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Wood and leaf anatomy of *Opiliaceae*

Abstract

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The wood and leaf anatomy of representatives of the 9 genera of the *Opiliaceae* are described in detail. It is possible to separate the genera on the base of both wood- and leaf anatomical characters. Herein the presence of cystoliths of varying shape and size is important. Some comments on the taxonomy and possible phylogeny of the familiy are given.

1. Introduction

The pantropical family *Opiliaceae* comprises 9 genera and about 35 species of shrubs, lianas and trees. The taxonomic delimitation of the family and the relationships to other families have often been subject of discussion (for a survey see Reed 1955). The family is now usually placed in the order *Santalales*. At the moment, P. Hiepko is revising the family (see Hiepko 1971, 1979, 1982).

Little has been published on either wood or leaf anatomy of the *Opiliaceae*. Solereder (1899, 1908) and Metcalfe & Chalk (1950) give short anatomical descriptions. Reed (1955) describes the anatomy of *Opiliaceae* and related families. His study, however, was based on few and mostly very small and young samples.

The aim of the present study is to describe and compare the wood and leaf anatomy of the *Opiliaceae* in the circumscription given by Hiepko, to discuss the relationships within the family, and to suggest a possible phylogenetic pathway.

2. Material and Methods

2.1. Wood anatomy

For this study, 48 wood samples and 8 slides (on loan from Harvard, Aw), representing 25 species were examined. Collector's numbers, localities and diameters if known, and numbers of the Utrecht wood collection (Uw) are given at the beginning of the generic descriptions.

Sections and macerations were prepared according to standard techniques and embedded in Canada balsam and in glycerine respectively. The terms used in this study are those proposed by the committee on nomenclature of the IAWA (1964). Ray height is based on the "frequently occurring

highest" rays, found in a frequency of 5-10%. L/H ratio of the ray cells gives an indication of radial length to axial height ratio as seen in radial sections.

Some characters usually included in wood anatomical descriptions are not given here: the shape of the vessels seen in transverse sections, end wall angles, intervascular pits and vessel-parenchyma pits. The reasons are given in the discussion on the taxonomic value of the wood characters.

The quantitative data are based on 25 measurements. The value given in the generic descriptions is the range of averages per species, followed by the minimum and maximum values found within the genus.

Exceptions are the figures for the number of rays per mm (averages out of 10 measurements), wall thickness and lumen diameter of the fibres, and the size of the fibre pits, which are estimated minimum and maximum values. The F/V-ratios, indicating the fibre length to vessel member length ratio, are calculated and the minimum and maximum values found within the genera are given.

2.2. Leaf anatomy

For this study, 53 mature leaves representing 29 species were examined. Collector's numbers and localities if known are given at the beginning of the generic descriptions. Most specimens were identified by Hiepko. Transverse microtome sections of the lamina including the midrib were made of the central part of the leaves as well as sections of the basal part of the petiole and completed with paradermal hand sections of the surfaces. The sections were stained with astra-blue/saffranin or with haematoxilin/saffranin. Cuticular preparations of all specimens were made and mounted in glycerine-gelatin after staining with Sudan IV. In the cuticular preparations measurements of epidermal cells and stomata were made on the abaxial surface. The values given represent single selected cells and stomata which are "representative" for the samples.

3. Results

3.1. *Agonandra* Miers ex Benth. & Hook. f.

About 10 species of trees in S and C America.

Wood Anatomy

Material seen: *A. brasiliensis* Miers: Brazil: Uw 18822 (*INPA*, Manaos *X 3104*; Amazonas, diam. 7 cm); Uw 26627 (*Jari Timber 273*; Amazonas, diam. 8 cm). - *A. excelsa* Griseb.: Brazil: Uw 12993 (*Lindeman & de Haas 1266*; Parana, diam. 5.5 cm); Uw 14175 (*Lindeman & de Haas 4784*; Parana, diam. 8.5 cm); Argentine: Uw 26692 (*Molfino s. n.*; diam. 8 cm). - *A. racemosa* (DC.) Standley: Mexico: Aw 24132 (slide). - *A. silvatica* Ducke: Surinam: Uw 3402 (*Lindeman 4995*; diam. 8 cm); Uw 11688 (*LBB 10947*; Nickerie R., diam. 12 cm); Uw 15336 (*Oldenburg & Norde 490*; Sipaliwini Savanna, diam. 15 cm); Brazil: Uw 8072 (*Krukoff 6953*; Amazonas, large tree); Peru: Uw 25867 (*Tessmann 4442*; large tree). - *A.* spec.: Ecuador: Uw 26733 (*Little 5*); Uw 26734 (*Ortega 265*).

The description is based on the samples of *A. brasiliensis, A. excelsa* and *A. silvatica.* (The slide of *A. racemosa* and the samples of *A.* spec. match well).

Growth rings absent or faint. Vessels diffuse, solitary with only incidentally two pores connected, 10 to 41 (9-84) per sq.mm, diameter 53 to 101 (36–144) μm, vessel member length 230 to 400 (80-550) μm. Tracheids scanty.

Fibres moderately to very thickwalled: diameter 16-20 μm, walls 4 to 12 μm. Pits distinctly bordered, frequent on radial and tangential walls, (4) 5-6 μm. Length 1040 to 2200 (680-3060) μm, F/V-ratio 4.6-5.8.

Rays homogeneous uni- and 2-3-seriate; uniseriate rays less than 5%, composed of procumbent cells; multiseriate rays composed of strongly procumbent cells with incidentally one row of weakly procumbent margin cells, height 220 to 800 μm. Cystoliths absent.

Parenchyma apotracheal, diffuse-in-aggregates, in strands of two cells.

N o t e : Although the genus is very homogeneous in all qualitative characters, the quantitative characters allow a distinction of the three species studied:

		A. brasiliensis	*A. excelsa*	*A. silvatica*
vessel	diameter (μm)	88 (60-115)	53 (36-67)	101 (64-144)
	frequency/mm^2	14 (9-22)	41 (26-84)	10 (5-13)
member	length (μm)	290 (150-380)	230 (80-370)	400 (200-550)
fibre	wall (μm)	4-8	3-6	5-12
	lumen (μm)	1-4	3-6	1-2
	length (μm)	1690 (1330-2150)	1040 (680-1380)	2200 (1450-3060)
ray	height (μm)	250-300	230-320	650-800
number per mm		5-7	6-8	3-4

L e a f A n a t o m y

Material seen: *A. brasiliensis* Miers: Brazil: *Ducke 18148,* R. Para. - *A. excelsa* Griseb.: Brazil: *Lindeman & de Haas 4787,* Parana, Fazenda Reserva. Argentine: *Schreiter 11484,* prov. Salta, Oran; *Hieronymus & Lorentz 653,* ibidem. - *A. granadensis* Rusby: Colombia: *Smith 1950,* Santa Marta. - *A. macedoi* Toledo: Brazil: *Black 48-3561,* Estado do Para, Caminho de Jubin para Condeixa. - *A. racemosa* (DC.) Standley: Mexico: *Langlassé 860,* Sierra Madre. - *A. silvatica* Ducke: Surinam: *LBB 10947,* R. Nickerie; Brazil: *Krukoff 6953,* Amazonas, R. Livramento.

In surface view:

Indumentum absent. Unspecialised epidermal cells polygonal, 30-40 × 15-25 μm, slightly elongate and larger above midrib and veins; cuticular flanges straight or slightly curved, sometimes pitted. Stomata exclusively abaxial, paracytic with 2-4 subsidiary cells, guard cells 25-35 × 18-25 μm.

In transverse section:

Lamina dorsiventral. Unspecialised cells flattened, adaxially much larger than abaxially. Stomata slightly raised or not, with well developed outer cuticular ledges.

Hypodermis absent. Mesophyll composed of 1-2 layers of poorly differentiated palisade parenchyma and loosely packed spongy tissue of large cells. Midrib adaxially flat, abaxially distinctly raised, with one vascular bundle (occasionally divided in three parts) with adaxially and abaxially supporting collenchyma strands. Veins: the larger ones accompanied by supporting collenchyma, the smaller ones embedded in the mesophyll. Petiole with a vascular system comparable with that of the midrib. Cystoliths not abundant, mostly frequent in ground tissue of petiole in clusters of up to twelve cystoliths, length of individual cystoliths 20-80 μm. Crystals absent.

N o t e : *A. excelsa* deviates from the description in the 2-3-layered, well differentiated palisade parenchyma, both ad- and abaxially, with only little spongy tissue in between. The stomata are equally frequent on ab- and adaxial sides. The supporting tissue along the veins is composed of sclerenchyma

cells, accompanied by solitary cystoliths. *A. granadensis* has smaller stomata (23-15 μm) with only 2-3 subsidiary cells, sunken below the level of the epidermis. In both *A. excelsa* and *A. granadensis* the vascular tissue of the petiole is distinctly divided in three or five parts.

3.2. *Cansjera* Juss.

Three species of lianas and erect shrubs, root parasites, from India and Ceylon to S China, New Guinea and N Australia.

Wood Anatomy

Material seen: *C. parvifolia* Kurz: Burma: Uw 26741 (*Helfer s. n.*, Herb. Lugd. Batav. 75). - *C. rheedei* J. F. Gmelin: Thailand: Uw 26562 (*Nooteboom 750*). Malaya: Uw 26693 (*T. & P. 590;* Endau, diam. 0.6 cm).

Growth rings faint. Vessels diffuse, solitary with only incidentally two pores connected, 33 to 34 (29-55) per sq.mm, diameter 60 to 63 (36-84) μm, vessel member length 370 to 400 (250-540) μm. Tracheids abundant, forming almost complete sheaths around the vessels.

Fibres thickwalled: diameter 15-20 μm, walls 3-8 μm. Pits distinctly bordered, frequent on radial and tangential walls, 4-5 μm. Length 970 to 980 (780-1300) μm, F/V-ratio 2.5-2.6.

Rays uniseriate and 2-3(4)-seriate; uniseriate rays 10 to 15%, composed of up to 8 upright cells; multiseriate rays composed of square and weakly upright cells with uniseriate margins of 1-4-weakly upright cells, height 1500 to 2000 μm. Cystoliths scanty, without stalks, in normal ray cells; surface granular or irregular.

Parenchyma scanty, diffuse, in strands of two cells.

Note: *C. parvifolia* deviates from the description given above in the following characters. Vessels: diameter 35 (17-53) μm, 126 (114-132) per sq.mm, vessel member length 290 (120-420) μm. Fibres: length 560 (450-730) μm, F/V-ratio 2.0. Rays uni- and biseriate, cystoliths absent.

Leaf Anatomy

Material seen: *C. leptostachya* Benth.: New Guinea: *Wichman 182,* Kemena. - *C. parvifolia* Kurz: Burma: *Helfer s. n.*, Tenasserim. - *C. rheedei:* J. F. Gmelin: Malay Peninsula: *Griffith 823,* Malacca; *FRI 5138,* Johore.

In surface view:

Indumentum absent or infrequent and almost entirely restricted to midrib and veins, hairs 4-8-celled, uniseriate. Unspecialized epidermal cells polygonal, 12-30 × 20-30 μm, strongly divided and squarish or short above midrib and large veins; cuticular flanges straight and pitted. Stomata mainly abaxial, paracytic with 2-4 subsidiary cells, guard cells 23-25 × 18-20 μm.

In transverse section:

Lamina homogeneous. Unspecialized epidermal cells square or flattened, adaxially of the same size as or slightly larger than abaxially. Stomata slightly raised with well developed outer cuticular ledges.

Hypodermis absent. Mesophyll homogeneous and compact, consisting of small cubic cells. Midrib ad- and abaxially slightly raised, with a single vascular bundle with ad- and abaxially supporting collenchyma caps. Veins: the larger ones accompanied by supporting collenchyma, the smaller ones embedded in the mesophyll. Petiole with a similar vascular system, but with the collen-

chyma arranged in strands divided by parenchyma. Cystoliths common, in the mesophyll mostly in pairs, in the ground tissue of the petiole in small clusters, crystalline part granular and distinctly refractive. Crystals abundant, minute: sometimes completely filling clusters of mesophyll cells, mostly near the abaxial epidermis.

Notes: *C. parvifolia* deviates from the description in the abundant branched, 4-12-celled hairs, both ab- and adaxially, with often minute crystals in their bases. Stomata occur in equal frequencies on both surfaces. The epidermal cells above midrib and veins are elongate. *C. rheedei (FRI 5138)* has 3-4 layers of relatively distinct palisade parenchyma.

3.3. *Champereia* Griff.

One species of trees (4-8 m high) occurring from S Burma to Formosa and W New Guinea.

Wood Anatomy

Material seen: *Ch. manillana* (Blume) Merr.: Thailand: Uw 26148 (*Geesink & Hiepko 7823;* Ban Phé, diam. 2.5 cm); Indonesia: Uw 26229 (*SAN 82729,* N Borneo; diam. 5.5 cm); Uw 26669 (*USw 28213,* Sumatra; diam. 2 cm); Aw 24130, 24131 (slides).

Growth rings faint. Vessels, diffuse, solitary with only incidentally two pores connected, 24 (14-38) per sq.mm, diameter 59 (34-100) μm, vessel member length 350 (150-540) μm. Tracheids scanty.

Fibres thickwalled: diameter 15-20 μm,. walls 3-8 μm. Pits distinctly bordered, frequent on radial and tangential walls, 4-6 μm. Length 1240 (830-1720) μm, F/V-ratio 3.5.

Rays uni- and 3-5-seriate. Uniseriate rays less than 10%, composed of upright cells; multiseriate rays composed of (weakly) procumbent cells (L/H-ratio 1.5-3), often with uniseriate wings of 1-4 square or weakly upright cells, height 800-1500 μm. Cystoliths frequent in the multiseriate rays, situated in large ideoblasts, attached to the outward tangential walls with stalks, frequently "twin" cystoliths in radially adjacent cells (stalks then attached to the common tangential wall); refractive part consisting of four lobes, cohering along the long sides.

Parenchyma apotracheal, diffuse-in-aggregates, in strands of 3-5 cells.

Note: Probably the Aw-slides have been prepared from samples with large diameters. The procumbent ray cells in these slides have the highest L/H-ratios (2-3), whereas in the Uw-material the L/H-ratio is 1.5-2.

Leaf Anatomy

Material seen: *Ch. manillana* (Blume) Merr.: Philippines: *Elmer 12800,* Palawan, Mt. Pulgar; *Elmer 12142a,* Magallanes, Mt. Giting-Giting; *Merrill 776,* Luzon, Manila.

In surface view:

Indumentum absent. Unspecialized epidermal cells polygonal, 12-15 × 17-20 μm; slightly modified above midrib and large veins and often strongly divided by thinner walls; cuticular flanges straight, not pitted. Stomata mainly confined to the abaxial surface, paracytic with 3-5 subsidiary cells, guard cells 18-20 × 15 μm.

In transverse section:

Lamina homogeneous. Unspecialized epidermal cells adaxially square or slightly upright, abaxially square or slightly flattened. Stomata slightly raised with well developed outer cuticular ledges.

Hypodermis strongly developed, consisting of 2-3 layers of strongly enlarged cells, except for the one-layered epidermis of slightly enlarged cells in *Elmer 12800.* Mesophyll homogeneous and compact, composed of cubic cells. Midrib adaxially slightly and abaxially distinctly raised, with a vascular bundle with ad- and abaxially supporting collenchyma caps. Veins: the larger ones accompanied by supporting tissue, the minor ones embedded in the mesophyll. Petiole with a single c-shaped vascular bundle supported by a continuous collenchyma cap nearly entirely surrounding the vascular tissue. Cystoliths abundant in the mesophyll, 4-12 together, crystalline part regularly built and sharply pointed, length of individual cystoliths 50-80 μm; cystoliths in vascular tissue much shorter and always in pairs. Crystals absent.

3.4. *Gjellerupia* Lauterb.

One species of shrubs and small trees in New Guinea.

Wood Anatomy

Material seen: *G. papuana* Lauterb.: New Guinea: Uw 26742 (*Gjellerup s. n.;* diam. 2 cm).

Growth rings present, composed of vessels, tracheids and parenchyma. Vessels diffuse, solitary with only incidentally two pores connected, 32 (23-53) per sq.mm, diameter 33 (24-45) μm, vessel member length 440 (180-670) μm. Tracheids present in the growth rings.

Fibres very thickwalled: diameter 10-14 μm, walls 5-6 μm. Pits minutely bordered, 2-3 μm. Length 1890 (1450-2250) μm, F/V-ratio 4.3.

Rays uni- and 2-3-seriate; uniseriate rays less than 5%, composed of up to 15 upright cells; multiseriate rays composed of square cells with uniseriate wings of 1-5 weakly upright cells, height 1200-1500 μm. Cystoliths abundant, without stalks, in normal ray cells; surface irregular. Parenchyma apotracheal, diffuse (to diffuse-in-aggregates), in strands of two, three or four cells.

Leaf Anatomy

Material seen: *G. papuana* Lauterb.: New Guinea: *Gjellerup 182,* Biwak Hollandia, Humboldt-Bay.

In surface view:

Indumentum restricted to midrib and veins, consisting of uniseriate, 1-4-celled hairs. Unspecialized cells polygonal, 30-35 × 20-23 μm, slightly elongate above midrib and veins; cuticular flanges straight or slightly curved, pitted or granulate. Stomata mainly confined to the abaxial surface, paracytic with 2-3 subsidiary cells, guard cells 25-27 × 15-17 μm.

In transverse section:

Lamina dorsiventral. Unspecialised cells adaxially much larger than abaxially. Stomata slightly raised with well developed outer cuticular ledges.

Hypodermis absent. Mesophyll composed of one layer of poorly differentiated palisade parenchyma and of spongy tissue composed of rather loosely packed, elongate cells. Midrib with a single vascular bundle with ad- and abaxially supporting collenchyma strands divided by parenchyma. Veins: the larger ones accompanied by supporting collenchyma, the smaller ones embedded in the mesophyll. Petiole with a similar vascular system as the midrib. Cystoliths abundant, in the mesophyll in sphere-like clusters of up to 20 (length of individual cystoliths up to 70 μm) but near the epidermis in pairs (length of individual cystoliths up to 40 μm), crystalline part irregular or granular. Crystals abundant, especially in the abaxially side of the leaf, variable in size and shape.

3.5. *Lepionurus* Blume

One species of small shrubs, occurring from Nepal and Assam to W Malesia.

Wood Anatomy

Material seen: *L. sylvestris* Blume: Indonesia: Uw 26670 (*USw 28597,* Sumatra; diam. 1.5 cm); Uw 26740 (*Backer s. n.,* Java; diam. 0.7 cm); Uw 26743 (*Lorzing 5723,* Sumatra; diam. 0.6 cm); Aw 1932, 1933 (slides).

Growth rings faint. Vessels diffuse, 40-80% in radial and tangential pore multiples of 2-3(8); vessels frequency difficult to count, but at least 30 per sq.mm, diameter 36 (22-58) μm, vessel member length 350 (190-530) μm. Tracheids common, mainly in the vessel multiples.

Fibres very thickwalled: diameter 10-16 μm, walls 4-8 μm. Pits minutely bordered, 2-3 μm. Length (800-2030) μm, F/V-ratio 3.5.

Rays uni- and 2-6-seriate; uniseriate rays 20-35%, composed of up to 10 upright cells; multiseriate rays composed of square und weakly upright cells with uniseriate wings of 1-3(8) upright cells; height 1000-1500 μm. Cystoliths scanty, without stalks, in normal ray cells; surface irregular. Parenchyma apotracheal, diffuse-in-aggregates, in strands of (2)3-4 cells.

Notes: In *L. sylvestris* intervascular pits are found. These are alternate, 4-6 μm and occasionally anastomosing. Uw 26670 was received as "*Champereia decemnervia* Merrill". On the basis of the wood structure the sample was identified as *L. sylvestris,* in spite of slighty longer fibres and abundant cystoliths. Hiepko (pers. comm.) confirmed, that "*Ch. decemnervia*" is an unpublished name for *L. sylvestris.*

Leaf Anatomy

Material seen: *L. sylvestris* Blume: Sumatra: *Lörzing 5723,* Sibolangit; *Forbes 2934.* Java: *Bakhuizen v. d. Brink Jr. 679.*

In surface view:

Indumentum absent. Unspecialised epidermal cells elongate or polygonal, 45-50 × 25 mm, slightly smaller but elongate above midrib and larger veins; cuticular flanges straight, more or less granulate. Stomata confined to the abaxial surface, paracytic with 2-3 subsidiary cells, guard cells 20-25 × 15 to 17 μm.

In transverse section:

Lamina dorsiventral. Epidermal cells flattened, adaxially much larger than abaxially. Stomata slightly raised with well developed outer cuticular ledges.

Hypodermis absent. Mesophyll consisting of 1-2 layers of poorly differentiated palisade parenchyma and of spongy tissue composed of rather compact elongate cells. Midrib adaxially occasionally, abaxially always distinctly raised, with a single vascular bundle (with occasionally a tendency to break up in some parts) with ad- and abaxially supporting strands of thinwalled collenchyma. Veins: always with one vascular bundle, the larger ones accompanied by strands of collenchyma, the smaller ones embedded in the mesophyll. Petiole with one vascular bundle which is always broken in at least two discrete parts by parenchyma; the vascular tissue supported by collenchyma strands divided by parenchyma. Cystoliths abundant, in spherelike clusters of 5-20, crystalline part irregular or granular, usually not refractive, length of individual cystoliths 50-120 μm; cystoliths in pairs usually present. Crystals minute, abundant.

3.6. *Melientha* Pierre

One species of small trees, occurring in Thailand, Malaya, Philippines and N Borneo.

Wood Anatomy

Material seen: *M. suavis* Pierre: Thailand: Uw 26147 (*Maxwell 75-452,* Chanthaburi prov.; diam. 2 cm); Uw 26744 (*Phengnaren 210,* Chon Buri; diam. 0.9 cm).

Growth rings distinct, composed mainly of vessels and tracheids. Vessels solitary with only incidentally two pores connected, 42 (25-64) per sq.mm, diameter 44 (24-60) μm, vessel member length 300 (150-480) μm. Tracheids common, mainly in the growth rings.

Fibres thickwalled: diameter 14-20 μm, walls 3-7 μm. Pits distinctly bordered, 5-6 μm. Length 1210 (850-1700) μm, F/V-ratio 4.0.

Rays uni- and 2-4-seriate; uniseriate rays less than 5%, composed of square cells; multiseriate rays composed of weakly procumbent cells with often uniseriate wings of 1-3 square cells; height 900-1000 μm. Cystoliths abundant, with stalks attached to the outward tangential walls of strongly enlarged cells (ideoblasts); frequently cystoliths in radially adjacent cells and then stalks attached to the joint tangential wall.

Parenchyma apotracheal, diffuse-in-aggregates, in strands of 3-5 cells.

Note: Uw 26744, the smaller sample, deviates from the description in a higher percentage of uniseriate rays (about 20%) and in less distinct growth rings.

Leaf Anatomy

Material seen: *M. suavis* Pierre: Malay Peninsula: *FRI 5386,* Ulu Kelantan; Philippines: *PNH 13753,* Mindanao, Misamis Or. prov., Claveria. – *M. suavis* subsp. *macrocarpa* Hiepko: Sabah: *RSNB 2518,* Mt. Kinabalu, Ulu Liwagu and Ulu Mesilau.

In surface view:

Indumentum absent. Unspecialised epidermal cells polygonal, 20-25 × 30-35 μm, squarish above midrib and veins; cuticular flanges straight, not pitted. Stomata mainly confined to the abaxial surface, paracytic with 3-5 subsidiary cells, guard cells 20-22 × 15 μm.

In transverse section:

Lamina dorsiventral. Unspecialised epidermal cells square or flattened, adaxially as large as or slightly larger than abaxially. Stomata slightly raised with well developed outer cuticular ledges.

Hypodermis consisting of one layer of slightly enlarged cells. Mesophyll consisting of 2-3 layers of poorly differentiated palisade parenchyma and of compact spongy tissue. Midrib adaxially slightly and abaxially distinctly raised, with a single vascular bundle with ad- and abaxially caps of collenchyma. Petiole also with a single vascular bundle, accompanied by continuous collenchyma caps, nearly entirely surrounding the vascular tissue. Cystoliths abundant in the mesophyll in clusters of 4-8, crystalline part regularly built and sharply pointed, length of individual cystoliths 60-90 μm; cystoliths in vascular tissue much smaller and always in pairs. Crystals absent.

3.7. *Opilia* Roxb.

Two species of lianas and shrubs (root parasites): *O. amentacea* Roxb. (including *O. celtidifolia* (Guill. & Perr.) Endl. ex. Walp.) and *O. campestris* Engl. (including *O. strobilifera* Hutch. & E. A. Bruce), occurring in Africa, SE Asia, New Guinea and Australia (cf. Hiepko 1982).

Because of the differences, separate descriptions are given for the lianas (*O. amentacea*) and for the shrubby species (*O. campestris*).

Wood Anatomy

Material studied: *O. amentacea* Roxb. group a: Australia: Uw 27027 (*Hyland 21128 V;* diam. 3.5 cm); New Guinea: Uw 26561 (*Jacobs 9600,* Lae; diam. 3 cm); Uw 26745 (*BW 15523,* Geelvink Bay; diam. 1.3 cm). - *O. amentacea* group b (*'celtidifolia'):* Cameroun: Uw 9482 (*Breteler 2261;* diam. 2.5 cm); Uw 9595 (*Breteler 2986;* diam. 2 cm); Togo: Uw 25866 (*Kersting A 88;* diam. 8 cm); Kenya: (*Hiepko 2623,* Nairobi dist.; diam. 1 cm). - *O. amentacea* ± group c (*'tomentella'*): Tanzania: Uw 25867 (*Goetze 1408;* Ubeya dist.; diam. 4.5 cm). - *O. campestris* Engl.: Kenya: (*Gillett 12657,* Dandu; diam. 0.6 cm; *Hiepko 2608,* Kajiado dist., diam. 2.1 cm); Tanzania: (*Richards 13430,* Nzega dist.; diam. 1.2 cm); Namibia: (*Dinter 5383,* Otavi; diam 0.8 cm). - *O. campestris* var. *strobilifera* (Hutch. & E. A. Bruce) Hiepko: Ethiopia: Uw 26694 (*Burger 3385,* Harar prov.; diam. 1.5 cm).

O. amentacea

Growth rings faint. Vessels solitary with only incidentally two pores connected, 13 to 23 (9-27) per sq.mm, diameter 106 to 137 (20-210) μm, vessel member length 260 to 300 (90-440) μm. Tracheids scanty.

Fibres thinwalled: diameter 15-18 μm, walls 3-4 μm. Pits distinctly bordered, 5-6 μm. Length 820 to 1150 (500-1500) μm, F/V-ratio 3.3.

Rays homogeneous, uni- and 3-5-seriate; uniseriate rays 10-15%, composed of up to 10 procumbent cells; multiseriate rays composed of procumbent cells, without uniseriate margins, height 1250-1500 μm. Cystoliths usually present, usually with stalks attached to one of the tangential walls, in large but normal ray cells; surface smooth or irregular.

Parenchyma apotracheal, scantily diffuse, in strands of 2-4 cells.

Note: The sample from Tanzania (*Goetze 1408;* ± group c) deviates in the following characters. Vessels: diameter 76 (24-140) μm, on av. 50 per sq.mm, vessel member length 330 (220-430) μm. Fibres: length 830 (410-1100) μm, F/V-ratio 2.5. Rays up to 3-seriate, height 1000-1100 μm.

O. campestris

Growth rings distinct, composed of vessels and tracheids. Vessels solitary with only incidentally two pores connected, over 60 per sq.mm, diameter 20 to 30 (11-47) μm, vessel member length 190 to 280 (100-400) μm. Tracheids abundant in growth rings.

Fibres very thickwalled: diameter 10-15 μm, walls 3.5 μm. Pits distinctly bordered, 3-5 μm. Length 490 to 710 (410-1100) μm, F/V-ratio 2.5-2.6.

Rays uni- and 2-seriate; uniseriate rays 25-50%, composed of up to 10 rows of (weakly) procumbent cells; multiseriate rays composed of procumbent cells with one or two rows of square or weakly procumbent margin cells, height 400-800 μm. Cystoliths abundant, without stalks, in normal ray cells (*Burger 3385*) or absent; surface irregular.

Parenchyma apotracheal, scantily diffuse, in strands of 1-2 cells.

Leaf Anatomy

Material seen: *O. amentacea* Roxb. group a: Philippines: *Elmer 12691,* Palawan prov., Brooks Point; New Guinea: *BW 15523,* Geelvink Bay. - *O. amentacea* group b (*'celtidifolia'*): Senegambie (?): *Alleizette 1227;* Cameroun: *Ledermann 2297,* Mbanti; Tanzania: *Stolz 1512,* Nyassa Highlands, Kyimbila. - *O. amentacea* ± group c (*'tomentella'*): Tanzania: *Goetze 1408,* Mbeya dist.; Mozambique: *Schlechter 11571,* Lourenço Marques. - *O. campestris* Engl.: Kenya: *Gillett 12657,* Dandu; Tanzania: *Greenway 4497,* E. Kilimanjaro dist.; Namibia: *Dinter 5383,* Otavi. - *O. campestris* var. *strobilifera* (Hutch. & E. A. Bruce) Hiepko: Ethiopia: *Burger 3385,* Harar prov.

O. amentacea
In surface view:

Indumentum absent. Unspecialised epidermal cells polygonal, 15-20 × 22-28 μm, strongly divided and short above midrib and veins; cuticular flanges straight or slightly curved, sometimes pitted, extending to the hypodermis. Stomata mainly confined to the abaxial surface, paracytic with 4 subsidiary cells, guard cells 25-28 × 18-22 μm.

In transverse section:

Lamina dorsiventral. Unspecialised cells flattened, adaxially as large as abaxially. Stomata slightly raised with well developed outer cuticular ledges.

Hypodermis consisting of one layer of large cells. Mesophyll composed of 2-3 layers of palisade parenchyma and compact spongy tissue of cubic cells. Midrib adaxially slightly, abaxially distinctly raised, with one vascular bundle with adaxially and abaxially strands of collenchyma, divided by parenchyma; the supporting tissue consisting of sclerenchyma in *Lederman 2297* and *Stolz 1512*. Larger veins and petiole with similar vascular and supporting tissue, the collenchyma never replaced. Cystoliths in the mesophyll near the epidermis abundant, often in pairs and quartets, paradermally orientated, length of individual cystoliths 40-60 μm; in the ground tissue of the petiole in spherelike clusters; in some specimens the parenchymatic tissues of the vascular system nearly entirely replaced by cells with paired cystoliths. Crystals absent.

N o t e : Two samples of *O. amentacea* ± group c *('tomentella')* deviate from the description given above in the homogeneous mesophyll. *Schlechter 11571* shows an indumentum similar to that of *O. campestris;* adaxial stomata occur in a frequency of ½-⅓ of the abaxial stomata. *Goetze 1408* shows even more adaxial stomata.

O. campestris
In surface view:

Indumentum consisting of 1-5-celled uniseriate hairs, equally distributed over both surfaces, hairs often branched above the midrib. Unspecialised epidermal cells square or slightly elongate, 15-25 × 25-30 μm, hardly modified above midrib and large veins; cuticular flanges straight, occasionally pitted. Stomata in equal frequencies on both surfaces, paracytic with 4 subsidiary cells, guard cells 25-30 × 17-20 μm.

In transverse section:

Lamina homogeneous. Unspecialised epidermal cells flattened, adaxially slightly larger than abaxially. Stomata slightly raised with well developed outer cuticular ledges.

Hypodermis absent. Mesophyll composed of cubic or anticlinally elongate cells. Midrib not or slightly raised, except incidentally abaxially, with one vascular bundle with adaxial and abaxial caps of collenchyma. Petiole with one vascular bundle, accompanied by strands of collenchyma divided by parenchyma. Cystoliths in the mesophyll near the epidermis abundant, often in pairs and quartets, paradermally orientated, length of individual cystoliths 40-65 μm; in the ground tissue of the petiole in spherelike clusters; paired cystoliths in the parenchymatic tissue of the vascular system abundant. Crystals: occasionally small crystals along the veins and in the mesophyll.

3.8. *Rhopalopilia* Pierre

About eight species of climbing or creeping shrubs, occurring in Africa.

Wood Anatomy

Material seen: *Rh. marquesii* Engl.: Zaïre: Uw 26695 (*Vermoesen 2523;* diam. 0.8 cm); Angola: *Gossweiler 8547;* diam. 0.5 cm). - *Rh. pallens* Pierre: Zaïre: (*Bouquet 600;* diam. 0.5 cm). - *Rh. umbellulata* (Baillon) Engl.: Tanzania: (*Semsei 2250,* Pangani; diam. 0.4 cm); (*Peter 44919,* Usaramo; diam. 0.4 cm).

Growth rings faint. Vessels diffuse, only incidentally two pores connected, over 60 per sq.mm, diameter 26 to 68 (13-90) μm, vessel member length 240-300 (150-420) μm.

Fibres thinwalled (diameter 10-12 μm, walls 2-3 μm) to thickwalled (diameter 6-8μm, walls 3 μm). Pits distinctly bordered, often frequent, 5-6 μm. Length 570 to 740 (350-980) μm, F/V-ratio 1.9-2.9.

Rays uniseriate and 2-6-seriate; uniseriate rays 0-50%, composed of upright cells; multiseriate rays composed of square and (weakly) upright cells without uniseriate margins, height 2000-3000 μm.

Parenchyma apotracheal, scantily diffuse, in strands of 1-2 cells.

Notes: *Rh. pallens* shows distinct growth rings, composed of frequent vessels and tracheids. The three studied species differ in the following quantitative characters:

		Rh. marquesii	*Rh. pallens*	*Rh. umbellulata*
vessel	diameter (μm)	55 (17-90)	26 (13-35)	41 (20-55)
member	length (μm)	295 (190-420)	260 (160-420)	265 (160-400)
fibre	wall (μm)	2-3	3	2-3
	lumen (μm)	3-8	1 (2)	1-8
	length (μm)	572 (470-730)	740 (530-860)	610 (350-850)
F/V-ratio		1.9	2.9	2.6
ray	height (μm)	3500	?	2000-3000
	width (cells)	4-6	4-5 (7)	2-6
cystoliths		x	-	-

Leaf Anatomy

Material seen: *Rh. altescandens* Mildbr. ex Sleumer: Cameroun: *Mildbraed. 4425,* Bezirk Molundu. - *Rh. marquesii* Engl.: Angola: *Gossweiler 8547.* - *Rh. pallens* Pierre: Cameroun: *Zenker 4338,* Bipinde; Zaïre: *Bouquet 600.* - *Rh. umbellulata* (Baillon) Engl.: Tanzania: *Semsei 2250,* Pangani; *Peter 44919,* Usaramo; *Faulkner 1919,* Tanga distr.

In surface view:

Indumentum variable: 1-2-celled hairs spread over the abaxial and less frequent over the adaxial surface in *Rh. pallens;* 5-8-celled, uniseriate hairs spread over the abaxial surface and adaxially confined to the midrib in *Rh. marquesii;* absent in *Rh. altescandens* and *Rh. umbellulata.* Unspecialised epidermal cells polygonal, 17-23 × 30-40 μm, strongly divided and short above midrib and large veins; cuticular flanges straight or slightly curved, pitted. Stomata mainly confined to the abaxial surface but adaxially also stomata present in *Rh. umbellulata (Semsei 2250):* paracytic with 4 subsidiary cells, guard cells 22-25 × 15-20 μm.

In transverse section:

Lamina dorsiventral. Unspecialised epidermal cells adaxially more flattened than abaxially. In

Rh. marquesii groups of silicified epidermal cells occur. Stomata slightly raised with well developed outer cuticular ledges.

Hypodermis absent. Mesophyll composed of 1-2 layers of weakly differentiated palisade parenchyma and compact spongy tissue, except for *Rh. altescandens* where the mesophyll is homogeneous, and *Rh. umbellulata* where relatively well differentiated 3-4 layered palisade parenchyma occurs; in the spongy tissue large ideoblasts occur, often filled with large granular deposits, possibly silica; these ideoblasts almost replacing the spongy tissue in *Rh. pallens* and *Rh. marquesii*. Midrib adaxially not or slightly raised, abaxially distinctly raised, with one vascular bundle with adaxially and abaxially caps of collenchyma, occasionally forming a continuous ring. Petiole with one vascular bundle and strands of collenchyma divided by parenchyma; in some species the ground tissue replaced by ideoblasts and then the collenchyma forming a continuous ring around the vascular tissue. Cystoliths common in the mesophyll, infrequent in ground tissue of petiole; usually in pairs, length of individual cystoliths 30-40 μm. Crystals abundant, minute, in and near the adaxial epidermis and often also in the collenchyma caps of midrib and veins, but absent in *Rh. altescandens*.

N o t e s : Cystoliths in clusters of 5-12, up to 80 μm, are present in *Rh. pallens* (*Zenker 4338*); *Rh. pallens* (*Bouquet 600*) lacks cystoliths entirely. The unspecialised epidermal cells in *Rh. altescandens* are about half as large as in the other species.

3.9. *Urobotrya* Stapf

The genus consists of two, geographically widely separated sections. The differences in wood anatomy of both sections are mainly quantitative and slight. Because of the discussion on the taxonomy of the genus, separate descriptions are given.

U. sect. *Lepionuroides* Hiepko
Five species of large shrubs in SE Asia.

W o o d A n a t o m y
Material seen: *U. floresensis* Hiepko: Flores: Uw 26770 (*Schmutz 3159,* Manggarai; diam. 3.2 cm). - *U. latisquama* (Gagnepain) Hiepko: Vietnam: (*Petelot 5952;* diam. 0.4 cm). - *U. siamensis* Hiepko: Thailand: Uw 26146 (*Geesink & Hiepko 7915,* Chanthaburi prov.; diam. 1.7 cm).

Growth rings faint. Vessels diffuse, solitary, with only incidentally two pores connected, 30 to 38 (24-45) per sq.mm, diameter 43 to 45 (29-67) μm, vessel member length 400 to 430 (180-600) μm. Tracheids scanty, scarsely distinguishable from fibres.

Fibres very thickwalled: diameter 15-20 μm, walls 4-8 μm. Pits distinctly bordered, 4-5 μm. Length 1180-1590 (680-1850) μm, F/V-ratio 3.3.

Rays uni- and 2-4-seriate; uniseriate rays 10-20%, composed of upright cells; multiseriate rays composed of square cells with uniseriate margins of 1-6 weakly upright cells, height 1200-1500 μm. Cystoliths abundant in *U. siamensis,* without stalks in normal square and upright cells; surface irregular.

Parenchyma apotracheal, diffuse-in-aggregates, in strands of 2-4 cells.

N o t e : *U. latisquama* differs in many aspects from the description given above: Growth rings faint, except for one distinct ring composed of vessels and tracheids. Vessels diffuse, 40-80% in radial pore multiples, over 40 per sq.mm, diameter 34 (18-48) μm, vessel member length 380 (190-560) μm. Tracheids abundant in growth rings and pore multiples. Fibre length 1045 (700-1300) μm. Rays: uni-

seriate rays 50%; multiseriate rays composed of weakly upright cells, with uniseriate margins of 1-3 upright cells.

Leaf Anatomy

Material seen: *U. floresensis* Hiepko: Flores: *Schmutz 4460,* Mangarai. - *U. latisquama* (Gagnepain) Hiepko: Vietnam: *Petelot 5952,* prov. de Vinh Yen. - *U. parviflora* Hiepko: Borneo: *Kostermans 21116,* Berau, Tdg. Redeb; Saba: *SAN 66802,* Tenom dist., near Kampong Pomila'an. - *U. siamensis* Hiepko: Thailand: *Kerr 10155,* Kanburi, Sisawat; *Geesink & Hiepko 7915,* Chanthaburi prov.

In surface view:

Indumentum variable: 2-6-celled, uniseriate hairs restricted to midrib and veins in *U. parviflora;* on the abaxial side only in *U. floresensis* and *U. latisquama;* absent in *U. siamensis.* Unspecialised epidermal cells polygonal, often elongate, 30-40 × 18-25 μm, nearly similar above midrib and veins; cuticular flanges straight or curved, usually pitted. Stomata almost entirely confined to the abaxial surface, paracytic with 2-4 subsidiary cells, guard cells 20-27 × 15-19 μm.

In transverse section:

Lamina dorsiventral. Unspecialised epidermal cells flattened, adaxially much larger than abaxially. Stomata slightly raised with well developed outer cuticular ledges.

Hypodermis absent. Mesophyll composed of 2-3-layered poorly differentiated palisade parenchyma (lacking in *U. parviflora, Kostermans 21116*) and loosely built spongy tissue. Midrib adaxially occasionally, abaxially always distinctly raised, with one vascular bundle (usually broken in several parts except in *U. latisquama*) with adaxially and abaxially supporting strands of collenchyma divided by parenchyma, (but collenchyma in two caps in *U. latisquama*). Petiole with a similar vascular system and supporting tissue. Cystoliths common in the mesophyll and ground tissue of the petiole, in clusters of 2-5, length of individual cystoliths 50-80 μm, (*U. siamensis*) or most cystoliths in pairs, length of individual cystoliths 30-50 μm (*U. floresensis, U. parviflora*) or in spherelike clusters of up to 20, length of individual cystoliths up to 110 μm (*U. latisquama*). Crystals usually present in low quantities.

U. sect. *Urobotrya*

Two species of shrubs in Africa.

Wood Anatomy

Material seen: *U. sparsiflora* (Engl.) Hiepko: Zaïre: (*Devred 2625;* diam. 0.5 cm); (*Louis 13340;* diam. 0.5 cm); (*Evrard 736;* diam. 0.4 cm); (*Gentil s. n.,* Kasai; diam. 0.4 cm).

Growth rings fairly distinct. Vessels diffuse, solitary with only incidentally two pores connected, over 80 per sq.mm, diameter 30 (15-45) μm, vessel member length 475 (280-750) μm.

Fibres rather thickwalled: diameter 10-15 μm. Pits distinctly bordered, 5 μm. Length 1000 (775-1375) μm. F/V-ratio 2.3.

Rays uniseriate and 2-5-seriate; uniseriate rays 30-40%, composed of up to 12 strongly upright cells; multiseriate rays composed of upright cells, with uniseriate margins of 1-3 (8) strongly upright cells; height 2000-3000 μm. Cystoliths absent.

Parenchyma apotracheal, scantily diffuse, in strands of 2-4 cells.

Notes: The samples are very thin, but show a marked homogeneity, especially in vessel member length and fibre length. The largest samples show the largest vessel diameters and the lowest ray

heights. In *Evrard 736* and *Gentil s. n.* a proportion of the fibres shows spiral thickenings. These fibres occur mainly near the vessels and show very few pits.

Leaf Anatomy

Material seen: *U. congolana* (Baillon) Hiepko: Equatorial Guinea: *Tessmann 154.* - *U. sparsiflora* (Engl.) Hiepko: Zaïre: *Devred 2625,* Kiyaka-Kwango.

In surface view:

Indumentum variable: hairs onecelled, restricted to midrib and veins, in *U. congolana;* 1-4-celled, uniseriate and uncinnate spread over the abaxial surface, in *U. sparsiflora.* Unspecialised epidermal cells polygonal, elongate, 40-50 × 25-45 μm, slightly modified and elongate above midrib and veins; cuticular flanges straight or curved, sometimes pitted. Stomata confined to the abaxial surface, paracytic with 4 subsidiary cells, guard cells 25-29 × 22-24 μm.

In transverse section:

Unspecialised epidermal cells flattened, adaxially slightly larger than abaxially. Stomata slightly raised with well developed outer cuticular ledges.

Hypodermis absent. Mesophyll consisting of 1-2 layers of weakly differentiated palisade parenchyma and spongy tissue with conspicuous intercellular spaces; throughout the mesophyll a "network" of branched lignified fibres, apparently not associated with the veins. Midrib adaxially not or slightly raised, abaxially distinctly raised, with a single vascular bundle, adaxially supported by thin-walled lignified fibres or by collenchyma, abaxially by sclerenchyma fibres. Larger veins accompanied by sclerenchyma fibres. Petiole with a single vascular bundle supported by collenchyma strands. Cystoliths in the mesophyll abundant; paired, length of individual cystoliths 50-60 μm (*U. congolana*) or spherelike clusters of up to 15, length of individual cystoliths 60-90 μm (*U. sparsiflora*); crystalline part irregular or granular; cystoliths in the ground tissue of the petiole solitary or paired, highly refractive. Crystals minute, abundant in epidermis and palisade parenchyma.

4. Discussion

4.1. Diagnostic and taxonomic value of wood anatomical features

Growth rings

Distinct growth rings, several vessels wide and containing a large proportion of tracheids, are found in *Gjellerupia, Melientha, Opilia campestris* and *Rhopalopilia pallens.* Single rings found in *Urobotrya latisquama* have the same composition. In all other *Opiliaceae* faint growth rings, indicated by slight differences in vessel diameter and frequency, and by fibre lumen differences are found. The occurrence of distinct growth rings perhaps has some diagnostic value on the species level.

Vessels

The vessels are solitary with only incidentally vessels radially or tangentially connected. Exceptions are *Lepionurus sylvestris* and *Urobotrya latisquama* (fig. 3). In both taxa 40-80% of the vessels are arranged in radial multiples.

This character, therefore at least has diagnostic value. Vessel arrangement is known to be taxonomically and systematically relevant in other plant groups.

The shape of the vessels has been omitted from the generic descriptions as the vessels are in all studied specimens round or oval.

Vessel diameter and frequency vary relatively little within the family. Perhaps these characters

have some diagnostic value, but because of the overlap between genera the taxonomic value is nil. Largest diameters are found in the climbing species of *Opilia* (fig. 2), and in *Agonandra*. The shortest average vessel member lengths are 190 and 260 μm in *Opilia* and *Rhopalopilia*, and more than 400 μm in *Gjellerupia* and *Urobotrya*. This feature has diagnostic value, as it is rather constant on the species level. On the generic level, overlap is considerable.

As the vessels are mostly solitary, intervascular pits are very rare and were often not found at all. Therefore they were not included in the descriptions. If present, they have a diameter of 5-6 μm.

Vessel-parenchyma and vessel-ray pits are half bordered; sometimes the slitlike apertures of the borders are coalescent. Incidentally round or oval "perforations" occur. Their diameter varies from 8 μm to 30 μm. They were found in all examined samples as well as in the few samples examined of the *Olacaceae* and *Santalaceae* (see also Metcalfe & Chalk, 1950, p. 364).

Since variations in size and occurrence appear to be related with the size of the vessels and the abundancy of the axial parenchyma, rather than with any taxonomic limits, they have been omitted from the generic descriptions. End wall angles were estimated from the maceration slides. They seem to be correlated with vessel diameters. As they apparently have no diagnostic or taxonomic value, they were not included in the descriptions.

Tracheids

Tracheids are found in large numbers in the taxa with distinct growth rings and in the specimens of *Cansjera* studied, were they ensheath the vessels. Sometimes they are difficult to recognize because of intermediates between narrow vessel members, tracheids and fibres. Vascular tracheids were observed in *Opilia amentacea*.

Fibres

Most *Opiliaceae* have thickwalled, sparsely pitted fibres. Exceptions are *Opilia amentacea*, *Rhopalopilia marquesii* and *Rh. umbellulata;* these have thinwalled and densely pitted fibres. All species with thinwalled fibres are lianas. The occurrence of thinner-walled and more densely pitted fibres in lianas as compared to shrubby or tree-shaped allies is quite common. Thus it does not seem to make sense to attribute taxonomic value to these characters. It is remarkable, that the fibres of *Cansjera rheedei*, also a liana, are thickwalled. It is an open question, in how far this is due to the fact that this species is a root parasite.

Most fibre pits in the *Opiliaceae* are distinctly bordered, 3-6 μm in diameter. In *Lepionurus* and *Gjellerupia* the borders are not over 3 μm. Differences in size of fibre pit borders in general are considered to be a useful and reliable diagnostic and taxonomic character, but the differences within *Opiliaceae* are fairly small and in some specimens the sizes vary only a few μms.

Average fibre lengths range from 490 μm in *Opilia campestris* to 2400 μm in *Agonandra silvatica*. Because of the overlap, the diagnostic value on generic level is nil. The F/V-ratio may be a useful diagnostic and taxonomic character. Within the family it ranges from 1.9 in *Rhopalopilia marquesii* to 6.2 in *Agonandra brasiliensis*. With the help of this character *Agonandra* can be distinguished: 4.5-6.2 against 1.9-4.6 in the rest of the family.

Rays

With the exception of one specimen of *Rhopalopilia marquesii* (Uw 26695), in all studied samples both uniseriate and multiseriate rays occur. The percentage of uniseriate rays varies from less than 5% to more than 50%, the lowest percentages are found in *Agonandra* (fig. 4), *Champereia*, *Gjellerupia* and *Melientha*. Commonly both uniseriate and multiseriate rays are composed of square and (weakly) upright cells (fig. 6, 8). In *Champereia* (fig. 5) and *Melientha* (fig. 7) the multiseriate parts of the rays are

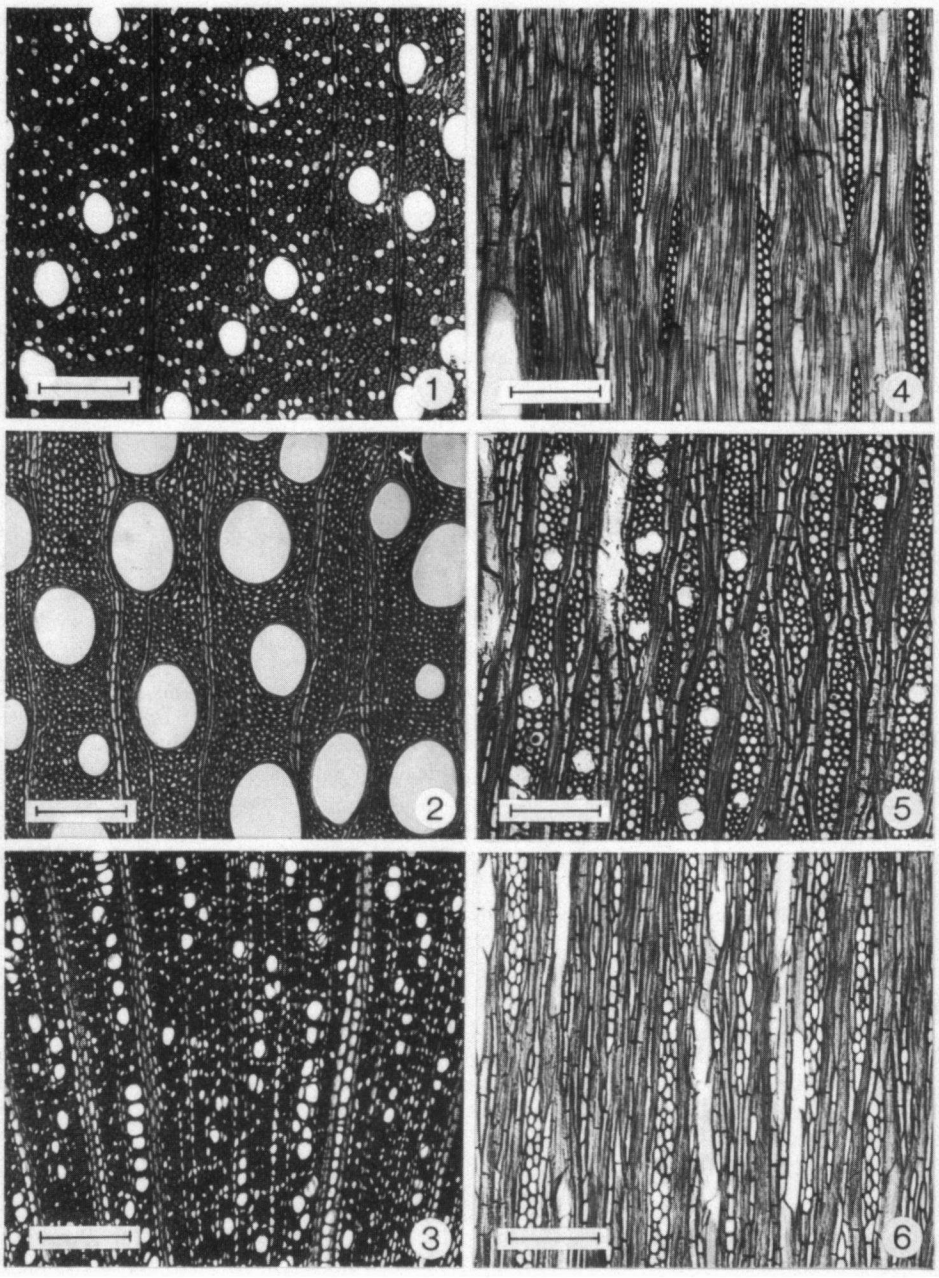

Fig. 1-6. Transverse and tangential wood sections of *Opiliaceae*. 1-*Agonandra brasiliensis* (Uw 18822), tr. 2-*Opilia amentacea* (Uw 9595), tr. 3-*Urobotrya latisquama* (*Petelot 5952*), tr. 4-*Agonandra silvatica* (Uw 8072), tg. 5-*Champereia manillana* (Uw 26669), tg. 6-*Urobotrya latisquama (Petelot 5952)*, tg. Standard 200 μm.

composed of procumbent cells, in *Opilia* (fig. 9) and *Agonandra* uni- and multiseriate rays are composed of procumbent cells, with at the utmost a few square margin cells.

Both features - percentage of uniseriates and ray cell type - have diagnostic value on the generic level. The composition of the rays is known to have taxonomic value in other plant groups. Because of the consistency within genera, the same may be assumed for *Opiliaceae*. Unfortunately, only small samples were available of *Cansjera, Rhopalopilia* and *Urobotrya* sect. *Urobotrya*. The wood in these samples might show juvenile characters. It remains to be investigated whether the square and upright cells will persist in subsequent growth zones, or be replaced by procumbent ray cells.

The width of the rays varies from 2- to 6-seriate, with the exception of one sample of *Rhopalopilia marquesii* (Uw 26695), where 7-15-seriate rays occur. The character may have some diagnostic value in addition to other characters. Ray height and presence of uniseriate wings vary within species, and lack diagnostic or taxonomic value, except perhaps in *Agonandra*, where *A. silvatica* can be recognized by its 650-800 μm high rays, in contrast to 230-320 μm high rays in other species.

Parenchyma

All *Opiliaceae* have apotracheal parenchyma. It can be described as diffuse-in-aggregates in *Lepionurus, Urobotrya* sect. *Lepionuroides, Agonandra* (fig. 1, 3), *Champereia* and *Melientha*. In *Cansjera, Gjellerupia, Opilia, Rhopalopilia,* and *Urobotrya sparsiflora,* less parenchyma was found, so that it may be described as diffuse. The differences, however, are slight. In a few samples of *Lepionurus* narrowly paratracheal parenchyma was found. The parenchyma strands are (predominantly) 1-2 celled in *Agonandra, Cansjera, Rhopalopilia,* and *Opilia campestris*. In the other taxa 3-4-celled strands are predominant with occasional strands up to 6 cells. Taken together, parenchyma distribution and number of cells per strand are useful in the identification of genera, in addition to other characters.

Cystoliths

The occurrence of cystoliths in wood is only known for the *Opiliaceae* and for one genus of *Hernandiaceae* and of *Acanthaceae* (ter Welle 1980). In *Opiliaceae,* they are a fairly constant phenomenon: in all species studied they occur, with the exception of the species of *Agonandra, Opilia campestris, Urobotrya floresensis, U. latisquama,* and *U. sparsiflora, Cansjera parvifolia, Rhopalopilia pallens* and *Rh. umbellulata*. Four types can be distinguished:

a: cystoliths in large ideoblasts (about three times the size of the normal procumbent ray cells) in the multiseriate rays; refractive part consisting of four lobes, which are joined along the length axis; pedicel not enclosed in the refractive part and usually attached to the outward tangential wall; radial twin cystoliths frequent (*Champereia, Melientha* [fig. 7]).

b: cystoliths in ideoblasts (slightly enlarged in comparison to the normal, square to slightly upright ray cells); refractive part with irregular surface; pedicel included in the refractive part and attached to one of the cell walls; tangential twin cystoliths scanty (*Rhopalopilia*).

c: cystoliths in normal (procumbent) cells in uni- and multiseriate rays; surface of the refractive part smooth or irregular; pedicel included in the refractive part and attached to one of the cell walls, but absent in some samples; tangential twin cystoliths scanty (*Opilia*, fig. 9).

d: cystoliths in normal (square and upright) cells in uni- and multiseriate rays; refractive part filling the cells entirely, granular or with irregular surfaces; pedicel absent (*Cansjera, Gjellerupia, Lepionurus* [fig. 8], *Urobotrya siamensis*).

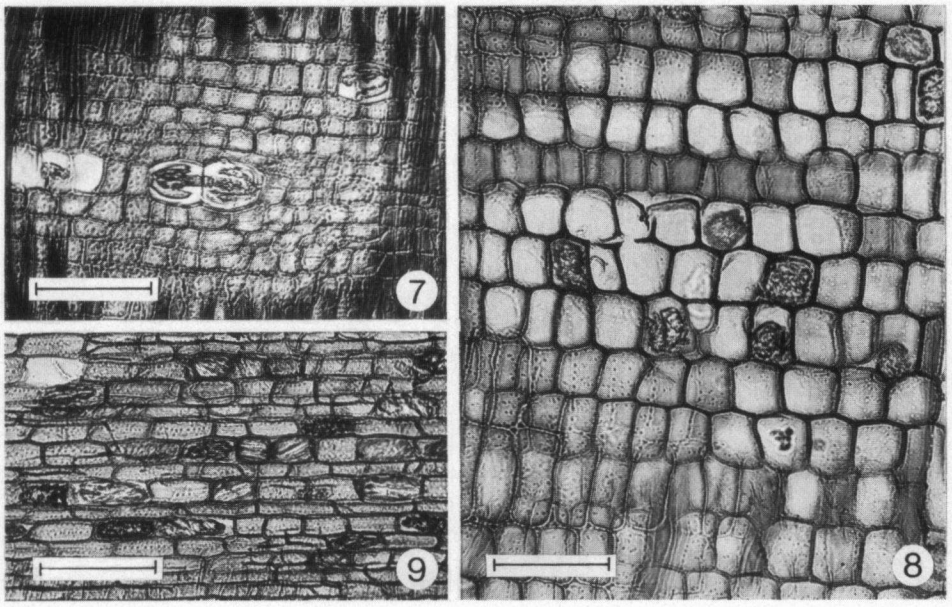

Fig. 7-9. Radial woodsections of *Opiliaceae*. 7-*Melientha suavis* (Uw 26147). 8-*Lepionurus sylvestris* (Uw 26670). 9-*Opilia amentacea* (Uw 25866). Standard 100 μm.

4.2. Diagnostic and taxonomic value of leaf anatomical features

Indumentum

The hairs found in *Opiliaceae* are mostly uniseriate, 1-8-cellular. Uncinate hairs are present in *Urobotrya sparsiflora* (fig. 14). In the samples of *Cansjera parvifolia* (fig. 13) hairs are nearly exclusively branched, in *Opilia amentacea* group c *('tomentella')* and *O. campestris* branched hairs were observed above midrib and veins, whereas uniseriate hairs are predominant elsewhere. (The branched hairs can be described as: three-to five-armed, multicellular, thickwalled trichomes [Theobald, Krahulik & Collins 1979, fig. 5.3., m-n]). In these last three taxa the hairs are distributed over both surfaces in the same way: sparsely with a higher frequency above midrib and veins. Other distribution patterns are: hairs restricted to midrib and veins, or adaxially hairs restricted to midrib and veins, abaxially hairs distributed over the entire surface. In several taxa no hairs were found. These four distribution types are not constant in all genera. Furthermore, in some species the frequency of the hairs varies. Diagnostic value may be found in the shape of the hairs.

Epidermal cells

In surface view the unspecialised cells in all *Opiliaceae* have straight or slightly curved anticlinal walls. Above midrib and large veins the cells are arranged in regular rows and appear to be more or less elongate. In five genera (*Cansjera, Champereia, Melientha, Opilia* p. p., and *Rhopalopilia*) the cells above the midrib and large veins are more strongly divided and are squarish. In *Champereia, Melientha, Opilia,* and *Cansjera* many thin anticlinal walls were observed, mainly restricted to the areas along midrib and veins.

In transverse section epidermal cells are square or flattened. The adaxial cells are much larger than the abaxial ones in *Agonandra, Gjellerupia, Lepionurus* and *Urobotrya* sect. *Lepionurus.* A smaller difference in size between adaxial and abaxial cells was observed in *Rhopalopilia* and *Urobotrya* sect. *Urobotrya,* whereas in *Cansjera, Champereia, Melientha* and *Opilia* the differences are negligible. Contrary to the situation in *Olacaceae* (Baas et al. 1982), where this feature varies at and below the species level, in our material these differences in size are constant.

Stomata

In most *Opiliaceae* the stomata are restricted to the abaxial surface. However, in *Agonandra excelsa, Cansjera parvifolia, Opilia amentacea* group c (*'tomentella'*) and *O. campestris,* stomata occur on both surfaces in about equal frequencies. In a single specimen of *O. amentacea* group c and of *Rhopalopilia umbellulata* adaxial stomata were observed in a frequency of about 1: 5 of the abaxial ones.

All stomata found in *Opiliaceae* are of the paracytic type (fig. 10). The number of subsidiary cells is often slightly variable (2-3 in *Lepionurus* and *Gjellerupia;* 2-4 in *Agonandra, Cansjera* and *Urobotrya* sect. *Lepionuroides;* 3-5 in *Champereia* and *Melientha*), but in *Opilia, Rhopalopilia,* and *Urobotrya* sect. *Urobotrya* always 4 subsidiary cells were found.

The size of the pairs of guard cells is fairly constant on the generic level. The smallest are found in *Champereia* and *Melientha* (18-22 × 15 μm), the largest in *Agonandra* (25-35 × 18-25 μm). An exception is *Agonandra granadensis,* which has much smaller stomata (25 × 15 μm). These appear in transverse section to be sunken below the level of the epidermis, whereas in all other *Opiliaceae* the stomata are in level with the epidermis or slightly raised. In *Gjellerupia, Lepionurus, Urobotrya latisquama, Champereia, Melientha,* and *Rhopalopilia* groups of silicified epidermal cells occur, often in clusters around the stomatal complexes. The frequence may vary considerable, and this feature is not recorded in the generic descriptions. However slight the differences may be, the stomatal features seem to have some diagnostic and taxonomic value.

Cuticle thickness

All *Opiliaceae* have cuticles abaxially 2-4 μm, adaxially 3-5 μm thick. The only exceptions are *Agonandra excelsa* and *Opilia amentacea* with cuticles up to 8 μm thick. This feature is not included in the generic descriptions.

Hypodermis

A hypodermis of one layer of slightly enlarged cells occurs in *Champereia, Melientha,* and *Opilia amentacea.* In two specimens of *Champereia* the hypodermis consists of 2-3 layers of strongly enlarged cells. Although the hypodermis in *O. amentacea* group c (*'tomentella'*) is rather indistinct, this character has diagnostic value on the species level.

Mesophyll

Usually a distinction can be made between palisade parenchyma and spongy tissue, although in many taxa the mesophyll is only weakly differentiated with 1-2 layers of palisade parenchyma. Palisade parenchyma consisting of 2-4 layers of relatively well differentiated cells was found in *Agonandra excelsa, Cansjera rheedei, Melientha, Opilia amentacea, Rhopalopilia marquesii* and *Rh. umbellulata. Agonandra excelsa* is the only taxon with palisade parenchyma both adaxially and abaxially (fig. 11).

In *Champereia, Cansjera leptostachya, C. parvifolia, Opilia amentacea* group c (*'tomentella'*) and *O. campestris* a homogeneous tissue consisting of cubic cells occurs. Independent of the presence of palisade parenchyma, the spongy tissue can be compact or looser with notable intercellular spaces.

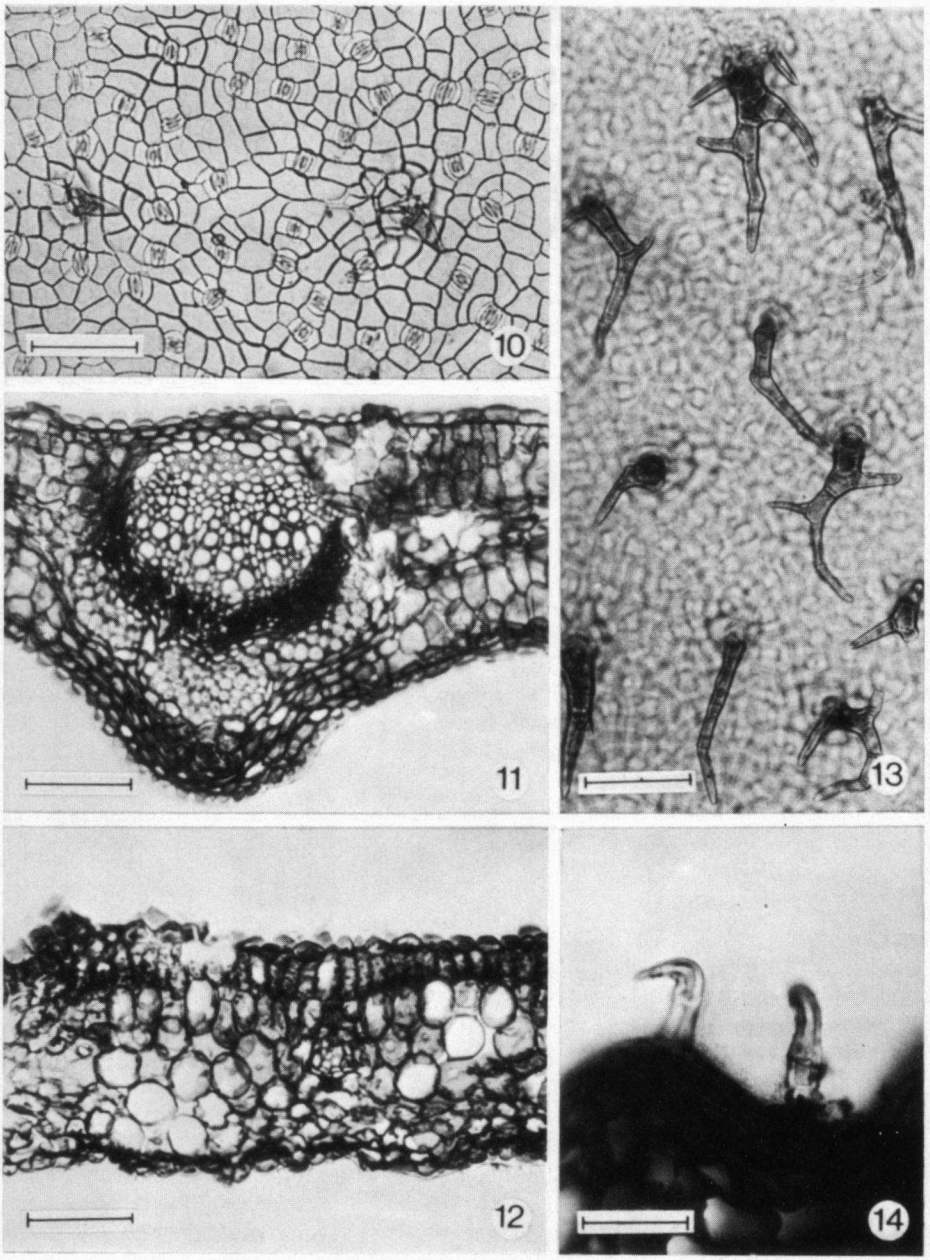

Fig. 10-14. 10-*Opilia campestris* (*Gillet 12657*), abaxial epidermis with stomata and short hairs. 11-*Agonandra excelsa*. (*Hieronymus & Lorentz 653*), tr. sect. of midrib and mesophyll. 12-*Rhopalopilia pallens* (*Bouquet 600*), tr. sect. of mesophyll. 13-*Cansjera parvifolia* (*Helfer s. n.*), branched hairs. 14-*Urobotrya sparsiflora* (*Devred 2625*), uncinnate hairs on lamina. Standard 100 μm.

Highly compact spongy tissue, consisting of small cubic cells, occurs in *Cansjera, Melientha, Champereia, Opilia,* and *Rhopalopilia.* In *Gjellerupia, Lepionurus,* and *Urobotrya* sect. *Lepionuroides* it is less compact with paradermally elongate cells. In *Agonandra* large cells with distinct intercellular spaces are found. In *Urobotrya* sect. *Urobotrya* the loosest spongy tissue of the family was observed.

The differences between "compact" and "loosely packed", and between "weakly" and "relatively well" differentiated are gradual, and probably directly influenced by ecological factors. The taxonomic value therefore seems to be nil. Nevertheless on the species level the structure of the mesophyll may have some diagnostic value.

Ideoblasts

In the spongy tissue of all representatives of *Rhopalopilia* strongly enlarged ideoblasts were found (fig. 12). In some species they replace the spongy tissue almost entirely. In some of them crystalline structures were found, in others silica-like balls. Perhaps they are allied to the "silica deposits" reported for *Schoepfia fragrans* (Baas et al. 1982) but they are much larger. It cannot be stated with certainty that the deposits consist of silica in spite of the resemblance with well-documented silica deposits. Staining with carbolic acid did not result in the expected orange-rose colour. As ideoblasts were not found in other *Opiliaceae,* this character has diagnostic, and probably taxonomic, value on the generic level.

Vascular system of midrib and veins

Midrib and large veins show very little variation: they have a single, open vascular arc-shaped bundle, which may be broken by parenchymatic tissue in *Agonandra excelsa, Lepionurus sylvestris* and *Urobotrya* sect. *Lepionuroides.* Abaxial and adaxial supporting tissue consists of collenchyma, except for *Agonandra excelsa, Urobotrya* sect. *Urobotrya* and some specimens of *Opilia amentacea* where sclerenchyma fibres were found. The supporting tissue is arranged in two continuous kidney-shaped caps in *Cansjera, Champereia, Melientha, Opilia campestris* and *Rhopalopilia.* In the other taxa the caps are broken by parenchymatic tissue. The minor veins are embedded in the mesophyll. They always end in complexes of brachysclereids, which show only limited variation.

Petiole

The vascular system of the petiole is highly similar to that of the midrib. A single open vascular arc is the basic type, which tends to become a closed vascular ring in *Champereia* and *Melientha.* The vascular arc may be divided in several parts in species of *Agonandra, Lepionurus* and *Urobotrya* sect. *Urobotrya.* The supporting tissue always consists of collenchyma and forms either two caps, or one continuous cap nearly surrounding the vascular tissue (*Champereia, Melientha,* and *Rhopalopilia* p. p.).

Cystoliths

One of the most conspicuous features, found in all examined taxa, is the presence of leaf cystoliths. They are usually most abundant in the mesophyll, but also occur in the ground tissue of the petiole and in the parenchymatic ray tissue of the vascular system. In the vascular tissue cystoliths always occur in pairs. In the mesophyll and ground tissue of the petiole most cystoliths are arranged in clusters consisting of more than six cystoliths (each of them up to 90 μm long), joined in a central point, thus forming a sphere.

Some deviations from this "normal" type allow us to recognize (groups of) genera.

– In *Champereia* and *Melientha* the crystalline parts of the cystoliths are regularly built, sharply pointed and highly refractive (fig. 16).

– In *Gjellerupia, Lepionurus, Urobotrya* sect. *Urobotrya* and *U. latisquama* large spheres can be found consisting of up to 20 cystoliths. In *Lepionurus* (fig. 15) and *Urobotrya latisquama* the individual

cystoliths are up to 120 μm long, in *Gjellerupia* and *U.* sect. *Urobotrya* the length does not exceed 90 μm. In this type the crystalline parts are not or only weakly refractive.

– The species of *Opilia* have most cystoliths arranged in pairs or quartets (fig. 17). Often they are paradermally situated near the epidermis. The crystalline parts are highly refractive.

– In all taxa some paired cystoliths can be found in the mesophyll and in the ground tissue of the petiole; they are dominant in *Cansjera* (fig. 18), *Rhopalopilia, Urobotrya floresensis* and *U. parviflora.*

– Solitary cystoliths accompany the bundles of sclerenchyma fibres around the vascular tissue in *Agonandra excelsa* (fig. 19).

Crystals

Crystals are absent in *Agonandra, Champereia, Melientha* and *Opilia amentacea.* In all other taxa rhombic crystals occur in varying quantities, sizes and shapes. Clusters of mesophyll cells filled with minute crystals occur in all specimens of *Cansjera,* and incidentally in a single specimen of *Lepionurus* and *Rhopalopilia.*

4.3. Comparison of wood and leaf features of *Opiliaceae;* comments on the generic delimitations and affinities.

Champereia and *Melientha*

The close affinity of these two genera, suggested by the morphological resemblances, is fully confirmed. In nearly all wood and leaf anatomical features they are similar, the most important differences with other genera being found in the presence of a c-shaped continuous collenchyma cap around the vascular tissue in the petiole and midrib, the vascular system tending to become a closed cylinder and the presence of wood cystoliths type a.

The differences between *Champereia* and *Melientha* are found in the presence of palisade parenchyma in *Melientha* against homogeneous mesophyll in *Champereia* (as pointed out by Baas et al. [1982], ecological factors may influence the structure of the mesophyll considerably), and in the more differentiated hypodermis in *Champereia.*

Opilia

The genus can be distinguished by the exclusive procumbent ray cells in uni- and multiseriate rays, wood cystoliths type c, and paradermal leaf cystoliths. The wood and leaf samples of *O. amentacea* from Australasia and Africa are highly similar which supports Hiepko's decision (1982) that it is impossible to separate the African populations as *O. celtidifolia.* Nearly the same can be said for *O. campestris* and *"O. strobilifera".* The two pairs of "species", however, show a marked difference between them in both wood and leaf features:

The climbing species *O. amentacea* shows the widest vessels within the family, thinwalled and densely pitted fibres, 3-5-seriate rays, 3-4-celled parenchyma strands; glabrous leaves with only abaxial stomata, a hypodermis, well differentiated palisade parenchyma, and sclerenchymatic supporting tissue along midrib and veins. The shrubby species *O. campestris* shows the narrowest vessels in the family, 1-2-seriate rays, 1-2-celled parenchyma strands; leaf indumentum of partly branched hairs, ad- and abaxial stomata, no hypodermis, an undifferentiated mesophyll consisting of cubic cells, and only collenchymatic tissue along the midrib. *O. amentacea* group c (*'tomentella'*) is wood anatomically next related to *O. amentacea* (group a and b), leaf anatomically to *O. campestris.* Morphologically, *O. amentacea* group c (*'tomentella'*) is very variable. The number of leaf samples studied is too small to give an indication about the anatomical variation, but the differences between *O. amentacea* group c (*'tomentella'*) and the other African samples of *O. amentacea* are considerable.

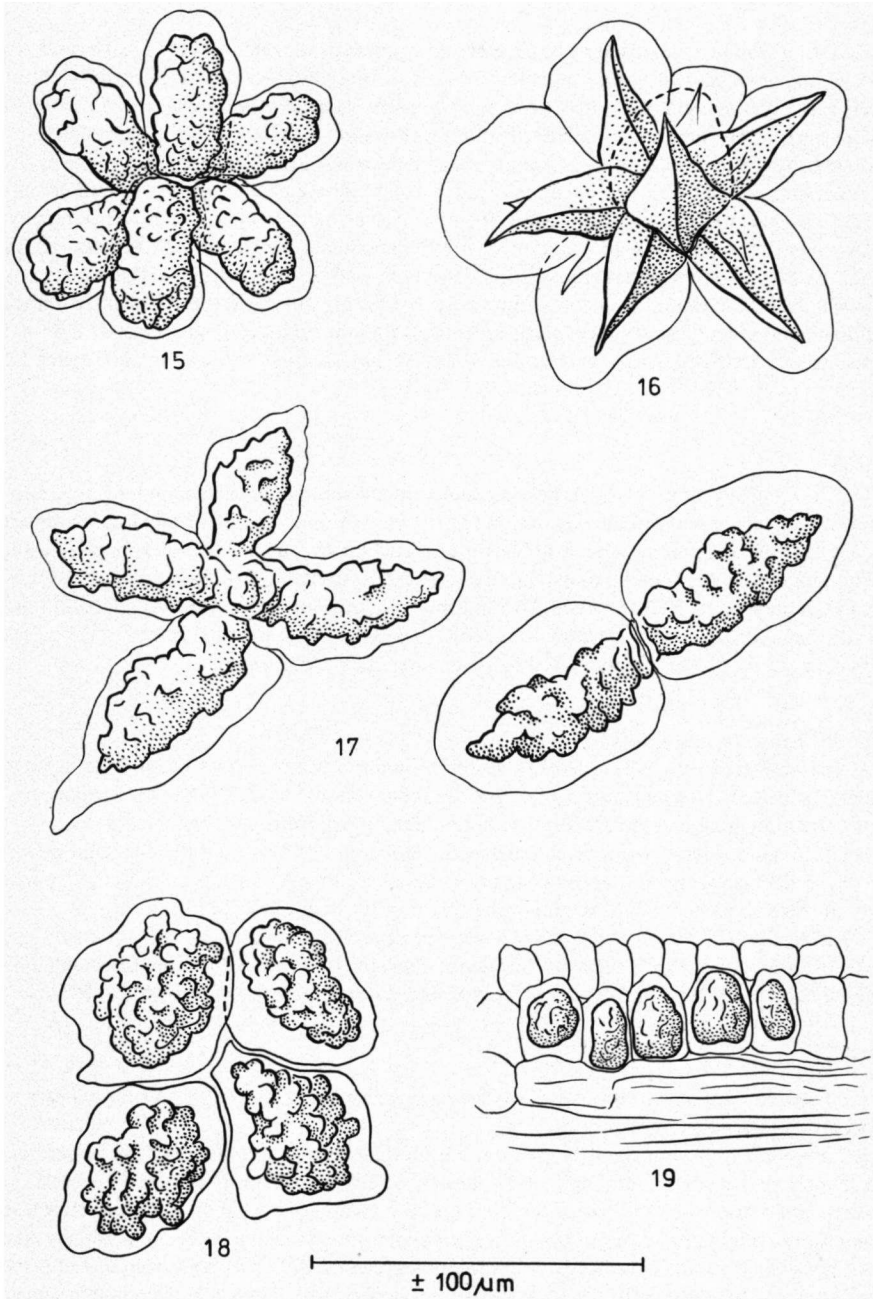

Fig. 15-19. Cystoliths in leaf mesophyll of *Opiliaceae*. 15-*Lepionurus sylvestris* (*Lörzing 5723*). 16-*Melientha suavis* subsp. *macrocarpa* (*RSNB 2518*). 17-*Opilia amentacea* (*Elmer 12691*). 18-*Cansjera rheedei* (*Griffith 823*). 19-*Agonandra excelsa* (*Schreiter 11484*).

Rhopalopilia

This genus can be recognized by its large ideoblasts in the spongy tissue of the leaves and – with the exception of *Rh. pallens* and *Rh. umbellulata* – the occurrence of wood cystoliths type b. The intrageneric variation is comparable with that within *Opilia:* the lianas *Rh. marquesii* and *Rh. umbellulata* are very similar and show some 'lianous' features: thinwalled, densely pitted fibres, relatively wide vessels and rays, whereas *Rh. pallens* is more similar in these respects to the shrubby species of *Opilia.* The four species studied of *Rhopalopilia* have abaxial stomata (except one specimen of *Rh. umbellulata* with about 20% adaxial stomata) and a clearly differentiated palisade parenchyma. The last character is most strongly pronounced in *Rh. umbellulata.* The indumentum of *Rh. marquesii* and *Rh. pallens* is rather remarkable (found elsewhere only in *Urobotrya sparsiflora*); it consists of abaxial hairs distributed over the entire surface whereas adaxially the hairs are confined to midrib and veins. The leaves of *Rh. altescandens* and *Rh. umbellulata* are glabrous. The wood and leaf features support therefore the transfer of *Opilia umbellulata* to *Rhopalopilia* (Engler 1909).

Cansjera

The genus differs from the other genera studied by the abundant vasicentric tracheids, and the clusters of cells filled with minute crystals in the leaves. Within the genus, comparable differences between shrubby and lianous species already mentioned for *Opilia* and *Rhopalopilia* can be found.

The small shrub *C. parvifolia* shows the smallest vessels; stomata and hairs (all branched) occur in equal frequencies on both surfaces and the mesophyll is homogeneously formed by cubic cells. In the lianas the hairs (all uniseriate) are confined to midrib and veins, the stomata are only abaxial, and in *C. rheedei* a relatively well differentiated palisade parenchyma was found.

Opilia, Rhopalopilia, and *Cansjera*

At first view these genera have a lot of features in common. Many characters, however, seem to be correlated with habit (see paragraphs on diagnostic and taxonomic value). When these characters are left out, the remaining common features, differentiating in regard to other genera, are:

- diffuse parenchyma distribution (also in *Gjellerupia*) in contrast to diffuse-in-aggregates;
- 1-2-celled parenchyma strands (except *O. amentacea*); this character occurs also in *Agonandra;*
- unbroken collenchyma caps supporting the midrib (except in *O. amentacea*);
- leaf cystoliths 2-4 mainly together (also in species of *Urobotrya*).

A close affinity between *Opilia* and *Urobotrya,* indicated by Engler (1909) and Sleumer (1935) in assigning subgeneric rank to *Urobotrya* within *Opilia,* is not supported by anatomical features.

Urobotrya

Urobotrya consists of two sections: *U.* sect. *Urobotrya,* occurring in Africa, und *U.* sect. *Lepionuroides* occurring in Asia.

U. latisquama is distinguished by the numerous pore multiples and the very large leaf cystoliths, both characters elsewhere found only in *Lepionurus.* The main difference between *Lepionurus* and *U. latisquama* seems to be the size of the fibre pit borders and the question arises whether *U. latisquama* should not better be retransferred to *Lepionurus,* under which it had been originally placed. This is, however, contradicted by the flower morphology, which differs strongly from that of *Lepionurus* and is exactly the same as in *Urobotrya siamensis* (Hiepko, pers. comm.). The remaining species *U. floresensis* and *U. siamensis* are rather similar. The only substantial difference is found in the abundance of the wood cystoliths (type d) in *U. siamensis,* in contrast to the absence of cystoliths in *U.*

floresensis.

Urobotrya sect. *Urobotrya* is characterized by a network of lignified fibres in the spongy tissue, which is not found in any other species. Furthermore, it differs from *Urobotrya* sect. *Lepionuroides* in the number of subsidiary cells of the stomata, and the absence of parenchyma bridges in the vascular tissue in the petiole. These differences are considerable, if compared with intergeneric differences between e. g. *Lepionurus* or *Gjellerupia* and *Urobotrya.*

Gjellerupia and *Lepionurus*

These monotypic genera were considered to be synonymous by Hatusima (1952). According to Sleumer (1935) and van Steenis (1963), *Gjellerupia* is most closely allied to *Agonandra.* Hiepko (1979) is of the opinion that *Urobotrya* is the closest ally of *Gjellerupia.*

Gjellerupia and *Lepionurus* contrast with all other taxa studied in their relatively small fibre pits. They differ in the vessel arrangement, and in some wood and leaf anatomical features considered to be less important.

Lepionurus resembles *Urobotrya latisquama* in the frequent vessel multiples, which occur nowhere else in the family. Here, the main difference is found in the size of the fibre pits.

Additional anatomical evidence that *Gjellerupia, Lepionurus* and *Urobotrya* sect. *Lepionuroides* are closely allied, is found in (a) the spongy tissue, which is always loosely built, (b) the adaxial epidermis cells being always much larger than the abaxial cells, (c) the number of subsidiary cells (mostly less than 4), and (d) the wood cystoliths, which, when present, are of type d.

Cansjera is comparable with *Gjellerupia, Lepionurus* and *Urobotrya* in the number of subsidiary cells and the presence of wood cystoliths type d. Some of the leaf characters of *Lepionurus, Gjellerupia* and *Urobotrya* are shared with *Agonandra.*

Agonandra

Geographically, *Agonandra* is excentric within the family as the only neotropical taxon. Although the samples studied hardly show anatomical features that do not occur elsewhere within the *Opiliaceae,* the genus can easily be recognized by the combination of the following features: all ray cells strongly procumbent forming low 2(-3)-seriate rays, high F/V-ratio, loosely built spongy tissue and absence of cystoliths in the wood. Within *Agonandra,* the species differ wood anatomically in quantitative characters (see description). Leaf anatomically, especially *A. excelsa* is deviating in the relatively well differentiated mesophyll (2-3 layers of palisade parenchyma, abaxially and adaxially), stomata abaxially and adaxially in equal frequencies, and solitary cystoliths accompanying the supporting tissue which consists of strongly developed bundles of sclerenchyma.

4.4. Speculations about relationships within *Opiliaceae*

In the foregoing paragraph we have argued, that most of the genera can be characterized by wood- and/or leaf anatomical features; that the differences within *Opilia, Rhopalopilia* and *Cansjera* are at least partly due to differences in life-form, that the two sections of *Urobotrya* differ in several aspects from each other and that *Urobotrya latisquama* strongly resembles *Lepionurus sylvestris.* This explains why in the following discussion we start from the monotypic genera *Lepionurus, Gjellerupia, Champereia* and *Melientha,* the two sections of *Urobotrya, Urobotrya latisquama,* and - ignoring some variation within the genera - *Cansjera, Opilia, Rhopalopilia* and *Agonandra.*

Taking the distribution of the anatomical features into account, we see several reticulate patterns. This hampers the presentation of a clustering of the indicated taxa on the basis of all recorded features. However, some features are known to be often variable even in taxa of low rank (i. e. vessel diameter)

or extremely difficult to split in distinct character states (i. e. relative abundancy of cystoliths and crystals in different plant tissues). Even when such features are abandoned, the remaining characters hardly enable us to arrange the *Opiliaceae* in a phylogenetic (cladistic) way (fig. 20).

The presence of vessel multiples and of small fibre pits, each present in the two genera *Gjellerupia, Lepionurus* and in *Urobotrya latisquama* makes it possible to combine these taxa in one way or an other. *Urobotrya* sect. *Lepionuroides* may be combined with this group. The "ancestor group" is then characterised by: solitary vessels, conspicuous bordered fibre pits, and wood cystoliths type d. *Urobotrya* sect. *Urobotrya* differs mainly in the presence of sclerenchyma fibres around the vascular tissue of midrib and large veins, and in the absence of wood cystoliths.

The presence of procumbent ray cells and a low number of uniseriate rays may be considered as phylogenetically relevant features. *Agonandra* and *Opilia* share homogeneous rays; *Champereia* and *Melientha* show (slightly) heterogeneous rays but like in *Agonandra* the number of uniseriate rays is strongly reduced. However, inclusion of *Agonandra* in one group with *Champereia, Melientha* and *Opilia* increases the character variation considerably (fig. 20). Remarkable in this respect is the complete absence of wood cystoliths in all samples studied of *Agonandra*. It is possible to hypothesize a separate line for *Agonandra*. That clears the way to link *Opilia* and *Rhopalopilia*, with leaf ideoblasts in *Rhopalopilia* and homogeneous rays in *Opilia* as main differentiating characters.

The hypothetical ancestor of the group *Champereia-Melientha-Opilia-Rhopalopilia* is characterized by: either (part of) the multiseriate rays composed of procumbent cells, or exclusively square / upright cells present (and then the rays comparable to the rays of the *Gjellerupia-Lepionurus-Urobotrya*-group); at least 10% of the rays uniseriate; wood cystoliths type a, b, or c.

The presence of wood cystoliths can safely be considered as a derived (apomorphic) character in *Opiliaceae*, as they are of very uncommon occurrence elsewhere. Considering the structure of the wood cystoliths, a development from solitary cystoliths with an irregular crystalline part in normal ray cells (type c, d) to clustered or paired, regularly built cystoliths in ideoblasts is obvious. However, this seems to conflict with the fact, that in all *Opiliaceae* the vascular system of midrib and veins show nearly exclusively paired cystoliths in ideoblastic cells.

It seems obvious from this analysis, that the hypothetical ancestor group of the *Opiliaceae* can be described wood anatomically as: vessels solitary, fibre tracheids with conspicuously bordered pits, rays heterogeneous (Kribs type I or II), and parenchyma scanty diffuse. This combination of features occurs in numerous dicotyledonous families and will be interpreted as "primitive" by most wood anatomists. In order to decide which leaf anatomical character states may be derived, an outgroup comparison is necessary. Baas et al. (1982) discuss the phylogenetic value of some leaf anatomical features in *Olacaceae*, often considered as close ally of *Opiliaceae*, and suggest a common ancestor for *Opiliaceae* and a specialised group ("group IV") of olacaceous genera. The most conspicuous difference between both groups is the presence of cystoliths in wood and leaves of *Opiliaceae*. We can confirm, that most leaf anatomical features found in *Opiliaceae* are also found in "group IV" of *Olacaceae*. Besides, our analysis of *Opiliaceae* nowhere contradicts the suggestion of "derived character states" (Baas et al. 1982: the presence of branched hairs and of a hypodermis are correlated in our material with an uncommon phenomenon: square epidermal cells over midrib and veins). However, their suggestion that this enables one to point to one common ancestor, or even to the olacaceous genus *Ximenia* as the direct ancestor (p. 206), must be contradicted. Within "group IV" and *Opiliaceae* specialised features (branched hairs, epidermis) occur incidentally, and not always correlated with each other. Thus these characters suggest a parallel development, a reticulate relationship, or a polyphyletic descendance of *Opiliaceae* and *Olacaceae*, rather than a common ancestor.

Restricting ourselves once more to the internal relations of opiliaceous taxa: with much caution it is possible to suggest a splitting of the family into two parts: one part consisting of the SE Asian taxa

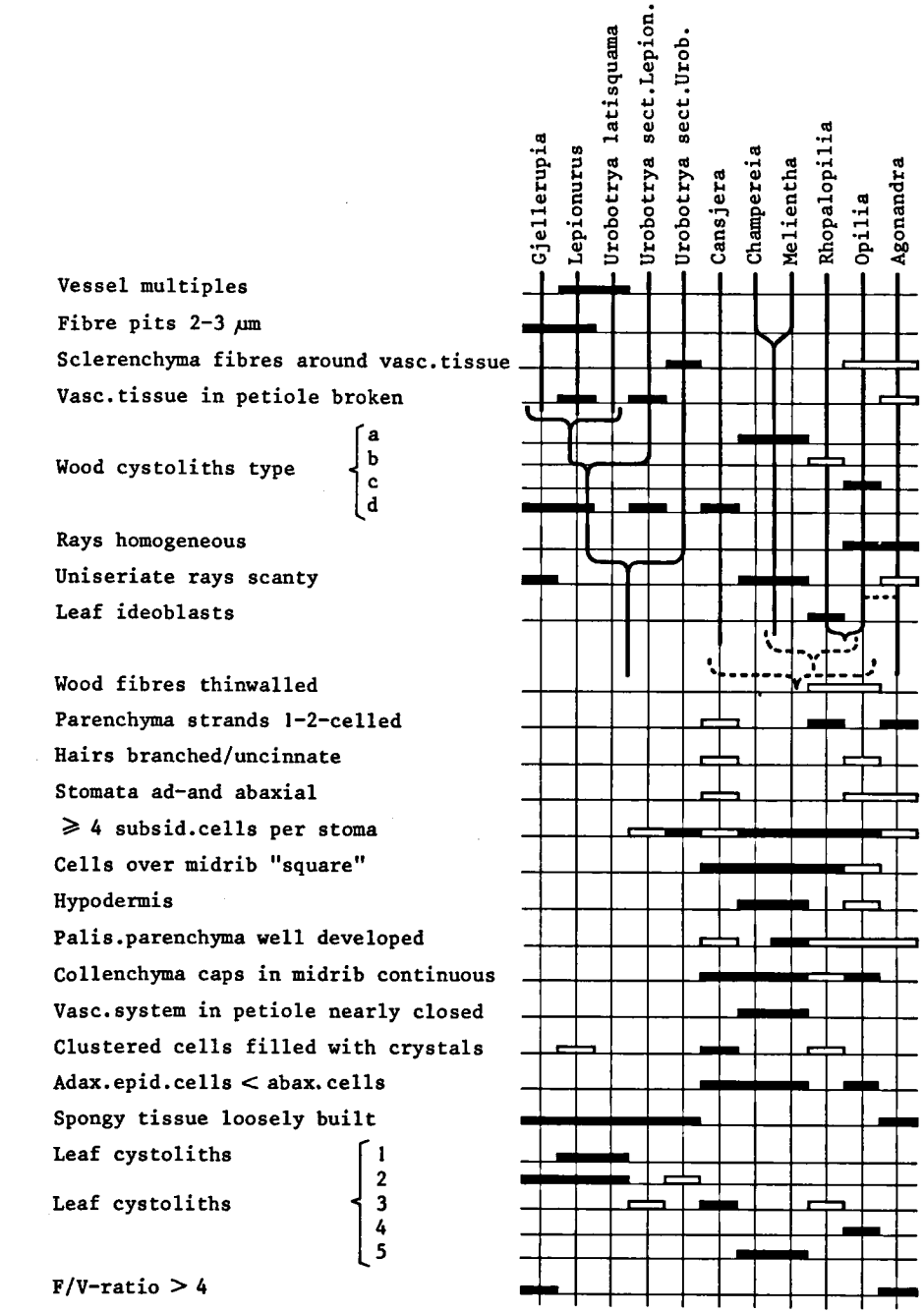

Fig. 20. Occurrence of some wood and leaf anatomical features in *Opiliaceae*. ■: feature always present. □: feature present in part of the material. The thick lines in the upper half of the figure indicate possible cladistic relations between the taxa. For further explanation see text.

Gjellerupia, Lepionurus and *Urobotrya* sect. *Lepionuroides,* with the African *Urobotrya* sect. *Urobotrya* as nearest taxon. The other one consists of *Champereia* and *Melientha* (SE Asia), and *Opilia* and *Rhopalopilia* (Africa), with *Cansjera* (SE Asia) perhaps closely allied to *Opilia.* In the second part the widest character variation occurs (fig. 20) including the most "derived" and the most "primitive" characters. The position of *Agonandra* (neotropics) remains uncertain.

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N o t e . After the manuscript has gone to the press, one more wood sample of *Rhopalopilia umbellulata* (Kenya : *Hiepko et al. 2634;* diam. 11 mm) has become available. The wood features of this sample fit in with the generic description, but come closest to the material of *Rh. marquesii,* rather than that of *Rh. umbellulata* (presence of cystoliths type b, and wide rays partly composed of procumbent cells). The discussion and conclusions of the paper are not affected.