MORPHOLOGY

The wood anatomy of the polyphyletic Icacinaceae s.l., and their relationships within asterids

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Wood samples from 53 species belonging to 41 genera of the Icacinaceae s.l. are investigated using light and scanning electron microscopy. The traditionally circumscribed Icacinaceae fall apart into four segregate families that are clearly nested within asterids, i.e., Icacinaceae s.str. (near or in Garryales), Cardiopteridaceae and Stemonuraceae (both Aquifoliales), and Pennantiaceae (Apiales). From a wood anatomical point of view, these families cannot easily be distinguished from each other. However, some features such as vessel distribution, perforation plate morphology, size and arrangement of vessel pits, fibre wall thickness, and the occurrence of cambial variants can be used to assign various species to one of the four families. The wood structure of the four segregate families is in general agreement with their suggested putative relatives, but the occurrence of lianas versus erect trees and shrubs is a confusing factor in getting clear phylogenetic signal from the wood structure. Maximum parsimony and Bayesian analyses using molecular data and combined anatomical-molecular data show that Icacinaceae s.str. are not monophyletic, and their closest relatives remain unclear. The combined analyses provide moderate support for a clade including *Cassinopsis*, the *Apodytes*-group, the *Emmotum*-group (all Icacinaceae s.str.), and the genus *Oncotheca*. This clade is situated at the base of lamiids and may be closely related to Garryales. The remaining lineage of Icacinaceae s.str., the *Icacina*-group represented by many climbing taxa exhibiting cambial variants, is strongly supported and might be sister to the rest of lamiids.

KEYWORDS: cambial variants, comparative wood anatomy, Garryales, Icacinaceae, LM, *Oncotheca*, SEM

INTRODUCTION

The traditionally circumscribed family Icacinaceae s.l. includes about 55 genera and 400 species (Kårehed, 2001). Representatives are small shrubs to tall trees or lianas that typically grow in humid lowland forests throughout the tropics. A small number of species prefer subtropical forests and savannas to more temperate areas of Africa, Asia, Australia and South America, while others sporadically occur in salt marshes or in high-altitude regions between 2,000–3,000 m (Guymer, 1984; Howard, 1942; Sleumer, 1972; Villiers, 1973; de Roon & Mori, 2003; de Stefano, 2004). Malesia is the main centre of diversity comprising about half of the genera, followed by (sub)tropical America (20%–25% of the genera) and Africa (15%). Many genera are endemic to major phytogeographical areas, with the pantropical genus *Citronella* being one of the few exceptions.

Frequent mistakes in species determination, complex nomenclatural issues and undersampled collections make Icacinaceae s.l. a poorly understood family of flowering plants (Howard, 1942; Sleumer, 1942a, b, 1972). Consequently, the taxonomic history shows much controversy (Table 1), and the family has been linked to various groups, including Olacaceae (De Candolle, 1824; Bentham, 1862) and the families Celastraceae and Aquifoliaceae (Miers, 1852; Engler, 1893). Subsequent authors followed the Celastrales connection (Rosidae, Cronquist 1981; *Cardiopteris* excluded), while Takhtajan (1997) recognised Icacinales as an order of its own in the Rosidae, including Aquifoliaceae, Icacinaceae (excluding *Cardiopteris* and *Metteniusa*), Phellinaceae and Sphenostemonaceae. Progress in molecular systematics has revealed that the Aquifoliaceae link is correct, but only for certain genera within Icacinaceae s.l. (Kårehed, 2001). A combined dataset of *ndhF*, *rbcL*, *atpB* and 18S rDNA together with morphology showed that the traditional Icacinaceae are polyphyletic, and must be divided into four different families within asterids sensu APG II (2003): Icacinaceae s.str.

Table 1. Taxonomic overview of the genera studied according to their family classification sensu Miers (1852), Engler (1893), Bailey & Howard (1941a), Sleumer (1942ab) and Kårehed (2001).

Genus	Miers (1852)	Engler (1893)	Bailey & Howard (1941b)	Sleumer (1942a, b)	Kårehed (2001)
Apodytes	Icacineae	Icacineae	Icacineae (I)	Icacineae	Icacinaceae s.str. (APO)
Calatola	–	–	Icacineae (I)	Icacineae	Icacinaceae s.str. (EMM?)
Cantleya	–	–	Icacineae (II)	Icacineae	Stemonuraceae
+Cardiopteris+	–	Cardiopterygoideae	–	Peripterygiaceae*	Cardiopteridaceae
Cassinopsis	–	Icacineae	Icacineae (I)	Icacineae	Icacinaceae s.str. (CAS)
+Chlamydocarya+	–	Phytocreneae	Phytocreneae (III)	Phytocreneae	Icacinaceae s.str. (ICA)
Citronella	–	Icacineae	Icacineae (I)	Icacineae	Cardiopteridaceae
Codiocarpus	–	–	–	–	Stemonuraceae
Dendrobangia	–	–	Icacineae (I)	Icacineae	Cardiopteridaceae
Desmostachys	Icacineae	Icacineae	Icacineae (III)	Icacineae	Icacinaceae s.str. (ICA)
Discophora	Sarcostigmateae	–	Icacineae (II)	Icacineae	Stemonuraceae
Emmotum	Emmoteae	Icacineae	Icacineae (I)	Icacineae	Icacinaceae s.str. (EMM)
Gastrolepis	–	–	Icacineae (II)	Icacineae	Stemonuraceae
Gomphandra	–	–	–	Icacineae	Stemonuraceae
Gonocaryum	Sarcostigmateae	Icacineae	Icacineae (II)	Icacineae	Cardiopteridaceae
Hartleya	–	–	–	–	Stemonuraceae
+Icacina+	Icacineae	Icacineae	Icacineae (III)	Icacineae	Icacinaceae s.str. (ICA)
+Iodes+	–	Iodeae	Iodeae (III)	Iodeae	Icacinaceae s.str. (ICA)
Lasianthera	–	Icacineae	Icacineae (II)	Icacineae	Stemonuraceae
+Lavigeria+	–	Icacineae	Icacineae (III)	Icacineae	Icacinaceae s.str. (ICA)
Leptaulus	–	Icacineae	Icacineae (II)	Icacineae	Cardiopteridaceae
+Mappia+	Icacineae	Icacineae	Icacineae (III)	Icacineae	Icacinaceae s.str. (ICA)
+Mappianthus+	–	Iodeae	Iodeae (III)	Iodeae	Icacinaceae s.str. (ICA)
Medusanthera	–	–	Icacineae (II)	Icacineae	Stemonuraceae
Merrilliodendron	–	–	Icacineae (III)	Icacineae	Icacinaceae s.str. (ICA)
Metteniusa	–	–	–	Icacineae	Cardiopteridaceae?
Oecopetalum	–	–	Icacineae (I)	Icacineae	Icacinaceae s.str. (EMM)
Ottoschulzia	–	–	Icacineae (I)	Icacineae	Icacinaceae s.str. (EMM)
Pennantia	Sarcostigmateae	Icacineae	Icacineae (I)	Icacineae	Pennantiaceae
+Phytocrene+	–	Phytocreneae	Phytocreneae (III)	Phytocreneae	Icacinaceae s.str. (ICA)
Platea	–	Icacineae	Icacineae (I)	Icacineae	Icacinaceae s.str. (EMM?)
+Polyporandra+	–	Iodeae	Iodeae (III)	Iodeae	Icacinaceae s.str. (ICA)
Poraqueiba	Icacineae	Icacineae	Icacineae (I)	Icacineae	Icacinaceae s.str. (EMM?)
Pseudobotrys	–	–	–	Icacineae	Cardiopteridaceae?
+Pyrenacantha+	–	Phytocreneae	Phytocreneae (III)	Phytocreneae	Icacinaceae s.str. (ICA)
+Rhaphiostylis+	Icacineae	Icacineae	Icacineae (III)	Icacineae	Icacinaceae s.str. (APO)
Rhyticaryum	–	Icacineae	Icacineae (III)	Icacineae	Icacinaceae s.str. (ICA)
+Sarcostigma+	Sarcostigmateae	Sarcostigmateae	Sarcostigmateae (III)	Sarcostigmateae	Icacinaceae s.str. (ICA)
Stemonurus	Sarcostigmateae	Icacineae	Icacineae (II)	Icacineae	Stemonuraceae
Whitmorea	–	–	–	–	Stemonuraceae

I, II and III refer to the groups of Bailey & Howard (1941b); APO, *Apodytes* group; CAS, *Cassinopsis*; EMM, *Emmotum* group; ICA = *Icacina* group. Names of climbing genera are marked with “+”. *Peripterygiaceae = Cardiopteridaceae.

(near or in Garryales, lamiids [euasterids I]), Cardiopteridaceae and Stemonuraceae (both in Aquifoliales, campanulids [euasterids II]), and Pennantiaceae (in Apiales, campanulids) (Kårehed, 2001). However, it is possible that the present delimitation of Icacinaceae s.str., including the *Apodytes* group, the *Emmotum* group, the *Icacina* group and the genus *Cassinopsis*, does not constitute a monophyletic entity (Table 1). Also the position of *Metteniusa* and *Pseudobotrys* within Cardiopteridaceae remains open for discussion (Kårehed, 2001).

Anatomical characters of the stem have been considered to represent key features for the intrafamily classification. In order to define the four tribes of the subfamily Icacinoideae (i.e., Icacineae, Iodeae, Sarcostigmateae and Phytocreneae), Engler (1893) used habit, type of vessel perforation, wood development in young stems, and presence of interxylary (included) phloem in the wood (the same author also recognised two monogeneric subfamilies: Cardiopteridoideae and Lophopyxioideae; the genus *Lophopyxis* is now included as a separate family in Malpighiales; Savolainen & al., 2000; APG II, 2003). Although Sleumer (1942a) followed the Icacinoideae classification, Bailey & Howard (1941a) pointed out that the four tribes proposed could not always be distinguished from each other based on the given characters. Therefore, Bailey & Howard (1941b) suggested an adjusted version of Engler's classification of Icacinoideae based on the nodal anatomy and the perforation plate morphology, resulting in three groups: group I (trilacunar, exclusively scalariform perforations), group II (trilacunar, simple and scalariform perforations) and group III (unilacunar, exclusively simple perforations) (Table 1). However the same authors (1941b: 184) questioned the validity of their own classification by stating that "It should not be inferred from this, however, that all of the genera in one of these categories [i.e., their three groups] are necessarily more closely related genetically to one another than to genera in the other categories." This statement appears to be true based on molecular data (Kårehed, 2001).

Based on predominantly juvenile twigs of 50 genera and more than 150 species, the wood structure of Icacinaceae s.l. has been intensively studied by Bailey & Howard (1941b–d). The authors found an enormous variation in the secondary xylem: taxa with wood characters traditionally regarded as primitive according to Bailey & Tupper (1918), such as solitary vessels, scalariform perforations with many bars and long vessel elements, as well as taxa that possess a so-called derived set of wood features, such as a high frequency of vessel groupings, simple perforations and short vessel elements, are present. Moreover, much variation is present in the distribution of the axial parenchyma, the structure of the rays, and the presence of so-called cambial variants (Bailey & Howard, 1941b–d). Nevertheless, this series of studies must be interpreted with caution because of the large number of juvenile wood samples included. It is generally known that the wood structure of juvenile twigs differs in many aspects from the wood of mature branches or trunks of the same plant. Not only quantitative characters, such as vessel diameter, vessel density, and ray width depend on this, also qualitative characters such as the initiation of specific cambial variants (amongst others successive cambia and interxylary phloem) only develop when a stem reaches a certain age (Obaton, 1960; Metcalfe & Chalk, 1983; Ursem & ter Welle, 1989; Carlquist, 2001). Next to the anatomical studies of Bailey & Howard, several other papers described the wood structure of a restricted number of Icacinaceae s.str. (Chalk & al., 1935; Metcalfe & Chalk, 1950; Détienne & al., 1982; Détienne & Jacquet, 1983; ter Welle & Détienne, 1994; Utteridge & al., 2005), Cardiopteridaceae (Metcalfe & Chalk, 1950; Normand, 1950; Détienne & al., 1982; Détienne & Jacquet, 1983; Bamber & ter Welle, 1994; ter Welle & Détienne, 1994), Stemonuraceae (Howard, 1943; Metcalfe & Chalk, 1950; Détienne & Jacquet, 1983; ter Welle & Détienne, 1994) and Pennantiaceae (Metcalfe & Chalk, 1950; Meylan & Butterfield, 1978; Patel & Bowles, 1978). Additional descriptions and micrographs of 21 genera belonging to all four families can be found on the InsideWood website (http://insidewood.lib.ncsu.edu/search). Wood anatomical papers that dealt with cambial variants of a small number of climbing Icacinaceae s.l. include Engler (1893), Sleumer (1942a), Obaton (1960), Ursem & ter Welle (1989), Bamber & ter Welle (1994), and Utteridge & al. (2005).

Major objectives of this study are: *(1)* providing a wood anatomical overview of the traditionally circumscribed Icacinaceae s.l. using original observations and literature data, *(2)* searching for wood anatomical synapomorphies that could define the segregate families Icacinaceae s.str., Cardiopteridaceae, Stemonuraceae and Pennantiaceae, *(3)* relating the wood anatomical diversity of the segregate families to their asterid relatives, and *(4)* evaluating the phylogenetic significance in the wood structure of the Icacinaceae segregates by carrying out phylogenetic analyses based on existing molecular and combined molecular-anatomical data at the asterid level.

MATERIAL AND METHODS

Wood anatomical descriptions and microtechniques. — In total, 61 wood specimens of Icacinaceae s.l., including 53 species and 41 genera, were investigated using light microscopy (LM) and scanning electron microscopy (SEM) (Appendix 1). Despite the undersampling of the traditional Icacinaceae in most botanical collections, the number of genera studied represents a good coverage of the segregate families at the genus level: Icacinaceae s.str. (23/34, including all lineages sensu Kårehed, 2001), Cardiopteridaceae (7/7), Stemonuraceae (10/12) and Pennantiaceae (1/1). Most samples were derived from mature sapwood, except for the juvenile twigs of *Cardiopteris moluccana*, *Chlamydocarya thomsonia*, *Gastrolepis austro-caledonica*, *Icacina claessensi*, *Lavigeria macrocarpa* (BR and Kw specimen in Appendix 1), *Leptaulus grandifolius*, *Mappianthus iodoides*, *Pyrenacantha lebrunii*, and *Pyrenacantha kirkii*. In order to increase our sampling, we were able to study a selection of the original slides of Bailey & Howard (1941a–d), including mostly juvenile stems of the genera *Cassinopsis*, *Chlamydocarya*, *Grisollea*, *Hosiea*, *Icacina*, *Iodes*, *Lavigeria*, *Mappia*, *Miquelia*, *Natsiatum*, *Nothapodytes*, *Oecopetalum*, *Phytocrene*, *Pittosporopsis*, *Pleurisanthes*, *Pyrenacantha*, *Rhaphiostylis* and *Sarcostigma*. Alcohol preserved material and fresh stems of lianas were requested from botanical gardens in order to make better sections, because most climbing taxa exhibit cambial variants including nonlignified tissues such as parenchyma and phloem (see Appendix 1). The specimen observed of *Pyrenacantha malvifolia*, a fast growing liana from the greenhouses of the Botanic Gardens in Kew, was omitted from the descriptions and Table 2 because of the huge amount of unlignified parenchyma and poorly developed fibres. This anatomical deviation is typical of fast growing plants in greenhouses, and should be treated with caution in comparative studies.

The methodology of wood sectioning and the subsequent steps are described in Lens & al. (2005b). The wood anatomical terminology follows the "IAWA list of microscopic features for hardwood identification" (IAWA Committee, 1989). We define tracheids as long, imperforate cells with more than one row of distinctly bordered pits in tangential and radial walls (usually between 8–10 µm in horizontal diameter), or with only one row of very large conspicuously bordered pits (often more than 10 µm in horizontal diameter). When distinctly bordered vessel-ray pits are mentioned, we mean that the pit pairs are half-bordered, because the pit on the vessel side is bordered, but predominantly simple on the parenchyma cell side.

Phylogenetic analysis. — In total, 26 wood anatomical characters (Appendix 2 in Taxon online issue) are combined with the existing molecular asterid matrix of Kårehed (2001) based on *ndhF*, *rbcL*, *atpB* and 18S rDNA, comprising in total 6,950 molecular characters, of which 2,251 are parsimony informative. A few adjustments have been carried out on the original Kårehed matrix: *(1)* all non-asterid taxa are omitted from the analysis because of the clear asterid origin of Icacinaceae s.l., *(2)* the original morphological data for Icacinaceae s.l. have been excluded, *(3)* only one end taxon per genus has been retained (except for *Pennantia*), excluding the taxa *Cassinopsis ilicifolia*, *Citronella moorei*, *Leptaulus daphnoides*, and *Pyrenacantha grandifolia*, *(4)* complete wood and sequence data of *Eucommia* (GenBank accession numbers AJ235469, AJ429113, L01917, L54066) and *Oncotheca* (accession numbers AJ429114, AF206976, AJ131950, AJ235549) have been included in order to investigate their relationship with Icacinaceae s.str. and Garryales, and *(5)* some sequences that were lacking in the original matrix have been added from GenBank, such as *ndhF* sequences of *Gonocaryum* (AJ400889) and *Medusanthera* (unpub. data), 18S sequences of *Gonocaryum* (AF206919), *rbcL* of *Apodytes* (AJ428895), *Cassinopsis* (AJ428896), *Gonocaryum* (AJ235779), *Pennantia corymbosa* (AJ494842), *P. cunninghamii* (AJ494843) and *Pyrenacantha* (AJ235791), and *atpB* sequences of *Gonocaryum* (AJ400883), *Pennantia corymbosa* (AJ494840), *P. cunninghamii* (AJ494841) and *Pyrenacantha* (AJ235575).

In total, 109 asterid taxa are included in the data matrix, of which the seven Cornales taxa are designated as outgroup. The genera *Anagallis*, *Boopis*, *Borago*, *Callitriche*, *Campanula*, *Codonopsis*, *Dipsacus*, *Hydrophyllum*, *Lamium*, *Menyanthes*, *Nymphoides*, *Panax* and *Proboscidea* are herbaceous, and are coded as unknown for all wood characters. Likewise, no data could be found for the woody genus *Phyla*, which is coded as unknown. Information from the other 95 genera was gathered using observations in Ericales (Lens & al., 2005a, b, 2007a, b) and Icacinaceae s.l. (this paper), while other groups were coded based on information from the InsideWood database (http://insidewood.lib.ncsu.edu/search/) and from extensive literature data (Howard, 1943; Metcalfe & Chalk, 1950; Carlquist, 1957, 1969a, b, 1978, 1981a, b, 1982, 1983, 1984, 1985, 1986, 1991, 1992, 1997; Obaton, 1960; Baas, 1973, 1975; Carpenter & Dickison, 1976; Giebel & Dickison, 1976; Stern, 1978; Styer & Stern, 1978; Mennega, 1980; Dickison, 1982; Carlquist & al., 1984; Dickison & Phend, 1985; Carlquist & Hoekman, 1986; Gornall & al., 1988; Gregory, 1988a–c; Ogata, 1988; Baas & al., 1988; Carlquist & Zona, 1988; Liang & Baas, 1990; Schweingruber, 1990; Carlquist & Hanson, 1991; Gasson & Dobbins, 1991; Ogata, 1991; Oskolski, 1996; Oskolski & al., 1997; Noshiro & Baas, 1998).

We have compiled the wood matrix following the strategy of Lens & al. (2007b): *(1)* the selection of characters is based on their variation within asterids and their stability at generic level (Appendix 2 in Taxon online issue), which is similar to most characters proposed by Herendeen & Miller (2000); *(2)* highly variable characters were excluded from the analysis (e.g., distinctness of growth rings, horizontal diameter of intervessel pits, presence of two distinct ray sizes, number of cells in multiseriate rays at their widest portions, and incidence of sheath cells) or coded using major character states only (axial parenchyma distribution); *(3)* only one of two dependent characters was taken into account, such as vessel diameter/density and vessel element/fibre length; *(4)* neotenous or paedomorphic characters (chars. 5, 10, 16–18), defined as juvenile characters of the primary xylem that have been protracted into the secondary xylem (Carlquist, 1962) and typical of taxa with secondarily derived wood, were not taken into account and were coded with a "?" (Appendix 2 in Taxon online issue); *(5)* ecologically dependent features (chars. 1, 3–4, 6, 8–10, 14) and habit related characters (chars. 3–4, 9) were not excluded from the matrix due to their possible phylogenetic value; *(6)* the continuously varying characters (chars. 4, 9–10) were coded following the gap weighting method of Thiele (1993) resulting in ordered, multistate characters with ten possible states and weight of 0.1 for each of the three characters; and *(7)* two additional multistate wood features are ordered (chars. 3, 5).

Maximum parsimony (MP) analyses were conducted with PAUP*4.0b10 (Swofford, 2002), employing a heuristic search with 2,500 random addition replicates, TBR branch swapping (one tree held at each step, MULTREES off). The shortest tree from each replicate was saved, and these trees were subsequently submitted to a second round of TBR swapping with the MULTREES option on. Bootstrap analyses were carried out using 10,000 bootstrap replicates, a random addition sequence with five replicates, and TBR swapping (one tree held at each step, MULTREES off). In order to assess the phylogenetic value of wood characters, both the adjusted molecular matrix of Kårehed (2001) and the combined molecular/anatomical matrix were analysed following the same strategy.

A Bayesian inference of phylogeny was conducted with the software programme MrBayes version 3.1.2 that calculates posterior probabilities using the Markov chain Monte Carlo (MCMC) algorithm (Huelsenbeck & Ronquist, 2001). The wood anatomy data and the indel data of the *ndhF* matrix were analysed under the standard discrete (morphology) model (Posada & Crandall, 1998). The MorphoCode characters were coded as unordered, because MrBayes allows only six different character states for one ordered character (the shift from ordered to unordered MorphoCode characters does not affect the topology in MP analyses). Models for nucleotide substitution were evaluated using MrAIC, version 1.4.2 (Nylander, 2004). The *ndhF* matrix was consequently analysed under the general time reversible model (GTR) with a gamma distribution of substitution rates. The other molecular markers were analysed under the same model but in addition with a proportion of invariant sites. When running the analyses, the dataset was partitioned and the partitions unlinked, so each had its own set of parameters. The Markov chain was run for 5,000,000 generations and every 100th tree was sampled. Three additional "heated" chains were used for each run (Metropolis-coupled Markov chain Monte Carlo; Huelsenbeck & Ronquist, 2001). At least two separate runs for each dataset were performed to evaluate if the chain had become stationary. Of the resulting 50,000 trees, the first 5,000 (burn-in) were discarded when calculating the posterior probabilities.

RESULTS

Wood descriptions. — The material studied is described according to the recent family classification of Kårehed (2001). For each genus examined, the numerator represents the number of species studied and the denominator includes the total number of species. Numbers without parentheses are ranges of means, while numbers between parentheses represent minimum or maximum values. Descriptions of continuous characters are based on mature wood samples. An asterisk after the genus names refers to genera with climbing species. A summary of selected wood features is shown in Table 2.

Icacinaceae s.str. (lamiids, near or in Garryales) (*Apodytes* 2/ca. 17, *Calatola* 2/8, *Cassinopsis* 2/4, *Chlamydocarya** 1/7, *Desmostachys* 1/7, *Emmotum* 1/7, *Icacina** 2/5, *Iodes** 1/24, *Lavigeria** 1/1, *Mappia** 1/7, *Mappianthus** 1/1, *Merrilliodendron* 1/1, *Oecopetalum* 1/2, *Ottoschulzia* 1/3, *Phytocrene** 1/19, *Platea* 2/8, *Polyporandra** 1/1, *Poraqueiba* 1/3, *Pyrenacantha** 3/24, *Rhaphiostylis** 1/10, *Rhyticaryum* 1/18, *Sarcostigma** 1/6; Figs. 1–4): Growth ring boundaries usually indistinct to completely absent (Fig. 1A–D), indistinct in *Cassinopsis* and *Emmotum*, and distinct in the young stems of *Icacina claessensi* and *Mappianthus iodoides*. Diffuse-porous. Vessels (0–)3–85 (–103)/mm^2, mostly solitary in all species (Figs. 1A–B), also a small percentage (usually 5%–25%) of radial multiples of 2–3(–4) in species of *Desmostachys*, *Merrilliodendron*, *Ottoschulzia*, *Phytocrene*, *Platea*, *Rhaphiostylis* and *Rhyticaryum*, additional tangential multiples (often between 10%–30%) of 2–3(–4) present in *Chlamydocarya*, *Desmostachys* (Fig. 1C), *Icacina*, *Iodes*, *Lavigeria*, *Mappia*, *Merrilliodendron*, *Phytocrene*, *Polyporandra* (Fig. 1D), *Rhaphiostylis* and *Sarcostigma*; vessel outline rounded to elliptical in the climbing species, but mostly slightly angular in the nonclimbing ones; perforation plates predominantly or entirely simple in most genera studied, but exclusively scalariform with (6–)8–80(–117) bars in *Apodytes*, *Calatola*, *Cassinopsis* (Fig. 1E), *Emmotum*, *Oecopetalum*, *Ottoschulzia*, *Platea* and *Poraqueiba*, exceptionally with reticulate portions in *Apodytes*. Intervessel pits opposite to alternate in species with predominantly simple perforations, pits 5–11 µm in horizontal diameter, intervessel pits scalariform to opposite in species with scalariform perforations (except for *Rhaphiostylis*), pits 5–40 µm in horizontal diameter, pit apertures coalescent in *Icacina*, *Iodes*, *Lavigeria* and *Sarcostigma*, nonvestured. Vessel-ray pits similar to intervessel pits in size and shape; vessel-

Table 2. Overview of selected wood anatomical characters within Icacinaceae s.l.

Species	Solitary vessels	Radial vessel multiples	Tangential vessel multiples	% of simple perforations	Bar number in scalariform perforations	Intervessel pit arrangement	Horizontal diameter of intervessel pits (µm)	Vessel-ray pits with reduced borders	Diameter of vessels (µm)	Density of vessels $(/mm^2)$
+*Chlamydocarya thomsoniana*+* ICA	+	–	±	>95	1–3–13	(O)–A	7–8	–	25–70–150	44–55–68
Desmostachys vogelii ICA	+	±	+	100	–	O–A	5	–	40–100–160	5–8–12
+*Icacina claessensi*+* ICA	+	–	±	100	–	O–A	6–8	–	40–120–220	11–14–17
+*Icacina mannii*+ ICA	+	–	±	100	–	(O)–A	6–9	–	35–155–250	6–9–12
+*Iodes africana*+ ICA	+	–	±	100	–	(O)–A	8–10	–	50–215–400	6–12–20
+*Lavigeria macrocarpa*+[3] ICA	+	–	±	>95	1–9–21	O–A	7–8	–	15–110–180	12–18–23
+*Mappia cordata*+[1] ICA	+	–	+	100	–	(O)–A	6–9	–	15–150–340	6–11–14
+*Mappia cordata*+[2] ICA	+	–	±	100	–	A	8–10	–	120–200–250	6–10–13
+*Mappianthus iodoides*+* ICA	+	–	–	100	–	O–A	4–5	–	35–70–80	20–35–47
Merrilliodendron megacarpum ICA	+	±	+	100	–	(O)–A	5–6	–	25–70–105	6–9–17
+*Phytocrene macrophylla*+ ICA	+	–	±	100	–	O–(A)	7–9	–	25–310–650	4–7–9
+*Phytocrene* sp.+ ICA	+	±	±	100	–	O–A	6–8	–	25–180–475	9–16–22
+*Polyporandra scandens*+ ICA	+	–	±	100	3–6–11	O–A	5–6	–	55–120–210	5–12–19
+*Pyrenacantha lebrunii*+* ICA	+	–	–	100	–	O–A	5–6	–	15–50–100	56–65–84
+*Pyrenacantha kirkii*+* ICA	+	–	±	100	–	A	6–8	–	20–42–60	120–140–160
Rhyticaryum longifolium ICA	+	±	–	100	–	O–A	7–10	–	60–80–110	0–3–6
+*Sarcostigma kleinii*+ ICA	+	–	±	100	–	O–A	7–10	–	35–120–250	7–10–16
Cassinopsis capensis CAS	+	–	–	0	13–25–31	O–A	6–8	–	20–34–50	67–85–103
Cassinopsis sp. CAS	+	–	–	0	39–70–117	S–O	5–12	+	75–90–125	21–25–31
Cassinopsis tinifolia CAS	+	–	–	0	32–40–49	(S)–O	5–7	±	32–55–70	31–40–59
Calatola columbiana EMM	+	–	–	0	21–40–57	O	5–6	–	50–80–115	8–13–17
Calatola venezuelana EMM	+	–	–	0	23–40–55	O–(A)	5–6	–	40–60–75	20–25–30
Emmotum fagifolium EMM	+	–	–	0	6–9–11	O	5–7	–	80–115–150	11–13–16
Oecopetalum mexicanum EMM	+	–	–	0	17–30–43	S–O	5–17	–	20–50–75	25–40–55
Ottoschulzia pallida EMM	+	±	–	0	6–8–11	O–(A)	5–6	–	25–45–70	25–33–38
Platea excelsa EMM	+	±	–	0	32–55–99	S–(O)	5–6	–	70–85–115	20–25–32
Platea hainanensis EMM	+	+	–	0	34–80–110	S–O	8–40	–	50–75–100	22–29–32
Poraqueiba guianense EMM	+	–	–	0	14–18–22	O	5–7	±	80–120–155	6–11–14
Apodytes dimidiata APO	+	–	–	0	23–30–35	O	5–7	–	55–75–95	12–17–22
Apodytes javanica APO	+	–	–	0	20–30–37	O	6–8	–	60–75–95	17–21–27
+*Rhaphiostylis ferruginea*+[1] APO	+	–	±	100	0	O–A	7–11	–	50–180–360	6–10–12
+*Rhaphiostylis ferruginea*+[2] APO	+	±	±	100	0	O–A	9–11	–	80–245–370	7–9–10
+*Cardiopteris moluccana*+* CAR	+	–	±	100	0	O–(A)	9–14	–	50–260–475	4–6–9

Vessel element length (µm)	Fibre length (µm)	Diffuse ax. parenchyma	Diffuse-in-aggregates ax. parenchyma	Banded ax. parenchyma	Scanty ax. parenchyma	Vasicentric ax. parenchyma	Multiseriate ray width (number of cells)	Multiseriate ray height (µm)	Prismatic crystals	Druses	Crystal sand	Styloid-like crystals	Clustered crystals	Type of cambial variants
225–370–600	400–750–1,200	–	+	+	+	+	2–3	200–335–875	r	r	–	–	–	fx, sc
500–730–1,000	1,100–1,630–2,200	–	±	±	+	+	2–6	1,000–3,350–7,500	r	–	–	–	r	–
250–540–1,100	750–1,020–1,500	–	+	+	±	+	4–6	2,300–3,780–7,100	–	–	–	–	–	–
250–860–1,200	900–1,360–1,900	–	±	+	±	+	5–32 (40)	> 5,000	r, ap	–	–	–	r	sc
300–495–725	600–960–1,200	–	±	+	–	+	2–6 (20)	200–1,300– >8,000	r	r	–	–	r	sc
400–690–950	700–1,070–1,600	–	±	±	–	+	6–10 (20)	> 9,000	–	–	–	–	–	sc
500–880–1,150	1,100–1,540–2,300	–	+	±	–	+	2–10	> 8,000	r, ap	–	–	–	–	sc
300–425–550	700–930–1,100	–	+	+	±	+	2–3 (6–9)	200–830–2,100	r	–	–	–	–	sc
550–790–850	650–1,130–1,450	–	+	+	+	±	2–7	> 6,000	–	–	–	–	–	–
200–450–700	700–970–1,300	–	+	+	–	+	2–4	300–800–1,650	r, ap	r	–	r	r	–
200–290–450	350–650–1,100	–	+	±	–	+	2–42	> 1,2000	–	r	–	–	r	fx, sc
70–175–300	250–610–1,000	–	±	+	–	+	2–19	150–1,120–3,700	r, ap	r	–	–	–	fx, sc
375–735–950	760–1,070–1,450	–	–	+	–	+	(2) 12–27	> 7,000	r, ap	r, ap	–	–	–	–
150–240–325	225–490–950	–	±	±	+	±	2	150–225–400	–	–	–	–	r	fx
150–250–350	400–550–750	–	+	–	+	–	–	–	–	–	–	–	–	fx
350–500–650	800–1,500–2,300	–	±	+	–	±	2–8	800–1,600–3,200	–	–	–	r	–	–
100–325–500	300–870–1,200	–	±	+	–	+	2	200–365–700	r, ap	–	–	r	r	ip
600–1,130–1,450	1,200–1,700–2,000	+	+	–	+	–	(2–4) 5–10	500–1,230–1,800	r	–	–	–	–	–
1,100–2,220–2,900	2,500–3,120–3,800	±	+	–	±	–	2–5	900–2,090–5,900	–	–	–	–	–	–
900–1,330–1,700	1,600–1,900–2,200	–	+	–	±	–	2–3 (4)	200–770–1,800	–	–	–	–	–	–
1,400–1,790–2,800	1,800–2,500–3,000	–	+	±	±	–	3–5	> 5,000	r	–	–	r	–	–
1,000–1,490–1,950	2,000–2,410–2,700	–	+	±	+	–	3–4	900–1,730–2,300	r	–	–	–	–	–
900–1,390–1,950	1,800–2,300–2,850	–	+	±	±	–	2–4 (16)	50–750– > 9,000	r	–	–	–	–	–
900–1,445–2,400	1,450–2,050–2,900	±	±	±	±	–	2–5	800–1,980–5,900	r	–	–	–	–	–
650–840–1,150	1,000–1,680–2,000	–	+	–	+	–	10–27	2,000–5,500–1,0000	r	–	–	–	–	–
1,000–1,495–2,100	1,800–2,170–2,600	–	+	±	±	–	2–5	500–870–1,550	–	–	–	–	–	–
1,300–2,000–2,700	2,300–2,860–3,300	–	+	–	+	–	3–5	700–1,460–2,600	r	–	–	–	–	–
1,200–1,620–2,100	1,900–2,400–2,900	–	+	±	±	–	2 (9–21)	50–2,450– > 7,000	r	–	–	–	–	–
1,200–1,760–2,200	2,250–2,880–3,300	–	+	–	±	–	2–3	300–770–1,200	–	–	–	r	r	–
1,200–1,800–2,400	2,300–2,910–4,700	–	+	–	±	–	2–4	350–1,110–3,300	–	–	–	–	–	–
500–680–900	800–1,170–1,700	–	+	–	–	+	(2–4) 4–8	350–1,110–4,250	r, ap	–	–	–	–	sc
500–700–950	750–1,150–1,500	+	+	–	±	+	(2–3) 4–6	>1,0000	ap	–	–	–	–	sc
300–470–950	1,100–1,600–2,200	–	–	+	+	±	2	200–365–650	–	r	–	–	–	pgt

Table 2. Continued.

Species	Solitary vessels	Radial vessel multiples	Tangential vessel multiples	% of simple perforations	Bar number in scalariform perforations	Intervessel pit arrangement	Horizontal diameter of intervessel pits (µm)	Vessel-ray pits with reduced borders	Diameter of vessels (µm)	Density of vessels (/mm^2)
Citronella silvatica CAR	+	–	–	0	37–50–65	O	5–8	–	60–100–140	16–25–32
Dendrobangia boliviana CAR	+	–	–	0	25–30–40	O	5–6	–	115–135–155	3–5–7
Gonocaryum crassifolium CAR	+	–	–	>95	0	O–A	5–7	–	50–70–110	18–25–31
Leptaulus daphnoides CAR	+	–	–	5–10	1–2–6	O	5–7	–	45–55–67	48–55–73
*Leptaulus grandifolius** CAR	+	–	±	>60	1–2–5	O–(A)	5–6	–	20–25–32	102–130–156
Metteniusa cf. *edulis* CAR	+	–	–	0	24–33–50	O–(A)	5–6	+	30–70–90	19–24–29
Pseudobotrys dorae CAR	+	–	–	0	17–35–51	(S)–O	5–10	–	30–40–55	32–45–63
Cantleya corniculata STE	+	–	–	100	0	O	8–9	+	75–105–125	5–7–10
Codiocarpus merrittii STE	+	+	–	>95	1–12–22	O–(A)	5–6	–	45–65–85	31–33–39
Discophora guianensis STE	+	+	–	80	3–10–21	O–A	5–8	–	50–75–105	20–27–36
*Gastrolepis austro-caledonica** STE	+	±	–	50	1–5–15	(S)–O	6–9	+	40–50–60	80–95–103
Gomphandra luzoninesis STE	+	–	–	75	1–18–64	O	5–7	–	60–100–120	5–7–10
Hartleya inopinata STE	+	±	–	50	1–5–30	S–O	6–12	+	55–75–95	11–18–21
Lasianthera africana STE	+	–	–	>90	1–3–5	O–A	5–6	+	30–45–55	34–45–50
Lasianthera apicalis STE	+	+	–	>70	1–7–44	S–O	6–13	–	80–135–175	9–12–15
Medusanthera laxiflora STE	+	±	±	>95	1–10–37	S–O–(A)	5–6	+	65–90–115	13–19–25
Stemonurus celebicus STE	+	±	±	>90	1–5–38	S–O	8–34	–	95–130–175	11–13–15
Stemonurus mallacensis STE	+	±	+	75	1–10–34	S–O–(A)	8–20	+	75–110–135	11–15–22
Stemonurus umbellatus STE	+	+	+	80	8–16–25	S–O	10–35	–	80–115–190	11–15–18
Whitmorea grandiflora STE	+	±	–	>90	1–5–21	S–O	8–13	–	65–80–100	4–7–10
Pennantia corymbosa PEN	+	?	?	0	18–28–45	O	3–4	–	30–40–55	69–85–112
Pennantia cunninghamii PEN	+	–	–	0	33–40–56	O	3–4	–	50–70–95	48–54–60

Species are arranged alphabetically according to the family classification of Kårehed (2001). Numbers between hyphens are mean values, flanked by minimum and maximum values; numbers/symbols between parentheses represent exceptional values/conditions; measurements for horizontal diameter of intervessel pits and multiseriate rays width are ranges. For specimens of the same taxon, superscript numbers after the species name refer to the order of the specimens in the species list (see Appendix 1). ►

ray pits sometimes scalariform with reduced borders to even simple in species of *Cassinopsis* and *Poraqueiba* (Fig. 1F); vessel-ray pitting occasionally unilaterally compound in *Cassinopsis tinifolia*, *Merrilliodendron* and *Phytocrene*. Wall sculpturing present as short fine ridges in the inner vessel wall of *Desmostachys* and *Iodes* (Fig. 2A). Tyloses occasionally present in *Icacina* and *Mappia*. Tangential diameter of vessels (20–)35–310(–650) µm, vessel elements (70–)175–2,200(–2,900) µm long. Tracheids present in *Chlamydocarya*, *Icacina*, *Iodes*, *Lavigeria*, *Polyporandra*, *Phytocrene*, *Rhaphiostylis* (Fig. 2B) and *Sarcostigma*, (250–)600–1,000(–1,500) µm long. Nonseptate fibres with large bordered pits (Fig. 2C) concentrated in tangential and radial walls, co-occurring with septate fibres having simple pits in *Sarcostigma* (Fig. 2D), fibres usually very thin- or thin- to thick-walled (thick-walled in

Vessel element length (µm)	Fibre length (µm)	Diffuse ax. parenchyma	Diffuse-in-aggregates ax. parenchyma	Banded ax. parenchyma	Scanty ax. parenchyma	Vasicentric ax. parenchyma	Multiseriate ray width (number of cells)	Multiseriate ray height (µm)	Prismatic crystals	Druses	Crystal sand	Styloid-like crystals	Clustered crystals	Type of cambial variants
850–1,390–1,950	1,900–2,520–3,100	–	+	–	+	–	4–7	> 5,000	r	–	–	r	–	–
1,100–2,230–2,800	3,300–4,240–4,900	–	+	±	+	–	(2–3) 5–8	> 6,000	r, ap	–	–	r	–	–
500–960–1,425	2,600–2,970–3,450	–	+	±	±	–	(3–4) 5–9	650–> 6,000	r	–	–	r	–	–
500–795–1,075	1,700–2,190–2,900	–	+	–	+	–	2–4	300–620–950	–	–	–	r	–	–
650–1,095–1,600	1,300–1,550–1,800	±	±	–	+	–	2–3	700–2,450–5,200	–	–	–	–	–	–
1,200–1,800–2,200	2,500–2,870–3,300	–	+	+	+	–	5–11	1,300–2,500–3,400	r	–	–	–	–	–
1,025–1,310–1,700	2,150–2,770–3,150	–	+	–	±	–	(6) 11–19	> 6,000	r	–	–	r	–	–
900–1,430–1,800	1,750–2,250–2,550	±	–	–	+	–	2–3	400–1,200–3,875	–	–	–	r	–	–
400–785–1,050	2,250–2,790–3,200	–	+	–	+	–	2–5	300–835–1,600	–	–	–	r	–	–
100–1,030–1,850	3,000–3,650–4,400	–	+	+	+	–	(2) 3–7	1,000–2,810–4,400	r	–	r	r	–	–
275–540–900	850–1,160–1,700	±	–	–	+	–	2–4	350–860–1,500	r	–	–	–	r	–
1,000–1,410–1,850	2,700–3,370–4,150	–	–	+	±	–	(6) 10–17	4,000–8,000–9,000	–	–	r	r	–	–
600–1,420–1,950	1,450–3,020–4,500	–	+	–	+	–	2–5	325–1,090–2,700	–	–	r	r	–	–
400–865–1,100	1,700–2,110–2,600	–	+	–	+	–	2–6	550–1,150–2,150	–	–	r	–	–	–
950–1,510–2,000	2,700–3,330–4,000	±	–	–	+	–	2–6	500–1,830–4,100	r	–	–	–	–	–
300–600–800	1,100–2,450–3,300	–	±	+	+	–	9–11	2,500–> 6,000	r	–	–	r	r	–
1,000–1,400–1,850	2,500–3,470–4,500	–	±	–	+	–	2–6	700–1,930–3,800	r	–	–	r	r	–
400–900–1,500	1,500–2,220–3,000	–	±	–	+	–	(2–4) 6–10	300–1,090–2,100	r	–	–	r	r	–
600–1,130–1,600	1,700–2,460–3,100	–	±	–	+	–	(2–4) 5–9	1,200–2,080–3,100	r, f	–	–	–	–	–
450–665–1,000	1,600–2,000–3,400	±	–	–	+	–	(2–4) 6–9	300–1,100–1,700	r	–	–	r	r	–
700–1,080–1,400	1,300–1,790–2,300	–	+	–	+	–	(2–3) 5–6	900–1,390–2,000	–	–	–	–	–	–
900–1,500–2,250	1,700–2,270–2,900	–	+	–	+	–	4–8	550–1,020–1,750	–	–	–	–	–	–

► Names of climbing species are marked with "+", juvenile wood samples with asterisks. Three-letter acronyms after genera refer to acronyms used in Table 1. Intervessel pit arrangement: A, alternate; O, opposite; S, scalariform. Type of crystals: ap, in axial parenchyma; f, in fibres; r, in rays. Type of cambial variants: fx, furrowed xylem; ip, included phloem; pgt, parenchymatous ground tissue; sc, successive cambia. + = present, ± = scarcely present, – = absent.

Poraqueiba), (350–)610–3,120(–3,800) µm long, pit borders (3–)5–8(–10) µm in diameter. Axial parenchyma in nonclimbing genera often a combination of diffuse-in-aggregates and scanty paratracheal parenchyma with a tendency to form short narrow bands in *Calatola*, *Desmostachys* (also wider bands, Fig. 1C), *Emmotum*, *Merrilliodendron*, *Oecopetalum*, *Platea*, and *Poraqueiba* (Fig. 1B), banded parenchyma 3–5 cells wide dominant in *Rhyticaryum*, vasicentric parenchyma and conspicuous band formation of (1–)2–10(–20) cells wide dominant in the climbing genera (Figs. 1D, 3E, bands absent in *Raphiostylis*), strands including 4–16 cells. Uniseriate rays scarce to abundant, (0–)1–29(–33) rays/mm, (30–)85–925(–2,500) µm long, consisting of square to upright cells. Multiseriate rays in nonclimbing genera generally 2–5-seriate (Fig. 2E–F, few multiseriate rays much wider in *Emmotum* (up to 16-seriate) and *Poraqueiba* (up to 21-seriate; Fig. 2G), and all multiseriate rays wider in *Ottoschulzia* (10–27-seriate); multiseriate rays in climbing genera extremely variable, but absent in the juvenile stem of *Pyrenacantha kirkii*, ranging from 2-seriate in *Sarcostigma* (Fig. 2D) up to 42-seriate in *Phytocrene macrophylla*, rays partly or entirely unlignified in *Icacina* (Fig. 3B), *Iodes*, *Lavigeria* (Fig. 3C), *Phytocrene* (Fig. 3D), *Polyporandra* (Fig. 1D), *Pyrenacantha*, *Mappia*, *Mappianthus* and *Rhaphiostylis*, multiseriate ray height (50–)365–5,500(–> 12,000) µm, density (0–)1–11(–15)

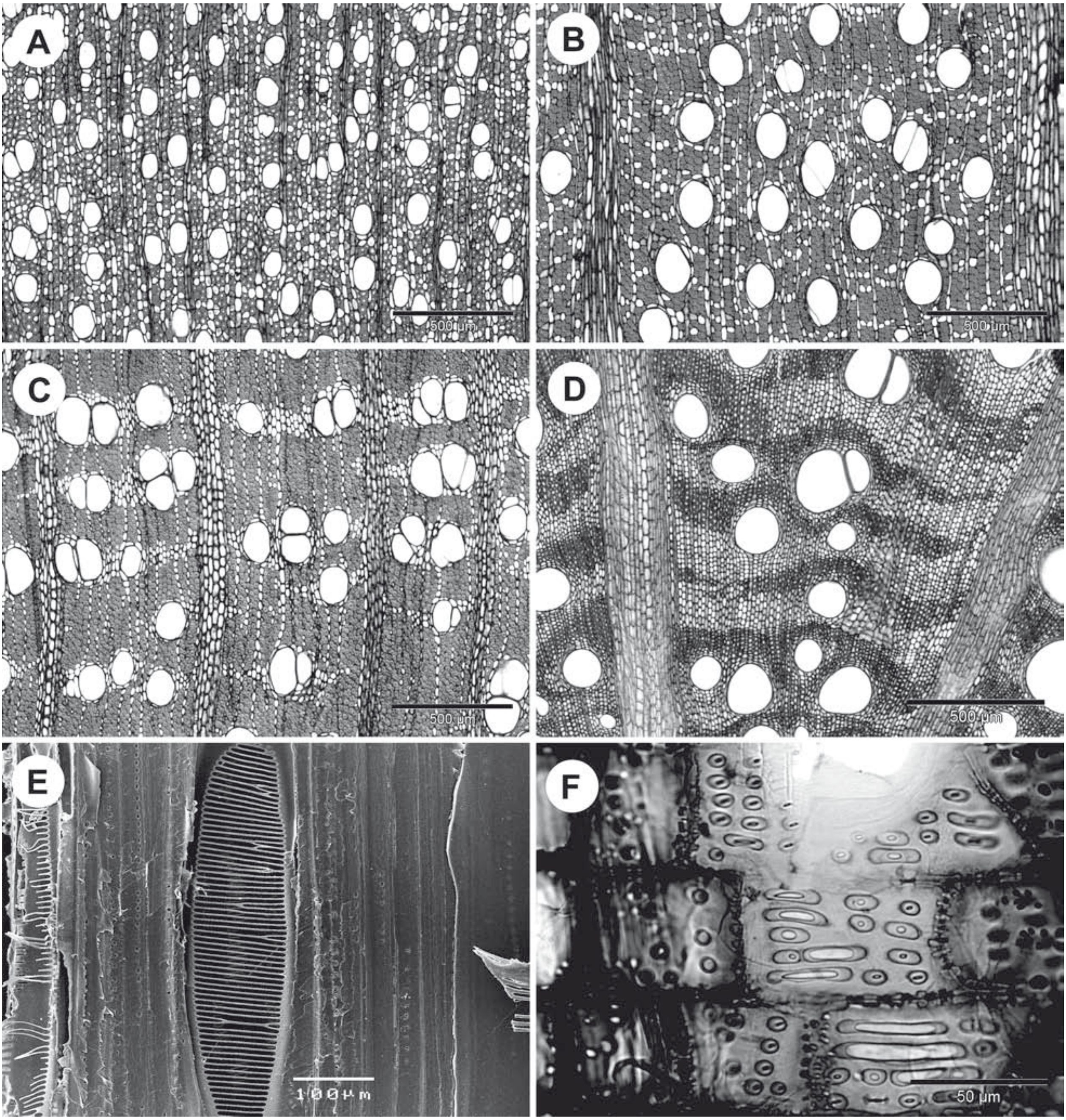

Fig. 1. LM micrographs (A–D, F) and SEM micrograph (E) of the wood structure in Icacinaceae s.str. A, *Apodytes dimidiata*, transverse section (TS), solitary vessels and mainly diffuse-in-aggregates axial parenchyma; B, *Poraqueiba guianense*, TS, solitary vessels and mainly diffuse-in-aggregates axial parenchyma with slight tendency to form short bands; C, *Desmostachys vogelii*, TS, vessels solitary and in short tangential multiples, axial parenchyma mainly paratracheal; D, *Polyporandra scandens*, TS, wide axial parenchyma bands and wide multiseriate rays; E, *Cassinopsis* sp., radial longitudinal section (RLS), scalariform perforation plate; F, *Poraqueiba guianense*, RLS, vessel-ray pitting opposite to scalariform with reduced borders.

rays/mm, rays consisting of homocellular (exclusively procumbent) body ray cells in *Apodytes*, *Emmotum*, *Poraqueiba*, *Platea*, and heterocellular (a mixture of procumbent, square and/or upright) body ray cells in the other genera, 1–4(>10) rows of upright to square marginal ray cells; indistinct sheath cells sometimes present in *Calatola*, *Cassinopsis* (Fig. 2F), *Desmostachys*, *Mappianthus*, *Platea* and *Rhyticaryum*; rays almost never fused. Dark amorphous contents sometimes present in *Apodytes*. Solitary prismatic crystals in body and marginal ray cells

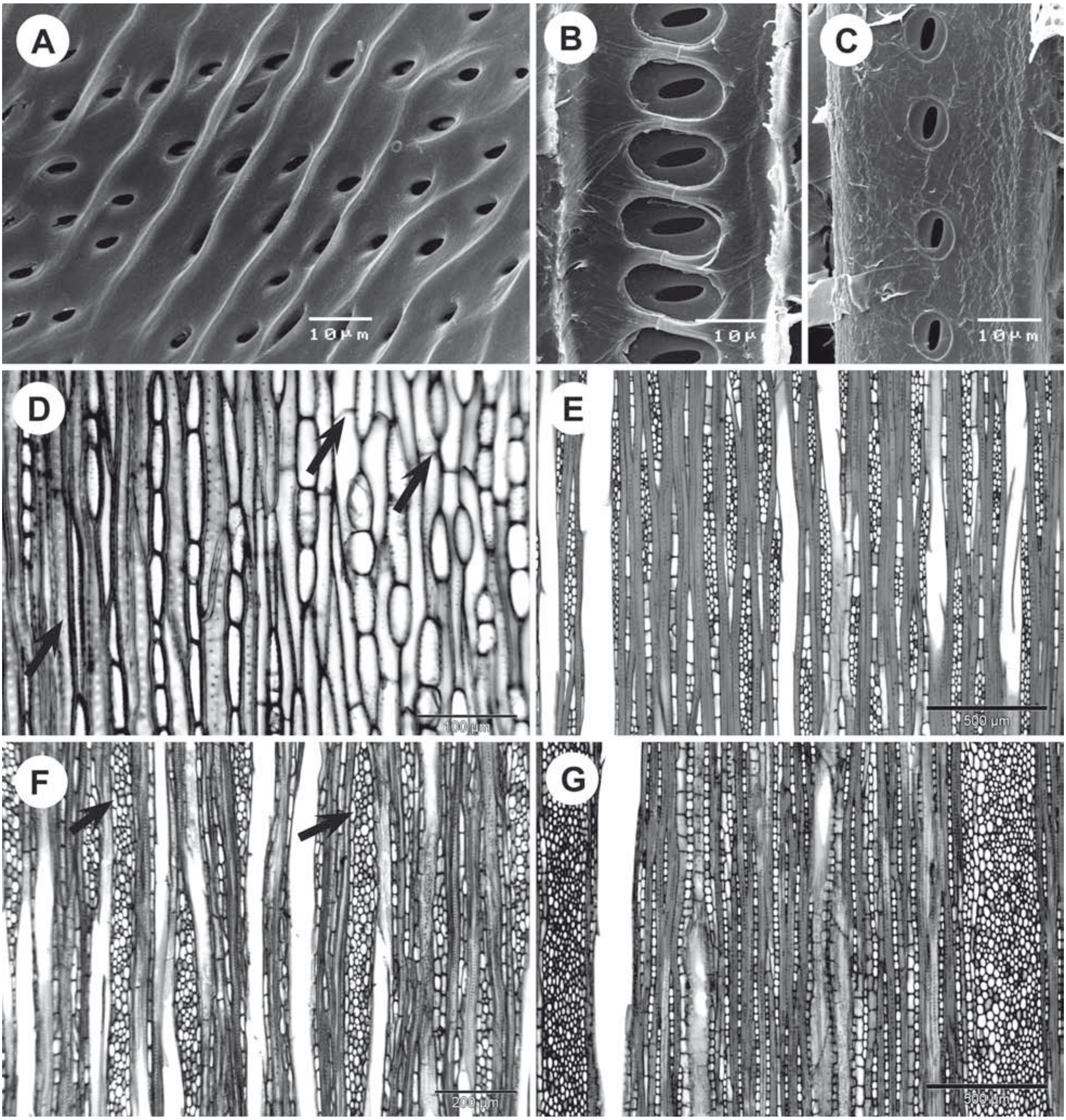

Fig. 2. Tangential longitudinal surfaces (TLS, SEM, A–C) and sections (LM, D–G) of Icacinaceae s.str. A, *Iodes africana*, short oblique wall thickenings in the inside wall of a vessel element; B, *Rhaphiostylis ferruginea*, tracheid with one row of conspicuously bordered pits; C, *Cassinopsis* sp., fibre with distinctly bordered pits; D, *Sarcostigma kleinnii*, uniseriate rays and septate libriform fibres (two arrows at right) that co-occur with fibre-tracheids having distinctly bordered pits (arrow at left); E, *Apodytes javanica*, 2–3-seriate rays with a variable number of rows of marginal ray cells; F, *Cassinopsis capensis*, multiseriate rays showing indistinct sheath cells (arrows); G, *Poraqueiba guianense*, large multiseriate rays co-occurring with uniseriate ones.

(usually nonchambered, but partly chambered in *Mappia* and *Sarcostigma*, absent in *Apodytes*, *Iodes*, *Rhyticaryum*, *Pyrenacantha*) and in axial parenchyma cells of species of *Icacina*, *Mappia* (chambered), *Merrilliodendron*, *Phytocrene*, *Polyporandra*, *Rhaphiostylis* and *Sarcostigma*, few small styloid-like crystals in rays of *Apodytes*, *Merrilliodendron*, *Rhyticaryum* and *Sarcostigma*, druses in nonlignified rays of *Iodes*, *Phytocrene* and *Polyporandra*, and in axial parenchyma of *Polyporandra*, few clustered crystals in nonchambered body and marginal ray cells of *Apodytes, Desmostachys, Icacina, Iodes, Merrilliodendron*, *Phytocrene*, *Pyrenacantha* and *Sarcostigma*, crystal

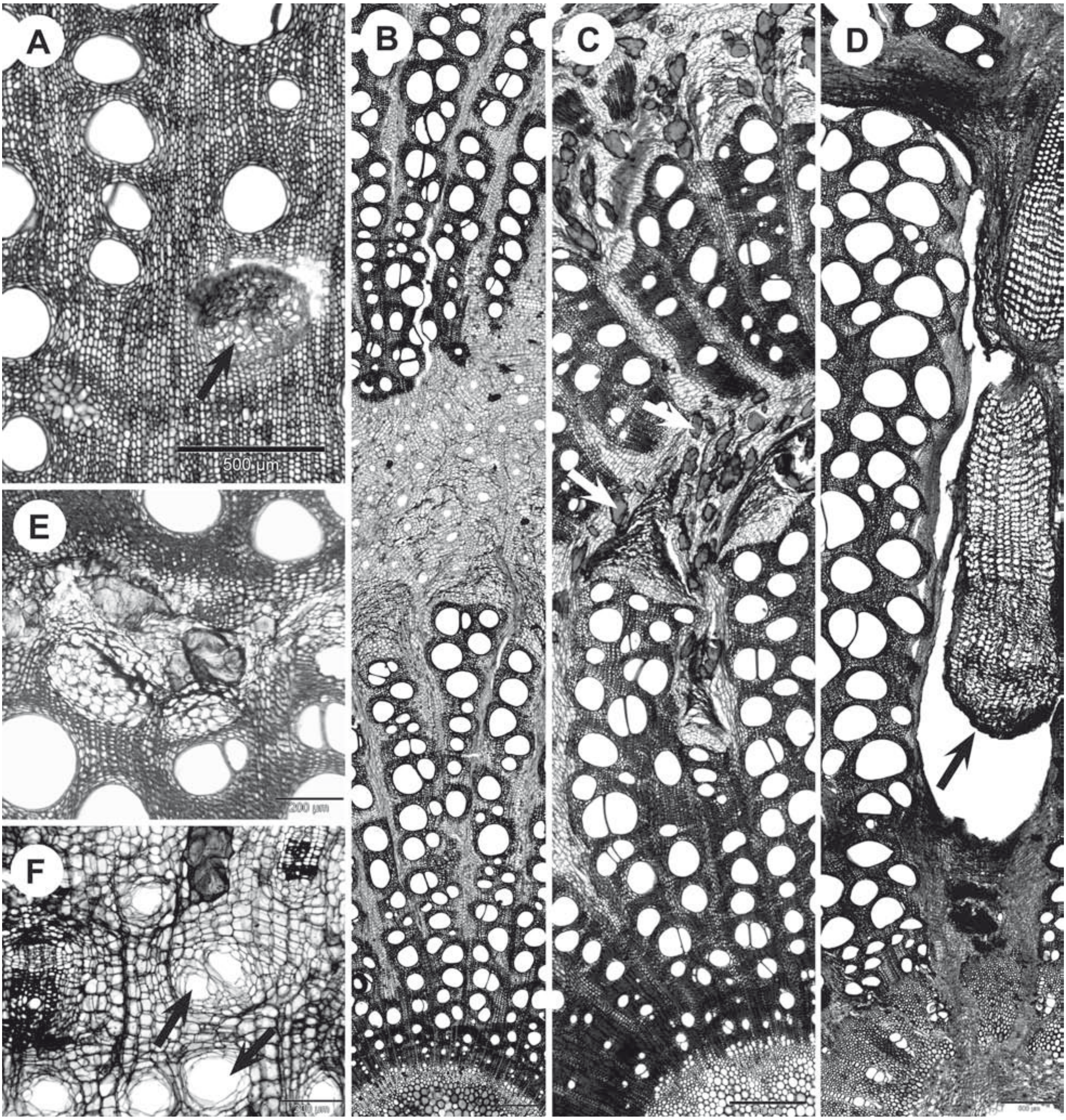

Fig. 3. Transverse sections (TS, LM) showing cambial variants in Icacinaceae s.str. A, *Sarcostigma kleinnii*, interxylary phloem (arrow); B, *Icacina mannii*, successive cambia; C, *Lavigeria macrocarpa*, successive cambia with thick-walled sclereids in the conjunctive tissue (arrows); D, *Phytocrene macrophylla*, successive cambia with elongated phloem zones (arrow); E, *Mappia cordata* (Tw specimen), detail of phloem region in between two regions of wood produced by successive cambia; F, *Icacina mannii*, detail of secretory canals (arrows) in the conjunctive tissue.

sand absent. Cambial variants observed as three types, and more than one type may occur within a single species: *(1)* interxylary phloem forming islands of phloem within the wood cylinder (*Sarcostigma*, Fig. 3A); *(2)* successive cambia (*Chlamydocarya* [only in furrows, Fig. 4B], *Iodes*, *Icacina* [Fig. 3B], *Lavigeria* [Fig. 3C], *Mappia* [Fig. 3E], *Phytocrene* [Fig. 3D], *Pyrenacantha* and *Rhaphiostylis*) with thick-walled sclereids in the conjunctive tissue, proliferation of parenchyma is obvious in species with successive cambia, especially in *Iodes* with abnormal position of the primary xylem; and *(3)* furrowed xylem with elongated zones of phloem in the furrows (*Chlamydocarya*

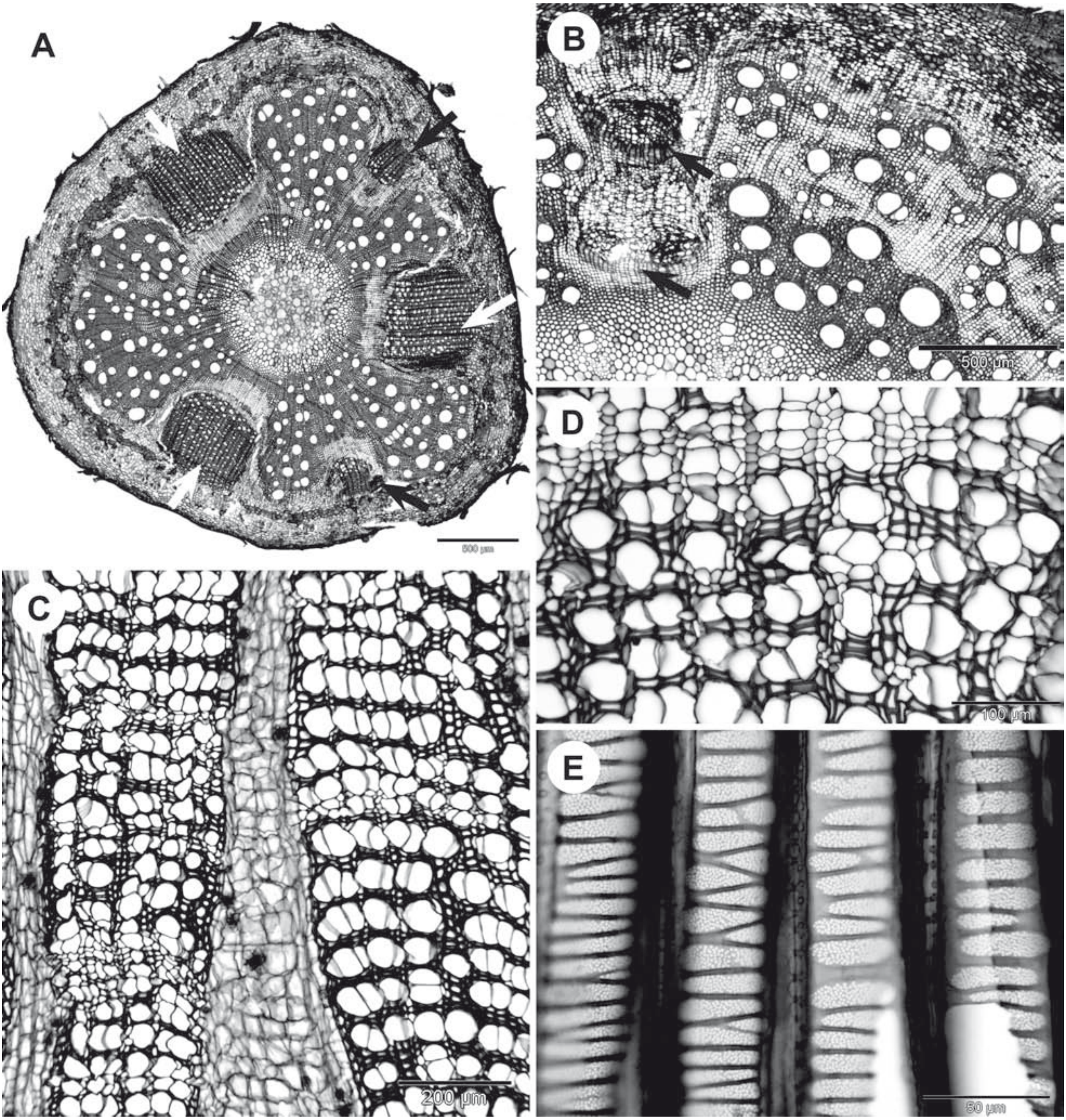

Fig. 4. Transverse sections (A–D) and tangential section (E) of cambial variants. A, *Pyrenacantha lebrunii*, entire juvenile stem with furrowed xylem, showing three well-developed (white arrows) and two initial (black arrows) phloem zones in the stem; B, *Chlamydocarya thomsonia*, successive cambia (arrows) constricted to the phloem zone; C, *Phytocrene* sp., elongated phloem zones separated by unlignified rays; D, *Phytocrene* sp., detail of phloem showing sieve tubes, companion cells, fibres and axial parenchyma; E, *Phytocrene* sp., sieve tubes with scalariform sieve plates.

[Fig. 4B], *Phytocrene* [Fig. 4D], *Pyrenacantha* [Fig. 4A]), in *Phytocrene* and *Pyrenacantha* phloem zones include mainly phloem fibres and tangential multiples of sieve tubes, together with few companion and phloem parenchyma cells (Fig. 4C–D); secretory canals in nonlignified conjunctive parenchyma and rays of *Icacina mannii* (Fig. 3F); phloem with typically scalariform sieve plates (Fig. 4E) and many druses.

Cardiopteridaceae (campanulids, Aquifoliales) (*Cardiopteris** 1/3, *Citronella* 1/10, *Dendrobangia* 1/1, *Gonocaryum* 1/ca. 20, *Leptaulus* 2/6, *Metteniusa* 1/3, *Pseudobotrys* 1/2; Fig. 5): Growth ring boundaries often indistinct to absent, more obvious in *Leptaulus*, *Metteniusa* and *Pseudobotrys*. Diffuse-porous. Vessels (3–)5–55(–73)/mm^2, predominantly solitary (Fig. 5B) with occasionally short tangential multiples of 2–3 in *Cardiopteris* (Fig. 5A) and *Leptaulus grandifolius*; vessel outline (slightly) angular, but oval to rounded in *Cassinopsis*; perforation plates exclusively or predominantly scalariform with (17–)30–50(–65) bars in *Citronella*, *Dendrobangia*, *Metteniusa* and *Pseudobotrys*, exclusively or predominantly simple in *Cardiopteris* and *Gonocaryum*, and simple/scalariform with few bars in *Leptaulus*, few reticulate perforations in *Gonocaryum* (Fig. 5D), reticulate portions in *Dendrobangia*. Intervessel pits opposite in *Citronella* and *Dendrobangia*, opposite to slightly scalariform in *Pseudobotrys*, opposite to slightly alternate in species of *Cardiopteris*, *Leptaulus* and *Metteniusa*, opposite to alternate in *Gonocaryum*, pits mostly 5–7 µm in horizontal diameter, up to 10 µm in *Pseudobotrys* and 9–14 µm in *Cardiopteris*, nonvestured. Vessel-ray pits similar to intervessel pitting in shape and size, except for *Metteniusa* showing opposite to scalariform pits with reduced pit borders (pit borders 8–20 µm in horizontal diameter). Wall sculpturing absent. Tyloses absent. Tangential diameter of vessels (30–)40–260(–475) µm, vessel elements (300–)470–2230(–2800) µm long. Tracheids present in *Cardiopteris* (Fig. 5E), (700–)1,050(–1,400) µm. Fibres nonseptate, fibres often thin- to thick-walled, thick-walled in *Pseudobotrys* and very thick-walled in *Gonocaryum*; pits conspicuously bordered and concentrated in tangential and radial walls (Fig. 5F), pit borders 5–9 µm in horizontal diameter; fibre length (1,175–)2,190–4,240(–4,900) µm. Axial parenchyma often diffuse-in-aggregates and scanty paratracheal (Fig. 5B), tendency to form short narrow bands in *Dendrobangia*, *Gonocaryum* and *Metteniusa*, in *Cardiopteris* lignified parenchyma concentrated around vessels (scanty and vasicentric) co-occuring with a nonlignified parenchymatous ground tissue (Fig. 5A); 3–11 cells per parenchyma strand. Uniseriate rays scarce to common, 0–11 rays/mm, but completely absent in *Pseudobotrys dorae* (Fig. 5F), (100–)330–1,070(–2,400) µm long, consisting of square to upright cells. Multiseriate rays narrow (2–4-seriate) in *Cardiopteris* and *Leptaulus*, up to 7-seriate in *Citronella*, up to 8-seriate in *Dendrobangia*, up to 9-seriate in *Gonocaryum*, and wider in *Metteniusa* (5–11-seriate) and *Pseudobotrys* (11–19-seriate, Fig. 5C), (300–)620–2,500(–> 6,000) µm high, 1–11 rays/mm, consisting of exclusively procumbent body ray cells in *Cardiopteris*, *Leptaulus*, a combination of procumbent and square body ray cells in *Citronella*, *Dendrobangia*, *Gonocaryum*, *Metteniusa* and *Pseudobotrys* and 1–6 rows of square to upright marginal ray cells; indistinct sheath cells in *Citronella* and *Dendrobangia*; a small percentage of rays fused in *Leptaulus*. Dark amorphous contents in ray cells. Few prismatic crystals in body and marginal ray cells of *Citronella* (sometimes in chambered cells), *Dendrobangia* (often in chambered cells, Fig. 5G), and in nonchambered cells of *Gonocaryum*, *Metteniusa* and *Pseudobotrys*, few small styloids present in rays of *Citronella*, *Dendrobangia*, *Gonocaryum* and *Leptaulus*, druses in nonlignified parenchyma of *Cardiopteris*, prismatic crystals also in chambered axial parenchyma cells of *Dendrobangia*, crystal sand absent. A specific type of cambial variants present in *Cardiopteris moluccana*: lignified islands consisting of vessels surrounded by paratracheal parenchyma, vasicentric tracheids (Fig. 5E) and fibres are embedded in nonlignified parenchymatous ground tissue (Fig. 5A).

Stemonuraceae (campanulids, Aquifoliales) (*Cantleya* 1/1, *Codiocarpus* 1/2, *Discophora* 1/2, *Gastrolepis* 1/1, *Gomphandra* 1/ca. 50, *Hartleya* 1/1, *Lasianthera* 2/2, *Medusanthera* 1/11, *Stemonurus* 2/ca. 20, *Whitmorea* 1/1; Fig. 6): Growth ring boundaries generally absent, indistinct in *Hartleya* and *Stemonurus*. Diffuse-porous. Vessels (4–)7–45(–50)/mm^2, exclusively solitary in *Cantleya* and *Lasianthera africana*, solitary and in radial multiples and/or tangential multiples of 2–4 in most genera (Fig. 6A), additional vessel clusters of 3–7 cells in *Stemonurus* (Fig. 6B); vessel outline often slightly angular; perforation plates exclusively simple in *Cantleya*, predominantly simple (> 90%) in *Codiocarpus*, *Medusanthera* (Fig. 6C) and *Whitmorea*, largely simple in *Lasianthera* (75% to > 90%), *Stemonurus* (75% to > 90%), *Discophora* (80%), and *Gomphandra* (75%), and simple/scalariform perforations equally abundant in *Hartleya*, scalariform perforations with (1–)3–18(–64) bars, occasionally double simple perforations in *Discophora*. Intervessel pits generally opposite to scalariform, although an alternate arrangement sometimes observed in *Discophora* and *Lasianthera*, pits 5–35 µm in horizontal diameter, nonvestured. Vessel-ray pits similar to intervessel pits in shape and size, except for the scalariform vessel-ray pitting with reduced pit borders in species of *Cantleya*, *Gastrolepis*, *Hartleya*, *Lasianthera*, *Medusanthera* and *Stemonurus*, vessel-ray pits unilaterally compound in *Medusanthera* (Fig. 6D). Wall thickenings absent. Tyloses absent. Tangential diameter of vessels (30–)45–130(–190) µm, vessel elements (300–)600–1,510(–2,000) µm long. Tracheids absent. Fi-

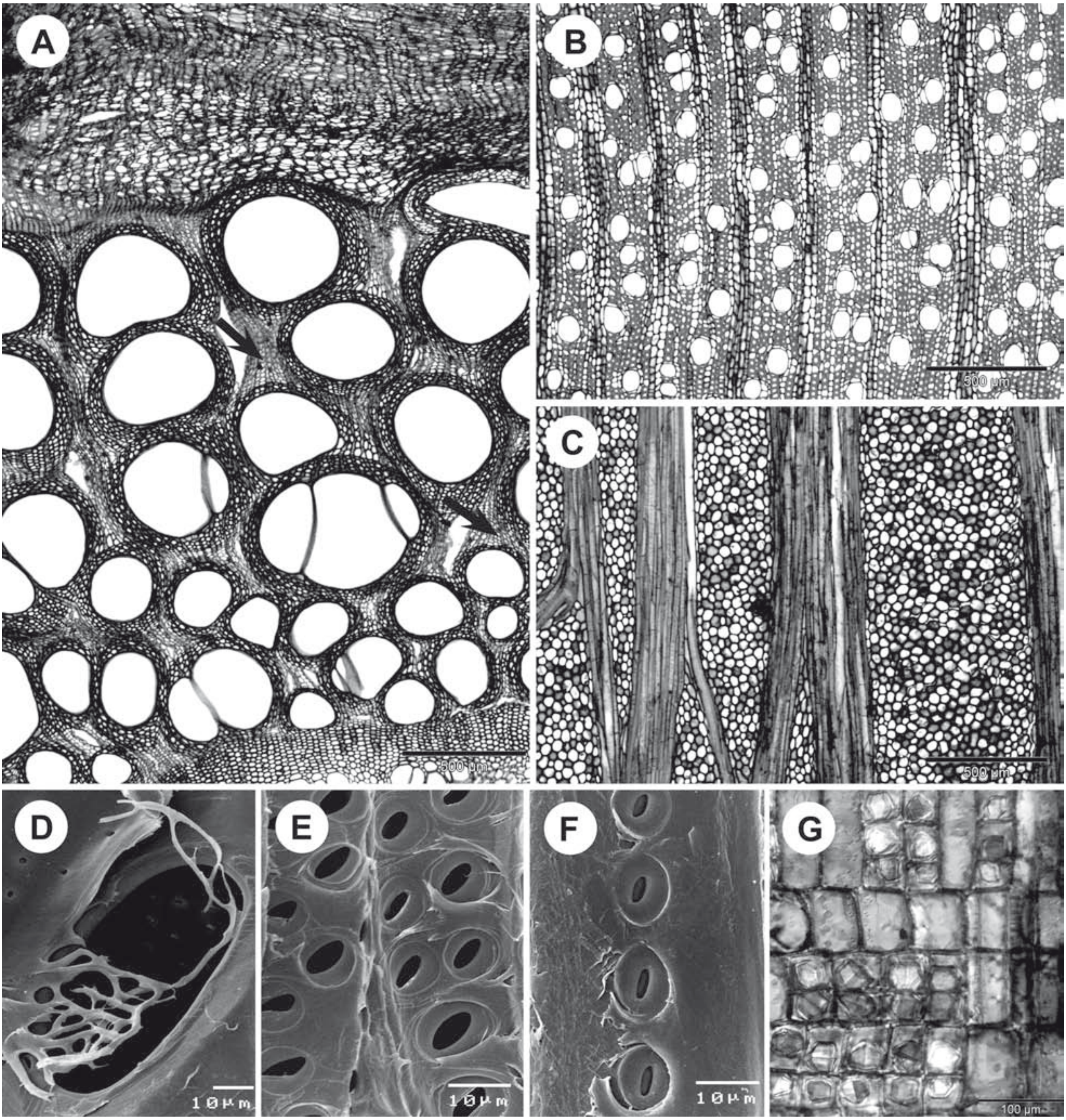

Fig. 5. LM (A–C, G) and SEM micrographs (D–F) showing the wood anatomical diversity of Cardiopteridaceae. A, *Cardiopteris moluccana*, transverse section (TS), islands of lignified cells (vessels, tracheids, fibres and axial parenchyma) embedded in unlignified parenchymatous ground tissue (arrows); B, *Citronella silvatica*, TS, solitary vessels, diffuse-in-aggregates axial parenchyma; C, *Pseudobotrys dorae*, tangential longitudinal section (TLS), wide multiseriate rays, uniseriate rays are lacking; D, *Gonocaryum crassifolium*, radial longitudinal section (RLS), part of reticulate vessel perforation; E, *Cardiopteris moluccana*, TLS, tracheids with conspicuously bordered pits; F, *Dendrobangia boliviana*, TLS, fibre-tracheid with distinctly bordered pits; G, *Dendrobangia boliviana*, RLS, prismatic crystals in chambered body and marginal ray cells.

bres nonseptate with distinctly bordered pits concentrated in tangential and radial walls, often thick- to very thick-walled (Fig. 6A–B) except in *Gastrolepis* and *Gomphandra*, (1,100–)2,000–3,650(–4,500) µm long, pit borders 4–9 µm in horizontal diameter. Axial parenchyma typically diffuse-in-aggregates and scanty paratracheal, paratracheal parenchyma dominant in species of *Gastrolepis*, *Lasianthera*, *Stemonurus* (Fig. 6B) and *Whitmorea*, tendency to banded axial parenchyma of 1–2 cells wide in *Discophora* (Fig. 6A), banded axial parenchyma prevailing in

Medusanthera (1–3 cells wide) and *Gomphandra* (1–2 cells wide); 4–14 cells per parenchyma strand. Uniseriate rays generally scarce to even completely absent in *Medusanthera*, 0–5 rays/mm, (50–)210–750(–1,550) µm high, consisting of square to procumbent ray cells. Multiseriate rays generally 2–7-seriate, up to 9-seriate in *Whitmorea* and up to 10-seriate in *Stemonurus*, rays wider in *Gomphandra* (10–17-seriate) and *Medusanthera* (9–11-seriate), (300–)835–2,810(–4,400) µm high in most genera, but much higher in *Gomphandra* (Fig. 6E) and *Medusanthera*,

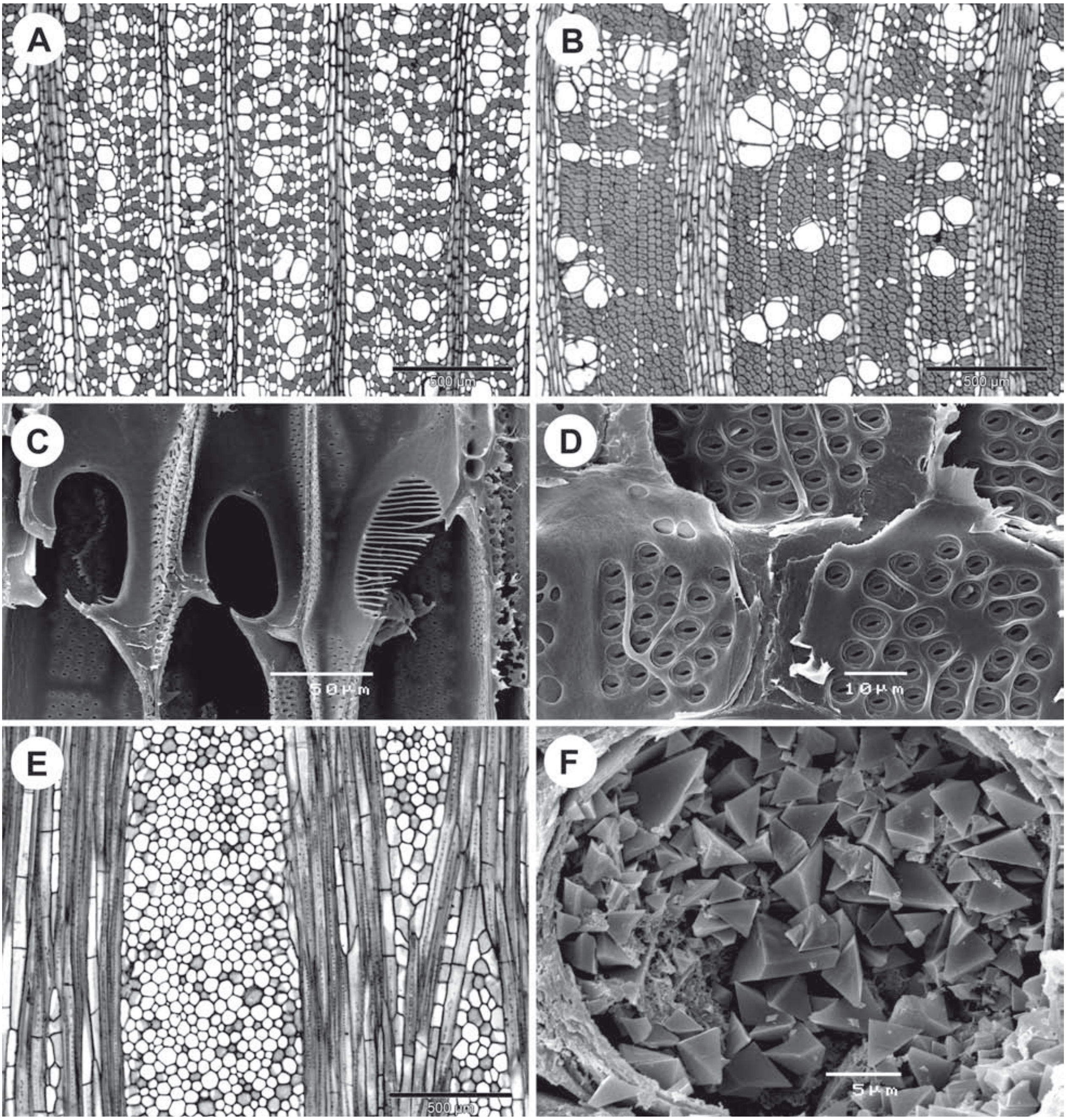

Fig. 6. LM (A–B, E) and SEM (C–D, F) micrographs showing wood anatomical variation in Stemonuraceae. A, *Discophora guianensis*, transverse section (TS), vessels solitary and in short radial multiples, axial parenchyma diffuse-in-aggregates with tendency to short narrow bands, fibres very thick-walled; B, *Stemonurus malaccensis*, TS, vessels sometimes in clusters, axial parenchyma mainly paratracheal, fibres very thick-walled; C, *Medusanthera laxiflora*, radial longitudinal section (RLS), vessel perforations simple or scalariform; D, *Medusanthera laxiflora*, RLS, unilaterally compound vessel-ray pitting; E, *Gomphandra luzoniensis*, tangential longitudinal section (TLS), wide multiseriate rays; F, *Lasianthera africana*, RLS, crystal sand in ray cell.

2,500–9,000 µm high, multiseriate ray density 1–9 rays/mm, rays consisting of procumbent body ray cells in *Cantleya*, *Codiocarpus*, *Stemonurus* and *Whitmorea*, or a mixture of procumbent and square cells in the other genera, and 1–5(–10) rows of square to upright marginal ray cells; a small percentage of rays fused in *Codiocarpus*, *Lasianthera*, *Stemonurus* and *Whitmorea*; indistinct sheath cells sometimes present in *Discophora*, *Gomphandra*, *Hartleya*, *Lasianthera* and *Stemonurus*; thick-walled sclereids in rays of *Medusanthera*. Dark amorphous contents in ray cells including crystal sand in *Discophora* and *Lasianthera*. Prismatic crystals present in rays of *Discophora*, *Gastrolepis*, *Lasianthera*, *Medusanthera*, *Stemonurus* (also in fibres of *S. umbellatus*) and *Whitmorea*, few small styloid-like crystals present in nearly all genera (except for *Gastrolepis* and *Lasianthera*), clustered crystals present in *Gastrolepis*, *Medusanthera*, *Stemonurus* and *Whitmorea*, crystal sand present in *Discophora*, *Gomphandra*, *Hartleya* and *Lasianthera* (Fig. 6F), crystals absent from axial parenchyma. No cambial variants.

Pennantiaceae (campanulids, Apiales) (*Pennantia* 2/3; Fig. 7): Growth ring boundaries indistinct (Fig. 7B) to distinct. Diffuse-porous. Vessels (48–)70(–30)/mm^2, predominantly solitary (Fig. 7A–B); vessel outline angular; perforation plates exclusively scalariform (Fig. 7C) with (18–)34(–56) bars, sometimes reticulate portions in *P. cunninghamii*. Intervessel pits opposite, pits 3–4 µm in horizontal diameter, nonvestured. Vessel-ray pitting comparable to intervessel pitting in shape and size. Helical thickenings present throughout vessel elements and in fibres in *P. corymbosa* (Fig. 7D), and sometimes in tails of vessel elements in *P. cunninghamii*. Tyloses absent. Tangential diameter of vessels (30–)55(–95) µm, vessel elements (700–)1,290(–2,250) µm long. Tracheids occasionally present, (1,400–)1,950(–2,700) µm long. Nonseptate fibres with distinctly bordered pits concentrated in tangential and radial walls, very thin-walled, (1,300–)2,030(–2,900) µm long, pit borders 4–6 µm in diameter. Axial parenchyma diffuse or diffuse-in-aggregates and scanty paratracheal; 5–10 cells per parenchyma strand. Uniseriate rays common, 5–9 rays/mm, consisting of square to upright cells, length (200–)500(–1,100) µm. Multiseriate rays often 4–8-seriate (Fig. 7E–F), (550–)1,200 (–2,000) µm high, 1–6 rays/mm, consisting of procumbent body ray cells with 1–4(>20) rows of upright to square marginal ray cells; indistinct sheath cells sometimes present in *P. cunninghamii* (Fig. 7E). Dark amorphous contents absent in rays. All types of mineral inclusions absent. No cambial variants.

Phylogenetic analyses based on maximum parsimony. — The maximum parsimony analysis of the molecular data finds 8,190 most parsimonious trees with length 15,756 (CI 0.278; RI 0.523), and generally lacks bootstrap support (BS) for the relationships between the major lineages of Icacinaceae s.str. (Fig. 8A). Regarding Icacinaceae s.str., the following groups are well supported within lamiids: *Emmotum*-group (BS 100; represented by only two out of six genera), *Apodytes*-group (BS 100), which is weakly supported as sister to *Oncotheca* (BS 58), and *Icacina*-group (BS 100; represented by 11 out of 25 genera). Other lineages within lamiids include *Garryales* (BS 99; including *Eucommia*), and a large clade consisting of Lamiales-Solanales-Gentianales plus *Vahlia* (Vahliaceae) and *Borago*-*Hydrophyllum* (Boraginaceae; BS 100), which are unplaced as to order. Within campanulids, Aquifoliales is the earliest diverging clade, including the monophyletic Cardiopteridaceae and Stemonuraceae (BS 82 and 98, respectively), which show a strong sister relationship (BS 100). Both families are in turn sister to the rest of Aquifoliales (BS 98). Aquifoliales is sister to a large clade (BS 100) comprising Asterales (BS 100), Apiales (BS 100), Dipsacales (BS 100), and *Berzelia*-*Escallonia* (BS 98). Apiales and Dipsacales are sisters (BS 80). The two species of *Pennantia* are strongly nested at the base of Apiales (BS 100).

The maximum parsimony analysis of the combined matrix reveals 120 most parsimonious trees with length 16,095.9 (CI 0.274; RI 0.521). The topology shows more resolution within the Icacinaceae s.str. relationships (Fig. 8B), although BS is often low to moderate. Within lamiids, the earliest diverging lineage is formed by a moderately supported monophyletic group (BS 72), including two poorly supported subclades: subclade 1 (BS 63) comprises *Cassinopsis*, which is sister to the *Emmotum*-group; and subclade 2 (BS 59) comprises *Oncotheca*, which is sister to the *Apodytes*-group. The following group that branches off includes Garryales (BS 99), which is very weakly supported (BS 51) as sister to the rest of the lamiids. Next, the *Icacina*-group (BS 100) is weakly supported (BS 59) as sister to a large clade (BS 100) comprising Lamiales-Solanales-Gentianales plus *Vahlia* and *Borago*-*Hydrophyllum*. Within campanulids, relationships and bootstrap supports are very similar to the molecular analysis, except for *Berzelia*-*Escallonia*, which are weakly supported (BS 53) as sister to Asterales. If the three MorphoCode characters are omitted from the analysis, the topology and BS remain similar.

Phylogenetic analyses based on Bayesian inference. — The Bayesian analysis of the molecular matrix (Fig. 9A) is generally better resolved than Fig. 8A, but posterior probabilities (PP) between different lineages of Icacinaceae s.str. are often too low to make conclusive comments on their relationships. In Fig. 9A, the first diverging evolutionary lineage of lamiids is formed by a weakly supported clade (PP 0.76) and is divided into two subclades: subclade 1 (PP 0.81) includes two branches, one (PP 0.69) including the *Emmotum*-group (PP 1.00), which is sister to *Cassinopsis*, and the other (PP 0.88) comprising the *Apodytes*-group (PP 1.00) and *Oncotheca*; subclade 2 includes Garryales (PP 1.00). The *Icacina*-group (PP 1.00) is the next lineage that diverges within lamiids (PP 0.87), followed by Gentianales, Solanales plus *Borago*-*Hydrophyllum* (PP 0.91), *Vahlia*, and Lamiales (PP 1.00). Within campanulids, the first diverging lineage is Aquifoliales (PP 1.00) including the well-supported sister families Cardiopteridaceae (PP 1.00) and Stemonuraceae (1.00), which are in turn sister to the rest of the order. Subsequent lineages include Asterales, which are sister to a clade formed by *Berzelia*-*Escallonia* (PP 1.00), Apiales (PP 1.00; including *Pennantia* at the base) and Dipsacales.

The Bayesian analysis of the combined data (Fig. 9B)

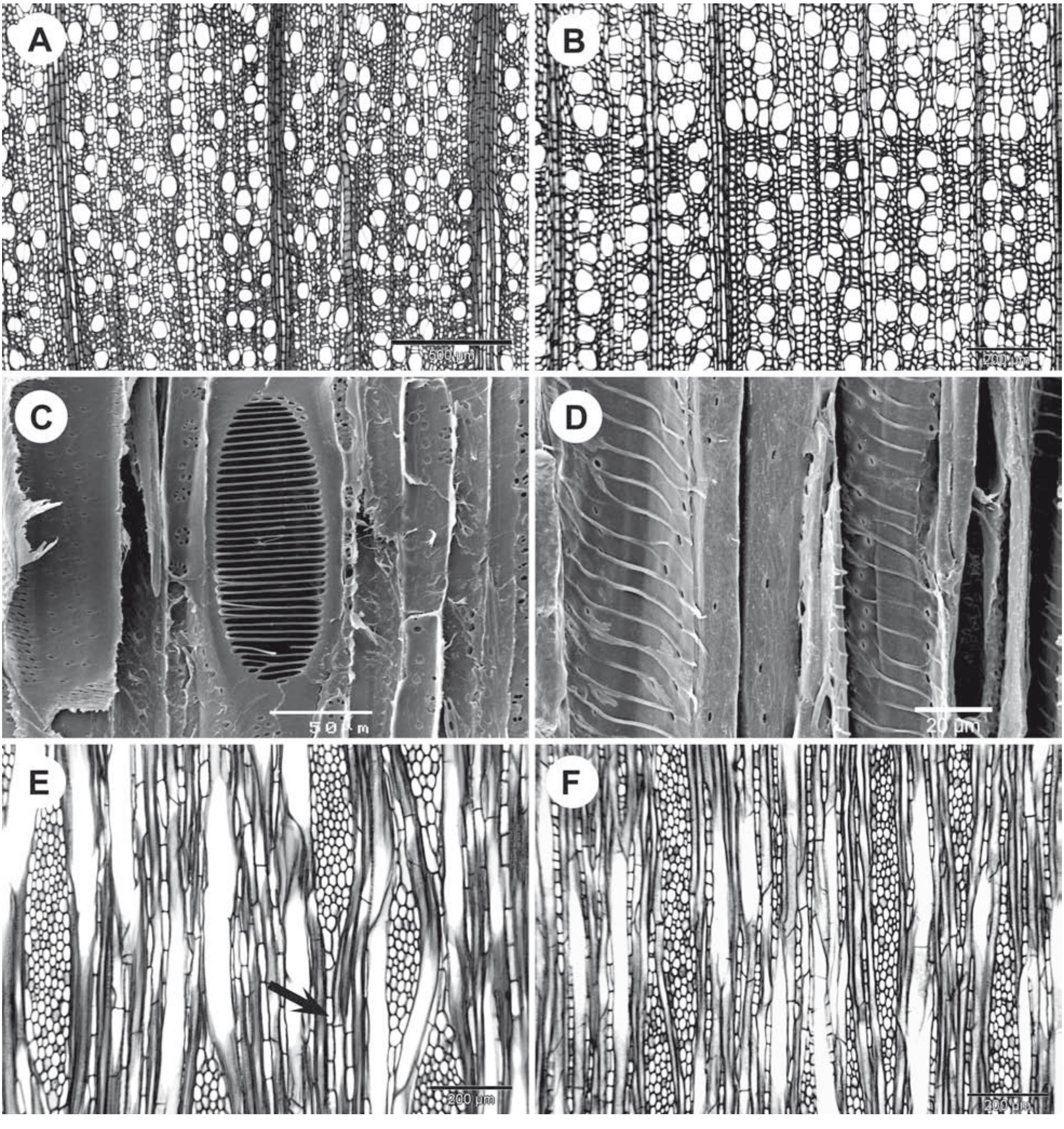

Fig. 7. Wood anatomical variation in Pennantiaceae based on LM (A–B, E–F) and SEM (C–D). A, *Pennantia cunninghamii*, transverse section (TS), mainly solitary vessels and thin-walled fibres; B, *Pennantia corymbosa*, TS, mainly solitary vessels and thin-walled fibres; C, *Pennantia cunninghamii*, radial longitudinal section (RLS), scalariform perforation plate; D, *Pennantia corymbosa*, RLS, helical thickenings in inside walls of vessels; E, *Pennantia cunninghamii*, tangential longitudinal section (TLS), multiseriate rays with long uniseriate ends (arrow); F, *Pennantia corymbosa*, TLS, uni- and multiseriate rays.

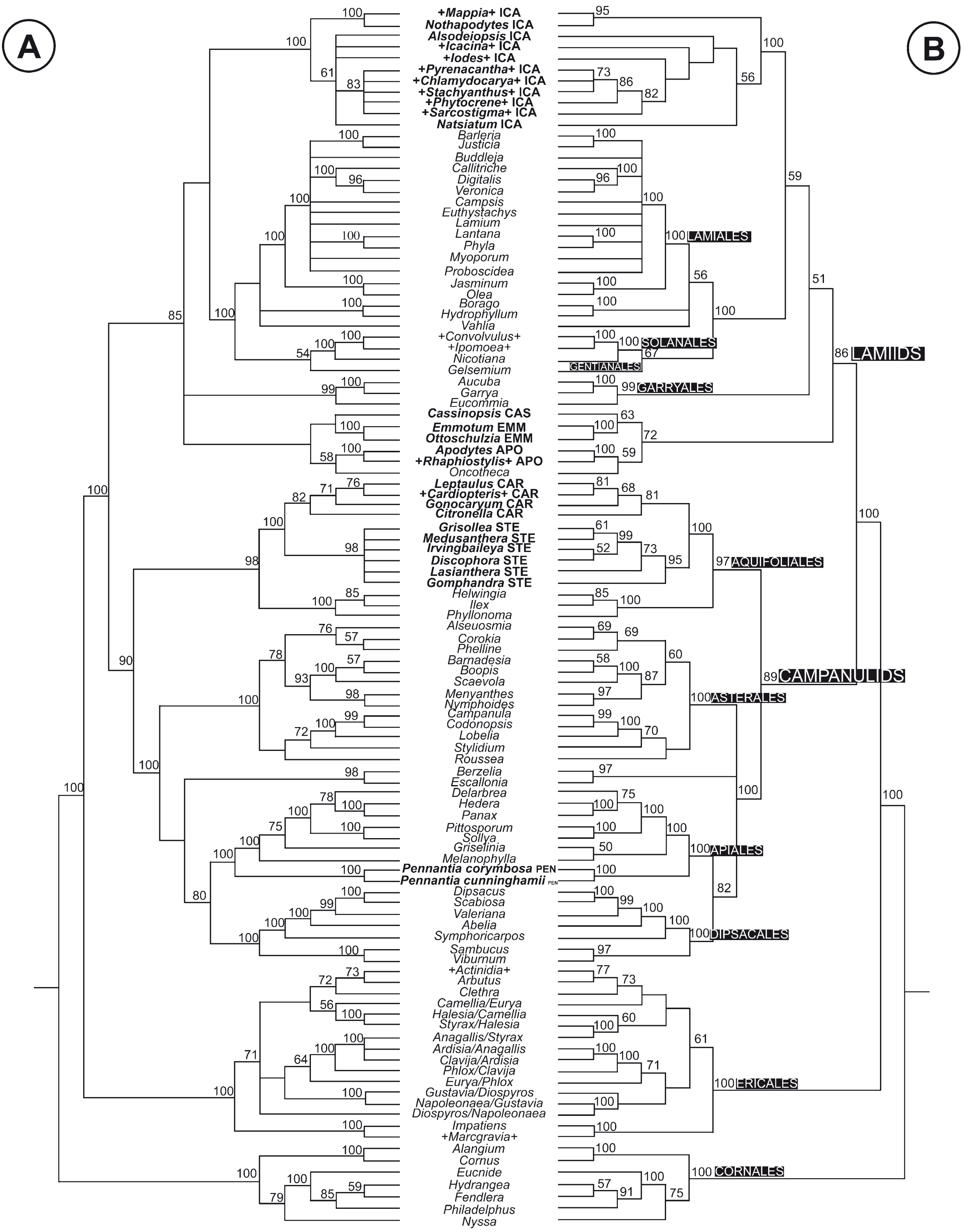

Fig. 8. Strict consensus trees of the maximum parsimony analyses based on molecular data (A) and combined wood anatomical-molecular data (B). Bootstrap values are given above the branches. Taxa written in bold represent Icacinaceae s.l.; genera marked with "+" refer to taxa with climbing members. APO, *Apodytes*-group of Icacinaceae s.str.; CAR, Cardiopteridaceae; CAS, *Cassinopsis*; EMM, *Emmotum*-group of Icacinaceae s.str.; ICA, *Icacina*-group of Icacinaceae s.str.; PEN, Pennantiaceae; STE, Stemonuraceae.

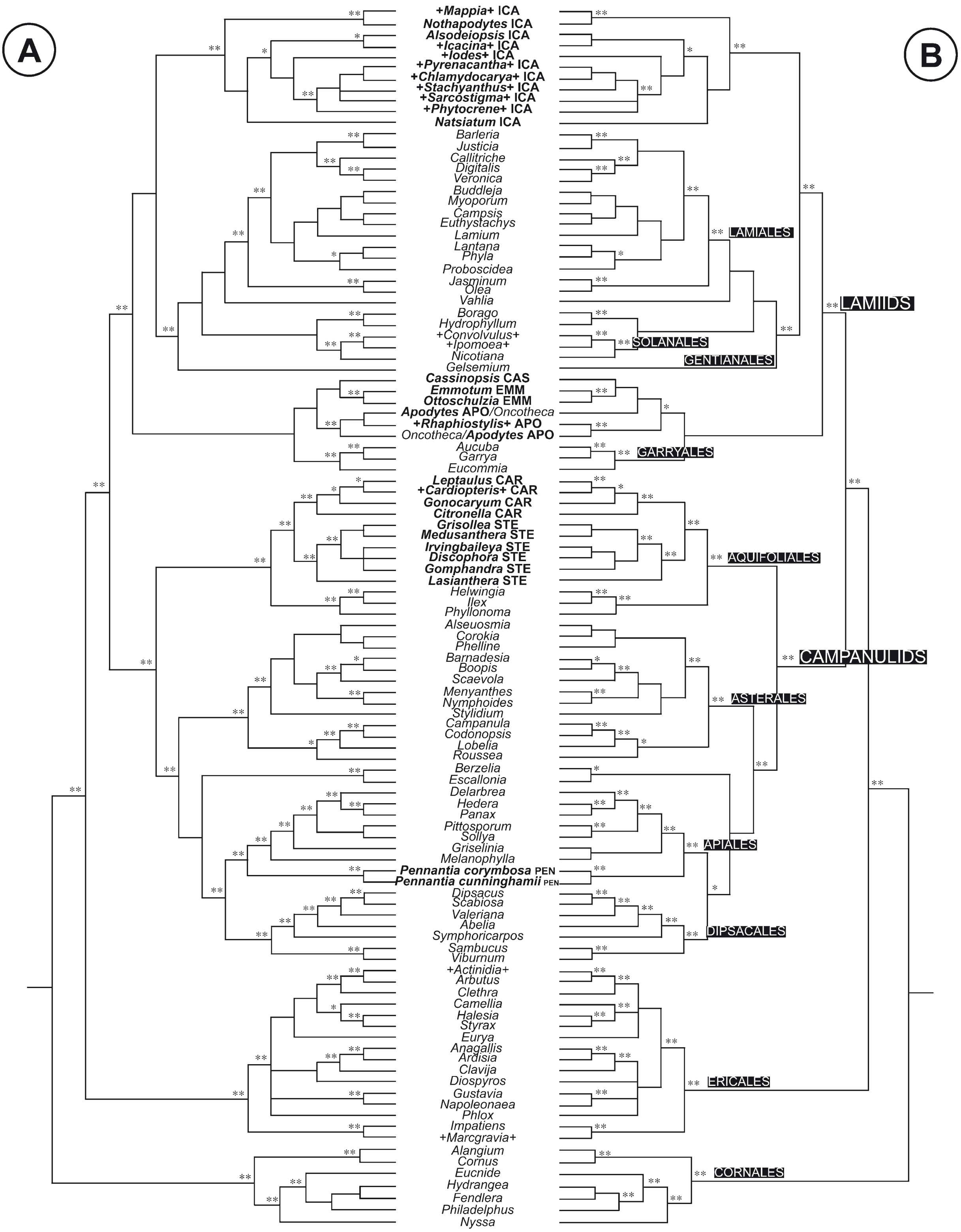

Fig. 9. Bayesian phylogenies based on the molecular data (A) and the combined anatomical-molecular matrix (B). Posterior probabilities (PP) are indicated as asterisks above the branches: one asterisk refers to PP-values between 0.95 and 0.99, two asterisks stand for maximum PP-values of 1.00; branches without asterisks have PP-values below 0.95. Taxa written in bold represent Icacinaceae s.l.; genera marked with "+" refer to taxa with climbing members. APO, *Apodytes*-group of Icacinaceae s.str.; CAR, Cardiopteridaceae; CAS, *Cassinopsis*; EMM, *Emmotum*-group of Icacinaceae s.str.; ICA, *Icacina*-group of Icacinaceae s.str.; PEN, Pennantiaceae; STE, Stemonuraceae.

results in a topology similar to that in Fig. 9A, notwithstanding some minor differences. For instance, the earliest diverging lineage within lamiids remains the same, although its support decreases from PP 0.76 to 0.53, and two well-supported subclades are present: subclade 1 (PP 0.99) includes the *Apodytes*-group (PP 1.00), which is sister to another group comprising the *Emmotum*-group, *Cassinopsis* and *Oncotheca*, although support for this sister relationship is almost lacking (PP 0.52); subclade 2 includes Garryales (PP 1.00). In the rest clade of lamiids (PP 1.00), the earliest diverging clade is formed by the *Icacina*-group with strong support (PP 1.00); the other large clade includes Lamiales-Solanales-Gentianales plus *Vahlia* and *Borago*-*Hydrophyllum* (PP 1.00). The relationships within campanulids are nearly identical to Fig. 9A.

DISCUSSION

Diagnostic wood characters of Icacinaceae s.str., Cardiopteridaceae, Stemonuraceae and Pennantiaceae. — The wood anatomical diversity of the distinctly polyphyletic Icacinaceae is huge (Figs. 1–7), as already mentioned by Bailey & Howard (1941a–d). Nevertheless, most of the diversity observed is due to differences in habit (lianas vs. erect trees and shrubs), while the wood anatomy of the climbing and especially the nonclimbing taxa separately is rather homogeneous. Consequently, the wood structure of the four currently circumscribed segregate families does not offer straightforward characters to define the family boundaries sensu Kårehed (2001). This is not surprising, because *(1)* Icacinaceae s.str. are probably not monophyletic (see also Figs. 8–9), and *(2)* Cardiopteridaceae and Stemonuraceae are strongly supported as sisters. Nevertheless, some wood features merit special emphasis because of their predictive value to assign a species to one of the four families.

Within Icacinaceae s.str., the *Icacina*-group (including the bulk of the climbing genera plus some nonclimbing ones) is rather homogeneous and can be easily distinguished from the other Icacinaceae lineages due to a combination of anatomical characters. These include simple vessel perforations, solitary vessels plus tangential multiples, a tendency to alternate vessel pitting, relatively short vessel elements and fibres (often between 300–700 μm and 600–1,000 μm respectively), banded and vasicentric axial parenchyma, high and wide multiseriate rays, and the occurrence of cambial variants. *Sarcostigma* has a peculiar anatomy within the *Icacina*-group because of: *(1)* interxylary phloem (Fig. 3A), *(2)* few septate libriform fibres that co-occur with the normal, distinctly bordered fibres (Fig. 2D), and *(3)* scarce, narrow (2-seriate) and low (<1 mm) multiseriate rays. Evidence from leaf anatomy (Van Staveren & Baas, 1973) and pollen morphology (Lobreau-Callen, 1973) also supports the isolated position of *Sarcostigma* as compared to the other lianas.

From a wood anatomical point of view, the remaining lineages within Icacinaceae s.str., i.e., *Cassinopsis*, *Apodytes*-group (without *Rhaphiostylis*) and *Emmotum*-group, are very similar and easily distinguishable from the *Icacina*-group due to a so-called primitive set of wood features in the Baileyan sense (Bailey & Tupper, 1918; Kribs, 1937). This combination of wood features, which is often encountered in basal angiosperm groups, includes: *(1)* exclusively scalariform perforations with usually many bars (range of means 8–80; Fig. 1E), *(2)* mainly opposite (to scalariform) vessel pitting (Fig. 1F), *(3)* very long vessel elements and fibres (range of means 840–2,220 μm and 1,680–3,120 μm, respectively), and *(4)* mainly diffuse-in-aggregates and scanty paratracheal axial parenchyma (Fig. 1A–B). Within the *Emmotum*-group, *Emmotum* and *Ottoschulzia* can be easily recognized by their scalariform perforations with less than 11 bars. The lianescent genus *Rhaphiostylis* does not share the characters just mentioned, but perfectly fits with the anatomy of the *Icacina*-group (except for the banded parenchyma).

The wood anatomical diversity within Cardiopteridaceae is more variable, especially in perforation plate morphology (exclusively scalariform, scalariform/simple, exclusively simple, and occasionally reticulate; Fig. 5C), axial parenchyma (diffuse-in-aggregates, banded and scanty paratracheal; Fig. 5B) and ray characters (large differences in width and height). If the climbing *Cardiopteris* is not considered, more or less stable wood characters are predominantly solitary vessels, mainly opposite (to slightly alternate) vessel pitting, and very long vessel elements and fibres (800–2,230 μm and 2,190–4,240 μm, respectively), but this set of wood characters is widely scattered within angiosperms. *Cardiopteris* can be defined by large circular vessel pits (9–14 μm vs. 5–8 μm in the other genera), narrow (2-seriate) and low (<1 mm) multiseriate rays, and especially by the nonlignified parenchymatous ground tissue containing lignified islands of xylem (represented by vessels, fibres, vasicentric tracheids and paratracheal parenchyma; Fig. 5A). The wood anatomy of the controversial genus *Metteniusa* is similar to the other genera of Cardiopteridaceae, but *Pseudobotrys* (the other genus that was placed in the family with hesitation) is strikingly different from all other taxa studied due to its deviating ray structure (no uniseriate rays, very wide multiseriate rays, Fig. 5C).

Stemonuraceae resemble Cardiopteridaceae in several aspects, amongst others the opposite to alternate intervessel pitting and the considerable length of vessel elements and fibres (mean ranges 600–1,510 μm and 2,000–3,650 μm, respectively). Nevertheless, Stemonuraceae exhibit a more homogeneous wood structure than Cardiopteridaceae, which can be demonstrated by: *(1)* a considerably higher percentage of vessel multiples (Fig. 6A), *(2)* mainly simple perforations that co-occur with few scalariform ones having on average 9 bars (Fig. 6C), *(3)* scalariform to opposite vessel pitting, *(4)* very thick-walled fibres (Fig. 6A–B), and *(5)* the tendency to form more paratracheal than apotracheal parenchyma (Fig. 6B). This set of characters is confirmed by additional observations in extra species of *Gomphandra* and *Lasianthera* from the Kew collection (pers. obs.). Furthermore, about half of the Stemonuraceae species have scalariform vessel-ray pits with strongly reduced pit borders (also present in *Cassinopsis*, *Metteniusa* and *Poraqueiba*; Fig. 1F), and the genera *Discophora*, *Gomphandra*, *Hartleya* and *Lasianthera* are the only ones that contain crystal sand in their wood rays (Fig. 6F; in contrast to Heintzelman & Howard (1948) who mentioned that crystal sand is always absent in their wood samples). Crystal sand outside the wood has also been observed in three other Stemonuraceae genera (*Cantleya*, *Medusanthera*, *Stemonurus*), but despite the phylogenetic significance of this character in many groups (e.g., Sapotaceae; pers. obs.), crystal sand outside the wood structure is also present in three genera of Cardiopteridaceae and six genera of Icacinaceae s.str. (Heintzelman & Howard, 1948).

The two species of *Pennantia* studied resemble very much the so-called primitive complex of wood characters that is also typical of the nonclimbing lineages of Icacinaceae s.str. and some Cardiopteridaceae (*Citronella*, *Dendrobangia*, *Metteniusa*, *Pseudobotrys*) in having mainly solitary vessels (Figs. 7A–B), exclusively scalariform perforations (Fig. 7C), predominantly opposite vessel pitting, fibres with distinctly bordered pits, and mainly diffuse-in-aggregates parenchyma that co-occur with scanty paratracheal parenchyma. Nevertheless, two wood features can be used to define *Pennantia* from the traditionally defined Icacinaceae, i.e., minute to small vessel pitting (3–4 μm) and the absence of prismatic crystals. In addition, the combination of width (4–8-seriate) and height (on average 1,000–1,400 μm) of the multiseriate rays in *Pennantia* usually offers additional distinguishing characters (Table 2).

Anatomy of climbers versus nonclimbers. — As mentioned before, the enormous wood anatomical diversity in the secondary xylem is largely attributed to differences in habit (lianas vs. erect trees and shrubs). The climbing group, represented by the taxa flanked with "+" in Figs. 8–9, can be characterised by mainly solitary vessels co-occurring with a small percentage of tangential multiples (Fig. 1C–D), exclusively or predominantly (> 95%) simple perforations, short to medium-sized vessel elements (range of means 175–880 μm), opposite to alternate vessel pitting, short to medium-sized fibres (range of means 610–1,540 μm), an abundance of banded and vasicentric axial parenchyma (Fig. 1D), high multiseriate rays (often more than 10 mm in length) with entirely or partly unlignified ray cells, and cambial variants (Fig. 3A–E). The nonclimbing group, represented by the bold genus names that are not flanked with "+" in Figs. 8–9, can easily be distinguished from the climbing group based on the perforation plate type (exclusively scalariform with often many bars, range of means 8–80, or a mixed occurrence of simple and scalariform perforations), vessel element length (typically long, but short in *Rhyticaryum*; range of means 500–2,230 μm), opposite or opposite to scalariform vessel pitting, diffuse-in-aggregates (to narrowly banded) and scanty paratracheal axial parenchyma, and long fibres (range of means 970–4,240 μm).

Due to the mixed occurrence of lianescent and erect genera in Icacinaceae s.str. and Cardiopteridaceae, the lianescent habit within these two families blurs the phylogenetic signal in the wood structure. For example, both members of the *Apodytes*-group (*Rhaphiostylis* lianas and *Apodytes* trees) have a completely different wood anatomy. Likewise, the wood structure of the only climbing genus of Cardiopteridaceae (*Cardiopteris*) is unique within the family, and even strongly deviates from the other lianescent genera of Icacinaceae s.str. (see next section). On the other hand, the wood structure of the few erect representatives in the *Icacina*-group (e.g., *Desmostachys*, *Merrilliodendron*, *Rhyticaryum*) reveals some interesting similarities compared to the common climbing *Icacina*-group members, such as exclusively simple perforations, a strong tendency to form alternate vessel pits, relatively short vessel elements (range of means 450–730 μm) and fibres (range of means 970–1,630 μm), and banded and/or vasicentric axial parenchyma. This means that these similarities are independent from differences in habit, indicating that this group may not be closely related with other Icacinaceae s.str. as shown by our phylogenetic analyses (Figs. 8–9).

Cambial variants. — Apart from the relatively young stems studied of *Mappianthus* and *Polyporandra*, all climbing taxa studied exhibit stems with cambial variants, which can provisionally be divided into four major types: *(1)* interxylary phloem (Fig. 3A), *(2)* nonlignified parenchymatous ground tissue with islands of lignified xylem (Fig. 5A), *(3)* successive cambia (Fig. 3B–E), and *(4)* furrowed xylem with elongated phloem zones (Fig. 4A–B). Interxylary phloem, irregularly scattered as islands in the wood cylinder, is typical of *Sarcostigma* (Fig. 3A; cf. Bailey & Howard, 1941a; Metcalfe & Chalk (1950) also reported successive cambia in *Sarcostigma*, but original slides and slides from four additional species in the Bailey & Howard collection only show interxylary phloem). The Bailey & Howard collection also demonstrates that the occurrence of interxylary phloem is not restricted to *Sarcostigma*: *Pleurisanthes flava* also has interxylary phloem islands that are more or less arranged in rings. The second type of cambial variants, represented by nonlignified ground tissue with islands of lignified xylem, is observed only in *Cardiopteris* (Fig. 5A; cf. Bamber & ter Welle, 1994). Another distinguishing anatomical character of *Cardiopteris* found in the literature is the presence of laticifers in the pith, bark and leaves (Thouvenin, 1891). However, laticifers in pith and bark are not present in our material of *C. moluccana*. It remains unknown whether all remaining climbing genera are characterised by successive cambia or not, because mature wood samples from many genera have not been investigated by us, nor in the literature due to lack of material. Furthermore, it seems that the presence of successive cambia may vary within a genus: Obaton (1960) observed a mature stem of 90 mm of *Pyrenacantha mangenotiana* that only exemplifies furrowed xylem with elongated phloem zones, while our study reveals elongated phloem regions as well as successive cambia in *P. malvifolia*, which is very similar to *Phytocrene* (Sleumer, 1942a; Metcalfe & Chalk, 1983; Fig. 3D). It can be suggested that all (except *Sarcostigma* and *Pleurisanthes*?) climbing genera within the *Icacina*-group have successive cambia because of several reasons: *(1)* the predictive value of successive cambia in different groups (for instance in Caryophyllales, Jansen & al., 2000; Carlquist, 2001), *(2)* the hypothesis that the *Icacina*-group is monophyletic (Figs. 8–9), *(3)* our observation that successive cambia are present in *Iodes* (a feature not mentioned in the literature due to lack of mature material), and *(4)* the recent observation of successive cambia in the new genus *Sleumeria* (Utteridge & al., 2005). If this should be true, two major types within the successive cambia-group could be distinguished based on the presence/absence of elongated phloem zones that are developed by the (unilaterally-active portion of the vascular) cambium at places opposite to the detachment of the leaves (Bailey & Howard, 1941a; Sleumer, 1942a; Obaton, 1960). Genera that show the cambial variant type with the peculiar phloem formation all belong to the former Phytocreneae (*Chlamydocarya*, Fig. 4B; *Miquelia*, *Phytocrene*, Fig. 3D; *Polycephalium*, *Pyrenacantha*, Fig. 4A; *Stachyanthus*), and it has largely been observed in young stems (confirmed by the original slides of Bailey & Howard; mature material only available from *Phytocrene* and *Pyrenacantha*). According to Carlquist (2001), the presence of elongated phloem regions in co-occurrence with successive cambia might be a unique feature among flowering plants. The young stems of *Chlamydocarya thomsonia* (Fig. 4B) and *Miquelia caudata* (slide collection Bailey & Howard) are remarkable in this regard, because they develop successive cambia that are restricted to the elongated phloem zones (cf. Sleumer, 1942a).

Taxonomic position of Icacinaceae s.l. — Previous analyses that dealt with the taxonomic position of Icacinaceae s.str. found that the family is nested at the base of lamiids, and may be closely allied with Garryales and *Oncotheca* (Savolainen & al., 2000; Kårehed, 2001; Stevens, 2001 onwards; Bremer & al., 2002; Cameron 2003), while the interfamily relationships of Cardiopteridaceae and Stemonuraceae (both Aquifoliales) and Pennantiaceae (Apiales) have been established with much greater confidence (Kårehed, 2001, 2003; Figs. 8–9). Our maximum parsimony and Bayesian analyses of both molecular and combined data strongly support the position of the latter three families, but the relationships between the distinct lineages of Icacinaceae s.str. remain enigmatic. We have found further support that the family Icacinaceae s.str. does not form a monophyletic entity, an idea that has already been proposed by Kårehed (2001). Although many more representatives should be studied to comment more thoroughly on the relationships within Icacinaceae s.str., our analyses (Figs. 8–9) add some new insights: *(1)* the *Apodytes*-group, *Emmotum*-group and *Cassinopsis* form together with the genus *Oncotheca* (Oncothecaceae) a monophyletic group with moderate to strong support based on the combined maximum parsimony and Bayesian analyses (Figs. 8B, 9B); this clade is nested at the base of the lamiids and might be closely related with Garryales, *(2)* the *Icacina*-group seems well supported and may not be directly related with other lineages of Icacinaceae s.str.; a possible sister relationship with a clade represented by Gentianales-Solanales-Lamiales plus Boraginaceae and Vahliaceae is plausible, especially based on the Bayesian analysis of the combined data (Fig. 9B).

Wood anatomical comparison within the asterids. — As discussed before, the four possible (non-climbing) candidates that may form the earliest diverging lineage within lamiids together with the *Apodytes* group, the *Emmotum*-group and *Cassinopsis* are *Aucuba*, *Eucommia* and *Garrya* (the only three genera in Garryales) and *Oncotheca* (Oncothecaceae). From a wood anatomical point of view, these three genera perfectly fit within this early diverging lamiid lineage because of the joint occurrence of: *(1)* predominantly solitary vessels, *(2)* exclusively scalariform perforations, *(3)* nonseptate fibres with distinctly bordered pits (simple to minutely bordered pits and sometimes septate in *Aucuba*), and *(4)* mainly diffuse to diffuse-in-agregates axial parenchyma (Baas, 1975; Carpenter & Dickison, 1976; Dickison, 1982; Noshiro & Baas, 1998; original observations). These four characters are part of the so-called primitive Baileyan syndrome, which is in agreement with other basal lineages in asterids (see further). When the wood structure of Garryales is compared with the *Icacina*-group, several characters may provide a link. For example, exclusively simple perforations and alternate intervessel pits characterise *Eucommia*, relatively short vessel elements are observed in *Garrya* and in *Eucommia* (400–830 µm and 150–350 µm, respectively), and mainly paratracheal parenchyma is present in *Aucuba*. A character that has never been found in Icacinaceae s.str., but that is clearly present in *Aucuba*, *Garrya* and *Eucommia*, is the presence of helical thickenings throughout vessel elements. However, the occurrence of helical thickenings is related to climate, especially to temperate and Mediterranean conditions (Baas & Schweingruber, 1987) or in areas that are drier or subject to freezing (Carlquist, 2001), and therefore, not indicative of finding relationships between the predominantly tropical lowland Icacinaceae s.str. and the more temperate genera *Aucuba*, *Garrya* and *Eucommia*.

Both Cardiopteridaceae and Stemonuraceae are strongly nested within Aquifoliales and are sister to three monogeneric families: Aquifoliaceae, Helwingiaceae and Phyllonomaceae (Kårehed, 2001; Bremer & al., 2002; Figs. 8–9). The detailed wood descriptions of *Ilex* (Baas, 1973) and *Helwingia* (Noshiro & Baas, 1998) and the brief wood description of *Phyllonoma* (Takhtajan, 1997) provide several similar characters compared to Cardiopteridaceae and Stemonuraceae. The occurrence of exclusively scalariform perforations in all three genera link them both more to Cardiopteridaceae than to Stemonuraceae, while other characters such as the distinct vessel multiples in several *Ilex* species refer to Stemonuraceae. The homogeneous wood anatomy of Aquifoliales notwithstanding, the genus *Helwingia* can be easily recognised due to its septate fibres with minutely bordered pits and the presence of silica grains (Noshiro & Baas, 1998).

The taxonomic position of the genus *Pennantia* as sister to the rest of Apiales is well established (Kårehed 2001, 2003; Figs. 8–9). Comparing the wood structure of *Pennantia* with Torricelliaceae (including *Aralidium*, *Melanophylla* and *Torricellia*) and the monotypic Griseliniaceae, two families that diverge just after Pennantiaceae as the second and third Apiales branch respectively, some interesting remarks can be made. Torricelliaceae have a strikingly different wood anatomy compared to *Pennantia* due to a so-called derived wood syndrome, including *(1)* pronounced vessel multiples, *(2)* predominantly or exclusively simple vessel perforations (except in *Aralidium*), *(3)* septate fibres with minutely bordered pits, and *(4)* exclusively scanty paratracheal parenchyma (Noshiro & Baas, 1998). This wood syndrome also characterises the other Apiales families Araliaceae (Oskolski, 1996), Pittosporaceae (Carlquist, 1981a), Myodocarpaceae (Oskolski & al., 1997) and Apiaceae (Rodriguez, 1957). *Griselinia* on the other hand, exemplifies a so-called primitive wood syndrome that is shared by *Pennantia*, which becomes evident when looking at the predominantly solitary vessels, scalariform perforation plates with more than 10 bars, opposite (to scalariform) vessel pitting, long vessel elements (often >1000 μm), fibres with distinctly bordered pits, and diffuse-in-aggregates axial parenchyma (Noshiro & Baas, 1998).

It is remarkable that all Icacinaceae s.l. lineages, of which most are characterised by the primitive Baileyan syndrome of wood characters, are nested at positions that can be considered as basal within lamiids (Icacinaceae s.str.), campanulids (Cardiopteridaceae and Stemonuraceae) and Apiales (Pennantiaceae). Likewise, the three first branching orders within asterids (Cornales, Ericales, Garryales) include families that have a nearly identical wood structure (most Cornales families—Noshiro & Baas, 1998; Ericaceae and relatives in Ericales—Lens & al., 2007b; both Garryales families—Noshiro & Baas, 1998). Likewise, additional asterid groups with a similar wood anatomy are often classified in families that have a basal position within asterid orders, even within the most derived orders such as Dipsacales (Columelliaceae—Stern & al., 1969; Adoxaceae—Moll & Janssonius, 1920) and Asterales (Rousseaceae—Gornall & al., 1988). As a consequence, the primitive set of wood features in the Baileyan sense can be interpreted as a symplesiomorphy for the entire asterids, and it has evolved to a so-called derived wood syndrome independently in several asterid orders. However, the phylogenetic significance of the primitive wood type at a lower taxonomic level must not be underestimated, as clearly demonstrated in Ericales (Lens & al., 2007b).

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Appendix 1. List of species studied with reference to their locality and vouchers. Institutional wood collections used in this study are abbreviated according to Index Xylariorum (Stern, 1988).

Apodytes dimidiata E. Mey ex. Bernh., Burundi, *Lewalle 3643* (L), 75 mm; ***Apodytes javanica*** Koord. & Valeton, Indonesia (Java), collector and number unknown (L), mature; ***Calatola columbiana*** Sleum., Colombia, *Cuatrecasas s.n.* (L), mature; ***Calatola venezuelana*** Pittier, Venezuela, *Williams 10118* (MADw 30905), mature; ***Cantleya corniculata*** (Becc.) R.A. Howard, Indonesia (Sarawak), collector and number unknown (L), mature; ***Cardiopteris moluccana*** Blume, New Guinea, *Jacobs 8700* (L), 12 mm; ***Cassinopsis capensis*** Harv. & Sond., South Africa, *Dentzman HJ 1774A* (MADw 10876), mature; ***Cassinopsis* sp.**, Madagascar, *Capuron 3291* (CTFw 12970), mature; ***Cassinopsis tinifolia*** Harv., Swaziland, *Prior 472* (Kw 75650), mature; ***Chlamydocarya thomsonia*** Baill., origin unknown, collector and number unknown (BR, living collection FB/S3745), 5 mm; ***Citronella silvatica*** Cuatrec., Colombia, *Cuatrecasas s.n.* (L), 50 mm; ***Codiocarpus merrittii*** (Merr.) Kowana, Philippines (Palawan), *Ridsdale s.n.* (L), 55 mm; ***Dendrobangia boliviana*** Rusby, Bolivia, collector and number unknown (L), mature; ***Desmostachys vogelii*** Stapf., Liberia, collector and number unknown (Kw 20719), mature; ***Discophora guianensis*** Miers, Surinam, *Lindeman 6918* (L), 69 mm; ***Emmotum fagifolium*** Desv., South America, collector and number unknown (L), mature; ***Gastrolepis austro-caledonica*** (Baill.) R.A. Howard, New Caledonia, *Lam 7207* (L), 4 mm; ***Gomphandra luzoniensis*** Merr., Philippines (Palawan), *Ridsdale s.n.* (L), mature; ***Gonocaryum crassifolium*** Ridl., Indonesia (Borneo), *Nooteboom 4048* (L), 45 mm; ***Hartleya inopinata*** Sleum., New Guinea, *Sinke 83* (L), 35 mm; ***Icacina claessensi*** De Wild., Democratic Republic of Congo, *Louis 6809* (Tw 38406), 12 mm; ***Icacina mannii*** Oliver, Africa, *Leeuwenberg 4223* (WAG, alcohol collection), 40 mm; ***Iodes africana*** Welw. ex Oliver, Cameroon, *Elad 579* (Kw 75203), mature; ***Lasianthera africana*** P. Beauv., Democratic Republic of Congo, *Constant 275* (CTFw 19859), mature; ***Lasianthera apicalis*** Thw., Sri Lanka, *Worthington 5272 I 206* (Kw 4586), mature; ***Lavigeria macrocarpa*** Pierre, Cameroon, collector and number unknown (BR, living collection FB/S3744), 9 mm; ***Lavigeria macrocarpa*** Pierre, Cameroon, *Parren 44* (Kw 75149), 11 mm; ***Lavigeria macrocarpa*** Pierre, origin unknown, *Leeuwenberg 5543* (WAG, alcohol collection), 21 mm; ***Leptaulus grandifolius*** Engl., Africa, *Bos 4090* (WAG, alcohol collection), 9 mm; ***Leptaulus daphnoides*** Benth., Uganda, collector and number unknown (L), mature; ***Mappia cordata*** Engl., Surinam, *Lindeman 4084* (L), 30 mm; ***Mappia cordata*** Engl., Surinam, *University of Utrecht s.n.* (Tw 35191), 28 mm; ***Mappianthus iodoides*** Hand.-Mazz., China, *Ting & Shih 861* (L), 6 mm; ***Medusanthera laxiflora*** (Miers.) R.A. Howard, New Guinea, *Pullen 7702* (L), 85 mm; ***Merrilliodendron megacarpum*** (Hemsl.) Sleum., New Guinea (New Britain), *Sayers s.n.* (L), 15 mm; ***Metteniusa*** cf. ***edulis*** H. Karst., Venezuela, *Whitford 46* (MADw 10656), mature; ***Oecopetalum mexicanum*** Greenm. & C.H. Thomps., Guatemala, collector and number unknown (Aw 19465), 26 mm; ***Ottoschulzia pallida*** Lundell, North America, *Curtis s.n.*

Appendix 1. Continued.

(Tw 53211), mature; ***Pennantia cunninghamii*** Miers., Australia, collector and number unknown (L), mature; ***Pennantia corymbosa*** Forst., New Zealand, *Dentzman A1471* (MADw 14277), mature; ***Phytocrene* sp.**, Philippines, *Coode 5369* (L), 26 mm; ***Phytocrene macrophylla*** var. ***dasycarpa*** Bl., Indonesia (Celebes), *Balgooy 3045* (L), 43 mm; ***Platea excelsa*** var. ***borneensis*** Bl., Indonesia (Celebes), *Hennipman 6106* (L), 180 mm; ***Platea hainanensis*** R.A. Howard, China (Guangdong), *Forest Research Institute s.n.* (Tw 41995), mature; ***Polyporandra scandens*** Becc., New Guinea, *Jacobs 9491* (L, alcohol collection), 20 mm; ***Polyporandra scandens*** Becc., Indonesia, *Van Balgooy 5060* (L), 18 mm; ***Poraqueiba guianense*** Aubl., South America, collector and number unknown (L), mature; ***Pseudobotrys dorae*** Moeser, New Guinea, *Pullen 7533* (L), 54 mm; ***Pyrenacantha kirkii*** Baill., Democratic Republic of Congo (Katanga), *Malaisse s.n. (*Tw 47294), 6 mm; ***Pyrenacantha lebrunii*** Boutique, Cameroon, collector and number unknown (BR, alcohol collection FB/S3743), 3.5 mm; ***Pyrenacantha malvifolia*** Engl., Somalia, *Bailes 205* (K, living collection 1981–1122), 12 mm; ***Rhaphiostylis ferruginea*** Eng., origin unknown, *Letouzey 4845* (CTFw 15550, MADw 36988), mature; ***Rhyticaryum longifolium*** K. Sch. & Laut., origin unknown, *Royen 3657* (L), 60 mm; ***Sarcostigma kleinii*** Wight & Arn., India, *Ridsdale 507* (L), 62 mm; ***Stemonurus celebicus*** Valet. ex Koord., Indonesië (Celebes), *Van Balgooy 3888* (L), mature; ***Stemonurus mallacensis*** (Mast.) Sleum., Indonesië (Borneo, Kalimantan), *De Vogel 1860* (L), 35 mm; ***Stemonurus umbellatus*** Becc., Indonesia (Borneo, South Kalimantan), *Labadie & Sacave s.n.* (Tw 42291), mature; ***Whitmorea grandiflora*** Sleum., Solomon Islands (Bougainville), *Schodde & Craven 3629* (L), mature.

Appendix 2. Wood matrix at the genus level including 109 asterid taxa arranged alphabetically, after implementing the gap weighting method of Thiele (1993) on characters 4, 9 and 10. Genera in bold have secondarily derived wood, which is illustrated by its paedomorphic wood features (indicated by asterisks). Paedomorphic features are coded as unknown. Herbaceous taxa are written in capitals; climbing taxa are marked with "+".

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Abelia	0	0	0	2	4	0	1	1	1	2	0	0	0	0	0	1	0,1	0	0	0	0	0	0	0	0	0
+Actinidia+	1,2	0	1	?	3	0	0	1	5	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Alangium	0,1	1	0,2	1	4	0	1	0	4	3	1	0	1	0	0	1	0	0	0	0	0	0	0	1	1	0
Alseuosmia	0	0	0	2	2	0	?	1	0	3*	1	1	0	0	2	?	?	?	?	0	0	0	0	0	0	0
Alsodeiopsis	0	1	2	0	3	0	0	0	?	?	0	0	0	0	0	1	?	0	0	0	0	0	0	1	?	0
ANAGALLIS	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Apodytes	0	0	0	2	2	0	0	0	2	7	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Arbutus	0,1	1	1,2	0	2	0	0	1	1	2	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0
Ardisia	0	1	1	?	4	0	0	0	2	2	1	1	0	0	1	2	2	1	0	0	0	0	0	1	0	0
Aucuba	0	0	0	3	2	0	0	1	1	4	1	1	0	0	1	1	1,2	1	0	0	0	0	0	0	0	0
Barleria	0	1	2	0	4	0	0	0	1	2*	1	1	0	0	1	1	0	1*	0	0	0	0	0	0	0	0
Barnadesia	0	1	2	0	4	0	0	0	1	0	1	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0
Berzelia	0	0	0	2	1,2	0	0	0	1	3	0	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0
BOOPIS	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
BORAGO	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Buddleja	0	1	2	0	4	0	0,1	1	1	0	1	1	0	1	1	1	0	0	0	0	0	0	0	1	0	0
CALLITRICHE	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Camellia	0	0	0	1	1	0	1	1	1	4	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0
CAMPANULA	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Campsis	0,2	1	2	0	4	0	0	1	4	1	1	1	0	1	1	1	0	0	0	0	1	0	0	0	0	0
+Cardiopteris+	0	2	2	0	2	0	0	0	9	2	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0
Cassinopsis	0	0	0	3	1	0	0,1	0	2	6	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
+Chlamydocarya+	0	2	2	0	3	0	0	0	?	?	0	0	0	1	0	1	?	1	0	0	0	1	?	0	0	0
Citronella	0	0	1,2	?	2	0	0	0	3	6	0	0	0	0	0	1	2	1	0	0	0	0	0	1	0	1
Clavija	0	1	2	0	4	0	0	0	1	1	1	1	0	0	1	2	1,2	0	0	0	0	0	0	0	0	0
Clethra	0	0	0	3	2	0	0	1	1	5	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
CODONOPIS	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Convolvulus	0	0	2	0	4	0	1	0	1	1*	0	0	0	1	1	1	0	0,1*	1	1	0	0	0	1	1	0
Cornus	0	0,1	0	3	1	0	0	1	2	5	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Corokia	0	0	0	1	3	0	0	1	0	2	1	1	0	0	2	1	0	1	0	0	0	0	0	0	0	0
Delarbrea	0	1	2	0	4	0	0	1	1	3	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0
Digitalis	0	0	2	0	4	0	0	1	0	?	1	0	0	1	1	1	0	1*	0	0	0	0	0	0	0	0
Diospyros	0,1	1	2	0	3	0	0	0	3	3	0,1	0	1	0	0	1	0	0	0	0	0	0	0	1	1	0
DIPSACUS	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Discophora	0	1	1	1	3	0	0	0	2	4	0	0	1	0	0	1	1	1	0	0	0	0	0	1	0	1
Emmotum	0	0	0	1	2	0	0	0	4	6	0	0	0	0	0	1	0,2	0	0	0	0	0	0	1	0	1
Escallonia	0	0	0	1	1	0	0	1	1	3	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Eucnide	0	1	2	0	0	0	0	0	2	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0
Eucommia	0	0	2	0	4	0	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Eurya	0	0	0	5	0,1,3	0	1	1	1	5	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Euthystachys	0	1	2	0	4	0	0	0	0	1	1	1	0	1	1	1	0	1	0	0	0	0	0	0	0	0

Appendix 2. Continued.

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**
Fendlera	0,2	0	0	0	3	0	1	1	1	2	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
Garrya	0	0	0	0	3	0	0	1	1	2	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0
Gelsemium	0	0	2	0	4	0	1	0	2	2	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0
Gomphandra	0	0	1	1	2	0	0	0	3	6	0	0	0	0	1	1	2	1	0	0	0	0	0	0	0	1
Gonocaryum	0	0	2	0	3	0	0	0	2	4	0	0	1	0	0	1	2	1	0	0	0	0	0	1	0	1
Griselinia	0	0	0	1	1	0	1	0	1	4	0	1	0	0	0	1	1,2	1	0	0	0	0	0	1	0	0
Grisollea	0	1	1	?	3	0	0	0	?	?	0	0	?	0	?	1	0	0	0	0	0	0	0	?	?	0
Gustavia	0	1	2	0	4	0	0,1	0	2	2	1	0	1	0	0	1	1	0	0	0	0	0	0	1	1	0
Halesia	1	1	0	1	2	0	1	0	1	4	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0
+Hedera+	1,2	1,3	2	0	4	0	0	1	1	3	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0
Helwingia	0	0	0	2	1	0	1	0	1	3	1	1	0	0	1	1	2	1	0	0	0	0	0	0	0	0
Hydrangea	0,1,2	0	0	2	0	0	0,1	1	2	2	0	1	0	0	0	1	2	1	0	0	0	0	0	0	0	0
HYDROPHYLLUM	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
+Icacina+	0	2	2	0	3	0	0	0	5	3	0	0	0	1	1	1	2	1	0	0	0	0	1	1	1	0
Ilex	0,1	0,1	0	2	2	0	0,1	1	2	5	0	0	0	0	0	1	1,2	0	0	0	0	0	0	1	0	0
Impatiens	0	0	2	0	0*	0	1	0	2	1*	1	0	0	0	0,1	2*	2*	1*	0	0	0	0	0	0	0	0
+Iodes+	0	2	2	0	3	0	0	0	7	2	0	0	0	1	1	1	2	1	0	0	0	0	1	1	0	0
Ipomoea	0	0	2	0	4	0	1	0	6	0*	0	1	0	0	1	0,1	0	1*	1	1	0	0	1	0	0	0
Irvingbaileya	?	?	1	?	1	?	?	?	?	?	0	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?
Jasminum	0,1	0	2	0	4	0	1	1	2	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Justicia	0	1	2	0	4	0	?	0	1	1*	1	1	0	0	1	?	?	?	0	0	0	0	0	0	0	0
LAMIUM	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Lantana	0	?	2	0	4	0	0	0	?	?	1	0	?	1	1	1	?	1	0	0	0	0	0	0	0	0
Lasianthera	0	1	1	0	1	0	1	0	3	5	0	0	1	0	1	1	0	1	0	0	0	0	0	1	0	1
Leptaulus	0	0	1	0	2	0	0	0	1	3	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1
Lobelia	0	1	2	0	0*	0	0	0	1	2*	1	1	0	0	1	2*	2*	1*	1	0	0	0	0	0	0	0
+Mappia+	0	2	2	0	3	0	0	0	6	2	0	0	0	1	1	1	2	1	0	0	0	0	1	1	1	0
+Marcgravia+	0	1	2	0	4	0	0	0	5	3	0	1	0	0	1	1	2	1	0	0	0	0	0	0	0	0
Medusanthera	0	1	2	1	1	0	1	0	3	2	0	0	1	0	0	2	1,2	1	0	0	0	0	0	1	0	0
Melanophylla	0	1	0	1	1	0	1	0	3	4	1	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0
MENYANTHES	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Myoporum	0,1	1	2	0	4	0	0	0	1	1	0,1	0	0,1	0	1	1	0	0	0	0	0	0	0	0	0	0
Napoleonaea	0	1	1	1	3	0	0	0	2	2	1	0	1	1	0	1	1	0	0	0	0	0	0	1	1	0
Natsiatum	0	2	2	0	3	0	0	0	?	?	0	0	0	1	1	1	?	1	0	0	0	0	?	?	?	0
Nicotiana	0	1	2	0	4	0	1	0	2	1*	0	0	0	0	0	1	0	1*	0	1	0	0	0	1	1	1
Nothapodytes	0	?	2	0	3	0	0	0	?	?	0	0	0	1	?	1	?	?	0	0	0	0	0	?	?	1
NYMPHOIDES	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Nyssa	0	1	0	2	1	0	0	1	2	8	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0
Olea	0	1	2	0	4	1	1	1	2	2	1	0	0,1	0	1	1	0	0	0	0	0	0	0	0	0	0
Oncotheca	0	0	0	1	3	0	1	0	2	5	0	0	1	0	0	1	0	1	0	0	0	0	0	1	0	0
Ottoschulzia	0	0	0	1	2	0	0	0	1	3	0	0	0	0	0	1	12	1	0	0	0	0	0	1	0	0
PANAX	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Pennantia corymbosa	0	0	0	2	2	0	0	1	1	4	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1

Appendix 2. Continued.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Pennantia cunninghamii	0	0	0	3	2	0	0	1	2	6	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Phelline	0	0	0	9	0	0	1	0	1	9	0	0	0	0	1	1	2	1	0	0	0	0	0	0	0	0
Philadelphus	01	0	0	2	1,2,3	0	1	0	1	2	0	0	0	0	0,1	1	2	0	0	0	0	0	0	0	0	0
Phlox	0	0	2	0	4	0	?	0	0	0*	1	0	0	0	1	?	?	?	0	0	0	0	0	0	0	0
Phyla	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Phyllonoma	?	?	0	?	2	0	?	?	?	?	0	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?
+Phytocrene+	0	2	2	0	3	0	0	0	8	0	0	0	0	1	0	1	2	1	0	0	0	1	1	1	1	0
Pittosporum	0	1,3	0,2	1	4	0	0	1	1	2	1	1	0	1	1	1	0	0	0	0	0	0	0	1	1	0
PROBOSCIDEA	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
+Pyrenacantha+	0	0	2	0	3	0	0	0	?	?	0	0	0	1	0	1	2	1	0	0	0	1	1	0	0	0
+Raphiostylis+	0	2	2	0	3	0	0	0	7	3	0	0	0	1	1	1	2	1	0	0	0	0	1	1	1	0
Roussea	0	?	0	1	0	0	0	0	?	?	0	0	0	0	1	?	?	?	?	0	0	0	0	0	0	0
Sambucus	0	1	2	0	4	0	1	0	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
+Sarcostigma+	0	2	2	0	3	0	0	0	4	1	0	0	0	1	0	1	0	1	0	0	1	0	0	1	1	0
Scabiosa	0	0	2	0	?	0	?	0	1	1*	0	0	0	0	2	1	0	1*	0	0	0	0	0	1	0	0
Scaevola	0	0	2	1	0*	0	0	0	2	1*	0	0	0	0	0	1	0,1	1*	0	0	0	0	0	1	0	0
Sollya	0	1	2	0	4	0	0	0	1	1	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0
+Stachyanthus+	0	2	2	0	3	0	0	0	?	?	0	0	0	?	?	1	?	?	0	0	0	1	?	?	?	0
Stylidium	0	0	2	0	4	0	?	0	0	2*	1	0	0	0	2	?	?	?	?	0	1	0	0	0	0	0
Styrax	0,2	1	0,1	1	4	0	1	0	2	3	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0
Symphoricarpos	1,2	0	2	0	4	0	0,1	1	1	?	0	0	0	0	0	1	?	0	0	0	0	0	0	0	0	0
Vahlia	0	0	2	0	4	0	0	0	0	1*	0,1	0	0	0	2	0*	?	?	0	0	0	0	0	0	0	0
Valeriana	0	1	2	0	4	0	0	0	2	0*	1	0	0	0	1	2*	2*	1*	0	0	0	0	0	1	0	0
Veronica	1	0	2	0	4	0	0	0	0	?	1	0	0	1	1	0*	?	?	0	0	0	0	0	0	0	0
Viburnum	0,1	0	0	6	1,2,3	0	1	1	1	3	0	0	0	0	0	1	1,2	0	0	0	0	0	0	0	0	0

The 26 features are listed and discussed below. Characters and their states are based on extensive literature information mentioned in the Material and Methods section.

1 Wood porosity: (0) diffuse-porous, (1) semi-ring-porous, (2) ring-porous. Diffuse-porous wood has a similar vessel width throughout the growth ring, while in ring-porous wood the vessels in the early wood are distinctly wider than in the late wood; semi-ring-porous wood is an intermediate condition in which the early wood vessels are somewhat larger than the late wood vessels.

2 Vessel grouping: (0) predominantly solitary, (1) solitary and in radial multiples, (2) solitary and in tangential multiples, (3) clusters common. Predominantly solitary vessels are coded as present when more than 90% of the vessels are solitary. If this percentage is lower, character state (1) is dominant. Character state (3) is only considered present if more than 50% of the vessels are arranged in clusters.

3 Vessel perforation plate: (0) exclusively or predominantly scalariform, (1) mixed simple and scalariform, (2) predominantly or exclusively simple. Character states (0) and (2) are present if more than 90% of the vessel perforations are scalariform or simple, respectively.

4 Number of bars in scalariform perforation plate (coded with Thiele's method): (0) 0–6 bars, (1) 8–20 bars, (2) 24–36 bars, (3) 40–49 bars, (5) 70 bars, (6) 95 bars, (9) 134 bars.

5 Arrangement of intervessel pitting: (0) scalariform, (1) scalariform to opposite, (2) opposite, (3) opposite to alternate, (4) alternate. Pits between vessels can be arranged in different ways. In taxa with exclusively solitary vessels, they are only present at the overlapping end wall region between two vessel elements. Although not recommended by Herendeen & Miller (2000), opposite to alternate vessel pitting is included, because this state is typical of several genera. Scalariform vessel-ray pitting is sometimes an indication of secondarily derived wood, especially in lineages where you would expect alternate pits (Carlquist, 1962).

6 Vestured pits: (0) absent, (1) present. Only "true vestures" sensu Jansen & al. (1998) are taken into account, thereby excluding warts and pseudovestures.

7 Vessel-ray pitting: (0) with distinct borders, (1) with reduced borders to simple. Vessel-ray pits are pits between vessel elements and ray cells, which can be easily seen in radial sections.

8 Helical thickenings in vessel elements: (0) always absent, (1) present in tails and/or body of vessel element. True helical thickenings are considered here; other helical sculpturing patterns such as grooves and ridges are not taken into account.

9 Tangential vessel diameter (coded with Thiele's method): (0) 15–25 µm, (1) 30–55 µm, (2) 60–80 µm, (3) 90–100 µm, (4) 115–125 µm, (5) 155–160 µm, (6) 170–175 µm, (7) 210–215 µm, (8) 245 µm, (9) 260 µm.

10 Length of vessel elements (coded with Thiele's method): (0) 120–220 µm, (1) 250–450 µm, (2) 470–650 µm, (3) 690–900 µm, (4) 930–1,120 µm, (5) 1,135–1,300 µm, (6) 1,390–1,560 µm, (7) 1,780 µm, (8) 1,800 µm, (9) 2,130 µm. The vessel element length of the taxa with secondarily derived wood is coded as unknown, because these taxa have a constantly declining length-on-age curve (Carlquist, 1962).

11 Type of imperforate elements: (0) with distinctly bordered pits in tangential and radial walls, (1) with minutely bordered to simple pits concentrated in radial walls. Character state (0) is often referred to as fibre-tracheids (or true tracheids) in the literature, while libriform fibres in the sense of Baas (1986) refer to character state (1).

12 Septate imperforate elements: (0) always absent, (1) occasionally or always present. In most cases, thin-walled septa occur in libriform fibres, but sometimes also in fibre-tracheids. When some species show septate fibres, but not in other species of the genus, we have coded this character as present for the genus.

13 Wall thickness of imperforate elements: (0) very thin- or thin- to thick-walled, (1) thick- to very thick-walled. According to the IAWA Committee (1989), thick- to very thick-walled fibres have fibre lumina that are much less than three or more times the double wall thickness, resulting in indistinctly open to almost closed fibre lumina.

14 Vasicentric tracheids: (0) absent, (1) present. Vasicentric tracheids are narrow imperforate cells that have numerous bordered pits in radial and tangential walls, and are always associated with vessels. Their presence is coded according to Carlquist (1985) and original observations.

15 Axial parenchyma distribution: (0) mainly apotracheal, (1) mainly paratracheal, (2) absent or extremely rare. We have chosen to use only three main character states instead of the numerous subtypes, because the variation within several genera is enormous. Apotracheal parenchyma can be defined as parenchyma that is not associated with vessels, while paratracheal parenchyma is always located adjacent to vessels.

16 Ray width: (0) exclusively uniseriate, (1) uniseriate and multiseriate, (2) exclusively multiseriate. The range of multiseriate ray width can vary considerably, even within a single specimen. As a consequence, the mean width of multiseriate rays is often difficult to determine. Therefore, ray width is coded as three main categories. Exclusively uniseriate or exclusively multiseriate rays are sometimes an indication for taxa with secondarily derived wood, so these character states are sometimes coded as unknown (Carlquist, 1962).

17 Multiseriate ray height: (0) shorter than 2 mm, (1) between 2–5 mm in length, (2) higher than 5 mm. The multiseriate ray height of some genera is sometimes higher than the length of the section, which makes the calculation of mean values impossible. Based on the range of the mean values within the genera coded, we have decided to use 2 mm and 5 mm as a boundary to define character states. Most of the genera included in the matrix fit well into the three arbitrary categories used. Very tall rays (character state 2) sometimes refer to taxa with secondarily derived wood, so they are coded as unknown for these taxa (Carlquist, 1962).

18 Composition of body ray cells: (0) exclusively procumbent, (1) mixture of procumbent, square and/or upright cells. The shape of body ray cells (the multiseriate part of a multiseriate ray) is determined in radial sections. Character state (1) is frequently used as a criterion for pointing out taxa with secondarily derived wood, so this character is coded as unknown for these taxa (Carlquist, 1962).

19 Laticifers in stems: (0) absent, (1) present. Because laticifers are sometimes present in the outer regions of the stem, but not in the wood, we have chosen to extend the presence of laticifers to the whole stem.

20 Intraxylary phloem: (0) absent, (1) present. Intraxylary phloem is phloem at the inner side of primary xylem.

21 Interxylary phloem: (0) absent, (1) present. Interxylary phloem or included phloem is present in the wood cylinder.

22 Furrowed xylem: (0) absent, (1) present. In this case, furrowed xylem is defined as xylem in which elongated tissues of phloem are protruding.

23 Successive cambia: (0) absent, (1) present. If more than one cambium takes part in producing wood at the inside and phloem at the outside, successive cambia are present.

24 Prismatic crystals in rays: (0) absent, (1) present. When the presence of prismatic crystals in rays is not constant within a genus, we have coded it as present.

25 Prismatic crystals in axial parenchyma: (0) absent, (1) present. When the presence of prismatic crystals in axial parenchyma is not constant within a genus, we have coded it as present.

26 Crystal sand in stem: (0) absent, (1) present. Crystal sand is sometimes present in the outer regions of the stem, but not in the wood. We have chosen to extend this character to the entire stem because of the rare occurrence within angiosperms (Carlquist, 2001).