Amazonas	rr
Guttiferae			
Clusia palmicida L.C. Rich.	Yw 35636	Surinam	rr
palmicida L.C. Rich.	Maguire 57527	Surinam	rr
palmicida L.C. Rich.	Maguire 55864	Surinam	rr
Oedematopus sp.	Maguire 45903	Guyana	(r)
Tovomita brasiliensis (Mart.) Walp.	Krukoff 6316	Br. Amazonas	rr
brasiliensis (Mart.) Walp.	Maguire 51724	Br. Amapa	rr
brevistaminea Engl.	L. & L. 2856	Surinam	rr
calodictyos Sandw.	L. & L. 2481	Surinam	rr
carinata Eyma	LBB 10721	Surinam	rr
cephalostigma Vesque	F.D. 5540	Guyana	rr
cephalostigma Vesque	L. & L. 427	Surinam	rr
grata Sandw.	Stahel 165	Surinam	rr
grata Sandw.	F.D. 3684	Guyana	rr
krukovii A.C. Smith	Krukoff 6384	Br. Amazonas	rr
macrophylla Walp.	Krukoff 7205	Br. Amazonas	rr
pyrifolia Pl. et Tr.	Krukoff 8714	Br. Amazonas	rr
schomburgkii Pl. et Tr.	Lindeman 3840	Surinam	rr
schomburgkii Pl. et Tr.	Krukoff 8975	Br. Amazonas	rr
secunda Poep. ap. Pl. et Tr.	Lindeman 4149	Surinam	rr
secunda Poep. ap. Pl. et Tr.	Schulz 8958	Surinam	rr
speciosum Ducke	Maguire 47079	Brazil	rr
stigmatosa Pl. et Tr.	Krukoff 6375	Br. Amazonas	rr
umbellata Benth. vel. aff.	Maguire 47111	Brazil	rr

Humiriaceae			
Sacoglottis guianensis Benth. var. guianensis	BAFOG 1239	Fr. Guiana	p, rr
guianensis Benth. var. guianensis	Lindeman 6252	Surinam	p, rr
guianensis Benth. var. guianensis	Lindeman 6381	Surinam	(p), rr
guianensis Benth. var. guianensis	Stahel 18	Surinam	pp, rr
guianensis Benth. var. guianensis	L. & L. 2869	Surinam	pp, rr
guianensis Benth. var. hispidula Cuatr.	Krukoff 6653	Br. Amazonas	pp, rr
Lauraceae			
Cryptocarya aschersoniana Mez	Hatschbach 13878	Br. Parana	rr
Licaria maguireana C.K. Allen	F.D. 2704	Guyana	rr
mahuba (Samp.) Kosterm.	Maguire 51845	Br. Amapa	rr
wilhelminensis C.K. Allen	Dan. & Jonk. 804	Surinam	rr
wilhelminensis C.K. Allen	Dan. & Jonk. 866	Surinam	rr
wilhelminensis C.K. Allen	Maguire 55307	Surinam	rr
Mezilaurus itauba (Meissn.) Taub.	Stahel 320	Surinam	rr
itauba (Meissn.) Taub.	Maguire 56549	Brazil	rr
itauba (Meissn.) Taub.	Krukoff 5221	Br. Amazonas	rr
itauba (Meissn.) Taub.	Krukoff 5317	Br. Amazonas	rr
synandra (Allen) Kosterm.	IANw 3871	Br. Amazonas	rr
Ocotea glaucinia (Meissn.) Mez	Maguire 24548	Surinam	ff
splendens (Meissn.) Mez	L. & L. 2282	Surinam	ff
splendens (Meissn.) Mez	Lindeman 5930	Surinam	ff
Lecythidaceae			
Allantoma lineata (Beg.) Miers	Maguire 51738	Br. Amapa	rr
Cariniana decandra Ducke	Krukoff 7193	Br. Amazonas	r
domestica (Mart.) Miers	Krukoff 5597	Br. Amazonas	(p), rr
estrellensis (Raddi) O.K.	L. & H. de H. 1638	Br. Parana	p, rr
estrellensis (Raddi) O.K.	Krukoff 5568	Br. Amazonas	r
micrantha Ducke	Krukoff 8796	Br. Amazonas	(p), r
multiflora Ducke	Krukoff 8164	Br. Amazonas	rr
pachyantha A.C. Smith	Krukoff 8690	Br. Amazonas	rr
pyriformis Miers	USw 9020	Colombia	p, rr
Crytophora rimosa W. Rodr.	IAN 20999	Br. Amazonas	rr, v^t

Table 1 (continued)

Species	Collection	Locality	Distribution
Lecythidaceae			
Couratari gloriosa Sandw.	Lindeman 6220	Surinam	r
guianesis Aubl.	Stahel 49	Surinam	r
krukovii A.C. Smith	Krukoff 1653	Br. Amazonas	r
macrosperma A.C. Smith	Krukoff 1513	Br. Amazonas	r
multiflora (Smith) Eyma	Stahel 44	Surinam	r
multiflora (Smith) Eyma	L. & L. 2198	Surinam	rr
oblongifolia Ducke ex Knuth	Schulz 7399	Surinam	r, v^t
panamensis Standl.	P.H. Allen USw 30147	Costa Rica	rr
panamensis Standl.	de Bruijn 1561	Venezuela	rr
stellata A.C. Smith	Stahel 137 a	Surinam	r
stellata A.C. Smith	L. & L. 2483	Surinam	r
stellata A.C. Smith	A.C. Smith 3561	Guyana	rr
stellata A.C. Smith	Krukoff 7254	Br. Amazonas	rr
stellata A.C. Smith	Krukoff 8893	Br. Amazonas	rr
Eschweilera alata A.C. Smith	F.D. 2564	Guyana	rr, v^t
amara (Aubl.) Ndz.	BBS 1077 B	Surinam	p, rr
amara (Aubl.) Ndz.	Schulz 7687	Surinam	rr
blanchetiana Miers	Maguire 51771	Br. Amapa	pp, rr
collina Eyma	Schulz 8338	Surinam	rr
collina Eyma	LBB 10898	Surinam	p, rr, v^t
confertiflora A.C. Smith	F.D. 4806	Guyana	pp, rr
coriacea Mart.	Krukoff 6450	Br. Amazonas	rr
corrugata (Poit.) Miers	BBS 30	Surinam	(p), rr
corrugata (Poit.) Miers	LBB 1022	Surinam	(p), rr, v^t
corrugata (Poit.) Miers	Schulz 8327	Surinam	(p), rr
decolorans Sandw.	L. & L. 2308	Surinam	rr
decolorans Sandw.	Dan. & Jonk. 1163	Surinam	rr
grata Sandw.	F.D. 2518	Guyana	(p), rr
grata Sandw.	Maguire 40502	Guyana	p, rr
grata Sandw.	Breteler 3870	Venezuela	p, rr
iquitosensis Knuth	Krukoff 8399	Br. Amazonas	rr
jarana (Huber) Ducke	Maguire 51861	Br. Amapa	p, rr
krukovii A.C. Smith	Krukoff 4847	Br. Amazonas	p, rr
krukovii A.C. Smith	Krukoff 6233	Br. Amazonas	p, rr
labriculata Eyma	Schulz 7662	Surinam	rr
longipes (Poit.) Miers	Stahel 45 a	Surinam	rr
longipes (Poit.) Miers	L. & L. 2164	Surinam	(p), rr
obtecta (Miers) A.C. Smith	Krukoff 6299	Br. Amazonas	rr
obversa (Berg) Miers	Krukoff 7183	Br. Amazonas	p, rr
obversa (Berg) Miers	Krukoff 4848	Br. Amazonas	rr

odora (Poepp.) Miers	Stahel 136 a	Surinam	rr
odora (Poepp.) Miers	Lindeman 5193	Surinam	rr
odora (Poepp.) Miers	Schulz 8352	Surinam	rr
odora (Poepp.) Miers	Krukoff 1665	Br. Amazonas	rr
pachysepala (Spruce) Mart.	Krukoff 7116	Br. Amazonas	rr
persistens (Sagot) Mennega	BAFOG 1049	Fr. Guiana	(p), rr
pittieri Knuth	USw 698	Panama	r
simiorum (R. Ben.) Eyma	BBS 170	Surinam	r
simiorum (R. Ben.) Eyma	Lindeman 3770	Surinam	r
subglandulosa (Steud.) Miers	BBS 104	Surinam	p, rr
subglandulosa (Steud.) Miers	Schulz 8335	Surinam	rr
subglandulosa (Steud.) Miers	Breteler 5097	Venezuela	rr
truncata A.C. Smith	Krukoff 7108	Br. Amazonas	p, rr
truncata A.C. Smith	Kurkoff 1531	Br. Amazonas	(p), rr, v^{t}
cf. wachenheimii R. Ben.	Lindeman 6954	Surinam	rr
Holopyxidium jaranum (Huber) Ducke	Krukoff 1995	Br. Amazonas	r
Lecythis davisii Sandw.	Lindeman 3703	Surinam	r
davisii Sandw.	Maguire 40551	Guyana	r
davisii Sandw.	BAFOG 158 M	Fr. Guiana	r
hians A.C. Smith	Krukoff 4630	Br. Amazonas	r
hians A.C. Smith	Krukoff 4811	Br. Amazonas	r
paraensis Huber	Maguire 51864	Br. Amapa	r
peruviana L. Wms.	MADw 22100	Peru	p, rr
usitata Miers	Krukoff 1130	Br. Amazonas	r
<u>Leguminosae</u>			
Dialium guianense (Aubl.) Steud.	Stahel 245	Surinam	pp
guianense (Aubl.) Steud.	Lindeman 3889	Surinam	pp
guianense (Aubl.) Steud.	Lindeman 4585	Surinam	pp
guianense (Aubl.) Steud.	Lindeman 6306	Surinam	pp
guianense (Aubl.) Steud.	BAFOG 223 M	Fr. Guiana	pp
guianense (Aubl.) Steud.	BAFOG 260 M	Fr. Guiana	pp
Dicorynia guianensis Amshoff	Stahel 36	Surinam	pp, rr^{r}
guianensis Amshoff	BBS 60	Surinam	pp, rr^{r}
guianensis Amshoff	L. & L. 389	Surinam	p, r^{r}
Sclerolobium albiflorum R. Ben.	BBS 1070 A	Surinam	(p), rr
albiflorum R. Ben.	BBS 1071 A	Surinam	(p), rr
albiflorum R. Ben.	Lindeman 5840	Surinam	rr
albiflorum R. Ben.	Schulz 9462	Surinam	rr
albiflorum R. Ben.	LBB 11030	Surinam	rr
albiflorum R. Ben.	BAFOG 28 N	Fr. Guiana	rr
guianense Benth.	Stahel 89	Surinam	rr
guianense Benth.	Schulz 8238	Surinam	p, rr
guianense Benth.	F.D. 3311	Guyana	rr
guianense Benth.	BAFOG 252 M	Fr. Guiana	rr
guianense Benth.	BAFOG 1197	Fr. Guiana	rr
guianense Benth.	Steyermark 88349	Venezuela	rr

Table 1 (continued)

Species	Collection	Locality	Distribution
<u>Meliaceae</u>			
Guarea carinata Ducke	IANw 3866	Brazil	rr
gnedesii C. DC.	Maguire 51840	Br. Amapa	rr
gomma Pulle	BBS 1070	Surinam	rr
gomma Pulle	LBB 11025	Surinam	rr
grandifolia C. DC.	LBB 10717	Surinam	rr
grandifolia C. DC.	O.N.S. 1254	Surinam	rr
guara (Jacq.) Wils.	L. & L. 1159	Surinam	rr
guara (Jacq.) Wils.	L. & L. 1464	Surinam	rr
rusbyi (Britton) Rusby	Krukoff 1528	Br. Amazonas	rr
rusbyi (Britton) Rusby	Krukoff 6492	Br. Amazonas	rr
Trichilia cardenasii Rusby	Krukoff 4631	Br. Amazonas	rr
cardenasii Rusby	Krukoff 4716	Br. Amazonas	rr
catigua A. Juss.	L. & H. de H. 639	Br. Parana	rr
ernesti Harms	Krukoff 5409	Br. Amazonas	rr
froesii A.C. Smith	Krukoff 1917	Br. Amazonas	rr
fuscescens Radlk.	Stahel 365	Surinam	rr
fuscescens Radlk.	Mennega 480	Surinam	rr
guianensis Klotzsch ex C. DC.	F.D. 3595	Guyana	rr
krukovii A.C. Smith	Krukoff 1021	Br. Amazonas	rr
krukovii A.C. Smith	Krukoff 6866	Br. Amazonas	rr
moritzii C. DC.	Schulz 8314	Surinam	rr
moritzii C. DC.	Maguire 47624	Brazil	rr
propinqua (Miq.) C. DC.	LBB 11022	Surinam	rr
roraimana C. DC.	Stahel 297	Surinam	rr
roraimana C. DC.	LBB 11046	Surinam	rr
roraimana C. DC.	F.D. 4023	Guyana	rr
subsessilifolia C. DC.	Stahel 182	Surinam	rr
surinamensis (Miq.) C. DC.	Schulz 7308	Surinam	rr
trinitensis A. Juss.	F.D. 5208	Guyana	r
trinitensis A. Juss.	Geyskes s.n.	Surinam	rr
trinitensis A. Juss.	O.N.S. 432	Surinam	rr
verrucosa C. DC.	Breteler 3536	Venezuela	rr
viridis Rusby	Krukoff 4711	Br. Amazonas	rr

Olacaceae			
Liriosma adhaerens Spruce	Krukoff 6328	Br. Amazonas	rr
cerifera A.C. Smith	Krukoff 6910	Br. Amazonas	rr
guianensis Engl.	O.N.S. 1285	Surinam	rr
pallida Miers	Krukoff 6205	Br. Amazonas	rr
Polygonaceae			
Neomillspaughia emarginata (Gross.) Blk.	MADw 11595	unknown	rr
Ruprechtia laxiflora Meissn.	L. & H. de H. 951	Br. Parana	rr
laxiflora Meissn.	L. & H. de H. 1716	Br. Parana	rr
marowijnensis Eyma	L. & L. 2002	Surinam	rr
ramiflora (Jacq.) Meyer	Breteler 5143	Venezuela	rr
Symmeria paniculata Benth.	Krukoff 1412	Br. Amazonas	rr
paniculata Benth.	Krukoff 6749	Br. Amazonas	rr
Triplaris boliviana Britton	Krukoff 5456	Br. Amazonas	rr
caracasana Cham.	Breteler 3653	Venezuela	rr
cumingiana Fisch. & Mey.	Stern 1859	Panama	r
guayaquilensis Wedd.	Acosta-Solis 11962	Ecuador	rr
melaenodendron (Bertol.) Stand. & Steyermark	USw 103	Panama	r
pavonii Meissn.	Krukoff 6249	Br. Amazonas	r
pavonii Meissn.	Krukoff 8423	Br. Amazonas	rr
punctata Stand.	Krukoff 5277	Br. Amazonas	rr
surinamensis Cham.	Stahel 50	Surinam	r
surinamensis Cham.	BBS 1053	Surinam	rr
surinamensis Cham.	BBS 1054	Surinam	rr

Table 1 (continued)

Species	Collection	Locality	Distribution
Proteaceae			
Euplassa cantareirae Sleum.	Reitz & Klein 6370	Br. Sta. Catarina	p, rr
Panopsis rubescens (Schott) Ducke var. simulans Macbride	Krukoff 1934	Br. Amazonas	p, rr
rubescens (Schott) Ducke var. simulans Macbride	Krukoff 7236	Br. Amazonas	r
sessilifolia (Rich.) Sandw.	Stahel 291	Surinam	(p), rr
sessilifolia (Rich.) Sandw.	F.D. 3040	Guyana	rr
sessilifolia (Rich.) Sandw.	Lindeman 6413	Surinam	(p), rr
sessilifolia (Rich.) Sandw.	BAFOG 1322	Fr. Guiana	rr
Roupala brasiliensis Pohl.	L. & H. de H. 2827	Br. Parana	p, rr
cataractarum Sleum.	Reitz 6030	Br. Sta. Catarina	p, rr
macrophylla Pohl.	Reitz & Klein 28181	Br. Sta. Catarina	p, rr
montana Aubl.	Stahel 249	Surinam	p, rr
montana Aubl.	O.N.S. 293	Surinam	p, rr
Rhabdodendraceae			
Rhabdodendron amazonicum (Spruce ex Benth.) Huber	Schulz 8322 a	Surinam	(p), rr
amazonicum (Spruce ex Benth.) Huber	LBB 10694	Surinam	(p), rr
amazonicum (Spruce ex Benth.) Huber	Fanshawe 2497	Guyana	rr
amazonicum (Spruce ex Benth.) Huber	Irwin 47524	Br. Amazonas	(p), rr
Rutaceae			
Erythrochiton brasiliensis Nees & Mart.	L. Williams 6761	Peru	p, rr
Galipea trifoliata Aubl.	van Donselaar 3437	Surinam	rr
Sabiaceae			
Meliosma sinuata Urb.	L. & H. de H. 341	Br. Parana	r
sinuata Urb.	L. & H. de H. 4923	Br. Parana	rr
sp.	Dan. & Jonk. 928	Surinam	r
sp.	Dan.. & Jonk. 1164	Surinam	r
Sapindaceae			
Toulicia pulvinata Radlk.	Stahel 368	Surinam	p
púlvinata Radlk.	LBB 10732	Surinam	p
reticulata Radlk.	Krukoff 4687	Br. Amazonas	p
reticulata Radlk.	Krukoff 4914	Br. Amazonas	p
reticulata Radlk.	Krukoff 5330	Br. Amazonas	(p)

Sapotaceae

Achrouteria pomifera Eyma	F.D. 913	Guyana	r
vs. Achrouteria pomifera Eyma	L. & L. 2506	Surinam	r
Calocarpum mammosum (L.) Pierre	USw 696	Panama	rr
Caramuri opposita (Ducke) Aubr. et Pellegr.	Maguire 51796	Brazil	p, rr
Chrysophyllum acreanum A.C. Smith	Krukoff 5593	Br. Amazonas	rr
auratum Miq.	Maguire 54831	Surinam	rr
marginatum (H. et A.) Radlk. var. marginatum	L. & H. de H. 1347	Br. Parana	rr
marginatum (H. et A.) Radlk. var. marginatum	L. & H. de H. 3312	Br. Parana	rr
nitidum G.F.W. Mey.	F.D. 4757	Guyana	rr
schomburgkianum A. DC.	Maguire 24309	Surinam	rr
Ecclinusa balata Ducke	Krukoff 7208	Br. Amazonas	rr
cuneifolia (Rudge) Aubrév.	Stahel 177	Surinam	rr
guianensis Eyma	Stahel 91	Surinam	rr
prieurii (A. DC.) Aubrév.	BAFOG 186 M	Fr. Guiana	rr
ramiflora Mart. var. tomentosa (Miq.) Monach	L. & L. 2221	Surinam	rr
sanguinolenta (Pierre) Engl.	L. & L. 463	Surinam	rr
Eremoluma sagotiana Baill.	L. & L. 2651	Surinam	rr
Franchetella gonggrijpii (Eyma) Aubrév.	Stahel 233	Surinam	p, rr
Lucuma ephedrantha A.C. Smith	Krukoff 5422	Br. Amazonas	(p), rr
Micropholis egensis (A. DC.) Pierre	Krukoff 7752	Br. Amazonas	rr
eugeniifolia Pierre	Maguire 24739	Surinam	rr
guianensis (A. DC.) Pierre	Stahel 14	Surinam	p, rr
martiana Pierre	BAFOG 1304	Fr. Guiana	rr
venulosa (Mart. et Eichl.) Pierre	L. & L. 2160	Surinam	rr
Nemaluma engleri (Eyma) Aubrév. et Pellegr.	Stahel 13	Surinam	rr
engleri (Eyma) Aubrév. et Pellegr.	BBS 198	Surinam	rr
Neopometia ptychandra (Eyma) Aubrév.	Lindeman 4837	Surinam	rr
ptychandra (Eyma) Aubrév.	BAFOG 55 M	Fr. Guiana	rr
Neoxythece cladantha (Sandw.) Aubrév.	Stahel 134 a	Surinam	p, rr
dura (Eyma) Aubrév. et Pellegr.	LBB 10802	Surinam	(p), rr
dura (Eyma) Aubrév. et Pellegr.	Schulz 7327	Surinam	p, rr
robusta (Mart.) et Eichl.) Aubrév. et Pellegr. var. longifolia Eyma	Stahel 30	Surinam	(p), rr

Table 1 (continued)

Species	Collection	Locality	Distribution
Sapotaceae			
Pouteria anibaefolia (A.C. Smith) Baehni	Krukoff 5124	Br. Amazonas	rr
caimito (Ruiz. et Pav.) Radlk.	L. & L. 670	Surinam	rr
casiocarpa (Mart.) Radlk.	Reitz & Klein 27498	Br. Sta. Catarina	rr
excelsa (A.C. Smith) Baehni	Krukoff 5177	Br. Amazonas	rr
glomerata (Miq.) Radlk. var. glabrescens Huber	Krukoff 6632	Br. Amazonas	rr
guianensis Aubl.	Stahel 9	Surinam	rr
gutta (Ducke) Baehni	Krukoff 1322	Br. Amazonas	rr
heterodoxa Stand. & L. Wms.	P.H. Allen s.n.	Costa Rica	rr
hispida Eyma	O.N.S. 434	Surinam	rr
inflexa (A.C. Smith) Baehni	Krukoff 1505	Br. Amazonas	rr
krukovii (A.C. Smith) Baehni	Krukoff 5700	Br. Amazonas	rr
melanopoda Eyma	Schulz 7453	Surinam	rr
mensalis Baehni	Maguire 24310	Surinam	rr
nuda Baehni	Maguire 24596	Surinam	r
pariry (Ducke) Baehni	Krukoff 5034	Br. Amazonas	rr
salicifolia (Spreng.) Radlk.	L. & H. de H. 3494	Br. Parana	rr
surinamensis Eyma	L. & L. 671	Surinam	rr
surinamensis Eyma	BAFOG 2 M	Fr. Guiana	rr
trichopoda Baehni	Krukoff 6344	Br. Amazonas	rr
trilocularis Cronquist	Krukoff 5283	Br. Amazonas	rr
triplarifolia Stand. & L. Wms.	P.H. Allen s.n.	Costa Rica	rr
Pradosia prealta Ducke	Maguire 51774	Br. Amapa	rr
schomburgkiana (A. DC.) Cronquist	F.D. 937	Guyana	r
Pseudocladia minutiflora (Britton) Aubrév.	Cowan & Lind. 39094	Surinam	rr
scytalophora (Eyma) Aubrév.	L. & L. 2408	Surinam	rr
Pseudolabatia filipes (Eyma) Aubrév.	F.D. 3759	Guyana	rr
Radlkoferella brachyandra Aubrév. et Pellegr.	BBS 95	Surinam	rr
brachyandra Aubrév. et Pellegr.	BBS 204	Surinam	rr
trigonosperma (Eyma) Aubrév.	Stahel 220	Surinam	rr
trigonosperma (Eyma) Aubrév.	Schulz 7293	Surinam	rr
trigonosperma (Eyma) Aubrév.	F.D. 4846	Guyana	rr
Richardiella rivicoa (Gaertn. f.) Pierre	Krukoff 1041	Br. Amazonas	rr
Sandwithiodoxa egregia (Sandw.) Aubrév. et Pellegr.	Stahel 122	Surinam	rr
Sarcaulus brasiliensis Eyma	Maguire 51839	Br. Amapa	rr
macrophyllus (Mart.) Radlk.	Krukoff 1419	Br. Amazonas	p, rr

Simarubaceae			
Quassia cuspidata (Spruce) Nooteboom	IANw 3898	Bràzil	rr
guianensis (Aubl.) D. Dietr.	IANw 2943	Brazil	rr
multiflora (A. Juss.) Nooteboom	Stahel 221	Surinam	rr
multiflora (A. Juss.) Nooteboom	L. & L. 1125	Surinam	rr
multiflora (A. Juss.) Nooteboom	Pr. & M. 11551	Br. Amazonas	rr
Styracaceae			
Styrax fanshawei Sandw.	F.D. 3403	Guyana	r
glabratus Schott ex Spreng.	Schulz 7142	Surinam	rr
guianensis A. DC.	Maguire 24424	Surinam	rr
leprosus Hook. et Arn.	L. & H. de H. 1335	Br. Parana	r
Theaceae			
Ternstroemia dentata (Aubl.) Sw.	Stahel 240	Surinam	r
dentata (Aubl.) Sw.	Heyligers 500	Surinam	r
punctata (Aubl.) Sw.	Maguire 23271	Guyana	r
Theophrstaceae			
Clavija lancifolia Desf.	Lindeman 4463	Surinam	rr
lancifolia Desf.	Flor. & Ms. 2475	Surinam	rr
lancifolia Desf.	Breteler 3535	Venezuela	rr
parviflora Mez	Krukoff 6742	Br. Amazonas	r
Tiliaceae			
Luehea candicans Mart.	L. & H. de H. 954	Br. Parana	r
divaricata Mart.	L. & H. de H. 1016	Br. Parana	rr
Verbenaceae			
Vitex compressa Turcz.	Stahel 349	Surinam	rr
compressa Turcz.	BBS 77	Surinam	rr
compressa Turcz.	L. & L. 1225	Surinam	rr
floridula Duchass. & Walp.	USw 684	Panama	rr
megapotamica (Spreng.) Mold.	Reitz 22680	Br. Sta. Catarina	ff
megapotamica (Spreng.) Mold.	L. & H. de H. 1058	Br. Parana	ff
megapotamica (Spreng.) Mold.	L. & H. de H. 1060	Br. Parana	f
Vochysiaceae			
Qualea acuminata Spruce	Krukoff 7169	Br. Amazonas	r
albiflora Warming	Stahel 31	Surinam	rr
albiflora Warming	Yw 35669	unknown	r
albiflora Warming	BBS 1076	Surinam	rr
coerulea Aubl.	BBS 1015	Surinam	r
coerulea Aubl.	BAFOG 316 M	Fr. Guiana	(r)
ingens Warming var. ingens	Maguire 56366	Brazil	r
rosea Aubl.	L. & L. 1195	Surinam	r
rosea Aubl.	BAFOG 317 M	Fr. Guiana	r

TABLE 2. Neotropical taxa without silica grains in the secondary xylem (between brackets the number of species investigated)

Acanthaceae	- Aphelandra (1), Trichanthera (1).
Annonaceae	- Anaxagorea (5), Annona (6), Bocageopsis (1), Cymbopetalum (2), Duguetia (10), Ephedranthus (1), Froesiodendron (1), Fusaea (1), Guatteria (8), Hornschuchia (1), Malmea (2), Oxandra (1), Panoxandra (2), Rollinia (5), Unonopsis (4), Xylopia (8).
Apocynaceae	- Ambelania (1), Aspidosperma (18), Bonafousia (3), Couma (1), Geissospermum (1), Himatanthus (2), Lacmellea (1), Macoubea (1), Malouetia (1), Parahancornia (1), Plumeria (2), Stemmadenia (1), Stenosolen (1), Tabernaemontana (1).
Aquifoliaceae	- Ilex (4).
Araliaceae	- Didymopanax (1), Schefflera (2).
Aristolochiaceae	- Aristolochia (1).
Bignoniaceae	- Adenocalymma (1), Anemopaegma (1), Arrabidaea (1), Cydista (1), Jacaranda (2), Mussatia (1) Paragonia (1), Phryganocydia (1), Potamogenos (1), Pseudocalymma (1), Roentgenia (1), Stizophyllum (1), Tabebuia (4).
Boraginaceae	- Cordia (10).
Celastraceae	- Maytenus (13), Plenckia (2).
Cochlospermaceae	- Cochlospermum (1).
Combretaceae	- Buchenavia (3), Combretum (1), Laguncularia (1), Terminalia (3).
Compositae	- Baccharis (1).
Convolvulaceae	- Bonamia (1), Dicranostyles (1), Maripa (1).
Cunoniaceae	- Caldcluvia (1), Lamanonia (1), Weinmannia (2).
Dichapetalaceae	- Dichapetalum (4), Gonypetalum (1), Tapura (3).
Dilleniaceae	- Curatella (1), Davilla (3), Doliocarpus (3), Pinzona (1), Tetracera (2).
Elaeocarpaceae	- Sloanea (9).
Gentianaceae	- Lisianthus (1).
Gnetaceae	- Gnetum (1).
Goupiaceae	- Goupia (1).
Hypericaceae	- Hypericum (3), Vismia (6).
Icacinaceae	- Calatola (1), Dendrobangia (1), Discophora (1), Emmotum (1), Leretia (1), Poraqueiba (1).
Lacistemaceae	- Lacistema (2).

Linaceae	- Hebepetalum (1), Roucheria (1).
Malpighiaceae	- Bunchosia (1), Byrsonima (4), Dolichopterys (1), Heteropteris (1), Hirarea (1), Lophopteris (1), Spachea (1), Tetrapteris (1).
Melastomataceae	- Bellucia (1), Clidemia (1), Henriettea (4), Henrietella (2), Loreya (1), Macairea (1), Meriania (3), Miconia (20), Mouriria (3), Myriaspora (2), Nepsera (1), Tibouchina (5), Tococa (1).
Monimiaceae	- Mollinedia (2), Siparuna (4).
Moraceae	- Anonocarpus (1), Bagassa (2), Batocarpus (1), Brosimum (8), Castilla (3), Cecropia (3), Clarisia (2), Coussapoa (2), Ficus (5), Helianthostylis (1), Helicostylis (3), Maquira (3), Naucleopsis (4), Perebea (2), Pourouma (5), Pseudolmedia (1), Sorocea (2), Trymatococcus (3).
Myristicaceae	- Iryanthera (4), Osteophloeum (1), Virola (6).
Myrsinaceae	- Ardisia (1), Conomorpha (4), Cybianthus (3), Rapanea (1), Stylogyne (1), Weigeltia (1).
Myrtaceae	- Blepharocalyx (1), Calycolpus (2), Calycorectus (1), Calyptranthes (5), Campomanesia (2), Catinga (2), Eugenia (7), Gomidesia (1), Marlierea (1), Mitranthes (1), Myrcia (11), Myrcianthes (1), Myrciaria (2), Plinia (1), Syzygium (1).
Nyctaginaceae	- Guapira (2), Neea (1), Pisonia (2).
Ochnaceae	- Elvasia (1), Ouratea (5).
Opiliaceae	- Agonandra (1).
Passifloraceae	- Passiflora (3).
Piperaceae	- Piper (3).
Polygalaceae	- Moutabea (1), Securidaca (1).
Rhamnaceae	- Gouania (1).
Rhizophoraceae	- Anisophyllea (1), Cassipourea (1), Rhizophora (3), Sterigmapetalum (1).
Solanaceae	- Brunfelsia (1), Cestrum (1), Cyphomandra (1), Solanum (3).
Sterculiaceae	- Basiloxylon (1), Guazuma (2), Herrania (1), Sterculia (2), Theobroma (2).
Symplocaceae	- Symplocos (3).
Trigoniaceae	- Trigonia (2).
Ulmaceae	- Ampelocera (1), Trema (1).
Violaceae	- Amphirrhox (2), Anchietea (1), Gloeospermum (1), Leonia (1), Paypayrola (1), Rinorea (2).

Normand (1966, 1967) reported the frequent occurrence of silica grains in the ray cells of *Q. tricolor*.

No silica grains were observed in *Callisthene* (1), *Erisma* (5), *Salvertia* (1), and *Vochysia* (13).

DISCUSSION

According to Amos (1952) the occurrence of silica grains is a very promising diagnostic character. In the present study, two or more samples of 117 siliceous species (including the Chrysobalanaceae) were investigated. In 110 species the presence of silica grains is constant (94%), in the remaining seven species the occurrence is variable.

The distribution of the grains over the various tissues is as follows: ray parenchyma 85%, axial parenchyma 20%, fibres 4%, and tyloses of the vessels 4%. Silica grains sometimes occur in more than one tissue and therefore the sum of the percentages is over 100%. The occurrence of tyloses being variable in a species, the presence of silica grains in tyloses is of no absolute diagnostic value. Species in which the grains are restricted to the axial parenchyma or to the fibres constitute only a small portion of the siliceous species. However, as in these species the occurrence of silica grains in those tissues is very constant it is also of diagnostic importance. However, when grains are not restricted to the axial parenchyma and fibres only, but also occur in other tissues of the same sample their presence in axial parenchyma and fibres is variable. Similarly the occurrence of silica grains in the rays is most constant in those species where the grains are restricted to the rays only. According to these results it is concluded that the occurrence of silica grains is a valuable diagnostic character on the species level, especially when the grains are restricted to one tissue.

In about 60% of all the material investigated, the occurrence of silica grains in a genus is constant. Therefore, though in many instances the presence of silica grains may be valuable as a diagnostic feature, it is not of such great importance at the genus level.

The diagnostic importance of the grains at the family level is very small. Besides the Chrysobalanaceae, only a few, mostly small or monotypic families, show a constant occurrence of the grains.

The surface of the grains may be smooth or granular. Grains with a smooth surface are less frequent than the ones with a granular surface. Although this smooth surface was not studied by means of scanning electron microscopy, it should be interpreted as 'not granular'. Grains with this type of surface are always small or medium sized ($\leq 10\ \mu$m). Granular surfaces show a considerable variation (Plate 2/6–11). At present this character has not been sufficiently studied. As Scurfield *et al.* (1974a) and Hirata *et al.* (1972) also described various types of granular surfaces, it might be of interest to study this phenomenon more extensively, especially with regard to its possible diagnostic value.

The size of the grains is very variable as pointed out by ter Welle (1976). The best way

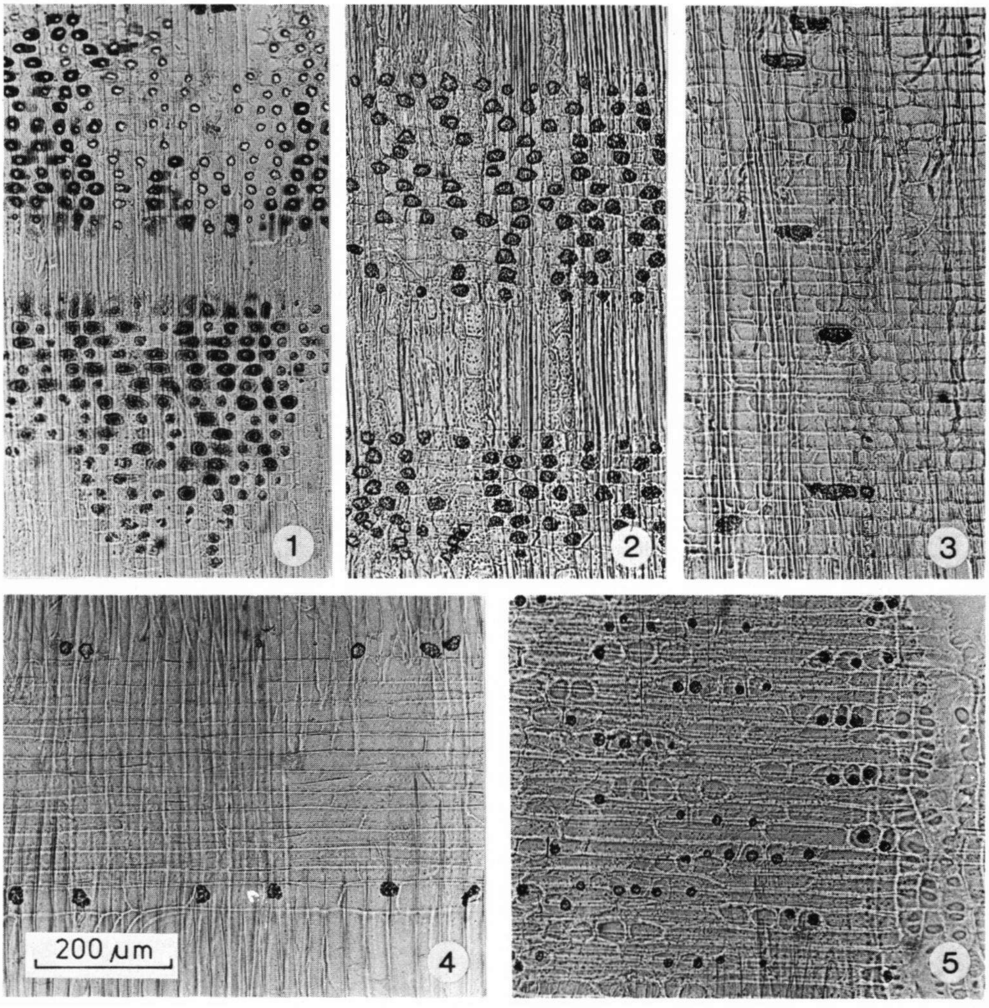

Plate 1.—Distribution patterns of silica grains in the rays; 1, *Licania leptostachya*. Globular grains in all ray cells; 2, *Licania majuscula*. Globular to oval grains in all ray cells; 3, *Lecythis davisii*. Oblong grains in part of the ray cells; 4, *Trattinickia demerarae*. Almost globular grains, restricted to the marginal ray cells; 5, *Mezilaurus itauba*. Globular grains grouped together in short horizontal bands of ray cells.

to make a good use of this character is probably found in introducing the following categories:

(1) grains small (≦ 5 µm),
(2) grains medium-sized (6–15 µm),
(3) grains large (≧ 15 µm).

Logically, this classification will apply to globular grains only.

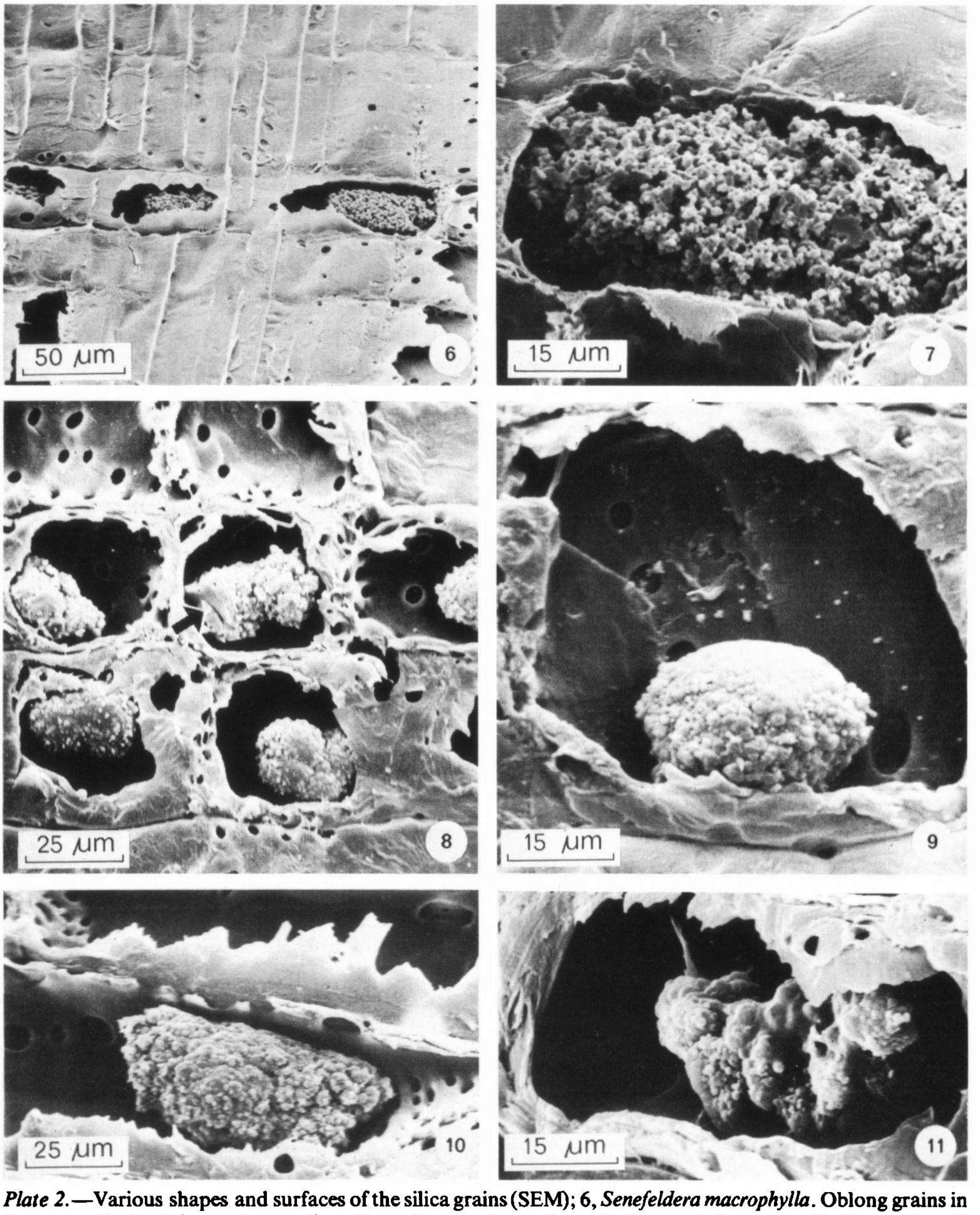

Plate 2.—Various shapes and surfaces of the silica grains (SEM); 6, *Senefeldera macrophylla*. Oblong grains in the ray cells; 7, *Achrouteria pomifera*. Strongly granular surface of silica grain in a ray cell. The entire cell lumen is filled; 8, *Erythroxylon citrifolium*. Silica grains with various shapes in the ray cells. Note the dense inner side of the broken grain (arrow); 9, Same sample as 8, showing an oval grain in a ray cell, the surface is less granular than that of the grains in 6 and 7; 10, *Couratari stellata*. Oblong grain. The granular surface is quite different from that of 7; 11, *Erythroxylon nitidum*. More or less oblong grain in a ray cell. The surface is irregular and varies from granular to nearly smooth.

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REFERENCES

AMOS, G. L. 1951. Some siliceous timbers of British Guiana. Caribb. Forester 12: 133–137.
AMOS, G. L. 1952. Silica in timbers. C.S.I.R.O. Bull. 267.
ARAUJO, P. A. DE & A. DE MATTOS FILHO. 1974a. Estrutura das madeiras brasilieras de angiospermas dicotiledoneas VII Proteaceae (*Panopsis sessilifolia* (Rid.) Sandw.). Rodriguesia 39: 61–71.
ARAUJO, P. A. DE & A. DE MATTOS FILHO, 1974b. Estrutura das madeiras brasilieras de angiospermas dicotiledoneas VIII Proteaceae (*Panopsis rubescens* (Pohl) Pittier). Rodriguesia 39: 71–85.
BALAN MENON, P. K. 1965. Guide to distribution of Silica in Malayan woods. Malay. Forester 28: 284–288.
BAMBER, R. K. & J. W. LANYON, 1960. Silica deposition in several woods of N.S.W. Trop. Woods 113: 48–54.
BARETTA-KUIPERS, T. 1976. Comparative wood anatomy of Bonnetiaceae, Theaceae, and Guttiferae. Leiden bot. Ser. (this issue).
BESSON, A. 1946. Richesse en cendres et teneur en silice des bois tropicaux. Agron. trop., Nogent 1: 44–56.
BRAZIER, J. D. & G. L. FRANKLIN, 1961. Identification of hardwoods. Forest Prod. Res. Bull. 46.
BURGESS, P. F. 1965. Silica in Sabah timbers. Malay. Forester 28: 223–229.
CHATTAWAY, M. M. 1948. The wood anatomy of the Proteaceae. Aust. J. scient. Res., Ser. B, 1: 279–302.
CRÜGER, H. 1857. Westindische Fragmente. Bot. Ztg. 15: 281–292, 297–308.
CUATRECASAS, J. 1961. A taxonomic revision of the Humiriaceae. Contr. U.S. natn. Herb. 35: 25–214.
DICKISON, W. E. 1972. Anatomical studies in the Connaraceae II. Wood anatomy. J. Elisha Mitchell scient. Soc. 88: 120–136.
ENGLER, A. & K. PRANTL, 1889. Proteaceae. *In*: Natürl. PflFam.
FRISON, E. 1942. De la présence de corpuscules siliceux dans les bois tropicaux en général et en particulier dans le bois du *Parinari glabra* Oliv. et du *Dialium klainei* Pierre. Bull. agric. Congo belge 28: 91–105.
GONGGRIJP, J. W. 1923. Over paalworm en tegen paalworm bestand hout. Indische Mercuur 46: 351–353, 369–371.
GONGGRIJP, J. W. 1932. Gegevens betreffende een onderzoek naar Nederlandsch-Indische houtsoorten, welke tegen den paalworm bestand zijn. Meded. Boschbouwproefstat. 25.
GOTTWALD, H. & N. PARAMESWARAN, 1967. Beiträge zur Anatomie und Systematik der Quiinaceae. Bot. Jb. 87: 361–381.
JOHNSON, L. A. S. & B. G. BRIGGS, 1975. On the Proteaceae—the evolution and classification of a southern family. Bot. J. Linn. Soc. 70: 83–182.
HIRATA, T., H. SAIKI, & H. HARADA, 1972. Observations of crystals and silica inclusions in parenchyma cells of certain tropical woods by scanning electron microscope. Bull. Kyoto Univ. Forests 44: 194–205.
KOEK-NOORMAN, J. 1969a. A contribution to the wood anatomy of South American (chiefly Suriname) Rubiaceae. I. Acta bot. neerl. 18: 108–123.
KOEK-NOORMAN, J. 1969b. A contribution to the wood anatomy of South American (chiefly Suriname) Rubiaceae. II. Acta bot. neerl. 18: 377–395.
KOEK-NOORMAN, J. 1970. A contribution to the wood anatomy of the Cinchoneae, Coptosapelteae, and Naucleeae (Rubiaceae). Acta bot. neerl. 19: 154–164.
KOEK-NOORMAN, J. 1972. The wood anatomy of Gardenieae, Ixoreae, and Mussaendeae (Rubiaceae). Acta bot. neerl. 21: 301–320.

KOEK-NOORMAN, J. 1974. The wood anatomy of Vanguerieae, Cinchoneae, Condamineae, and Rondeletieae (Rubiaceae). Acta bot. neerl. 23: 627–653.
KOEPPEN, R. C. 1967. Revision of *Dicorynia* (Cassieae, Caesalpiniaceae). Brittonia 19: 42–61.
KÜSTER, E. 1897. Die anatomische Charaktere der Chrysobalaneen, insbesondere ihre Kieselablagerungen. Bot. Zbl. 69: 46–54, 97–106, 129–139, 161–169, 193–202, 225–234.
MAGUIRE, B. 1972. Bonnetiaceae. Mem. N.Y. bot. Gdn. 23: 131–165.
MENNEGA, A. M. W. 1966. Wood anatomy of the genus *Euplassa* and its relation to other Proteaceae of the Guianas and Brazil. Acta bot. neerl. 15: 117–129.
MENNEGA, A. M. W. 1972. A survey of the wood anatomy of the new world Hippocrateaceae. *In*: Research trends in plant anatomy (eds.: A. K. M. Ghouse & M. Yunus).
MENNEGA, A. M. W. 1977. Stem structure of Menispermaceae of the New World (in press).
METCALFE, C. R. & L. CHALK. 1950. Anatomy of the Dicotyledons.
MILLER, R. B. 1975. Systematic anatomy of the xylem and comments on the relationship of Flacourtiaceae. J. Arnold Arbor. 56: 20–102.
MURTHY, L. S. V. 1965. Silica in Sarawak timbers. Malay. Forester 28: 27–45.
NORMAND, D. 1950. Atlas des bois de la Côte d'Ivoire. 1.
NORMAND, D. 1966. Les Kouali, Vochysiacées de Guyane, et leurs bois. Bois Forêts Trop. 110: 3–11.
NORMAND, D. 1967. Les Kouali. Vochysiacées de Guyane, et leurs bois. Bois Forêts Trop. 111: 5–17.
PARENTE, M. Z. G. 1959/1961. Anatomia do lenho secondaris de *Triplaris gardneriana* Wedd. Archos Jard. bot. Rio de J. 17: 251.
PAULA, J. E. DE, 1974. Anatomia de madeira. Guttiferae. Acta amazonica 4: 27–64.
PAULA, J. E. DE, & J. L. DE HAMBURGO ALVES. 1973. Anatomia de *Anacardium spruceanum* Bth. ex Engl. (Anacardiaceae da Amazônia). Acta amazonica 3: 39–53.
PENNINGTON, T. D. & B. T. STYLES. 1975. A generic monograph of the Meliaceae. Blumea 22: 419–540.
PETRUCCI, G. B. 1903. Concrezioni silicea intracellulari nel legno secondario di alcune Dicotiledoni. Malpighia 18: 23–27.
PRANCE, G. T. 1968. The systematic position of *Rhabdodendron* Gilg & Pilg. Bull. Jard. bot. État Brux. 38: 127–146.
PRANCE, G. T. 1972. A monograph of the Rhabdodendraceae. Flora Neotropica, Monograph 11.
RECORD, S. J. & R. W. HESS. 1943. Timbers of the new world.
ROBYNS, A. 1963. Essai de monographie du genre *Bombax* s.1. (Bombacaceae). Bull. Jard. bot. État Brux. 33: 1–313.
SCHULTES, R. E. 1952. Studies in the genus *Micrandra* I. The relationship of the genus *Cunuria* to *Micrandra*. Bot. Mus. Leafl. Harv. Univ. 15: 201–220.
SCURFIELD, G., C. A. ANDERSON, & E. R. SEGNIT, 1974a. Silica in woody stems. Aust. J. Bot. 22: 211–231.
SCURFIELD, G., C. A. ANDERSON, & E. R. SEGNIT, 1974b. Silicification of wood. Scanning electron microscopy Part 2: 389–396. I.T.T. Research Institute, Chicago.
SHARMA, M. & K. R. RAO, 1970. Investigations on the occurrence of silica in indian timbers. Indian Forester 96: 740–754.
SOUTHWELL, C. R. & J. D. BULTMAN, 1971. Marine borer resistance of untreated woods over long periods of immersion in tropical waters. Biotropica 3: 81–107.
WEBBER, I. E. 1936. Systematic anatomy of the woods of the Simarubaceae. Amer. J. Bot. 23: 577–587.
WEBBER, I. E. 1941. The woods of the 'Burseraceae'. Lilloa 6: 441–465.
WEBSTER, G. L. 1975. Conspectus of a new classification of the Euphorbiaceae. Taxon 24: 593–601.
WELLE, B. J. H. TER, 1976. On the occurrence of silica grains in the secondary xylem of the Chrysobalanaceae. I.A.W.A. Bulletin 1976/2: 19–29.