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Occurrence, Morphology and Taxonomic Implications of Crystalline and Siliceous Inclusions in the Secondary Xylem of the Lauraceae and Related Families*

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Summary. Crystalline inclusions were observed in more than 50 %, silica in nearly 20 % of about 1500 wood specimens representing ± 750 species from 40 genera of the laurel family. Both types of inorganic cell deposits are described and classified with regard to composition, habit, size, degree of isolation and location. Their diagnostic value and taxonomic implications on the specific, generic and suprageneric level are discussed with respect to intra as well as extrafamiliar relationships.

Introduction

A large number of plants are known to deposit excess inorganic materials in their tissues, consisting mostly of calcium salts and of silicium dioxide (SiO_2). Among the calcium salts the most common is calcium oxalate which is found in the majority of plant families.

Crystals in wood occur most frequently in ray and/or axial parenchym cells, but also in fibers and vessel tyloses. Siliceous compounds may be found either as "dense silica" (Scurfield, 1974), lining or even filling the cell cavity, or as individual bodies in the cell lumina, varying considerably in size and shape. Particulate silica inclusions are present exclusively either in rays, axial parenchyma, fibres and vessel tyloses or jointly in any two of these tissues.

Both forms of inorganic inclusions, crystals and silica, have been proven to be of diagnostic value and taxonomic significance in wood anatomy. At the same time, one should regard these features with considerable prudence with respect to their diagnostic limits at the specific, generic and family levels. Prompted by these findings, both

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encouraging and cautioning, the present paper attempts to examine in detail the occurrence, morphology and taxonomic implications of crystals and silica in the woods of the Lauraceae, a family which poses an yet unsurmounted challenge to botanists and wood anatomists alike with regard to a satisfactory intra-family classification. Crystals of traumatic or abnormal origin will not be considered.

Materials and Methods

In the course of a general structural survey of the laurel family more than 1500 wood specimens have been examined in detail for the presence of crystals and silica. In addition, microscopic slides of 18 more or less closely related families belonging to the orders Laurales, Magnoliales, Aristolochiales and Piperales (Takhtajan, 1973) were checked for the same purpose.

Observations were carried out with temporarily and permanently mounted slides using normal and polarized light. Scanning electron microscopy (SEM) was also employed to obtain better information about geometry and surface structure of the inorganic inclusions. Finally, micro-chemical tests and energy dispersive X-ray analysis (EDXA) were applied to selected specimens to ascertain the chemical composition of the minerals involved.

Results

The laurels constitute a very large plant family with a total number of species estimated between 2000 and 2500 (Kostermans, 1957), more recently up to 4000 (Kostermans, 1974), belonging to approximately 40 genera. Of the nearly 750 species (as well as 150 specimens with generic identification only) analysed, more than 400 or nearly 50 % were found to contain crystalline inclusions and 140 or nearly 20 % to bear particulate silica bodies. With the exception of two sole species crystals and silica proved to be mutually exclusive.

Crystalline Inclusions

Location: The occurrence of crystalline inclusions in lauraceous woods is restricted almost entirely to the ray parenchyma. Only in few instances (less than 10 %) were they observed in the axial parenchyma, although never exclusively, and notably in specimens with generally large quantities of crystals in the rays. Neither fibers nor vessel tyloses were found to contain crystals under the light microscope. Irregular "crystalline masses" were observed in the fiber lumina of a few genera, appearing as compact plugs. Although these plugs do not show definite crystal geometry, they are birefringent, thus revealing their crystalline nature.

Chemical Composition: Although the scope of the current anatomical study did not allow for detailed analyses, various techniques were applied to some selected specimens representing typical crystalline inclusions.

EDXA: In all specimens studied calcium has been determined to be the major component of the crystalline material.

Microchemical tests: The chemical behaviour towards dilute (10 %) acetic, hydrochloric and sulfuric acids shows convincingly that the crystals in lauraceous specimens tested consist of calcium oxalate.

Polarization optics: Both morphology and specific birefringent properties lead to the assumption that the monohydrate form of calcium oxalate dominates in most specimens investigated, while only one species, *Caryodaphnopsis tonkinensis*, contains the typical bipyramidal crystals known from the tri-hydrate form. With reference to the above mentioned "crystalline masses" neither EDXA nor microchemical tests resulted in clarification of the possible chemical composition. Dilute acids and organic solvents, such as alcohol, xylene, acetone and benzene, had no visible effect. Further tests with trichlorethylene and hydrofluoric acid (4 %) revealed that possibly two birefringent substances are involved, one organic and another inorganic, the former enclosing small particles of the latter.

Crystal habit and morphology: With regard to crystal formation, degree of individualization and morphology, the microscopic and SEM observations have led to the following results:

- All crystals, independent of size, shape or location, occur free in their parenchymatic cells. There is convincing evidence corroborated by their smooth and untainted surfaces that no membranes or sacks are present around individual crystals or crystal aggregates.
- As a rule there are no solitary crystal per cell. Depending on size and shape, from two to more than hundred (crystal sand) may be found in one cell. Solitary crystals have been observed occasionally when their dimensions nearly equal those of the surrounding cells.
- Crystals in Lauraceae are of a very simple structure, occurring predominantly as solid figures with six (hexahedron) or, less frequently, eight (octohedron) plane surfaces. Their transverse sections are either square or rectangular. Contact twin formation is quite common.
- According to their form and regardless of their size the crystals in the secondary xylem of Lauraceae may be classified tentatively in the following categories (Fig. 1):

  A) Isodiametric or Elongated Prisms

  This is the most common form, extremely variable in size: crystal sand (1,5–5 μm) as exemplified by most species of *Actinodaphne* (Fig. 3, A).

  Square to elongated (10–30 μm) prisms as found to be typical of the genera *Cryptocarya* and *Ravensara*, but occurring also scattered in individual species throughout the family (Fig. 3 B).

  Rather large, elongated prisms (40–70 μm) as in *Nectandra grandis* and some species of *Aniba* (Fig. 3 C).

CRYSTALLINE INCLUSIONS IN LAURACEAE

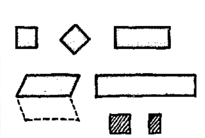
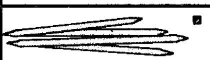
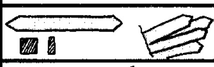
TYPE	DESCRIPTION	FORM	OCCURRENCE
A	ISODIAMETRIC OR ELONGATED PRISMS According to size and habit: "CRYSTAL SAND" "ROD-LIKE" "ELONGATED" (CHATTAWAY 1955)		*ACTINODAPHNE* +++, *ENDLICHERIA* +, *PERSEA* (+) → "X-sand" *CRYPTOCARYA/RAVENSARA* +++, *PHOEBE* ++, OTHER SCATTERED SPECIES → "squarish to rod-like" *ANIBA* +, *NECTANDRA* +, OTHER SCATTERED SPECIES → "elongated, large"
B	ACICULAR CRYSTALS		*LITSEA CHINENSIS* *NECTANDRA LUCIDULA*
C	SPINDLE-SHAPED CRYSTALS		*DEHAASIA* ++, *LINDERA* +, *ACTINODAPHNE* (+), *AIOUEA* +, *ENDLICHERIA* ++, *LICARIA* +, OTHER SCATTERED SPECIES
D	STYLOID CRYSTALS		*OCOTEA SUAVEOLENS*, *NECTANDRA SANGUINEA*, *APOLLONIAS CANARIENSIS*
E	TABLETOID CRYSTALS		*ANIBA* +++, *ENDLICHERIA* +, *NECTANDRA* +
F	PYRAMIDAL CRYSTALS		*CARYODAPHNOPSIS TONKINENSIS*
G	"CRYSTALLINE MASSES"		*DEHAASIA* +++, *OCOTEA* (+), *LICARIA* (+)

Fig. 1. Diagrammatic presentation of crystalline inclusions in Lauraceae. +++ nearly all species, ++ common, + rare

SILICEOUS INCLUSIONS IN LAURACEAE

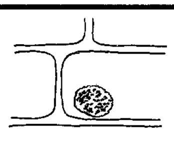
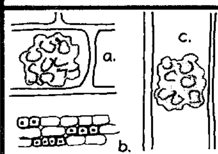
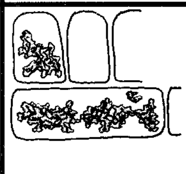
TYPE	DESCRIPTION	FORM	OCCURRENCE
A	SMOOTH GRAINS 5-12μ Ø		*LITSEA* + *ENDLICHERIA* (+) *BEILSCHMIEDIA* (only south-american)
B	ROUGH GRAINS "Cauliflower" 8-35μ Ø		in rays: *LICARIA WILHELMINENSIS* a. *MEZILAURUS* +++ b. *BEILSCHMIEDIA* (+) in fibres: *NOTHAPHOEBE* ++ c. *OCOTEA SPLENDENS*
C	AGGREGATE GRAINS up to 70μ in radial direction		*BEILSCHMIEDIA* +++ *ENDIANDRA* +++ *POTAMEIA* +++ *TRIADODAPHNE INAEQUITEPALA* *CRYPTOCARYA* +

Fig. 2. Diagrammatic presentation of siliceous inclusions in Lauraceae. +++ nearly in all species, ++ common, + rare

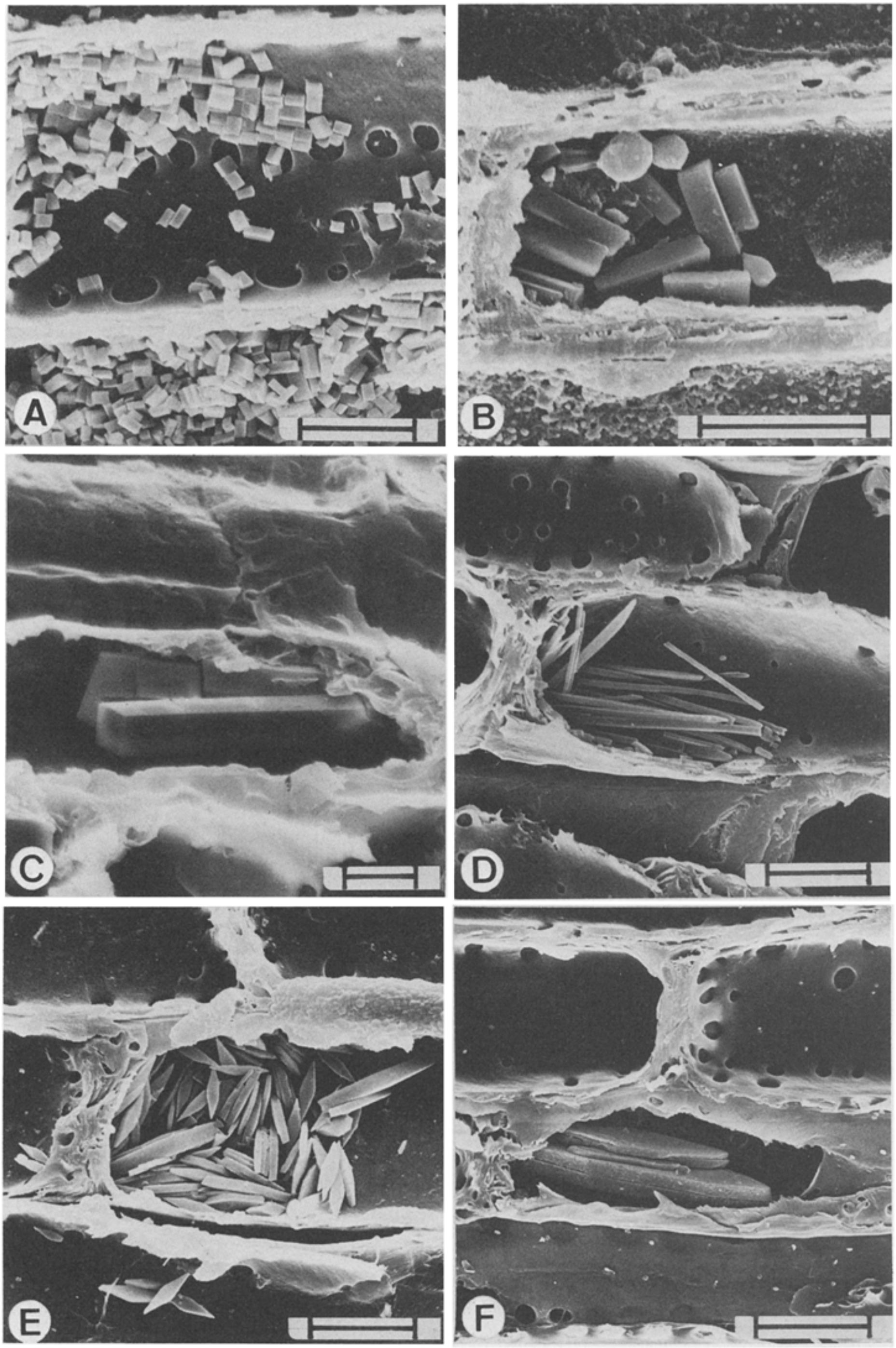


Fig. 3. A Crystal sand in ray of *Actinodaphne glomerata*, **B** Small prismatic crystals in ray of *Cryptocarya moretoniana*, **C** Large prismatic crystal in ray of *Nectandra grandis*, **D** Crystal needles (acicular) in ray of *Litsea chinensis*, **E** Spindle-shaped crystals in ray of *Actinodaphne tadulingami*, **F** Styloid crystals, stacked, in ray of *Nectandra sanguinea*

Note: The marked distance on each photograph equals 10 μm

B) Acicular Crystals
Needle-like crystals with pointed ends, generally about 20x longer than wide, of rare occurrence, e. g. in *Litsea chinensis* and *Nectandra lucidula* (Fig. 3, D).
C) Spindle-chaped Crystals
Slightly to strongly elongated structures with wedgelike extremes, either with parallel or, occasionally, curved lateral plains; typical of *Dehaasia*, *Lindera spp.*, *Aiouea spp.*, *Endlicheria spp.*, also scattered in other parts of the family (Fig. 3, E).
D) Styloid Crystals
Rather large, elongated structures with square to rectangular cross sections; rare, either single *(Apollonias)*, in tightly stacked piles (*Nectandra sanguinea*) or else as fascicular bundles (*Ocotea suaveolens*) (Fig. 3, F).
E) Tabletoid Crystals
Square to rectangular crystals, either single or in twin formation, often with slightly curved edges; typical of most species of *Aniba*. A rare and rather unique example of crystal formation in wood apparently not previously described (Fig. 4, G).
F) Pyramidal Crystals
Single or mostly bi-pyramidal forms with a square base and twin formations thereof; of extremely rare occurrence, observed only in *Caryodaphnopsis tonkinensis* (Fig. 4, H).
G) Crystalline Masses
Birefringent substances (plugs) without any geometrical form, located in the fiber lumina; typical of nearly all species of *Dehaasia*; scattered in a few other genera (Fig. 4, J).

Siliceous Inclusions

Location: similar to what has been shown for crystals, silica bodies are located almost exclusively in the ray parenchyma. There are, however, some taxonomically significant exceptions to this rule, where silica is formed exclusively in the fibers as in *Ocotea splendens* and in at least 4 species of *Nothaphoebe*. No silica was found in vessel tyloses.

Chemical Composition: EDXA showed that silicium is the major component in all specimens. As the chemical composition of siliceous inclusions in plants has been established early by a number of researchers as silica ($SiO_2 \cdot nH_2O$), no additional investigations were carried out.

Habit: with regard to formation, morphology and surface structure of silica in lauraceous woods, microscopic and SEM observations gave the following results:
- Silica occurs exclusively in its particulate form, i. e. as free individual bodies in the cell lumina; dense silica was not observed.
- As a rule there is only one grain per cell; in the case of large and loosely aggregate grains, various particles may be discerned.

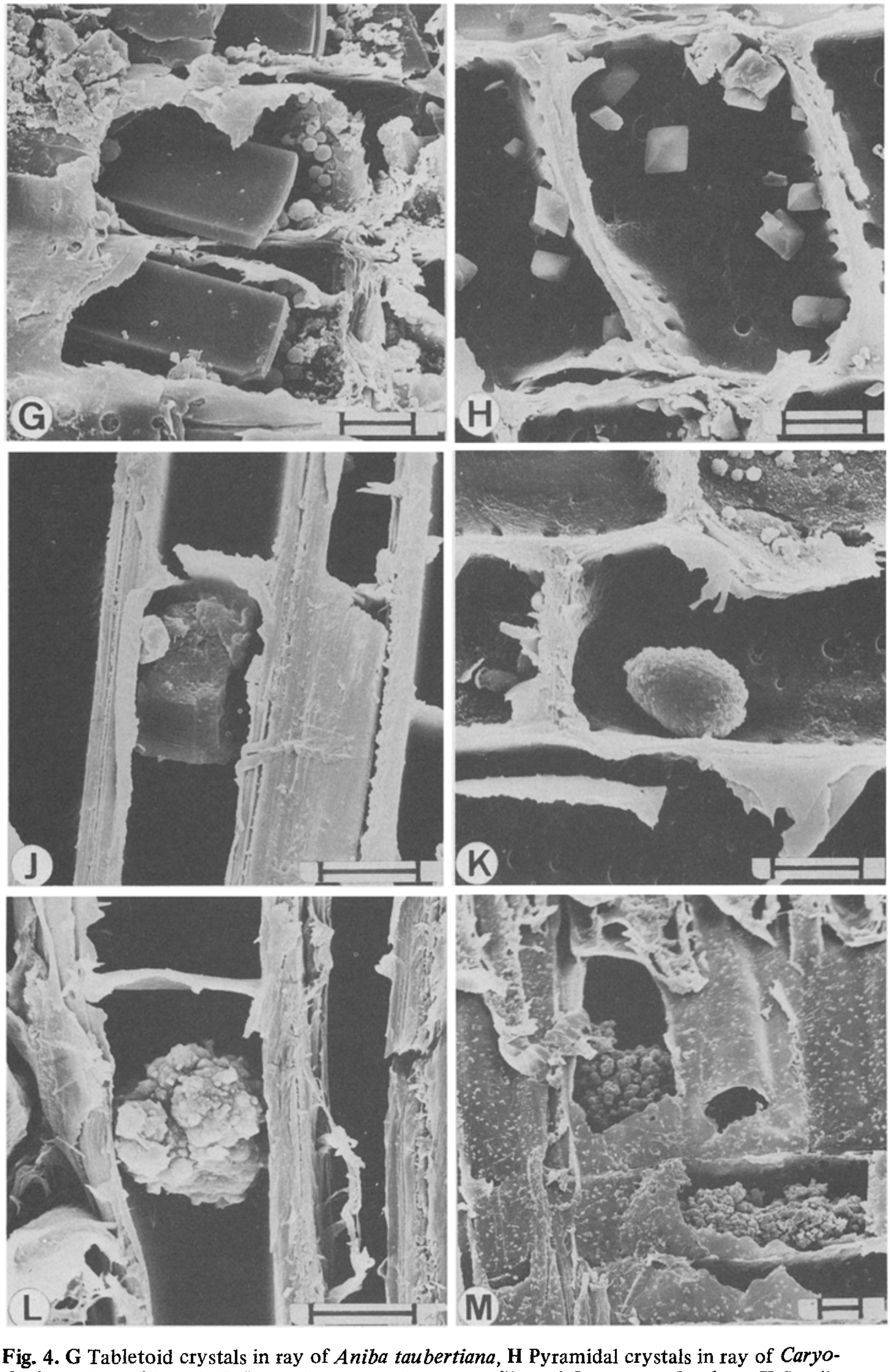


Fig. 4. G Tabletoid crystals in ray of *Aniba taubertiana*, H Pyramidal crystals in ray of *Caryodaphnopsis tonkinensis*, J Crystalline masses in septate fibre of *Ocotea petalanthera*, K Small and smooth silica grain in ray of *Endlicheria? krukovii*, L Large and rough silica grain in septate fibre of *Nothaphoebe sp.*, M Aggregate silica in ray of *Bleischmiedia micrantha*

Note: The marked distance on each photograph equals 10 μm

- Silica-bearing parenchymatic cells or fibers are similar to silica-free cells, with one notable exception: 2–5 seriate cell chains in the rays of the genus *Mezilaurus*, a unique feature among silica-containing woody plants (Amos, 1952; ter Welle, 1976).
- According to their size, form and surface structure silica inclusions in lauraceous timbers may be classified tentatively in the following categories (Fig. 2):

A) Smooth Grains
Small (5–12 μm), nearly globular particles appearing as rather smooth, glassy bodies (microscopic observation), with an only slightly roughened, compact surface structure (SEM); rather rare, observed only in some species of *Litsea*, *Beilschmiedia* (only South American) and one species of *Endlicheria* (Fig. 4, K).

B) Rough Grains
Small to large (8–35 μm) more or less globular grains of a more irregular outline as in A and lacking somewhat the glassy appearance. With a compact, coarsely ragged surface resembling a densely grown head of cauliflower; typical of *Mezilaurus* in non-seriate and seriate cells and for those taxa, where silica is located in the fibers (Fig. 4, L).

C) Aggregates
By far the most common type, rather variable in size (15–70 μm); of irregular outline and deeply fissured surface structure; apparently aggregations of many smaller or primary grains; common in nearly all species of *Beilschmiedia* (except South American), *Endiandra*, *Potameia* and some species of *Cryptocarya* (Fig. 4, M).

Discussion

Information on crystalline and siliceous inclusions in woody plants has been assembled on numerous occasions, largely to assist in timber identification. There is no doubt that in wood anatomy these inorganic substances play a major, but mostly supporting role as discriminatory features at the specific, generic or family level. With regard to crystalline inclusions in Lauraceae the following criteria might eventually prove useful to the taxonomist, especially when combined with other structural evidence:

- No special crystalline configurations such as druses or raphides were observed.
- Crystals appear to possess no surrounding membranes or sacks.
- Solitary crystals are the absolute exception and might be considered a matter of size rather than of a genetic origin.
- Crystal-containing cells are similar to crystal-free cells; in no instance the presence of subdivided strands, enlarged idioblasts or sclerosed cell walls was evident in connection with crystals.

– As a rule crystal formation assumes the more simple configurations, e. g. prisms, styloids, tabletoids, with normally six or eight plane surfaces.
– At the generic level the almost exclusive presence of crystal sand in *Actinodaphne,* tabletoid crystals in *Aniba* and that of crystalline masses in the fibers of *Dehaasia* proved to be of considerable diagnostic significance.

Siliceous inclusions, because of their more restricted distribution in Lauraceae, may be considered more useful to the taxonomist than crystals, as revealed by the following observations:

– The bulk of silica inclusions is concentrated in a structurally well defined group of genera: *Bleischmiedia*, *Endiandra*, *Potameia*, *Triadodaphne* (in the latter three nearly obligatory) and in about 15 % of the species of *Cryptocarya*. The silica bodies encountered in these taxa are located in the ray – rarely in the axial – parenchyma and belong mostly to the aggregate type (C).
– At the generic level the unique feature of seriated, silica-bearing ray cells characterizes the genus *Mezilaurus* even beyond the realm of the laurel family.
– Diagnostic significance may be attributed to the very restricted occurrence of silica grains exclusively in the fibers, as in *Ocotea splendens* (and possibly some closely related species) and *Nothaphoebe spp.*.

In this context it is worthwhile to note that virtually all information in the literature on silica inclusions in Lauraceae stems from publications concerned with either general taxonomic considerations (Amos, 1952; ter Welle, 1976 and others) or with important technical aspects such as resistance to marine borers and the problems of mechanical conversion of silica-bearing timbers (Gonggrijp, 1923; Southwell & Bultman, 1971 and others). All major contributions to the wood anatomy and taxonomy of this family, or parts of it, lack any specific information on silica contents (Moll & Janssonius, 1934; Dadswell & Eckersley 1940; Stern 1954; Metcalfe & Chalk, 1957; Desch, 1957; Kostermans, 1957 and others).

With regard to phylogenetic affinities between Lauraceae and related families any statement based solely on such secondary features as discussed in this paper, must remain highly hypothetical. While distribution patterns and habit of silica do not permit any conclusions, as this substance is lacking in almost all the families checked, crystal configurations encountered allow for the formation of at least two groups of crystal-bearing taxa: one containing solitary, multi-faceted "rhomboidal" crystals (non-existent in Lauraceae), represented by families belonging exclusively to the order *Magnoliales* (Takhtajan); the other containing crystalline inclusions similar to those found in Lauraceae, represented by *Austrobaileyaceae*, *Hernandiaceae*, *Monimiaceae* and *Myristicaceae*, the former 3 included in *Laurales*, the latter in *Magnoliales* by Takhtajan. The position of *Myristicaceae* in the latter group, based solely on crystalline evidence and on the presence of silica inclusions in some genera, is in agreement with Hutchinson's (1964) systematic concept that places Myristicaceae in the *Laurales,* rather than supporting Takhtajan's placement of this familiy in the *Magnoliales*. It thus gives some support to Gottwald's (1977) contention of a "Myristical" structural concept somewhere between *Laurales* and *Magnoliales*.

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