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LEAF ANATOMY OF CINNAMOMUM SCHAEFFER (LAURACEAE) WITH SPECIAL REFERENCE TO OIL AND MUCILAGE CELLS

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SUMMARY

The morphology and distribution patterns of oil and mucilage cells in the leaf of 150 species of *Cinnamomum* are described. Idioblasts are always present in the palisade and the spongy parenchyma. Usually both oil and mucilage cells occur; in some species either oil or mucilage cells are present. Both types of idioblasts possess a suberized wall layer. The idioblasts vary between species in size/shape, stainability and number. Variations in the distribution pattern can partly be explained by the proposed homology of the oil and mucilage cells.

Other leaf anatomical characters are also mentioned, such as lamina and cuticle thickness, bundle sheath extensions, sclerification of the epidermal, the palisade, and the spongy parenchyma cells, number of palisade layers, presence or absence of a hypodermis, the indumentum and papillate abaxial epidermal cells, and the venation pattern.

Most species differ from each other in only one or few leaf anatomical characters (including oil and mucilage cells). A great many combinations in character distribution were observed. However, the distribution pattern in approximately one-fifth of all studied species deviated largely from the typical leaf anatomical character distribution pattern occurring in the majority of *Cinnamomum* species. There was a maximum of seven differing features out of the sixteen features studied. Within this group almost all neotropical *Cinnamomum* species are included. The latter species lack sclerified epidermal cells and almost all have penninerved instead of the generally occurring triplinerved leaves.

Cluster analyses based on all leaf anatomical features studied revealed that the distribution patterns of the oil and mucilage cells play a significant part in the grouping of the species. Therefore oil and mucilage cells possess at least some diagnostic value within the genus *Cinnamomum*. The systematic significance of oil and mucilage cells at the infrageneric level remains uncertain for lack of a detailed infrageneric classification of *Cinnamomum* for comparison with the idioblast distribution patterns.

INTRODUCTION

In a previous study on oil and mucilage cells in species of the genus *Annona* (Bakker & Gerritsen, 1992) we explored the systematic value of these idioblasts. Since the distribution of the idioblasts showed large variation within groups of species it was concluded that oil and mucilage cells had little or no taxonomic value below the genus level. This can partly be understood in the light of the proposed homology of oil and mucilage cells (Bakker & Gerritsen, 1989, 1990, 1992; Bakker et al., 1991).

In the present paper the diagnostic (discriminating) and systematic value of oil and mucilage cells will be investigated for the genus *Cinnamomum* Schaeffer.

Cinnamomum is a genus with about 200 accepted species (Kostermans, 1964, 1986, 1988). A number of neotropical species previously placed in other genera such as *Oreodaphne, Persea, Laurus, Ocotea,* and *Phoebe* have been transferred to *Cinnamomum* (Kostermans, 1961, 1988; Van der Werff, 1991a, b). The not neotropical species are present in the Malesian area, Australia, Asia, and the Pacific Islands (Kostermans, 1961, 1968, 1969, 1970a, b, 1983, 1986, 1988; Hyland, 1989). The genus is especially known for the production of cinnamon and camphor (Pax, 1889; Hegnauer, 1966; Kostermans, 1986). The use of the bark (cinnamon) dates from ancient times (see Kostermans, 1986). Nowadays, the plants are also used as medicine and in the cosmetic and perfume industry.

Leaf anatomical descriptions of *Cinnamomum* species are scarce. General notes were given by Pax (1889), Solereder (1899), Metcalfe & Chalk (1950) and Metcalfe (1987). Perrot (1891) described the histology of oil and mucilage cells in species of Lauraceae, including five *Cinnamomum* species. Later only two detailed leaf anatomical studies were published for a restricted number of *Cinnamomum* species (Santos, 1930; Marlier-Spirlet, 1946).

The genus *Cinnamomum* is poorly understood and poses many taxonomic difficulties. The two sections distinguished by Meissner (1864): *Malabathrum* Meissn. and *Camphora* Nees, are still accepted nowadays as the only subdivision of the genus (Kostermans, 1986). The sections, besides their different smells, also can be distinguished by bud morphology and leaf arrangement (Kostermans, 1986).

In the present paper the distribution of oil and mucilage cells and other leaf anatomical features are described for 150 species of *Cinnamomum*. A comparison of the leaf anatomical character distribution in the species is carried out by means of cluster analysis and the results are discussed in the light of the existing classification in order to evaluate the diagnostic and/or systematic value of the oil and mucilage cells below the genus level.

MATERIAL AND METHODS

Material and fixation

The 207 specimens of the 150 species of *Cinnamomum* studied are listed in Table 1. In this study leaves from herbarium vouchers, kept in Leiden, were boiled in water until they permanently sank in water, and then were stored in a FAPA-solution.

Fresh leaves of *C. burmanni, C. camphora, C. daphnoides, C. iners, C. kinabaluense, C. loureirii, C. obtusifolium, C. parthenoxylon, C. sericeum, C. tamala, C. verum,* and *C. spec.*, grown in greenhouses of several Botanical Gardens in Western Europe (in Table 1 marked with an asterisk), were collected and fixed in FAPA-solution. Fresh leaves from *C. burmanni* (Leiden, Java), *C. camphora* (Berkeley, Bogor), *C. iners* (Wageningen, Bogor), *C. kinabaluense* (Bogor), *C. parthenoxylon* and *C. verum* (Delft) were fixed in modified Karnovsky fixative followed by OsO_4 and embedded in Epon (see Bakker & Gerritsen, 1989).

Table 1. List of material examined of *Cinnamomum*. All material is herbarium material located in L.

altissimum Kosterm.: Chelliah FRI 6543, Malaysia — ***amoenum*** (Nees) Kosterm.: Smith & Klein 11260, Brazil — ***angustitepalum*** Kosterm. **1**: Kostermans 12974, Borneo — ***angustitepalum* 2**: Brain anak Tada S 16253, Borneo — ***archboldianum*** Allen **1**: Craven & Schodde 1239, New Guinea — ***archboldianum* 2**: bb. 25066, New Guinea — ***archboldianum* 3**: Koster BW 6854, New Guinea — ***archboldianum* 4**: Streimann & Stevens LAE 54854, New Guinea — ***archboldianum* 5**: Foreman & Vinas LAE 60127, New Guinea — ***archboldianum* 6**: Schodde & Craven 5014, New Guinea — ***archboldianum* 7**: Aet & Idjan 394, New Guinea — ***archboldianum* 8**: Carr 14814, Papua New Guinea — ***archboldianum* 9**: Carr 13253, Papua New Guinea — ***archboldianum* 10**: Stevens LAE 54769, New Guinea — ***aromaticum*** Nees: Schewe s.n., s.l. — ***aureo-fulvum*** Gamble: Wong Khoon Meng FRI 32230, Malaysia — ***baileyanum*** (F. Muell.) Francis: Hyland 7547, Australia — ***bejolghota*** (Ham.) Sweet: Schewe s.n., Asia — ***bintulense*** Kosterm.: Ding Hou 349, Borneo — ***bodinieri*** Gamble/Lev.: Beauvais 132, China — ***brevipedunculatum*** Chang: Ching-en Chang 6643, Taiwan — ***bullatum*** Kosterm.: Womersley NGF 11335, New Guinea — ***burmanni*** (Nees) Blume **1**: Schewe s.n., Japan — ***burmanni* 2**: de Vriese & Teijsmann s.n., Sumatra — ***burmanni* 3**: de Vriese & Teijsmann s.n., Java — ***burmanni* 4**: Boerlage 1888, Java — ***burmanni* 5**: Keith For. Dep. No. 5999, Borneo — ***burmanni* 6**: Perrottet s.n., Philippines — ***burmanni* 7**: Teijsmann s.n., Celebes — ***burmanni* 8**: Schmutz 2836, Lesser Sunda Islands — ***burmanni* 9**: Iboet 514, Lesser Sunda Islands — ***burmanni* 10**: Kostermans s.n., Java — ***burmanni* 11***: Hortus Botanicus Leiden, The Netherlands — ***burmanni* 12***: Baas s.n., Cibodas, Java — ***calciphilum*** Kosterm.: Paul et al. S 37382, Borneo — ***cambodianum*** Lec.: Poilane 23247, Cambodia — ***camphora*** (L.) Presl **1**: d'Aleizette 558m, Japan — ***camphora* 2***: Bot. Gardens Kew No. 00073 12261, U.K. — ***camphora* 3***: Royal Bot. Garden Edinburgh No. 69 6417, U.K. — ***camphora* 4***: Bot. Garden Techn. Univ. Delft, The Netherlands — ***camphora* 5***: Bot. Garden Utrecht No. 73GR00538, The Netherlands — ***camphora* 6***: Van der Werff s.n., Berkeley, U.S.A. — ***camphora* 7***: Bot. Garden Bogor No. XXB 112, Java — ***camphora* 2***: Baas s.n., Cibodas, Java — ***camphora variegata* 9***: Bot. Gardens Kew No. 00073 12262, U.K. — ***cappara-coronde*** Blume: Kostermans 25596, Ceylon — ***caryophyllus*** (Lour.) Moore: Bordeneuve (Chevalier 40969), Indochina — ***celebicum*** Miq.: bb. 5555, Celebes — ***chittagongense*** Kosterm.: King 249, India — ***cinereum*** Gamble: Corner s.n., Malaysia — ***citriodorum*** Thw.: Kostermans 23455, Ceylon — ***clemensii*** Allen: Eyma 5093, New Guinea — ***cordatum*** Kosterm.: Whitmore FRI 20470, Malaysia — ***coriaceum*** Cammerl.: bb. 14079, Borneo — ***corneri*** Kosterm.: Carson SAN 28012, Borneo — ***crassinervium*** Miq.: Puasa, B.N.B. For. Dep. 3159, Borneo — ***crispulum*** Kosterm.: Poilane 21913, Indochina — ***cubense*** (Nees) Kosterm.: Sintenis 1036, Puerto Rico — ***culitlawan*** (L.) Kosterm.: Labill., Blackw.t.? 391, Moluccas — ***curvifolium*** (Lour.) Nees: Poilane 32.126, Indochina — ***cuspidatum*** Miq. **1**: Suppiah FRI 11901, Malaysia — ***cuspidatum* 2**: de Wilde & de Wilde-Duyfjes 12889, Sumatra — ***damhaense*** Kosterm.: Chevalier 37468, Asia — ***daphnoides*** Sieb. & Zucc. **1**: Koidzumi s.n., Eur./Asia — ***daphnoides* 2***: Bot. Gardens Kew No. 00073 12263, U.K. — ***deschampsii*** Gamble: Corner SFN 31000, Singapore — ***dewildei*** Kosterm.: bb. 2796, Sumatra — ***doederleinii*** Engl.: Fosberg 37185, Ryukyu Islands — ***dubium*** Nees **1**: Kostermans 24095, Ceylon — ***dubium* 2**: s.n., Java — ***durifolium*** Kosterm.: Poilane 9030, Asia — ***ebaloi*** Kosterm.: Ebalo 1198, Philippines — ***effusum*** (Meissn.) Kosterm.: Sousa 7876, Mexico — ***elephantinum*** Kosterm.: Béjaud 742m, Cambodia — ***ellipticifolium*** Kosterm.: Balus? 12288, Burma — ***elongatum*** (Vahl) Kosterm.: Curtiss 309, West Indies (Central America) — ***englerianum*** Schewe: Ledermann 9806, New Guinea — ***eugenoliferum*** Kosterm.: bb. 32907, New Guinea — ***fouil-***

(Table 1 continued)

loyi Kosterm.: Endert 3840, Borneo — ***frodinii*** Kosterm.: Henty & Katik NGF 49456, New Guinea — ***gigaphyllum*** Kosterm.: Telussa BW 5161, New Guinea — ***glaucescens*** (Wall.) Drury: Poilane 1272, Asia — ***goaense*** Kosterm.: Stocks s.n., Asia — ***grandiflorum*** Kosterm.: Hoogland 5052, New Guinea — ***griffithii*** Meissn. **1**: J.C. 1641, Malaysia — ***griffithii* 2**: Kostermans 5283, Borneo — ***iners*** Reinw./Blume **1**: Pierre 5170, Asia — ***iners* 2**: Kostermans? s.n., Java — ***iners* 3***: Bot. Gard. Agricult. Univ. Wageningen No. 72 PTO 1275, The Netherlands — ***iners* 4***: Bot. Gard. Bogor No. XXB 74, Java — ***insulari-montanum*** Hay.: Kao 9834, Taiwan — ***javanicum*** Blume **1**: bb. 2729, Sumatra — ***javanicum* 2**: s.n., Java — ***kami*** Kosterm.: Frodin NGF 28255, New Guinea — ***keralaense*** Kosterm.: Kostermans 26283, South India — ***kinabaluense*** Heine **1**: Aban Gibot SAN 66838, Borneo — ***kinabaluense* 2***: Bot. Gard. Bogor No. XXA 85, Java — ***kunstleri*** Ridley: Poilane 31019, Indochina — ***laubatii*** F. Muell.: Irvine 1668, Australia — ***ledermannii*** Schewe: Powell UPNG 1639, Papua New Guinea — ***litseafolium*** Thw.: Davidse 8455, Ceylon — ***longitubum*** Kosterm.: Poilane 29260, Asia — ***loureirii*** Nees **1**: Yoshida 2201, Japan — ***loureirii 2****: Royal Bot. Gard. Edinburgh No. 100 029, U. K. — ***lucens*** Miq.: Meebold 14876, Burma — ***macrocarpum*** Hook. f.: Kostermans 24534, South India — ***macrophyllum*** Miq.: Kostermans 1230, Moluccas — ***magnifolium*** Kosterm.: Poilane 29510, Indochina — ***mairei*** Lév.: s.n., Asia — ***malabaricum*** Garc.?: Ridsdale 495, Asia — ***malabathrum*** (Burm. f.) Blume: Kostermans 26119, South India — ***malayanum*** Kosterm.: Kochummen FRI 16657, Malaysia — ***melastomaceum*** Kosterm.: Poilane 29636, Indochina — ***melliodorum*** Kosterm.: Sayers NGF 24238, New Guinea — ***mendozae*** Kosterm.: Mendoza PNH 42310, Philippines — ***mercadoi*** Vid.: Merrill Sp. Blanc. No. 758, Philippines — ***microcarpum*** Kosterm.: Martin S 38157, Borneo — ***microphyllum*** Ridley: Whitmore FRI 15582, Malaysia — ***mollissimum*** Hook. f.: Corner SFN 30885, Malaysia — ***montanum*** (Sw.) Berchth. & Presl: Krug & Urban 5259, Jamaica — ***myrianthum*** Merr.: Conklin PNH 37897, Philippines — ***myrtifolium*** Kosterm.: Chevalier 35.993, Cambodia — ***nalingway*** Kosterm.: Kostermans 270, Asia — ***nooteboomii*** Kosterm.: bb. 6628, Sumatra — ***obtusifolium*** Nees *: Royal Bot. Gard. Edinburgh No. 35 0159, U. K. — ***oliveri*** F. M. Bailey: Tadman s.n., Australia — ***osmeophleum*** Kan.: Kao 9650, Taiwan — ***ovalifolium*** Wight: Hoogland 11550, Ceylon — ***ovatum*** Allen: Jean 38.397, Indochina — ***pachyphyllum*** Kosterm.: Sinclair & Kish bin Salleh SFN 39922, Malaysia — ***paiei*** Kosterm.: Paie & Mamit S 29332, Borneo — ***panayense*** Kosterm.: Martelino & Edaño BS 35653, Philippines — ***parthenoxylon*** Meissner *: Bot. Gard. Bogor No. XXB41, Java — ***perrottetii*** Meissn.: Kostermans 25803, India — ***piniodorum*** Schewe: Versteegh BW 3919, New Guinea — ***podagricum*** Kosterm.: Sayers NGF 21699, New Guinea — ***poilanei*** Kosterm.: Poilane 33772, Indochina — ***politum*** Miq.: Smythies S 7803, Borneo — ***polyadelphum*** (Lour.) Kosterm.: Poilane 28504, Indochina — ***porphyrospermum*** Kosterm.: de Wilde & de Wilde-Duyfjes 12984, Sumatra — ***porrectum*** (Roxb.) Kosterm. **1**: Bodinier 1118, China — ***porrectum* 2**: Burkill KEP 76692, Malaysia — ***porrectum* 3**: Rahmat si Toroes 4694, Sumatra — ***propinquum*** F. M. Bailey: Hyland 6577, Australia — ***pseudopedunculatum*** Hay.: Tuyama s.n., Bonin Island — ***psychotrioides*** (H. B. K.) Kosterm.: Tokatia a/1541, Mexico — ***racemosum*** Kosterm.: Shea & Minjuk SAN 76182, Borneo — ***reticulatum*** Hay.: Chang 3771, Taiwan — ***rhynchophyllum*** Miq. **1**: Thorenaar 52, Sumatra — ***rhynchophyllum* 2**: Clemens 22194, Borneo — ***rhynchophyllum* 3**: Sinanggui SAN 56217, Borneo — ***rhynchophyllum* 4**: Gibot SAN 37019, Borneo — ***rhynchophyllum* 5**: Kostermans 4559, Borneo — ***rhynchophyllum* 6**: de Wilde & de Wilde-Duyfjes 15545, Sumatra — ***rhynchophyllum* 7**: Forbes 2969, Sumatra — ***rhynchophyllum* 8**: Ogata KEP 105031, Malaysia — ***rhynchophyllum* 9**: Grashoff 733, Sumatra — ***riedelianum*** Kosterm.: Riedel s.n., Brazil — ***rigidum*** Gillespie: Webster & Hildroth 14198, Fiji — ***riparium*** Gamble: Ridsdale 628, South India — ***rivulorum*** Kosterm.: Kostermans 27831, Ceylon — ***rupestre*** Kosterm.: Ridsdale SMHI 264, Philippines — ***scalarinerve***

(Table 1 continued)

Kosterm.: Chevalier 38.371, Indochina — ***scortechinii*** Gamble: Poilane 11143, Asia — ***sellowianum*** (Nees & Mart.) Kosterm.: Hatschbach 17399, Brazil — ***sericans*** Hance: Pierre 5170, Asia — ***sericeum*** Siebold *: Royal Bot. Gard. Edinburgh No. 69 6418, U.K. — ***sessilifolium*** Kan.: Hosakawa 5954, Ponape. Pacific — ***simondii*** Lec.: Chevalier 32075, Indochina — ***sinharajense*** Kosterm.: Kostermans 27486, Ceylon — ***sintok*** Blume: Kostermans s.n., Java — ***solomonense*** Allen: Waterhouse 129A-B, Solomon Islands — ***soncaurium*** (Ham.) Kosterm.: Hansen & Smitinand 12882, Thailand — ***spec.****: Royal Bot. Gard. Edinburgh No. 69 6352, U.K. — ***subavenopsis*** Kosterm.: Boschproefstation Cel/IV-94, Celebes — ***subavenium*** Miq. **1**: Put 3526, Thailand — ***subavenium*** **2**: Kostermans 37, Sumatra — ***subcuneatum*** Miq.: Lörzing 11289, Sumatra — ***subpenninervum*** Kosterm.: Poilane 9680, Asia — ***sulphuratum*** Nees: Hook. f. & Thomson 2617, Asia — ***tahyanum*** Kosterm.: Othman et al. S 41520, Borneo — ***tamala*** (Ham.) Th. Nees & Eberm. **1**: Tatemi Shimizu et al. T-20932, Thailand — ***tamala*** **2***: Bot. Gardens Kew No. 00073 12264, U.K. — ***tampicense*** (Meissn.) Kosterm.: s.n., Mexico — ***tazia*** 'Hamilton' Hook. f.: Bot. Garden Calcutta s.n., Asia — ***tepalinum*** Kosterm.: Koelz 29958, India — ***tonkinense*** (Lec.) Chev.: Poilane 32261, Indochina — ***trichophyllum*** Quis. & Merr.: Meijer 9759, Celebes — ***triplinerve*** (R. & P.) Kosterm.: Dombey 201, Peru — ***tsoi*** Allen: Poilane 24801, Annam — ***vaccinifolium*** Kosterm.: Sleumer & Vink BW 14254, New Guinea — ***velutinum*** Ridley: Whitmore FRI 12116, Malaysia — ***verum*** Presl **1**: Hasskarl s.n., Japan — ***verum*** **2**: Wight 2511, India — ***verum*** **3**: Sedies? s.n., Mauretania — ***verum*** **4***: Bot. Gard. Berlin-Dahlem, Germany — ***verum*** **5***: Bot. Gard. Techn. Univ. Delft, The Netherlands — ***verum*** **6***: Bot. Gard. Agric. Univ. Wageningen, The Netherlands — ***vesiculosum*** (Nees) Kosterm.: Klein 3.269, Brazil — ***vimineum*** Nees: Loh FRI 19170, Malaysia — ***virens*** R.T. Baker: Jones 2693, Australia — ***wightii*** Meissn.: Kostermans 25731, India — ***xanthoneurum*** Blume: Versteegh & Vink BW 8309, New Guinea — ***xylophyllum*** Kosterm.: Kostermans 12981, Borneo — ***zollingerii*** (de Lukm.) Kosterm. **1**: Walker et al. 6059, Okinawa Island — ***zollingerii*** **2**: Fosberg 38155, Ryukyu Islands.

Sectioning, staining and microscopy

The methods used for sectioning and staining of the leaves are identical to those described for *Annona* leaves in Bakker & Gerritsen (1992). Thick (30 µm) transverse sections of FAPA-fixed leaves were stained for oil with Sudan IV or Chrysoidin/Acridin red. Mucilage was stained with Alcian Blue. For suberin the Berberin and Anilin Blue fluorescent staining method was applied. Ultrathin and 1 µm sections of Epon-embedded material were examined with transmission electron microscopy (TEM) and light microscopy (LM) respectively (see Bakker & Gerritsen, 1992; Bakker et al., 1991).

Some leaf fragments were air-dried, gold-sputtered and examined with the scanning electron microscope (SEM).

Examination and measurements

In the 30 µm sections the number of oil and/or mucilage cells in the palisade and/or spongy parenchyma was counted and calculated per mm leaf width. In the same sections the lamina thickness was measured and the number (per mm leaf width) and length of hairs was determined (see Bakker & Gerritsen, 1992). The presence/absence of an indumentum was verified by examination of the leaves with a stereo microscope and partly with a scanning electron microscope (SEM).

Phenetic analysis

Phenetic analyses were carried out with the help of NTSYS-pc, version 1.30 (Rohlf, 1986), a computer program for numerical taxonomic and multivariate analyses. Each analysis consists of a two-step procedure, i.e., the computation of the overall similarity among taxa and the representation thereof by a phenogram. In the first step a datamatrix, based on Table 2, is used to calculate the (dis)similarity among taxa expressed as Manhattan distances. In the second step, creating a phenogram, the pairwise distances among taxa serve as input for the analysis, using UPGMA (Unweighed Pair-Group Method using arithmetic Averages) as a cluster criterion.

RESULTS

Oil and mucilage cells

30 µm sections – Light microscopy

Sudan IV — Oil cells were recognized by the stained contents (red, orange, pink, brown; depending on the species). The oil is present as small irregular bodies (Fig. 1A), clustering globules (Fig. 1B), a distinctly stained mass (Fig. 1C), or a homogeneous oil drop. The oil drop may be visibly attached to the wall by a cupule (Fig. 1D). Other oil cells did not contain oil but could be distinguished by the presence of a cupule (Fig. 1E) and/or a characteristic fold in the cell wall (Fig. 1E, F). These oil cells had a glossy pink appearance. Mucilage cells were unstained and empty. The suberized layer was visible as a thin red line in the oil and mucilage cells.

Chrysoidin/acridin red — The oil cells were recognized as described for the Sudan IV-staining, but generally the idioblasts were less clear because of the strong background staining. Mucilage cells were unstained (empty) or faintly yellowish.

Alcian Blue — Oil cells stained glossy greenish-blue or were empty (Fig. 2A) and could be distinguished from the mucilage cells by a thick dark blue cell wall, sometimes containing a cupule, or by the ring-like appearance of the cytoplasm. In mucilage cells the retained mucilage distinctly stained blue and sometimes extruded from the cells (Fig. 2A, B, D). The mucilage often showed (circular) striation (Fig. 2C). The presence of elder pith fragments (used to clamp leaf fragments for sectioning) sticking to the sections also indicated the presence of mucilage in the leaf. In control samples the mucilage was stained less densely and generally spread out over the section as a result of the dissolution of the mucilage in water, thereby obscuring the mesophyll (Fig. 2D).

30 µm sections – Fluorescence microscopy

The cell walls of oil and mucilage cells showed autofluorescence of the suberized wall layer. When stained specifically for suberin (Berberin) this layer appeared as a thin yellow/whitish thin line in the cell wall. This staining reaction has been described earlier for oil and mucilage cells of *Cinnamomum burmanni* (Bakker et al., 1991).

1 µm sections – Light microscopy

Both idioblast types were easily distinguished from each other by their overall cytoplasmic composition. Oil cells were also characterized by the presence of a cupule. Mucilage cells showed the distinctly purple-stained mucilage and/or the characteristic pattern of the cytoplasmic strands.

Transmission electron microscopy

The suberized wall layer was already observed against the inner side of the cell wall in a young oil cell in the leaf of *Cinnamomum camphora* (Fig. 3A) and turned out to be always present in mature oil (Fig. 3D) and mucilage cells. The composition of the cytoplasm of the oil and mucilage cells in the leaf is very similar to that described for the idioblasts in the shoot apex of *C. burmanni* (Bakker & Gerritsen, 1989; Bakker et al., 1991). In a very young oil cell, present in the palisade parenchyma, electron dense oil droplets and characteristic plastids were present in the cytoplasm (Fig. 3B). The plastids lacked thylakoids but contained starch, dark globules and very small white globules (Fig. 3B). In another young oil cell in the palisade parenchyma a thickened part of the inner wall layer was observed: the cupule base (Fig. 3C). In mature oil cells in leaves of different *Cinnamomum* species a cupule was generally observed (Fig. 3D), showing the cupule base from which the cupule projects into the cytoplasm surrounding the oil cavity. These observations are identical to those described earlier for cupules in oil cells of *C. burmanni* (Bakker & Gerritsen, 1989; Bakker et al., 1991) and *Annona muricata* (Bakker & Gerritsen, 1990).

Shape and size

In most species the oil cells are oblong-ovoid in the palisade parenchyma (Fig. 1A, C, D) and more or less globular in the spongy parenchyma (Fig. 1B, E, F). The mucilage cells generally are ovoid in the palisade parenchyma (Fig. 2A, B, D) and globular in the spongy parenchyma (Fig. 2B, C). The sizes of the idioblasts vary per species (Figs. 1A–F & 2A–D). In general mucilage cells are larger than oil cells.

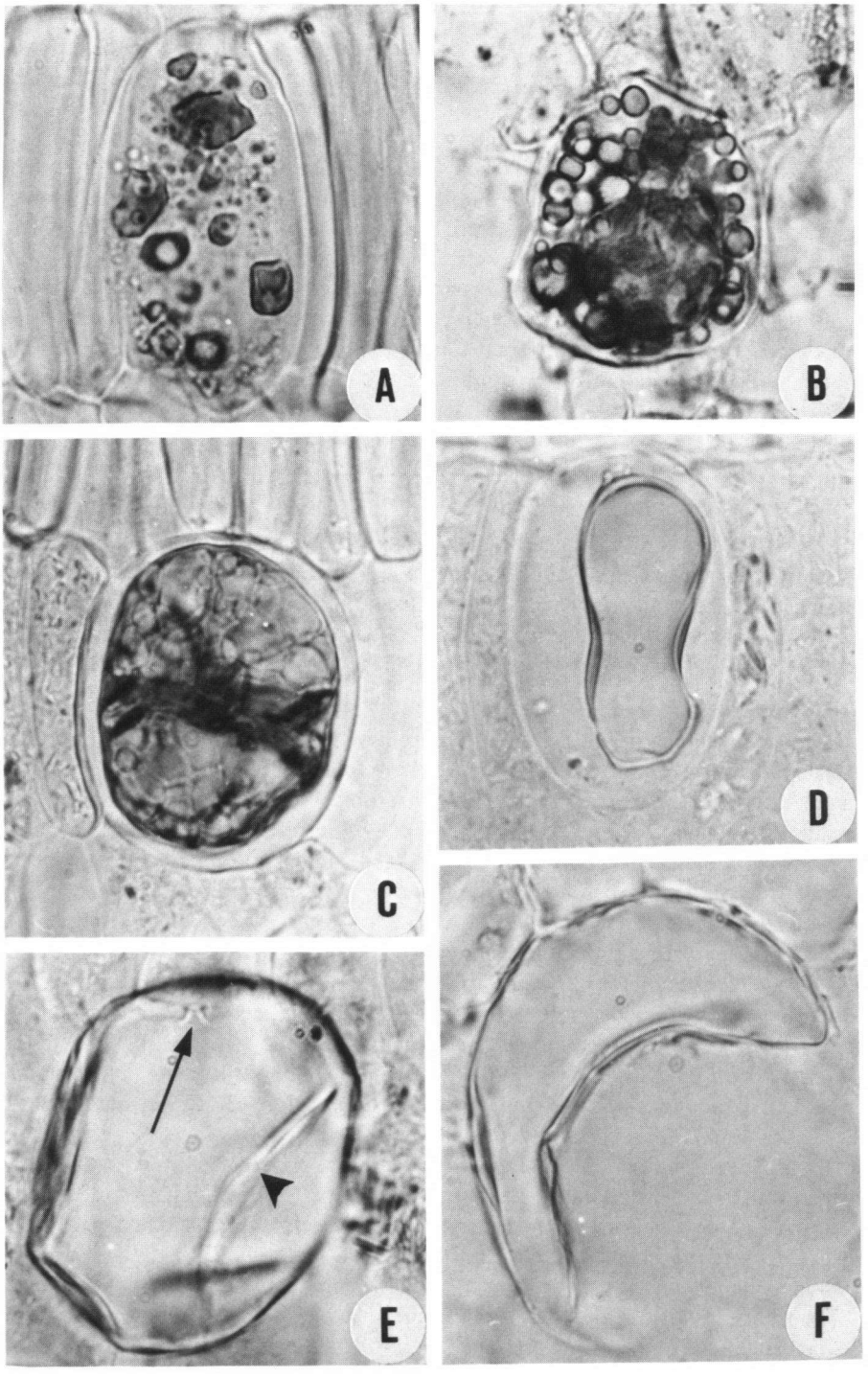
Distribution

Oil and/or mucilage cells are always present in both the palisade and the spongy parenchyma (Table 2). Most species possess both oil and mucilage cells in the leaves. The majority of these species contain the two idioblast types in both the palisade and the spongy parenchyma. The exclusive presence of oil cells in the leaf occurred in c. 17% of the species and only 5 species contained exclusively mucilage cells in the leaves (*Cinnamomum archboldianum* [no. 4 and 5], *C. magnifolium, C. nalingway, C. rivulorum* and *C. sinharajense*).

In the spongy parenchyma idioblasts are usually located against the lower side of the palisade parenchyma (Fig. 2A, B) and against the abaxial epidermal cells.

Of 18 species of which more than 1 specimen was studied 11 were constant for the distribution of the oil and mucilage cells in the palisade and spongy parenchyma (*C. angustitepalum* [2 specimens], *C. burmanni* [12], *C. cuspidatum* [2], *C. daphnoides* [2], *C. javanicum* [2], *C. loureirii* [2], *C. porrectum* [3], *C. rhynchophyllum* [9], *C. subavenium* [2], *C. tamala* [2] and *C. verum* [6]). The other species showed variation in their distribution patterns. Small variations concern the presence/absence of oil or mucilage cells in one of the mesophyll layers (*C. griffithii* [2] and *C. zollingerii* [2]). Larger variations occur when part of the specimens lacks one type of idioblast (*C. archboldianum* [10], *C. camphora* [9], *C. dubium* [2] and *C. iners* [4]). *Cinnnamomum kinabaluense* [2] showed two different distribution patterns (Table 2).

The frequency of the idioblast types in the leaf was found to be highly variable between species (Table 2). Between specimens of the same species only minor variations occurred in the number of idioblasts. The maximum number in the palisade


A
B
C
D
E
F

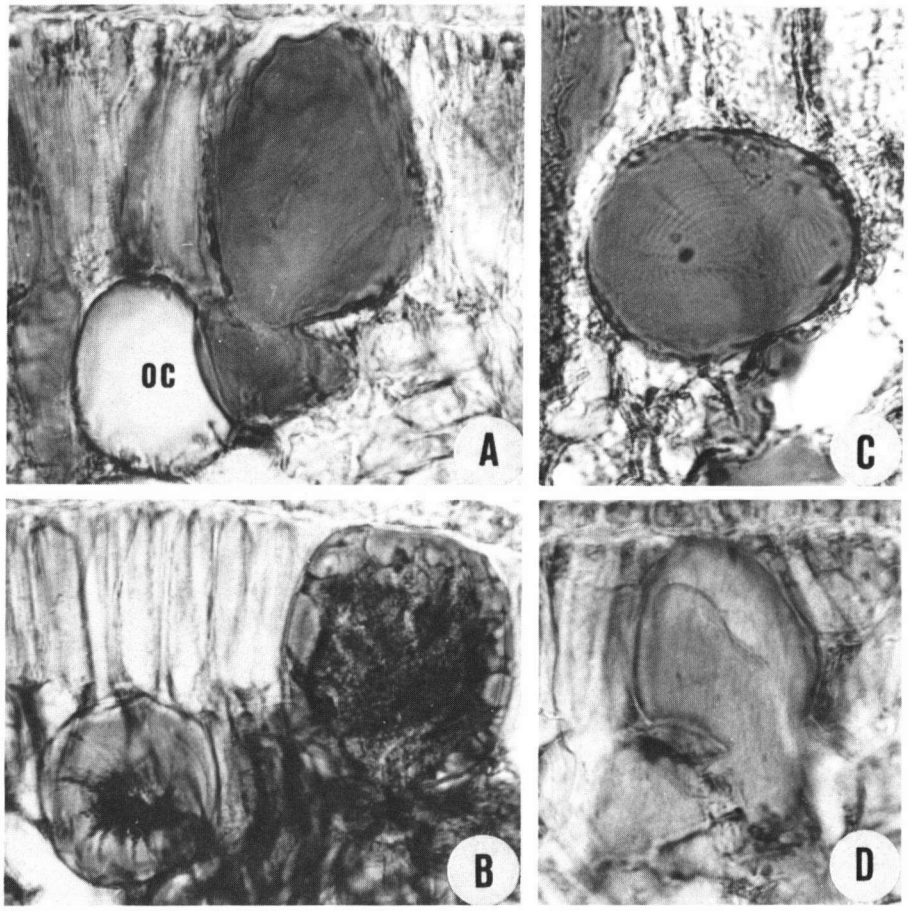


Fig. 2. Transverse 30 μm thick sections of *Cinnamomum* species. A–D: Mucilage cells stained with Alcian Blue. Light microscopy. All × 345 — A: *C. virens*. Mucilage cell in the palisade parenchyma showing extrusion of the stained mucilage from the cell into another cell. Also note the neighbouring unstained oil cell (oc) in the spongy parenchyma. — B: *C. nalingway*. Mucilage cells in the palisade and spongy parenchyma, both extruding mucilage into the intercellular spaces of the spongy parenchyma. Note the darker stained mucilage in the centre of the cells. — C: *C. vaccinifolium*. Mucilage cell in the spongy parenchyma. Note the circular striations in the mucilage. — D: *C. magnifolium*. Mucilage cell in the palisade parenchyma. Note the less densely stained mucilage extruded from the cell and spread out over the section.

Fig. 1. Transverse 30 μm thick sections of *Cinnamomum* species. A–F: Oil cells stained with Sudan IV. Light microscopy. All × 725.— A: *C. cubense*. Oil cell in the palisade parenchyma showing loose pieces of stained oil. — B: *C. crispulum*. Oil cell in the spongy parenchyma filled with a mass of globules of stained oil. — C: *C. vesiculosum*. Oil cell in the lower layer of the palisade parenchyma filled with a heterogeneous oil drop. — D: *C. tampicense*. Oil cell in the palisade parenchyma filled with a large oil drop. — E: *C. brevipedunculatum*. Empty oil cell in the spongy parenchyma showing a cupule (arrow) and a fold in the cell wall (arrowhead). — F: *C. vimineum*. Large empty oil cell in the spongy parenchyma showing the fold in the cell wall.

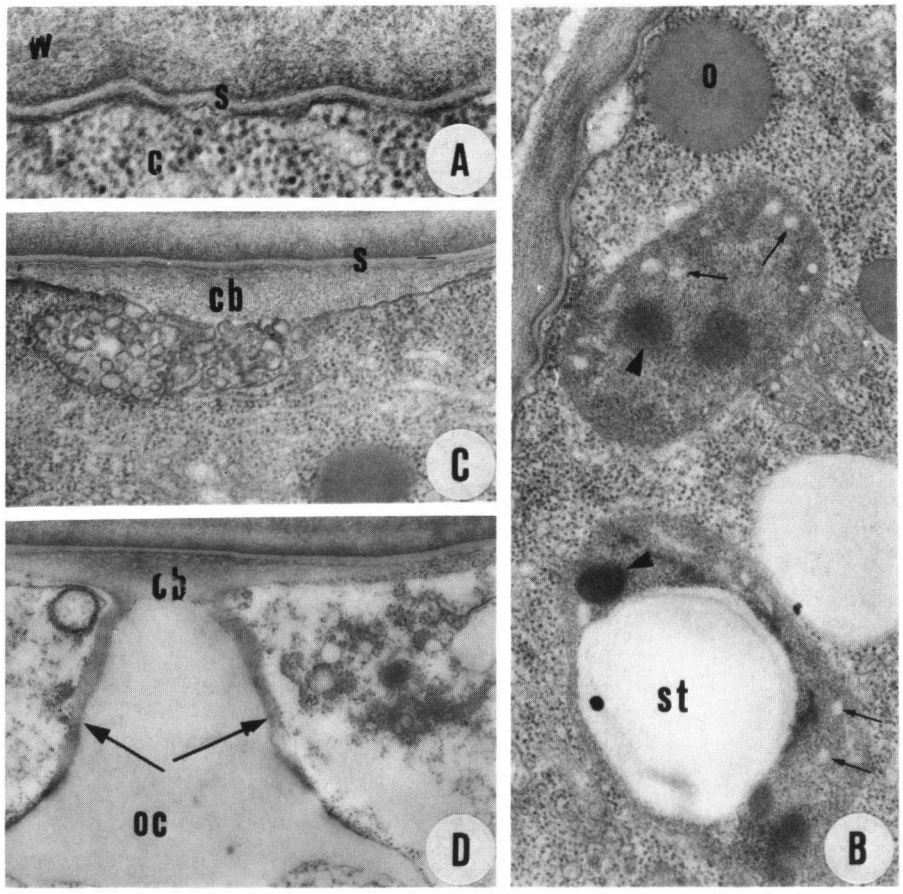


Fig. 3. *Cinnamomum camphora 8.* A–D: Transmission electron microscopy. — A: Detail of the cell wall of a very young oil cell in which only a suberized wall layer (s) has been deposited between the primary cell wall (w) and the cytoplasm (c); × 58,200. — B: Detail of the cytoplasm of young oil cell depicted in A. Note the specific plastids containing starch (st), dark globules (arrowheads), and small white globules (small arrows). The plastids lack thylakoids. Note the large oil globule (o) in the cytoplasm; × 27,250. — C: Detail of the cell wall of a young oil cell showing the development of a cupule base (cb) deposited against the suberized wall layer (s). The cupule base is the thickened part of the inner wall layer which is deposited against the suberized layer throughout the whole oil cell; × 27,250. — D: Detail of a developed cupule in an older oil cell in the palisade parenchyma. Note the cupule base (cb) from which the cupule proper (arrows) projects into the cytoplasm and surrounds the oil cavity (oc); × 16,930.

Fig. 4. Transverse 30 µm thick sections of leaves of *Cinnamomum* species. A–F: Stained with Sudan IV. Light microscopy. — A: *C. vaccinifolium.* Extremely thick, densely stained cuticle (17 µm) showing an irregular outer surface; × 400. — B: *C. glaucescens.* Adaxial epidermis with large non-sclerified epidermal cells. Note the cutinized (stained) anticlinal walls; × 400. — C: *C. wightii.* Vertically transcurrent lower order vein with sclerenchymatous bundle sheath extensions; × 400. — D: *C. velutinum.* Detail of the uppermost part of a vertically transcurrent lower order vein showing the continuation of the sclerified bundle sheath cells with the sclerified adaxial epidermal cells; × 1,000. — E: *C. sintok.* Layer of aligned sclerified outer periclinal walls of the palisade cells underneath the small epidermal cells; × 400. — F: *C. sericeum.* Hypodermis (hy) underneath the adaxial epidermis. Note the sclerenchymatous cells in this layer (arrow); × 400.

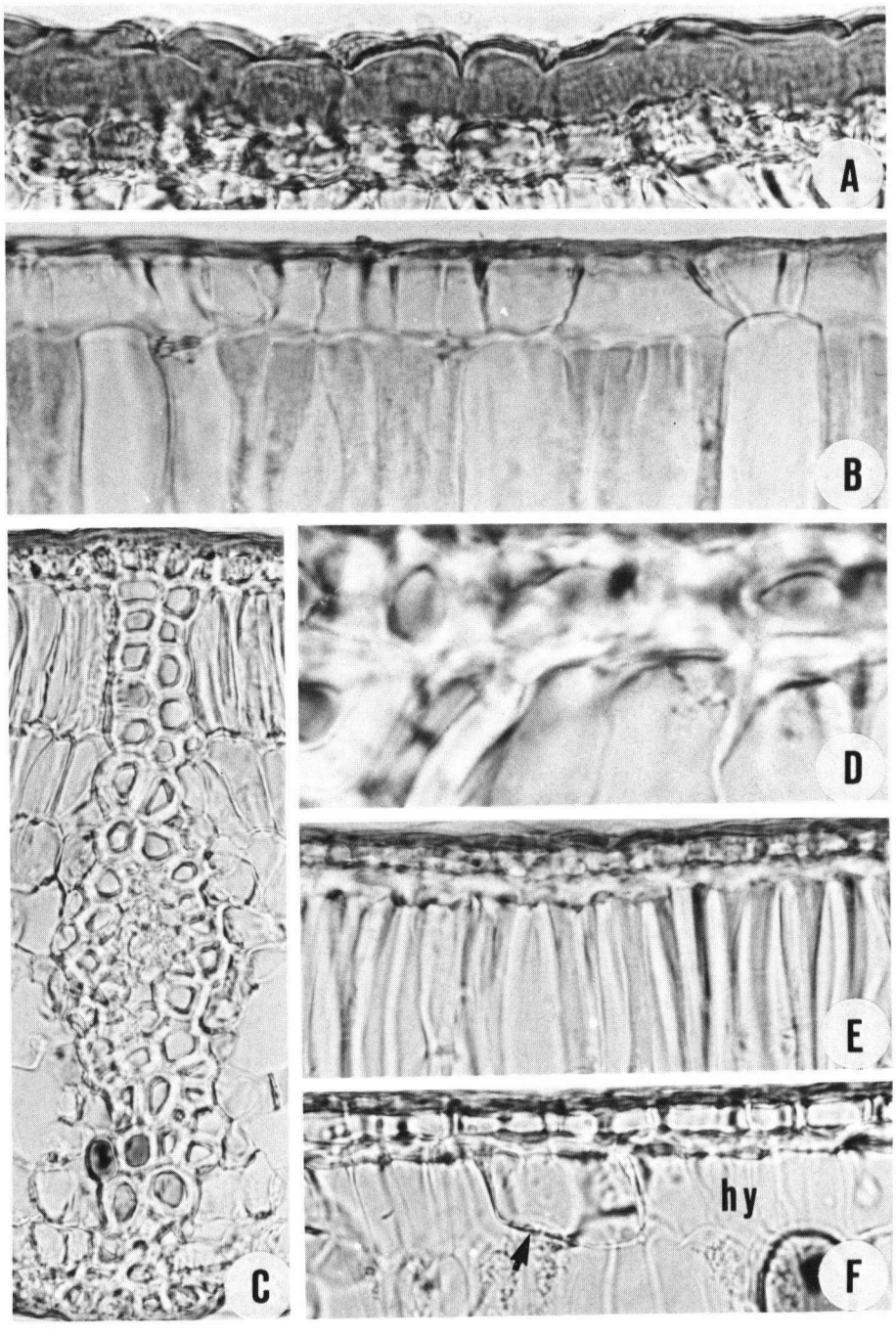

A
B
C
D
E
hy
F

Table 2. Distribution of leaf anatomical features in *Cinnamomum* species.

species	oil		muc		t	cu	ep	hy	p	s	pa	ad. ha		ab. ha		v	e
	p	s	p	s								f	l	f	l		
altissimum	–	3	2	2	2	2	+	–	1t	+	–	–		–		t	+
amoenum	4	2	–	–	3	2	–	–	3–	±	–	1	3s	5	3s	p	+
angustitepalum 1	–	p	4	4	4	2	++	–	1c	–	–	–		2	3cs	p	+
angustitepalum 2	–	2	4	3	4	3	++	–	1c	–	–	–		?		t	+
archboldianum 1–3,6–10	2	2	4	3	2	2	+	–	1c*	+	–	–		–		t	+
archboldianum 4, 5	–	–	4	3	2	2	+–	–	1c*–	+–	–	–		–		t	+
aromaticum	p	p	1	4	3	2	++	–	1c	–	+	–		2	2s	t	+
aureo-fulvum	4	3	p	p	3	3	+	–	1c	–	–	–		5	2s	t	+
baileyanum	2	2	4	2	3	2	+	–	1c*	±	–	–		1	1s	p	+
bejolghota	2	–	2	2	4	2	+	–	1t	±	++	–		–		t	+
bintulense	4	4	–	–	2	2	+	–	1t	+	–	–		3	4t	t	+
bodinieri	2	4	3	2	3	2	–	–	1–	–	±	–		4	2s	p	+
brevipedunculatum	–	3	3	4	3	2	+	–	1c	–	±	–		–		t	+
bullatum	1	2	4	3	3	2	+	–	1t	+	–	–		3	3t	t	+
burmanni 1–12	2	3	3	3	2	2	+	–	1c	–±	–±	–		–		p	+
calciphilum	1	3	4	4	4	2	+	–	1c*	±	–	–		–		p	+
cambodianum	4	2	4	3	3	2	++	–	1c	–	±	–		–		t	+
camphora 1	p	p	p	p	2	1	–	–	1–	–	±	–		–		p	+
camphora 2, 3, 5, 6	3	4	2	2	2	1	–	–	1–	–	±	–		–		p	+
camphora 7, 8	4	3	–	–	2	1	–	–	1–	–	±	–		–		p	+
camphora 4, 9	4	3	–	–	2	1	+	–	1c	–	±	–		1		p	+
cappara-coronde	1	4	2	3	3	2	+	–	1t	+	–	–		–		t	+
caryophyllus	2	4	1	2	3	2	+	–	1t	±	–	–		3	3s	t	+
celebicum	1	3	4	2	2	1	+	–	1t	+	–	–		–		t	+
chittagongense	–	2	2	2	3	2	+	–	1t	+	–	–		–		t	+
cinereum	3	4	4	2	2	2	++	–	1t	+	–	–		–		p	+
citriodorum	3	4	2	3	3	2	+	–	1c*	±	–	–		1	2s	p	+
clemensii	p	p	p	p	3	2	–	–	1t	+	–	–		3	2i	t	+

species	oil		muc		t	cu	ep	hy	p	s	pa	ad. ha		ab. ha		v	e
	p	s	p	s								f	l	f	l		
cordatum	2	1	4	4	4	3≈	±	–	2t	+	–	–		–		t	+
coriaceum	–	2	3	4	3	2	+	–	1t	±	+	–		–		t	+
corneri	2	5	–	–	3	2	+	–	1t	+	–	–		–		t	+
crassinervium	–	2	5	4	3	2	+	–	1c*	+	–	–		–		t	+
crispulum	1	4	2	2	2	2	+	–	1c*	±	–	–		–		t	+
cubense	5	4	3	–	2	2	–	–	2c*	±	±	–		–		p	+
culitlawan	2	3	4	4	2	2	+	–	1c*	±	–	–		–		t	+
curvifolium	–	2	2	3	2	2	+	–	1t	+	–	–		1	1i	t	+
cuspidatum 1, 2	2	4	4	2	2	2	+	–	1c*	+	–	–		–		t	+
damhaense	4	5	?	?	2	2	+	–	1c	–	–	–		1	2t	t	+
daphnoides 1, 2	4	3	1	1	4	3	+	–	2c	±	–	1–	4s	4	4s	t	+
deschampsii	4	3	3	2	3	1	+	–	1c*	±	±	–		3	2s	t	+
dewildei	1	2	1	2	3	2	±	–	1t	±	–	–		–		t	+
doederleinii	3	4	2	2	3	2	+	–	1t	+	–	1	3s	3	3s	t	+
dubium 1	2	4	–	–	2	1	+	–	1c*	±	±	–		2	2s	t	+
dubium 2	3	4	2	2	2	2	+	–	1t	±	±	–		3	2s	t	+
durifolium	1	1	4	2	4	2	+	–	1c	–	–	–		–		t	+
ebaloi	1	2	4	3	3	2	+	–	1t	±	–	–		1	2s	t	+
effusum	4	3	2	–	3	3≈	–	–	2c	±	–	–		–		p	+
elephantinum	–	2	4	4	3	2	+	–	1t	±	–	–		–		t	+
ellipticifolium	1	1	5	4	3	2	+	–	1–	–	+	–		3	2s	t	+
elongatum	5	4	1	–	2	2	–	–	2c*	–	++	–		–		p	+
englerianum	5	3	4	5	3	2	+	–	1–	–	±	–		4	2s	t	+
eugenoliferum	1	2	4	4	3	2	+	–	1c*	±	–	–		–		t	+
fouilloyi	4	4	–	–	2	2	+	–	1t	+	–	–		2	3s	t	+
frodinii	3	3	5	4	2	1	+	–	1t	±	–	–		2	1i	t	+
gigaphyllum	1	3	4	4	3	2	+	–	1c*	±	–	–		2	2s	t	+
glaucescens	5	5	–	–	3	1	–	–	1–	–	–	–		–		p	+
goaense	–	3	4	2	3	2	+	–	1c*	±	+	–		2	2s	t	+
grandiflorum	2	3	4	2	2	1	+	–	1c*	±	–	–		2	1s	t	+

(Table 2 continued)

species	oil		muc		t	cu	ep	hy	p	s	pa	ad. ha		ab. ha		v	e
	p	s	p	s								f	l	f	l		
griffithii 1	2	4	3	2	2	1	±	–	1c	±	–	–		–		t	+
griffithii 2	1	–	4	3	2	1	+	–	1c*	±	–	–		3	3i	t	+
iners 1–3	3	2	2	2	2	2	+	–	1c*	±–	±	–		3	2i	t	+
iners 4	4	2	–	–	3	2	+	–	1c	–	±	–		2	2s	t	+
insulari-montanum	1	3	4	4	3	2	+	–	1c	–	–	–		–		t	+
javanicum 1, 2	2	3	4	1	2	2	+	–	1t	+	±	–		4	3s	t	+
kami	3	4	5	4	4	3	±	–	2c	±	–	–		–		t	+
keralaense	2	4	4	4	3	2	+	–	1c*	±	–	–		–		t	+
kinabaluense 1	–	1	4	4	4	3	+	–	2c	±	–	3	4i	4	3s	t	+
kinabaluense 2	4	5	–	–	2	2	–	–	1–	–	–	–		3	5s	t	+
kunstleri	–	2	1	1	3	2	+	–	1t	+	–	–		2	2s	t	+
laubatii	1	3	4	2	2	2	+	–	1c*	+	±	–		–		t	+
ledermannii	1	3	5	3	2	2	+	–	1t	±	–	–		3	4t	t	+
litseafolium	2	3	3	2	4	2	+	–	1c*	–	–	–		–		t	+
longitubum	3	4	4	3	3	2	+	–	1c	–	–	–		–		t	+
loureirii 1, 2	2	3	2	2	2	2	+	–	1tc	+	–	–		–3	3t	t	+
lucens	2	2	3	2	2	2	+	–	1c	–	±	–		2	3s	t	+
macrocarpum	4	4	2	1	3	2	+	–	2c*	+	–	–		–		t	+
macrophyllum	2	2	3	2	4	2	++	–	1c*	+	–	–		2	3s	t	+
magnifolium	–	–	2	2	3	2	+	–	1t	+	–	–		–		t	+
mairei	3	4	–	–	3	2	+	–	1c*	±	–	–		3	2t	t	+
malabaricum	2	4	–	–	2	2	+	–	1t	±	–	–		1	2s	t	+
malabathrum	1	2	4	3	3	2	+	–	1t	±	±	–		3	2s	t	+
malayanum	–	p	p	p	1	1	–	–	1–	±	–	–		–		t	+
melastomaceum	1	2	5	5	4	2	+	–	1c*	–	–	1	2s	3	3s	t	+
melliodorum	2	3	4	3	3	2	+	–	1t	+	–	1	3i	2	1s	t	+
mendozae	2	4	3	2	2	2	++	–	1t	+	–	–		–		t	+
mercadoi	1	4	3	2	2	2	+	–	1t	+	–	–		–		t	+
microcarpum	4	3	–	–	3	2	++	–	2t	+	–	–		1	2t	t	+

species	oil		muc		t	cu	ep	hy	p	s	pa	ad. ha		ab. ha		v	e
	p	s	p	s								f	l	f	l		
microphyllum	4	5	2	4	3	2	+	–	1t	±	–	2	1i	4	2s	t	+
mollissimum	4	4	–	–	2	2	+	–	1t	+	+	–		3	3s	t	+
montanum	3	3	5	2	2	2	–	–	2c*	±	±	–		4	2s	p	+
myrianthum	2	4	4	2	3	2	+	–	1t	±	–	–		–		t	+
myrtifolium	–	4	2	1	3	2	+	–	1c*	±	–	–		–		t	+
nalingway	–	–	5	5	3	2	+	–	1t	±	+	–		3	2s	t	+
nooteboomii	3	5	2	2	2	2	++	–	1c	–	–	1	1s	3	2s	t	+
obtusifolium	3	4	–	–	3	1	+	–	1c*	±	±	–		–		t	+
oliveri	4	4	2	2	3	2	+	–	1c*	±	–	–		–		p	+
osmeophleum	1	4	2	4	2	2	+	–	1c	–	±	–		–		t	+
ovalifolium	3	4	–	–	4	2	+	–	1c*	±	±	3	4t	4	2s	t	+
ovatum	–	3	1	2	3	2	++	–	1c	±	±	–		–		t	+
pachyphyllum	1	4	4	4	3	1	++	–	1t	±	++	–		–		t	+
paiei	2	4	–	–	3	2	+	–	1t	±	±	–		1	2t	t	+
panayense	1	4	4	3	3	2	+	–	1t	+	–	–		–		t	+
parthenoxylon	3	4	2	2	2	1	–	–	1–	–	±	–		–		t	+
perrottetii	2	3	2	2	3	2	+	–	1t	±	++	–		3	4i	t	+
piniodorum	1	2	4	4	2	2	+	–	1t	±	–	–		–		t	+
podagricum	3	3	4	2	2	2	+	–	1c*	–	–	–		2	3s	t	+
poilanei	–	2	1	1	2	2	+	–	1c*	±	–	–		–		t	+
polítum	–	3	4	3	3	2	+	–	1t	+	–	–		–		t	+
polyadelphum	–	1	4	3	3	2	+	–	1c*	–	±	–		–		t	+
porphyrospermum	2	4	2	1	3	2	+	–	1t	±	–	–		–		t	+
porrectum 1–3	2	3	3	4	3	2	–	–	1c–	–	–±	–		–1	2s	p	+
propinquum	3	2	1	–	3	2	+	–	1c	–	–	–		–		t	+
pseudopedunculatum	4	3	4	3	4	3	±	–	2c*	±	–	–		–		t	+
psychotrioides	2	2	5	4	2	2	–	–	1–	–	–	–		2	2s	p	+
racemosum	p	p	p	p	2	1	++	–	1c	–	–	–		–		t	+
reticulatum	1	2	5	4	3	2	+	–	1c	–	–	–		–		t	+
rhynchopyllum 1–10	4	5	–	–	2	1	++	–	1c*	±	–±	–		–3	3i	t	+

(Table 2 continued)

species	oil p	oil s	muc p	muc s	t	cu	ep	hy	p	s	pa	ad. ha f	ad. ha l	ab. ha f	ab. ha l	v	e
riedelianum	3	3	–	–	3	1	–	–	1c*	±	–	–		–		p	–
rigidum	–	5	4	3	3	2	+	–	1t	±	–	–		–		t	+
riparium	3	4	–	–	2	2	±	–	1c*	±	+	–		2	2s	t	+
rivulorum	–	–	3	4	2	2	++	–	1c	–	–	–		–		p	+
rupestre	2	2	5	4	4	2	++	–	1c*	–	±	–		4	4i	t	+
scalarinerve	2	4	1	4	2	1	+	–	1t	–	±	–		3	3s	t	+
scortechinii	3	3	2	4	3	2	+	–	1c*	–	+	–		3	3s	t	+
sellowianum	5	2	–	–	3	3	–	–	2c*	±	±	–		4	3cs	t	+
sericans	4	2	2	1	3	2	+	–	1t	–	±	–		3	3s	t	+
sericeum	2	3	2	2	3	1	±	+	1–	–	–	–		–		t	+
sessilifolium	2	3	4	4	3	2	+	–	1t	±	–	–		–		t	+
simondii	4	4	–	–	2	1	–	–	1c	–	±	–		2	1i	t	+
sinharajense	–	–	5	4	4	2	+	–	1c	±	–	–		–		t	+
sintok	2	2	2	1	3	1	+	–	1t	±	–	–		–		t	+
solomonense	1	–	4	3	2	1	+	–	1c*	+	–	–		–		t	+
soncaurium	2	2	3	2	2	2	+	–	1c	±	±	–		–		t	+
spec.	2	3	2	2	3	1	+	–	1c*	±	–	1	?	3	3s	p	+
subaveniopsis	2	4	–	2	2	2	+	–	1c	–	–	–		2	2t	t	+
subavenium 1, 2	2	4	1	1	2	2	+	–	1c	±–	–+	–		2	2s	t	+
subcuneatum	1	1	4	2	2	2	++	–	1t	–	–	–		1	?	t	+
subpenninervum	–	4	3	4	3	2	+	–	1t	±	–	–		–		p	+
sulphuratum	3	4	2	2	3	2	+	–	1t	±	+	–		2	3i	t	+
tahijanum	3	4	–	–	2	1	+	–	1t	+	–	–		–		t	+
tamala 1, 2	2	4	1	2	2	2	+	–	1c*	–	–	–		–		t	+
tampicense	2	4	4	1	2	1	–	–	1–	–	–	–		2	2i	p	+
tazia	2	4	2	2	2	2	+	–	1t	–	–	–		–		t	+
tepalinum	–	2	4	3	3	1	+	–	1t	±	–	–		–		t	+
tonkinense	2	2	2	3	2	2	+	–	1c*	–	–	–		–		t	+
trichophyllum	2	3	4	2	2	1	+	–	1c*	+	+	–		2	3s	t	+

species	oil		muc		t	cu	ep	hy	p	s	pa	ad. ha		ab. ha		v	e
	p	s	p	s								f	l	f	l		
triplinerve	5	4	–	–	2	1	–	–	2–	–	++	–		–		t	+
tsoi	1	2	2	2	3	2	+	–	2t	+	–	–		–		t	+
vaccinifolium	2	3	4	2	4	4≈	+	–	2c	±	–	–		3	2s	t	+
velutinum	3	2	4	4	3	2	+	–	2c*	–	–	–		2	3s	t	+
verum 1–6	1	4	3	3	2	1	+	–	1c*	±	±	–		-2	1t	t	+
vesiculosum	4	4	–	–	3	2	–	–	2c*	–	–	–		2	3s	p	+
vimineum	4	4	–	–	2	2	+	–	1t	+	–	–		–		t	+
virens	1	4	4	3	3	1	+	–	1t	±	–	–		–		p	+
wightii	2	2	4	2	3	2	+	–	2t	+	–	–		2	1t	t	+
xanthoneurum	2	3	3	5	2	2	++	–	1t	–	–	–		–		t	+
xylophyllum	1	4	4	3	3	2	++	–	1t	+	–	–		–		t	+
zollingerii 1	2	3	–	1	3	2	++	–	1c	–	–	–		–		t	+
zollingerii 2	1	2	4	3	3	2.	+	–	1c	–	–	–		–		t	+

Explanation of Table 2:

oil = oil cells; **muc** = mucilage cells; **p** = palisade parenchyma; **s** = spongy parenchyma; – = absent; 1 = ≤ 0.1 cell/mm leaf width; 2 = 0.1–1 cell/mm; 3 = 1–2 cells/mm; 4 = 2–5 cells/mm; 5 = 5–10 cells/mm; p = present, frequency undetermined; ? idioblast type indistinct.

t = lamina thickness: 1 = ≤ 100 µm; 2 = 100–200 µm; 3 = 200–300 µm; 4 = > 300 µm.

cu = adaxial cuticle thickness: 1 = ≤ 3 µm; 2 = 3–8 µm; 3 = 8–13 µm; 4 = > 13 µm; ≈ = irregular surface. — **ep** = adaxial epidermis cells: – = not sclerified; ± = slightly sclerified; + = moderately distinctly sclerified; ++ = strongly sclerified. — **hy** = hypodermis: – = absent; + = present. — **p** = palisade parenchyma: 1 = unilayered; 2 = 2-layered; 3 = 3-layered; – = not sclerified; c = (upper layer) with thickened and sclerified outer periclinal wall; c* = (upper layer) with thickened outer periclinal and anticlinal walls sclerified; t = (upper layer) totally sclerified. — **s** = spongy parenchyma: – = not sclerified; ± = weakly sclerified; + = sclerified. — **pa** = papillate abaxial epidermis: – = flat; ± = lowly domed outer periclinal walls; + = dome-shaped papillae; ++ = club-shaped papillae.

ad. ha = adaxial hairs; **ab. ha** = abaxial hairs; **f** = frequency; – = absent; **l** = ≤ 0.1 hair/mm leaf width; 2 = 0.1–1 hair/mm; 3 = 1–2 hairs/mm; 4 = 2–5 hairs/mm; 5 = 5–10 hairs/mm; **l** = length: 1 = ≤ 50 µm; 2 = 50–100 µm; 3 = 100–200 µm; 4 = 200–300 µm; 5 = > 300 µm; ? = undetermined; s = thick-walled (solid); t = thin-walled; i = intermediate wall thickness; c = curly hair type.

v = venation: p = penninerved; 1 main vein distinct; t = (more or less) triplinerved.

e = transcurrent bundle sheath extensions of the lower order veins: – = absent; + = present.

parenchyma was 8 cells/mm leaf width for oil cells (*C. camphora* 7) and 10 cells/mm leaf width for mucilage cells (*C. psychotrioides*). In the spongy parenchyma the maximum number was 11 oil cells (*C. rhynchophyllum* 8) and 8 mucilage cells/mm leaf width (*C. englerianum*). The frequency of both idioblast types together in the leaf ranges from 0.5 to over 17 idioblasts per mm leaf width (*C. englerianum*).

Other leaf anatomical characteristics (Table 2)

Lamina thickness — Four categories of lamina thickness were distinguished (Table 2). Most species are between 100 and 300 µm thick. Only one species (*C. malayanum*) is less than 100 µm thick. Sixteen species have a very thick lamina (over 300 µm; Table 2).

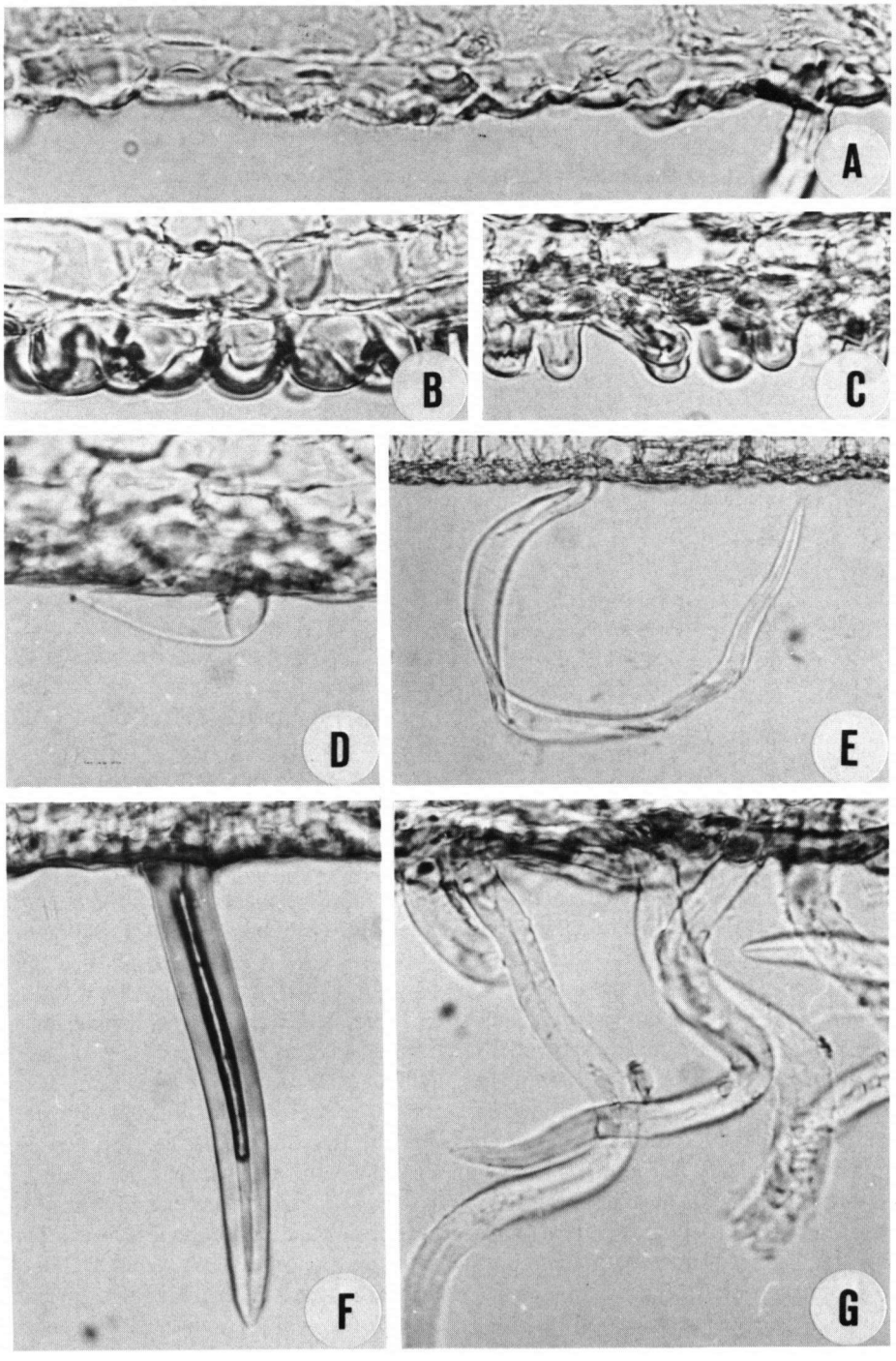
Lower order veins — The lower order veins are vertically transcurrent and possess sclerified bundle sheath extensions, showing birefringence and (auto-)fluorescence (Fig. 4C; Table 2). Only in *C. riedelianum* such bundle sheath extensions were lacking, and the veins were embedded in the mesophyll.

Cuticle — The cuticle (including the cuticular layer) stained bright to dark red, pink or orange with Sudan IV. Four classes in the cuticle thickness were recognized (Table 2). Most species had a cuticle thickness between 3 and 8 µm; 28 species had thinner cuticles; *C. tampicense* has a cuticle only 2 µm thick; 9 species had thick cuticles of which the cuticle of *C. vaccinifolium* showed the maximum value of 17 µm (Fig. 4A). The outer cuticle surface is almost always flat. In 3 species, however, an irregular surface was observed: *C. cordatum, C. effusum* and *C. vaccinifolium* (Fig. 4A; ≈ in Table 2).

Adaxial and abaxial epidermis — In most species the adaxial epidermal cells are small, square to rectangular in shape (Fig. 4A), and show various degrees of birefringence and (auto)fluorescence of the cell walls which indicate sclerification (Fig. 4C, D). Some species showed strong sclerification. Other species possessed large epidermal cells which were hardly sclerified (Fig. 4B; Table 2). The adaxial epidermal cells had cutinized anticlinal walls (Fig. 4B). Generally, the cells of the abaxial epidermis show flat periclinal outer walls (Table 2). Some species have lowly domed outer periclinal epidermal walls (Fig. 5A; Table 2). Other species possess papillae varying from dome-shaped (Fig. 5B; + in Table 2) to club-shaped (Fig. 5C; ++ in Table 2). Generally, the cells of the abaxial epidermis show sclerification identical to that occurring in the adaxial epidermal cells.

Hypodermis — A hypodermis occurred in only 1 species: *C. sericeum* (Table 2). Some of the hypodermal cells were sclerified (Fig. 4F).

Fig. 5. Transverse 30 µm thick sections of *Cinnamomum* species. A–G: Stained with Sudan IV. Light microscopy. — A: *C. bodinieri*. Abaxial epidermis with lowly domed outer periclinal walls; × 435. — B: *C. cubense*. Abaxial epidermis of the leaf with dome-shaped papillae; × 435. — C: *C. bejolghota*. Papillate abaxial epidermis of the leaf showing more or less club-shaped papillae; × 435. — D: *C. wightii*. Short, thin-walled appressed hair on the abaxial surface of the leaf; × 435. — E: *C. bintulense*. Long, broad, thin-walled hair on the abaxial surface of the leaf; × 175. — F: *C. fouilloyi*. Very thick-walled erect hair on the abaxial surface of the leaf; × 435. — G: *C. sellowianum*. Curly, thick-walled hairs on the abaxial surface of the leaf; × 435.


A
B
C
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E
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G

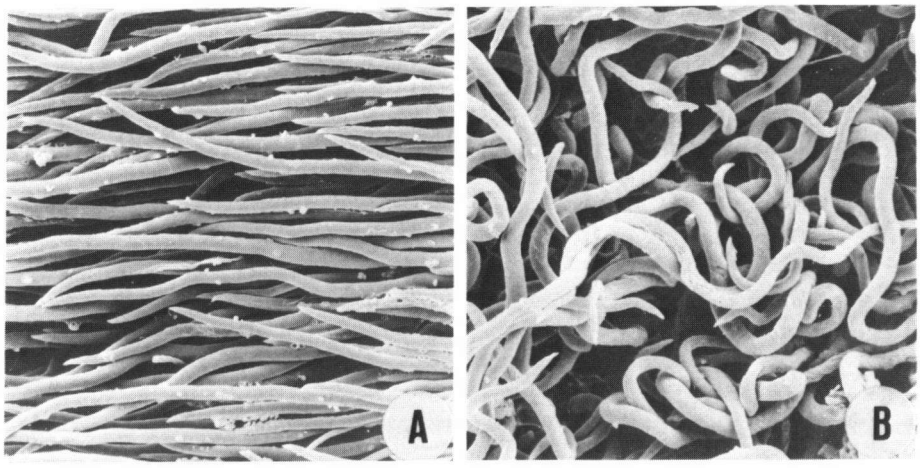


Fig. 6. Scanning electron micrographs of *Cinnamomum* leaves. — A: *C. aureo-fulvum*. Dense aligned hairs; × 260. — B: *C. sellowianum*. Curly erect hairs; × 260.

Mesophyll — Almost all species studied possessed a distinctly 1-layered palisade parenchyma. The presence of a 2-layered palisade parenchyma was recorded in 19 species (Table 2). Only in *C. amoenum* a 3-layered palisade parenchyma was observed. In many species the palisade cells (of the upper layer in case of a multi-layered palisade) were (more or less) entirely sclerified (c* en t in Table 2). In the partially sclerified cells the sclerified parts in the anticlinal walls had tapering ends on the lower side of the cells when seen in transverse section (Fig. 4D, E). In approximately 20% of the species only the upper periclinal wall was thickened and sclerified, thus forming a kind of cap (Fig. 4D; c in Table 2). Where sclerification of the palisade cells (and adaxial epidermal cells) was present a layer of 'fused' sclerified caps was mostly apparent underneath the epidermis (Fig. 4E). Only 13 species had non-sclerified palisade cells (Fig. 4B; Table 2).

In about two-thirds of the species studied a slight to distinct sclerification was observed in the cells of the spongy parenchyma (Table 2). A subepidermal layer against the abaxial epidermis mostly showed distinct sclerification.

Trichomes — Trichomes were absent in about 50% of the species (Table 2). In the other species solitary unicellular trichomes were present. Most of these species bore trichomes on their abaxial surface only. The frequencies varied from few to abundant (Fig. 6A, B; Table 2). The length of these hairs varied from c. 30 μm (e.g. *C. wightii*, Fig. 5D) to over 250 μm (e.g. *C. kinabaluense 2*, Table 2; Fig. 5E). In only ten species trichomes were also present on the adaxial side of the leaf, usually in low frequencies (Table 2). The length of the adaxial trichomes varied from c. 50 μm to 250 μm (Table 2). The trichomes were of different types: erect (Fig. 5F), appressed (Fig. 5D) or curly (c in Table 2; e.g. *C. sellowianum*, Figs. 5G, 6B). In most cases the hairs were thick-walled (Fig. 5F, G). Some species showed thin-walled hairs (Fig. 5D, E) or hairs with an intermediate wall-thickness.

Venation pattern — In *Cinnamomum* the triplinerved leaf (subpalmate venation pattern) occurs generally (t in Table 2). The nervature can be described as acrodromal. The main vein and two (sub)basal lateral veins are conspicuous and in some cases even an additional lateral vein pair is distinct. However, some species have penninerved (pinnately nerved) leaves (p in Table 2).

General leaf anatomy in Cinnamomum

The lamina thickness ranges from 100 to 300 μm. The upper cuticle is 3–8 μm thick and is flat. The adaxial epidermal cells are small, rectangular to square in transverse section and possess more or less sclerified walls. These walls are continuous with the sclerenchymatous bundle sheath extensions of the vertically transcurrent lower order veins. There is no hypodermis. The palisade parenchyma consists of one layer of cells of which the outer periclinal wall is more or less thickened and sclerified, thus forming a cap. In most species the aligned sclerified caps in the outer periclinal wall form a kind of layer underneath the adaxial epidermis. The anticlinal walls of the palisade cells show sclerification. The cells of the spongy parenchyma also show sclerification. Oil and/or mucilage cells are always present in the palisade and spongy parenchyma. The outer periclinal walls of the abaxial epidermal cells are more or less flat and sclerified. Hairs, if present, are unicellular, thick-walled, and mostly occur on the abaxial side. The majority of the species differed from this general pattern in only one or a few features. However, about one-fifth of all species studied deviated more strongly with a maximum number of seven out of the sixteen features studied.

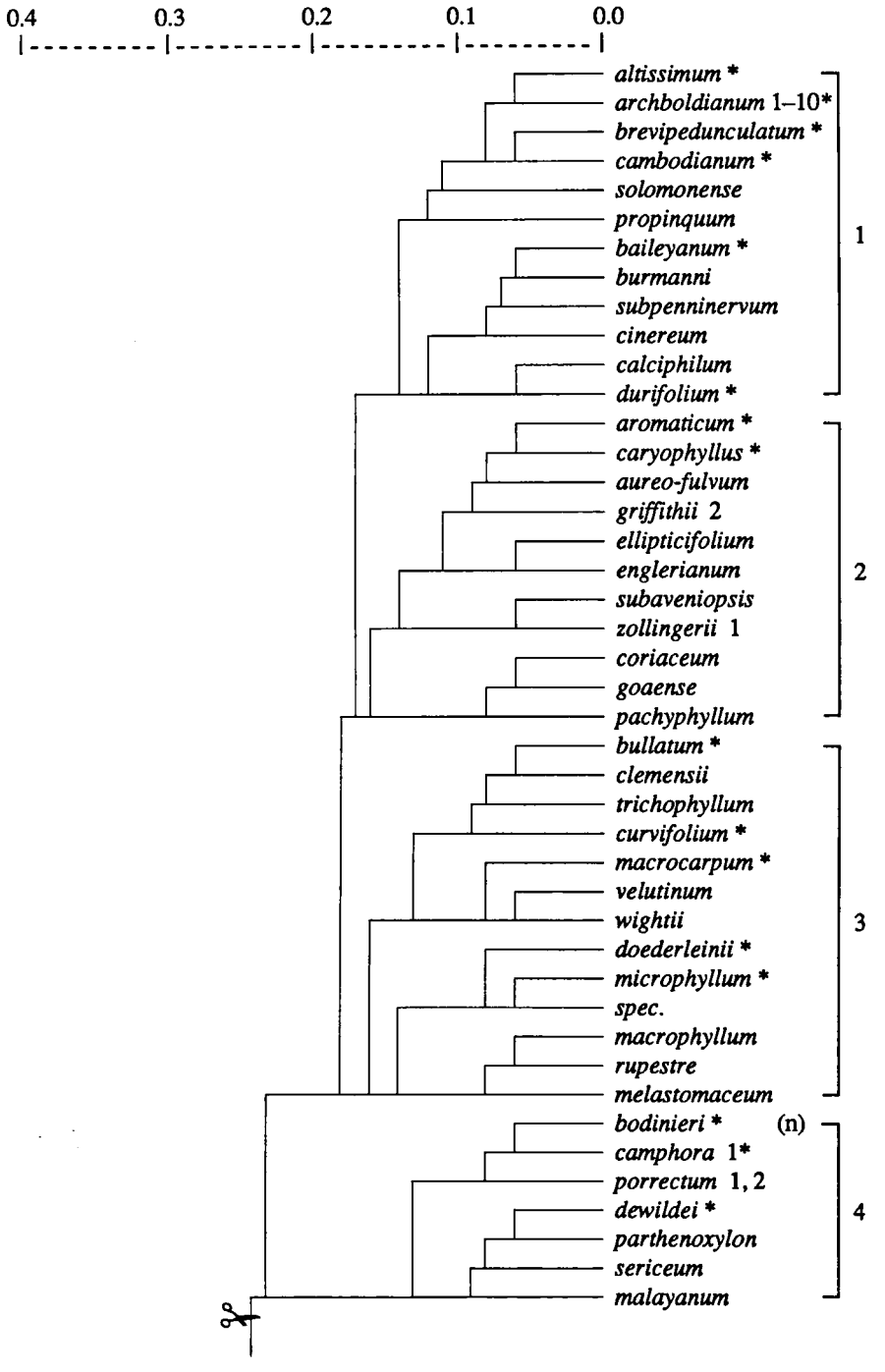
Phenetic analysis

All leaf anatomical features presented in Table 2 were coded for cluster analysis (Table 3a) and a datamatrix was generated for the calculation of the similarity among the species/specimens. Several groups of leaf anatomically identical species were entered as single species (Table 3b). The first mentioned species of each of these groups was used in the analysis. The resulting phenogram of the cluster analysis based upon Manhattan distances is presented in Figure 7.

Ten arbitrary clusters can be recognized: cluster 1: *C. altissimum–C. durifolium*; cluster 2: *C. aromaticum–C. pachyphyllum*; cluster 3: *C. bullatum–C. melastomaceum*; cluster 4: *C. bodinieri–C. malayanum*; cluster 5: *C. angustitepalum* and *C. bejolghota*; cluster 6: *C. cubense–C. montanum*; cluster 7: *C. cordatum–C. kinabaluense 1*; cluster 8: *C. archboldianum 4–C. nalingway*; cluster 9: *C. amoenum–C. triplinerve*, and cluster 10: *C. bintulense–C. ovalifolium*. Most *Cinnamomum* species are clustered at low distance values, especially clusters 1 to 3 (Fig. 7) which include two-thirds of all species studied. The neotropical *Cinnamomum* species (n in Fig. 7) are especially present within the clusters 6 and 9, which show more deviation (higher Manhattan distance) from the species placed in the upper part of the phenogram (Fig. 7).

When analyzing the variation in idioblast distribution patterns within the clusters it was striking that three clusters were constant for the idioblasts (Table 4). The species/specimens of cluster 8 were characterized by the absence of oil cells, while the species in the clusters 9 and 10 lacked mucilage cells. In the clusters 3–7 only 1 or 2 species/specimens deviated from the general pattern within a cluster (see Table 4).

Figure 7


0.4
0.3
0.2
0.1
0.0
altissimum *
archboldianum 1–10*
brevipedunculatum *
cambodianum *
solomonense
propinquum
baileyanum *
burmanni
subpenninervum
cinereum
calciphilum
durifolium *
aromaticum *
caryophyllus *
aureo-fulvum
griffithii 2
ellipticifolium
englerianum
subaveniopsis
zollingerii 1
coriaceum
goaense
pachyphyllum
bullatum *
clemensii
trichophyllum
curvifolium *
macrocarpum *
velutinum
wightii
doederleinii *
microphyllum *
spec.
macrophyllum
rupestre
melastomaceum
bodinieri * (n)
camphora 1*
porrectum 1, 2
dewildei *
parthenoxylon
sericeum
malayanum
1
2
3
4

(Fig. 7 continued)

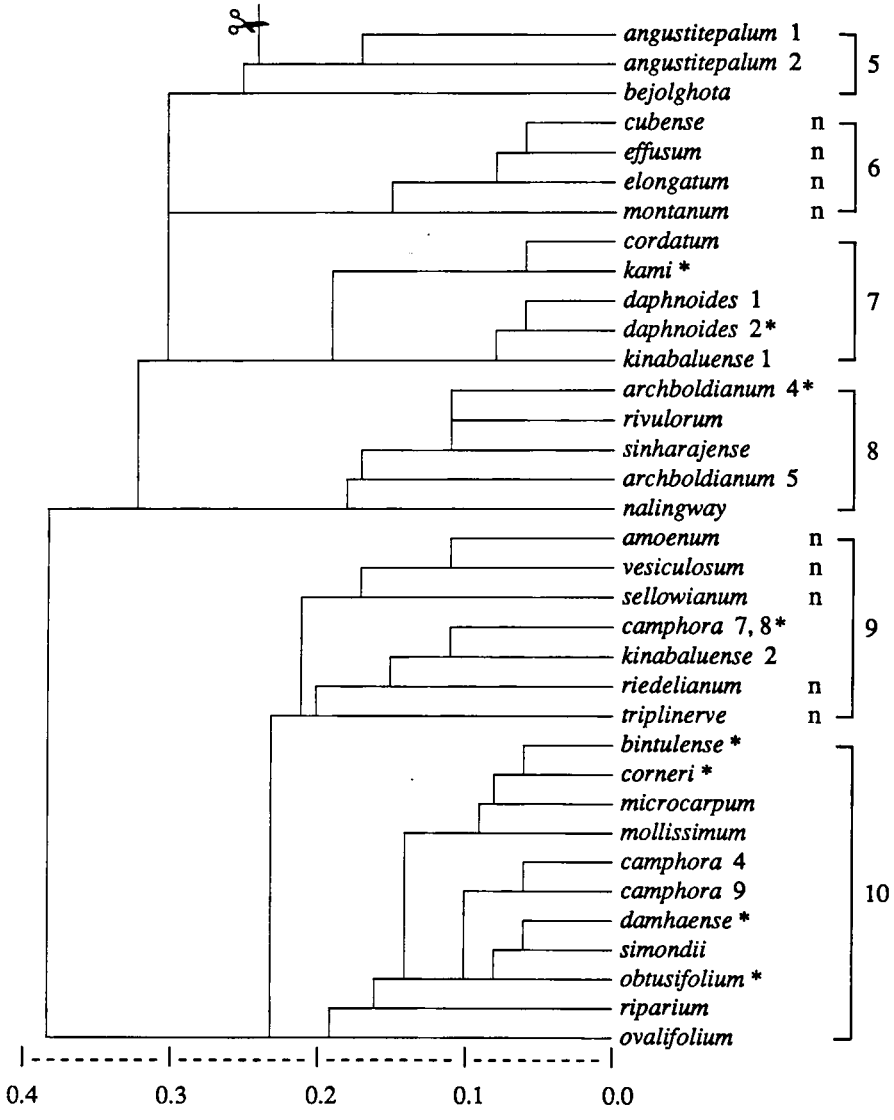


Fig. 7. Phenetic cluster analysis of *Cinnamomum* species based on a datamatrix derived from Table 2. The scale on the X-axis reflects Manhattan distances between species or groups of species; * refers to groups of identically coded species listed in Table 3b (n = neotropical species).

Table 3a. Coding characters of Table 2 for cluster analysis.

1.	Oil cells in lamina:	0 = present;	1 = absent.
2.	Mucilage cells in lamina:	0 = present;	1 = absent.
3.	Oil cells in palisade parenchyma:	0 = absent;	1 = present.
4.	Oil cells in spongy parenchyma:	0 = absent;	1 = present.
5.	Mucilage cells in palisade parenchyma:	0 = absent;	1 = present.
6.	Mucilage cells in spongy parenchyma:	0 = absent;	1 = present.
7.	Lamina thickness:	0 = ≤ 300 µm;	1 = > 300 µm.
8.	Cuticle thickness:	0 = ≤ 8 µm;	1 = > 8 µm.
9.	Adaxial epidermal cells:	0 = not or slightly sclerified; 1 = distinctly or	
10.	Adaxial hypodermis:	0 = absent;	1 = present. [strongly sclerified.
11.	Palisade parenchyma layers:	0 = 1 layer;	1 = 2 or 3 layers.
12.	Palisade parenchyma cells:	0 = not sclerified;	1 = more or less sclerified.
13.	Spongy parenchyma cells:	0 = not or lightly sclerified;	1 = sclerified.
14.	Adaxial papillae:	0 = absent;	1 = present.
15.	Adaxial hairs:	0 = absent;	1 = present.
16.	Abaxial hairs:	0 = absent;	1 = present.
17.	Venation:	0 = triplinerved;	1 = penninerved.
18.	Bundle sheath extensions:	0 = absent;	1 = present.

Table 3b. Groups of identically coded *Cinnamomum* species.

C. altissimum; *C. crassinervium*; *C. chittagongense*; *C. politum*.
C. archboldianum 1–3, 6–10; *C. cappara-coronde*; *C. celebicum*; *C. cuspidatum* 1, 2; *C. laubatii*; *C. loureirii* 1; *C. mendozae*; *C. mercadoi*; *C. panayense*; *C. xylophyllum*.
C. archboldianum 4; *C. magnifolium*.
C. aromaticum; *C. perrottetii*; *C. scortechinii*; *C. subavenium* 2; *C. sulphuratum*.
C. baileyanum; *C. citriodorum*.
C. bintulense; *C. fouilloyi*.
C. bodinieri; *C. porrectum* 3; *C. psychotrioides*; *C. tampicense*.
C. brevipedunculatum; *C. elephantinum*; *C. myrtifolium*; *C. ovatum*; *C. poilanei*; *C. polyadelphum*; *C. rigidum*; *C. tepalinum*.
C. bullatum; *C. javanicum*; *C. loureirii* 2.
C. burmanni; *C. oliveri*; *C. virens*.
C. cambodianum; *C. crispulum*; *C. culitlawan*; *C. eugenoliferum*; *C. insulari-montanum*; *C. keralaense*; *C. longitubum*; *C. myrianthum*; *C. osmeophleum*; *C. piniodorum*; *C. porphyrospermum*; *C. racemosum*; *C. reticulatum*; *C. sessilifolium*; *C. sintok*; *C. soncaurium*; *C. tamala* 1, 2; *C. tazia*; *C. tonkinense*; *C.verum* p.p.; *C. xanthoneurum*; *C. zollingerii* 2.
C. camphora 1; *C. camphora* 2–6; *C. porrectum* 1, 2.
C. camphora 7, 8; *C. glaucescens*.
C. caryophyllus; *C. deschampsii*; *C. dubium* 2; *C. ebaloi*; *C. frodinii*; *C. gigaphyllum*; *C. grandiflorum*; *C. iners* 1–3; *C. ledermannii*; *C. lucens*; *C. malabathrum*; *C. podagricum*; *C. scalarinerve*; *C. sericans*; *C. subavenium* 1; *C. subcuneatum*; *C. verum* p.p.
C. corneri; *C. tahijanum*; *C. vimineum*.
C. curvifolium; *C. kunstleri*.
C. damhaense; *C. dubium* 1; *C. iners* 4; *C. mairei*; *C. malabaricum*; *C. paiei*; *C. rhynchophyllum* p.p.
C. daphnoides 2; *C. vaccinifolium*.
C. dewildei; *C. griffithii* 1.
C. doederleinii; *C. melliodorum*.
C. durifolium; *C. litseafolium*.
C. kami; *C. pseudopedunculatum*.
C. macrocarpum; *C. tsoi*.
C. microphyllum; *C. nooteboomii*.
C. obtusifolium; *C. rhynchophyllum* p.p.

The general idioblast distribution pattern in the clusters 1–4 was that oil and mucilage cells are present in both layers. Clusters 1 and 2 showed more variation in the idioblast distribution than clusters 3 and 4. About 80% of the species within the former clusters possessed the general idioblast distribution. The remaining species/specimens within these clusters only lack one idioblast type in one of the mesophyll layers.

The idioblast characters are more constant than the other leaf anatomical characters such as the presence or absence of sclerified epidermis, palisade and spongy parenchyma cells, the layering of the palisade parenchyma, the lamina and cuticle thickness, and the venation pattern (Table 4). The combination of the idioblast distribution pattern and other constant leaf anatomical characters can be used to distinguish the clusters (Fig. 7) from each other (Table 4).

DISCUSSION

The leaf anatomical features studied (Table 2) confirm and greatly extend the existing knowledge on *Cinnamomum* leaf anatomy (Santos, 1930; Marlier-Spirlet, 1946). These features, including the idioblasts, did not show obvious correlations enabling the recognition of species groups. In order to get some insight in the overall similarities of the individual species/specimens of *Cinnamomum* cluster analyses were applied. A tentative cladistic analysis was not carried out, as the number of taxa is out of proportion as compared with the number of features. Moreover, such an analysis yielded already unsatisfactory trees in a study on oil and mucilage cells in *Annona* (Bakker & Gerritsen, 1992) in which only c. 40 taxa were used.

Some *Cinnamomum* species of which more than one specimen was studied ended up in different clusters (Fig. 7), e.g. *C. archboldianum* in the clusters 1 and 8; *C. camphora* in the clusters 4, 9 and 10, and *C. kinabaluense* in the clusters 7 and 9. However, slightly different specimens of most other species ended up in the same clusters, e.g. *C. angustitepalum* and *C. daphnoides*.

In the clusters 1 and 2 the idioblast distribution patterns show the largest variation (Table 4). However, these variations are less obvious than in the idioblast distribution in leaves of *Annona* (Bakker & Gerritsen, 1992). The other leaf anatomical features were not useful in discriminating these clusters. In the clusters 3–7 only one or two species show minor idioblast variations. Cluster 3 always possesses mucilage cells in both mesophyll layers and oil cells in the spongy parenchyma. The remaining leaf anatomical features were not discriminating. Species in cluster 4 can be recognized by the combination of the following features: presence of both idioblast types in both layers, non-sclerified epidermal cells, and a weakly or not sclerified spongy parenchyma. Cluster 5 does not possess a discriminating leaf anatomical character distribution. Cluster 6 lacks mucilage cells in the spongy parenchyma and is additionally characterized by the possession of non-sclerified epidermal cells and spongy parenchyma, a two-layered sclerified palisade parenchyma and penninerved leaves. Cluster 7 is characterized by the presence of oil and mucilage cells in both layers, a thick lamina and cuticle, a two-layered sclerified palisade parenchyma and tripli-

Table 4. Constant leaf anatomical features per cluster.

feature	oil		muc		l	c	e	p	s	pa	ad	ab	v
cluster	p	s	p	s									
1		+*	+	+*		<	+	1+		–	–		
2		+*		+	<		+	1	–		–		t
3		+	+	+		<		+					
4	+*	+	+	+	<	<	–	1	–	–	–		
5	–*	+*	+	+	>		+	1+	–		–		
6	+	+	+	–*	<		–	2+	–		–		p
7	+*	+	+	+	>	>		2+	–				t
8	–	–	+	+		<		1			–		
9	+	+	–	–	<		–		–				
10	+	+	–	–		<		+					

Legend:

Clusters: for species composition of each cluster see Figure 7 and Table 3b.

Features: oil: p = oil cells in palisade parenchyma
s = oil cells in spongy parenchyma
muc: p = mucilage cells in palisade parenchyma
s = mucilage cells in spongy parenchyma
\+ = present; – = absent
+* = present, but absent in one species
–* = absent, but present in one species

l = lamina thickness
< = lamina thickness ≤ 300 µm
> = lamina > 300 µm

c = cuticle thickness
< = cuticle thickness ≤ 8 µm
> = cuticle > 8 µm

e = adaxial epidermis
\+ = sclerified; – = non-sclerified

p = palisade parenchyma
1 = uni-layered; 2 = two-layered
\+ = sclerified; – = non-sclerified

s = spongy parenchyma
\+ = distinctly sclerified; – = weakly or non-sclerified

pa = papillae; – = absent

ad = adaxial hairs; – = absent

ab = abaxial hairs

v = leaf venation
t = triplinerved; p = penninerved

veined leaves. The distribution pattern of the idioblasts is constant in the following three clusters (Table 4). Cluster 8 lacks oil cells and clusters 9 and 10 are characterized by the absence of mucilage cells.

At least in the latter three clusters the idioblast distribution pattern is the discriminating factor. Therefore, oil and mucilage cells possess some diagnostic value, generally in combination with other leaf anatomical features.

A classification of *Cinnamomum* species was presented by Meissner (1864). He placed 54 *Cinnamomum* species in two sections: *Malabathrum* and *Camphora* (see also Pax, 1889). No more recent literature is available on the infrageneric taxonomy of *Cinnamomum* (Kostermans, 1986). In an attempt to correlate the leaf anatomical characters of the species (Table 2) with the existing classification, we analyzed the position of the species in the phenogram (Fig. 7). In the present paper 23 out of the 42 species included in section *Malabathrum* (Meissner, 1864) are discussed. Of these species 18 are placed in the upper part of the phenogram (Fig. 7: clusters 1–3). The five other species are placed in cluster 7 and 10. All these species possess sclerified epidermal cells and/or palisade cells. Only two out of the twelve species belonging to section *Camphora* (Meissner, 1864) were studied here (*C. camphora* and *C. parthenoxylon*). These species are placed in the clusters 4, 9 and 10 (Fig. 7) and lack sclerified epidermal and palisade cells (Table 2). A few other not neotropical species (*C. bodinieri, C. clemensii, C. glaucescens, C. kinabaluense 2, C. malayanum, C. porrectum* and *C. simondii*) also lack sclerification (Table 2) and are almost all located in the same clusters. Because of the low number of species studied in section *Camphora* little can be concluded about characters on sectional level, but from the fact that both sections have species in cluster 10 it is evident that there is no clear leaf anatomical distinction between them.

Of the 11 neotropical species in the present study, 10 were transferred from other genera such as: *Phoebe* (*C. cubense, C. effusum, C. elongatum*), *Oreodaphne* (*C. amoenum, C. tampicense, C. vesiculosum*), *Laurus* (*C. montanum, C. triplinerve*), *Ocotea* (*C. psychotrioides*) and *Persea* (*C. riedelianum*). Almost all neotropical species are placed in the clusters 6 and 9 (Fig. 7). Furthermore *C. cubense, C. effusum* and *C. elongatum* (cluster 6) are closely related as is the case with *C. amoenum* and *C. vesiculosum* (cluster 9). The first three species were included in the genus *Phoebe* and the latter two in *Oreodaphne*.

It is striking that nine of these species have penninerved leaves (Table 2; not *C. sellowianum* and *C. triplinerve*). Of the remaining 139 *Cinnamomum* species only 15 showed this type of leaf venation (Table 2). Triplinerved and penninerved leaves have been reported before in *Cinnamomum* (Klucking, 1987; Hyland, 1989). In addition, all neotropical species possessed non-sclerified epidermal cells (Table 2). Further, eight of eleven neotropical species showed a 2- or 3-layered palisade parenchyma against eleven of the remaining not neotropical species (Table 2). Therefore, it can be concluded that the neotropical species show more differences from the general occurring leaf anatomical pattern in *Cinnamomum* than does the majority of the species studied. Richter (1981) already recognized a South American group of *Cinnamomum* species based on wood and bark anatomy.

The presence of oil cells, and to a lesser extent also of mucilage cells, is characteristic for the Lauraceae (Pax, 1889; Solereder, 1899; Metcalfe & Chalk, 1950; Metcalfe, 1987). In the present study oil and/or mucilage cells are always present in *Cinnamomum* in both mesophyll layers of the leaf (Table 2). In *Annona* (Annonaceae) the idioblasts were always present in the spongy parenchyma only (Bakker & Gerritsen, 1992). The variation in number, staining reaction, and size/shape of oil and mucilage cells in *Cinnamomum* was similar to that found in *Annona* species (Bakker & Gerritsen, 1992). The different staining colours and/or appearances of the oil cells in different species (Fig. 1) have been attributed to the different compositions of oil in the cells (Perrot, 1891; Kurata, 1952). The presence of oil and mucilage cells in leaves of the neotropical *Cinnamomum* species studied, which formerly were placed in other genera, are in agreement with the literature concerning the leaf anatomy of American Lauraceae, including *Phoebe, Persea, Ocotea,* and *Oreodaphne* (Petzold, 1907).

Eleven species of which in the present study more than one specimen was studied were constant for their idioblast distribution pattern. However, seven other species (*C. archboldianum, C. camphora, C. dubium, C. griffithii, C. iners, C. kinabaluense, C. zollingerii*) showed variable distribution patterns (Table 2). It is not likely that these specimens were determined incorrectly. The variation in idioblast distribution can partly be explained by the suggested homology of the two types of idioblasts (Bakker et al., 1991; see also below). Moreover, it is possible that different ecological conditions also played a part in the variation found in *C. camphora, C. iners,* and *C. kinabaluense*. It is not known which genetic and/or ecological triggers play a part. Ontogenetic and seasonal variations have been reported to effect the number of oil and mucilage cells in the camphor tree, *C. camphora* (Shirasawa, 1903). Leaf oil composition varied between varieties of *C. cassia* (Cheng et al., 1989). The variations were used to identify types of *C. camphora* (Shi et al., 1989) and were applied in numerical chemotaxonomical studies in *Cinnamomum* (Tao & Zhong, 1988). Experimental studies under varying conditions are needed in order to explain the apparent variations in idioblast distribution in *Cinnamomum* species.

Since infrageneric classifications within *Cinnamomum,* based upon other characters such as macromorphology and pollen morphology, are very scarce, the idioblast distribution patterns could not be correlated with diversity patterns in other characteristics. Therefore little can be concluded about the systematic significance of the oil and mucilage cells.

In the literature oil and mucilage cells are mentioned as occurring together and were supposed to develop from one type into the other (Tschirch, 1889, 1914; Janssonius, 1926, 1934; West, 1969). Baas & Gregory (1985) and Gregory & Baas (1989) critically discussed this phenomenon and suggested further research. In earlier papers we described the ultrastructure and development of oil and mucilage cells of *Cinnamomum* (Bakker & Gerritsen, 1989; Bakker et al., 1991) and *Annona* (Bakker & Gerritsen, 1990), especially to investigate the possible homology of both idioblast types. We found that a suberized wall layer, typical plastids, an extraplasmatic space for storage of the secreted product, and a cupule were present in both oil and mucilage cells (Bakker et al., 1991), which indicated a homologous development of both idio-

blast types. In addition, the first zone of deposited mucilage in mucilage cells resembled the inner wall layer in oil cells. The present observations on oil and mucilage cells in a large number of *Cinnamomum* species also support this homology. A suberized layer was always detected in both idioblast types at the light microscopical and ultrastructural level.

CONCLUSIONS

Oil and/or mucilage cells are always present in both mesophyll layers in all *Cinnamomum* species. The idioblasts show variations in shape/size, stainability, number, and distribution pattern. The latter variation can partly be understood by the proposed homology of both idioblast types. Oil and mucilage cells possess some diagnostic value in combination with other leaf anatomical characters. Because of the lack of a comparative classification of *Cinnamomum*, the systematic significance remains questionable. Further studies on the classification of *Cinnamomum* are necessary to evaluate the systematic value of oil and mucilage cells at the infrageneric level.

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