

The background of the cover features two black and white micrographs of plant tissue. The left image shows a cross-section of a stem with a central vascular cylinder, displaying various cell types and their arrangement. The right image shows a longitudinal section of a stem, highlighting the layered structure of the cortex and the vascular bundles.

**IAWA
BULLETIN**

1976/3

EDITORIAL

On Tuesday, June 7 of this year, Dr. Wilfred A. Côté personally handed over the essential IAWA records to us thereby officially transferring the office of the International Association of Wood Anatomists to the Netherlands, after it had been at Syracuse for six and a half successful years. Dr. Côté's efforts on behalf of the Association, and those of his co-editor Dr. Carl de Zeeuw, did not cease at this juncture, however, since they had agreed to complete the 1976 sequence of IAWA Bulletins, albeit without the editorial responsibility, now resting on our inexperienced shoulders.

It is difficult to describe in a short editorial the full significance of the work that Dr. Côté has done for our Association. The results can be seen in a regular quarterly bulletin of excellent quality and lay-out; a vast increase of the membership from about 160 to 270, and a doubling of the number of library subscriptions from 20 to 40 during his term of office. These are hard facts which are self-explanatory with regard to the involvement and energy spent by our former Executive Secretary. However, these achievements, although of vital importance for the IAWA, only show the tip of the iceberg of all that went on at Syracuse. The major aim of the Association—to provide contacts between wood anatomists—was impressively served by Dr. Côté as many of you have experienced in correspondence with his office at Syracuse, and as we can testify from the extensive files now at Leiden. The IAWA certainly owes a great debt of gratitude to Dr. Côté and to those who assisted him.

To succeed Dr. Côté and Dr. de Zeeuw is, for obvious reasons, a pleasant as well as a very difficult task. Pleasant and easy, because of the fine example set, which simply has to be followed. Difficult, because it will be very hard to come up to the high Syracuse standards. In this first editorial it is therefore appropriate to ask your help and support for our efforts to maintain the IAWA activities at the same high level both qualitatively and quantitatively. We need support from all members in the field of increasing the circulation of the Bulletin, in providing copy for scientific contributions as well as notes and requests; the last but not least we will appreciate your understanding and clemency if, for financial or other reasons, we will sometimes fail in our aims to achieve the results so successfully obtained by our predecessors.

Pieter Baas

Peter B. Laming

Office of the Executive Secretary
Rijksherbarium
Schelpenkade 6, Leiden
The Netherlands

RADIAL VESSELS IN RAYS

by

G.J.C.M. van Vliet¹

In the course of a wood anatomical survey of the Combretaceae (van Vliet, in preparation), radial vessels were found in the rays of the genera *Quisqualis* and *Combretum*: scandent or erect members of this family. To my knowledge this feature has never been recorded in the literature before. However, the radial vessels are common in most of the wood samples studied of these two closely related genera.

In *Quisqualis* and *Combretum* the rays are uni- or biseriolate, rarely triseriate. They are mainly homogeneous and composed of procumbent cells only, but may also contain erect cells, particularly in the juvenile wood near the pith. In tangential sections simple perforations can be found in the tangential ray cell walls (Fig. 2), and when studying radial sections (Fig. 1 and 3), radial files of cells are present which are connected through perforations in the tangential walls. (The perforations occur in oblique walls.) Of these radial files, mostly only one terminal cell was observed with a perforation in one tangential wall only and one perforation in a radial wall, leading to a vascular tracheid or a very narrow vessel. In one case, both terminal cells of a radial file were observed, and each was connected with an axial element, through a perforation (Fig. 1). A perforation in the radial wall of a cell somewhere in the middle of a radial vessel has never been found. The maximum number of cells recorded for a radial vessel of which no terminal cells were visible was 29 cells. Mostly these radial files of ray vessels are in one level; however, the vessels shift to a lower or higher level (Fig. 1). Branching of a radial vessel has been observed once: one of the radial vessels having a perforation of the ventral wall and being connected through a vertical ray vessel element with another radial vessel running two ray cell levels lower. Radial vessels have been observed in the following species: *Quisqualis latialata* (Engl.) Exell, *Combretum collinum* Fresen, *C. erythrophyllum* (Burch.) Sond., *C. fruticosum* (Loefl.) Stuntz., *C. gallabatense* Schweinf., *C. imberbe* Wawra, *C. kraussii* Hoechst., *C. molle* R. Br. and *C. zenkeri* Engl. and Diels. They were not observed in the samples studied of *Combretum apiculatum* Sond. and *C. multispicatum* Engl. and Diels.

Perforations in ray cells have been described in the literature before, but these perforations were always found in the radial walls between one ray cell and a vessel member. Such a ray cell always has two perforations, one in each radial longitudinal wall and serves as a link between two vessel members of an

axial vessel, deviating from its vertical course and obliquely passing through a ray. Chalk and Chattaway (1933) and Carlquist (1960) referred to such cells as perforated ray cells. McLean and Richardson (1973) used the term "vascular ray cell." The latter term is, in my opinion, most confusing because the term vascular rays is often used to refer to the entire ray tissue of the secondary xylem. Perforated ray cells of this type, although not uncommon in a number of families, have not been observed in *Combretum* or *Quisqualis*, or in other Combretaceae studied by me.

Carlquist (1961) stated that perforated ray cells of the common type are vessel members, derived from ray initials, and that they are somewhat intermediate between ray cells and vessel elements in morphology. The lateral wall pits are like those of the vessels (Carlquist, 1960), bordered and alternate, although the pits are smaller and have reduced borders (cf. Fig. 2).

For the radial vessel elements reported here, similar suggestions can be advanced. There can be no doubt about the fact that they arose from ray initials, and their morphology recalls ordinary ray cells in shape and size. However, the presence of perforations and vestured pits (Fig. 4 and 6), as well as the fact that they usually form a radial tube of substantial length, all constitute characters typical for true vessel members.

The presence of these radial vessels in the genera *Combretum* and *Quisqualis* has many aspects that need further attention. It would be interesting to study the ontogeny and morphogenesis of these radial vessels. Moreover, the general theories on the determination of xylem mother cells to vessel elements and on vessel differentiation should be tested for these genera which combine a radial and an axial vessel system. Functional aspects would also deserve further attention. The taxonomic and diagnostic implications of this character will be discussed in a future paper (van Vliet, in preparation).

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¹Rijksherbarium, Schelpenkade 6, Leiden, The Netherlands.

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Figures 1, 2, 5: *Combretum molle* R. Br.
Figures 3, 4, 6: *Quisqualis latialata* (Engl.). Exell.

Figure 1. Radial section. Light micrograph, showing a file of radial vessel elements (white arrows) of which both terminal cells have a perforation (p) in the radial wall, connecting them with a vascular tracheid. Both terminal cells are on a level different from the greater part of the radial vessel. On the left a terminal cell and some elements of another radial vessel (black arrows) are visible. $\times 600$.

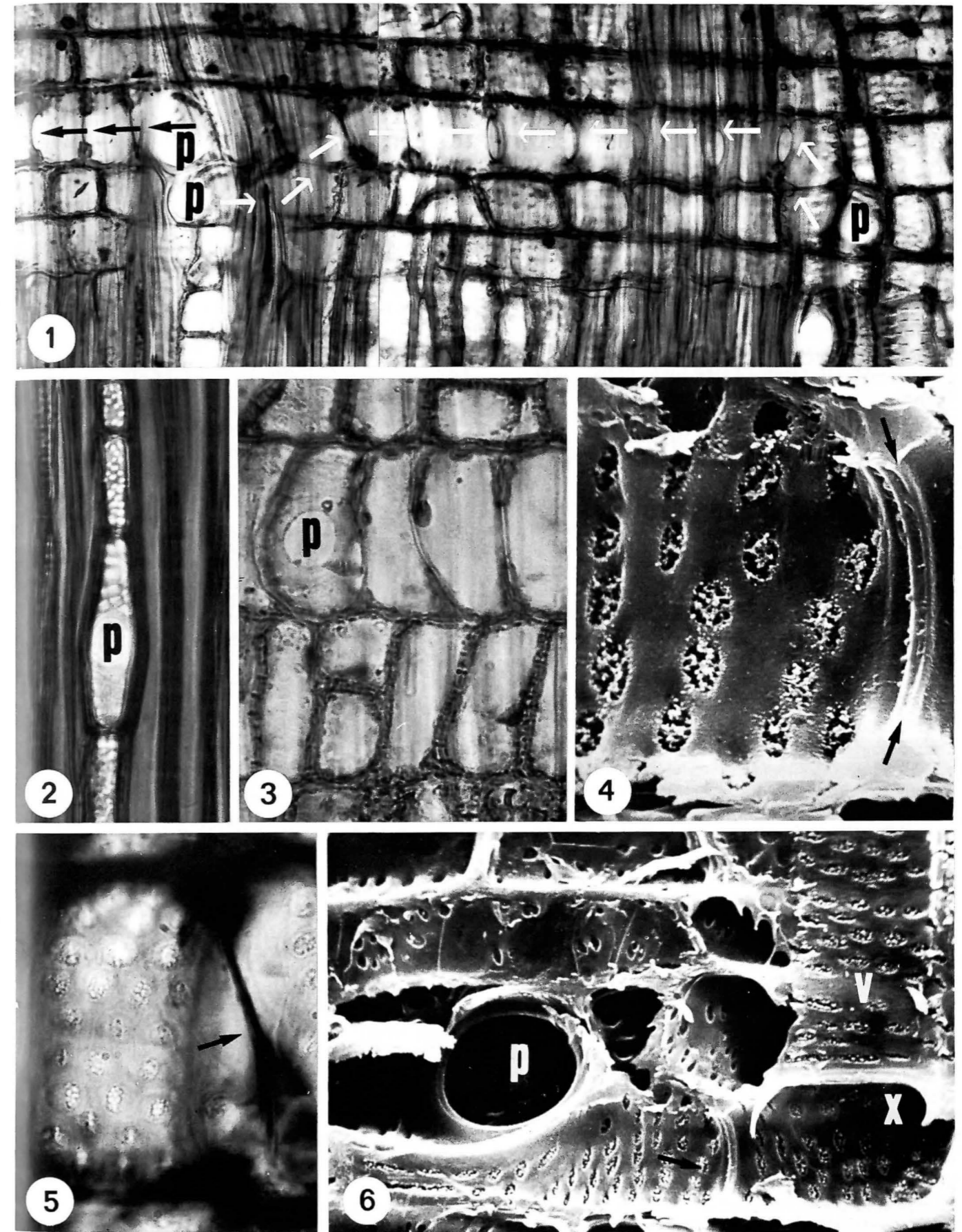
Figure 2. Tangential section. Light micrograph, showing a perforation (p) in the tangential wall of a ray cell. $\times 600$.

Figure 3. Radial section. Light micrograph, showing 'erect' radial vessel elements. The terminal cell has a perforation (p) in the radial wall. $\times 800$.

Figure 4. Radial surface. Scanning electron micrograph, showing a perforation rim in a radial vessel (arrows). Note the vestured pits. $\times 3100$.

Figure 5. Radial section. Light micrograph, showing vestured radial vessel to parenchyma pits. On the right a perforation in a tangential wall (arrow). $\times 2400$.

Figure 6. Radial surface. Scanning electron micrograph, showing radial vessel elements with a perforation in the radial (p) and the tangential wall (arrow), and a narrow vessel (v) with a perforation (x) probably leading to a radial vessel. Note the vestured pits in the radial and axial vessel elements and the unvestured pits in the ray parenchyma cells. $\times 900$.



JUVENILE CHARACTERS IN THE WOOD OF CERTAIN RUBIACEAE WITH SPECIAL REFERENCE TO *RUBIA FRUTICOSA* AIT.

by

Jifke Koek-Noorman¹

The great and numerous, although mostly quantitative, differences which often exist in the structure of the secondary xylem of large trees and shrubs or subshrubs belonging to the same or allied genera have been emphasized in the past by several anatomists. Most wood anatomists will be very careful when comparing such wood structures and will hesitate to draw conclusions based upon noted differences.

However, in other cases there may be a rather good agreement between small and large woody allies. Within the Rubiaceae we found a number of taxa in which this is the case. For instance, a mainly woody tribe like the Psychotriaceae is very homogeneous in its wood structure, not only as far as the large trees and shrubs of genera like *Psychotria*, *Mapouria*, *Ronabea*, *Rudgea*, *Naletonia* (Koek-Noorman, 1969 a,b) are concerned, but also when we take into consideration representatives of *Amarocarpus* (small shrubs), *Declieuxia* (herbs and subshrubs), and the subherbaceous species of *Psychotria*. The genera *Coprosma* (trees), *Plocama* (shrubs), *Pomax* (herbs), and *Othiophora* (herbs), belonging to the Anthospermeae, resemble each other in many wood anatomical characters which are considered to be of diagnostic value within the Rubiaceae. The same can be said for the genera *Spermacoce*, *Hemidiodia* and *Diodia* (Spermacoceae). These herbs show in the very small rings of secondary xylem a structure comparable to that of the Anthospermeae mentioned above.

A specimen of *Diodia brasiliensis* Spr., with a diameter as large as 2 cm, showed an unaltered structure also in the last formed growth ring. In those three tribes, classified in one subfamily Rubioideae, the agreement between the specimens studied is rather good, and their wood structure fits in the overall picture of the family Rubiaceae.

This statement does not apply to the Rubieae, a chiefly herbaceous tribe classified in the same subfamily Rubioideae. Most of the representatives available to me have very small stems. However, all thin specimens resemble each other as well as they resemble a wood sample of *Rubia fruticosa* Ait., with a diameter of 2 cm. The following description is based on this largest specimen available: *Rubia fruticosa* Ait., Uw 20251, Ridsdale and Baas 5, Carachico, along the coast, Canary Islands N. Tenerife, (Plate I: 1, 2, 3).

General Characters

Scandent shrub, stem oval in transverse section, diam. 2 x 2.5 cm (diam. of the xylem body: 1.5 x 2 cm); wood pinkish to brown, semi-ringporous; growth rings 11-12, marked by a zone with small vessels and thick-walled fibers, separated by a narrow terminal band of parenchyma from a zone with larger pores and thinner-walled fibers; width of the growth rings 0.5-1.8 mm.

Microscopic Characters

Vessels—mostly solitary, some in short radial multiples; in the early wood round to oval, diam. 70-100 μ m, in the late wood more or less angular, diminishing to less than 30 μ m; 74-100 per sq. mm; perforations simple, with rather wide rims (in one element a perforation transitional between scalariform and reticulate was observed); end walls nearly transverse; intervacular pitting alternate, vested, 6-9 μ m; length of the vessel members in the last formed growth ring (220-)295(-450) μ m.

Fibers—non-septate; bordered pits frequent on tangential and radial cell walls, apertures oval, extended, borders 4-6 μ m; cell walls 3-4 μ m thick, lumen diameter 12-16 μ m; fiber length in the last formed growth ring (420-)400(-680) μ m.

Rays—absent (some vague uniseriate rows of upright parenchyma cells in tangential section suggest the presence of rays. However, radial series are not recognizable).

Parenchyma—apotracheal, diffuse between the fiber tissue and in terminal bands of one cell wide; strands consisting of one or two cells, length of strands in the last formed growth ring (220-)270(-330) μ m; raphides present in many cells.

Most remarkable is the absence of rays. This phenomenon has been reported for several dicotyledonous woods of different taxa. Carlquist related raylessness with his theories on paedomorphosis (1962) and on insular woodiness (1969). An elaborate review of his theories is beyond the scope of this short note. It is relevant here, that in normally developed wood the elements of the first formed secondary xylem are much shorter than those of the

¹Institute for Systematic Botany, State University of Utrecht, The Netherlands

primary xylem. When such a shortening is absent, an abrupt change in length of the cambial initials has not taken place, and a "juvenile" characteristic may be said to result. Carlquist (1962) summarized a great number of characters which may be "transferred" from the primary xylem to the secondary xylem because of protracted or permanent juvenilism. Those characters are not necessarily correlated with each other which means that paedomorphosis may result in wood with a mixture of juvenile (mostly primitive) and mature (more advanced) characters. One of the characters, considered to be a possible indicator of juvenilism, is the predominance of erect ray cells, or raylessness.

Carlquist (1970) noted that raylessness occurs in the following classes of dicotyledonous woods: (1) Groups in which cambial activity is limited or finite; (2) Groups in which woodiness is in the process of increase rather than decrease, with the herbaceous condition as (phyletic) starting point; (3) Groups in which fusiform cambial initials are relatively short, so that there is no great difference between length of fusiform and ray initials; and (4) Groups in which a form of juvenilism or paedomorphosis occurs. Usually raylessness occurs in taxa combining several of these characteristics. For *Rubia fruticosa* the characteristics of (1), (3) and (4) can be demonstrated. I would not like to speculate on the phyletic increase or decrease of woodiness in *Rubia*, but cambial activity is certainly limited; the fusiform initials as reflected in vessel members and parenchyma strands are short, and there are signs of juvenilism if we consider the length-on-age graphs for axial elements (Fig. 1). We see an absence of a more or less steep fall and rise in the line considered to be normal for the transition from primary xylem and first formed secondary xylem to more mature wood. The graphs for *Rubia* resemble Carlquist's graph for *Talinum guadalupense* as given in his paper of 1962. The slight shortening in length of parenchyma strands suggested by the second mean value (233 μ m, Fig. 1.) is not very significant, and a possible shortening of the cambium initials is contradicted both by the highest value found in that zone (350 μ m) and by the flat line for the vessel members. Unfortunately the available material does not lend itself to a statistical approach. The mean length of vessel elements is 270-290 μ m, which is much shorter than in most other truly woody Rubiaceae, where generally the average vessel element length lies between 400 and 900 μ m. The shorter vessel elements in *Rubia* suggest that the fusiform cambial initials are shorter in *Rubia* than in other Rubiaceae. We have no data on length of ray initials of herbaceous Rubiaceae.

The length-on-age graph for *Rubia* can be compared with that of *Diodia brasiliensis* Sprengel, Kirkbride

1746, Uw 20851 (Plate I: 7, 8, 9). This collection was made in Serra de Bocaina, E. do Sao Paulo, Brazil, alt. ca. 1640 m, probably on a mesic site. The climate is mild atlantic. Our specimen of *Rubia fruticosa*, however, was collected in a dry locality at sea level, where also succulent *Euphorbias*, *Tamarix* and Cactaceae were found. *Diodia*, a shrub reaching up to one meter, had a diameter of about 2 cm wood, which is rather uncommon, as the representatives of the herbaceous tribe Spermacoceae usually do not have a diameter of more than about 5 mm of wood. As said before, the structure of the secondary xylem of this specimen fits in with that of large trees and shrubs of Rubiaceae. The shortening of the vessel elements at the transition to secondary xylem is present: in the maceration, taken from the first mm from the pith outwards, we see vessel elements with spiral secondary walls and very oblique end walls, which are about one and a half times as long as the secondary vessel elements. Towards the bark the length of vessel elements and fibers increases about 25%. In the 6th and last growth ring we do not see further elongation (Fig. 1).

Mabberley (1974) criticized Carlquist's interpretation of the different length-on-age graphs of vessel elements as indicators of paedomorphosis by referring to the paper of Philipson and Butterfield (1967). They explained the strong rise of vessel element length in the first growth rings by the fact that the rate of increase of the circumference of the cambium for an equal increment of radial growth is much higher in young stems than in older specimens. That means that the number of pseudotransverse divisions of initials will not be sufficient to supply the needs of the rapidly expanding perimeter of the cambium. Compensation is supposedly found in an elongation of the daughter initials beyond the length of their parents. According to Mabberley, in pachycaul trees with a wide pith, the first pseudotransverse cambial divisions take place at a greater distance from the center of the stem than in leptocaul trees. Because of a comparatively lower increase in circumference per unit of radial growth, a strong elongation of the daughter initials compared to their parents is not necessary, and the steep rise in vessel element length will not be present. Baas (1976), however, criticizes the hypothesis of Philipson and Butterfield, thereby also invalidating Mabberley's inferences. Although the pith of the sample of *Rubia fruticosa* (3 mm) is wider than those of the specimens of *Diodia brasiliensis* (0.6 mm, 1 mm), I also do not believe that the interpretation given by Mabberley mentioned above applies in this case. The material of *Crucianella* (pith 0.2 mm), *Galium* (pith 0.1, and 1 mm) and *Relbunium* (pith 0.1 mm) was too poor to allow macerations on fixed distances from the pith. But they show only small variations in vessel element length, and their over-all

structure is similar (Plate I: 4, 5, 6). The data for *Diodia*, like those for *Rubia*, do not allow statistical treatment, but I find the differences between *Rubia* and *Diodia* remarkable.

The parenchyma strands of *Rubia* are composed of one or two cells, contrary to those of the many other Rubiaceae studied on earlier occasions in which they are nearly always composed of 8 (4-12) cells. Comparison with *Diodia brasiliensis* is not possible because it lacks parenchyma. Although other "juvenile" characters are absent (Carlquist, 1962) this combination resembles the descriptions given by Carlquist (1962) as illustrations of his theory of pedomorphosis.

Taking for granted Carlquist's pedomorphosis theory, interpreting certain wood anatomical characters as primary xylem characters perpetuated into the secondary tissues, *Rubia* and the related genera *Relbunium*, *Galium* and *Crucianella* seem to provide interesting examples in addition to those given by Carlquist himself. It is noteworthy, however, that contrary to Carlquist's repeated belief that pedomorphosis is closely associated with phyletically increased woodiness due to mild climatic conditions, this phenomenon also occurs in some notably xerix representatives of the Rubiaceae (*Rubia*, *Crucianella*). Furthermore, juvenile characters are absent in the secondary xylem of representatives in the same size class of other, also essentially herbaceous tribes, as illustrated by *Diodia brasiliensis*, growing in mesic sites.

These two facts do not fit very comfortably with pedomorphosis theory. The conclusion is that the tribe Rubieae is very anomalous within the subfamily Rubioideae and within the Rubiaceae as a whole, as based upon its wood anatomy.

Material Studied:

Rubieae:

1. *Galium eriocarpum* Bartl. ex DC. Chile: Zollner 5020, diam. 0.7 cm.
2. *Relbunium* sp. Brazil: Rambo 34848, diam. 0.4 cm.
3. *Rubia fruticosa* Ait. N. Tenerife, Canary Isl.: Ridsdale and Baas 5, diam. 2 × 2.5 cm.
4. *Crucianella maritima* L. Palestine: Meyers and Dinsmore 3300, diam. 1 cm. Portugal. Pris Calo - Mondega. Wilezek 2451, diam. 0.3 cm.

Anthospermeae:

1. *Coprosma* sp. New Guinea: NGF 48391, diam. 0.7 cm.
2. *Othiophora* sp. E. Transvaal: Syde 100, diam. 0.4 cm.
3. *Plocama pendula* Ait. N. Tenerife, Canary Isl.: Ridsdale and Baas 4, diam. 4 × 6 cm.
4. *Pomax umbellata* Soland. ex Gaertn. S. Australia: Whibley 743, diam. 0.4 cm.

Psychotrieae:

1. *Amarocarpus* sp. New Guinea: NGF 23100, diam. 0.7 cm.

2. *Declieuxia dianthenoides* Standl. Brazil: Anderson e.a. 36266, diam. 1 cm.
3. - *deltoidea* Muell. Arg. Brazil: Anderson e.a. 35594, diam. 0.7 cm.
4. - *fruticosa* (Willd. ex R. and S.) Ktze. Brazil: Kirkbride 1703, diam. 0.8 cm.
5. - *spergulifolia* Mart. and Zucc. Minas Gerais, Brazil: Anderson 8918, diam. 0.8 cm.
6. *Psychotria angulata* Korth. Selangor, Malaya: Fl. Malaya 2809, diam. 1.4 cm.
7. - *aff. myrmecophila* K. Sch. and Lauterb. New Guinea: W.M. Doctors v. Leeuwen 9311, diam. 1 cm.

Spermacoaceae:

1. *Diodia brasiliensis* Spr. Brazil: Hatschbach 9059, diam. 0.3 cm; Kirkbride 1746, diam. 1.6 × 2 cm.
2. *Hemidiodia ocumifolia* (Willd.) K. Schum. Tobago: Krug and Urban 4450, diam. 0.8 cm.
3. *Spermacoce verticillata* L. Brazil: Mart. 590, diam. 0.5 cm.

Acknowledgments

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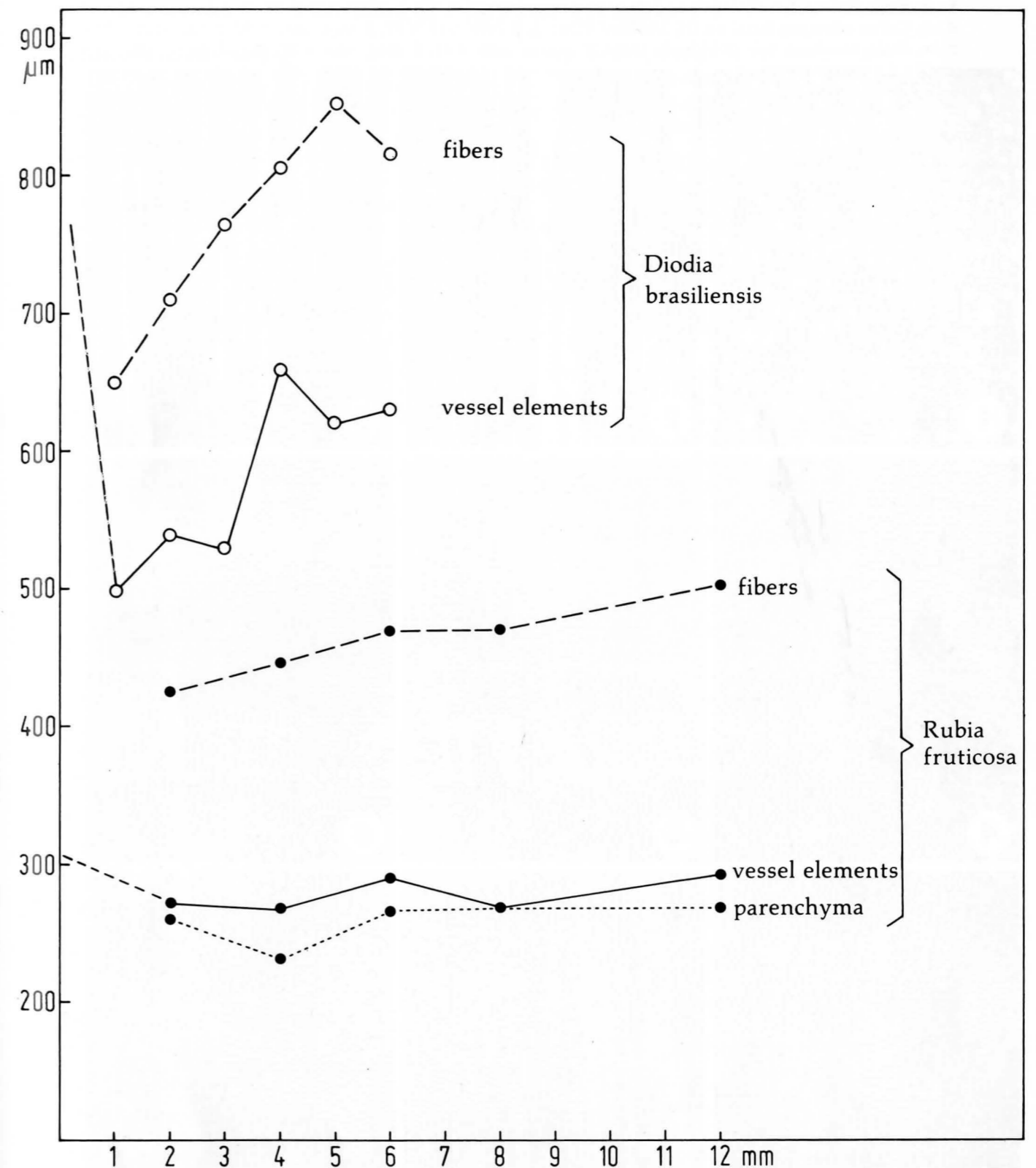
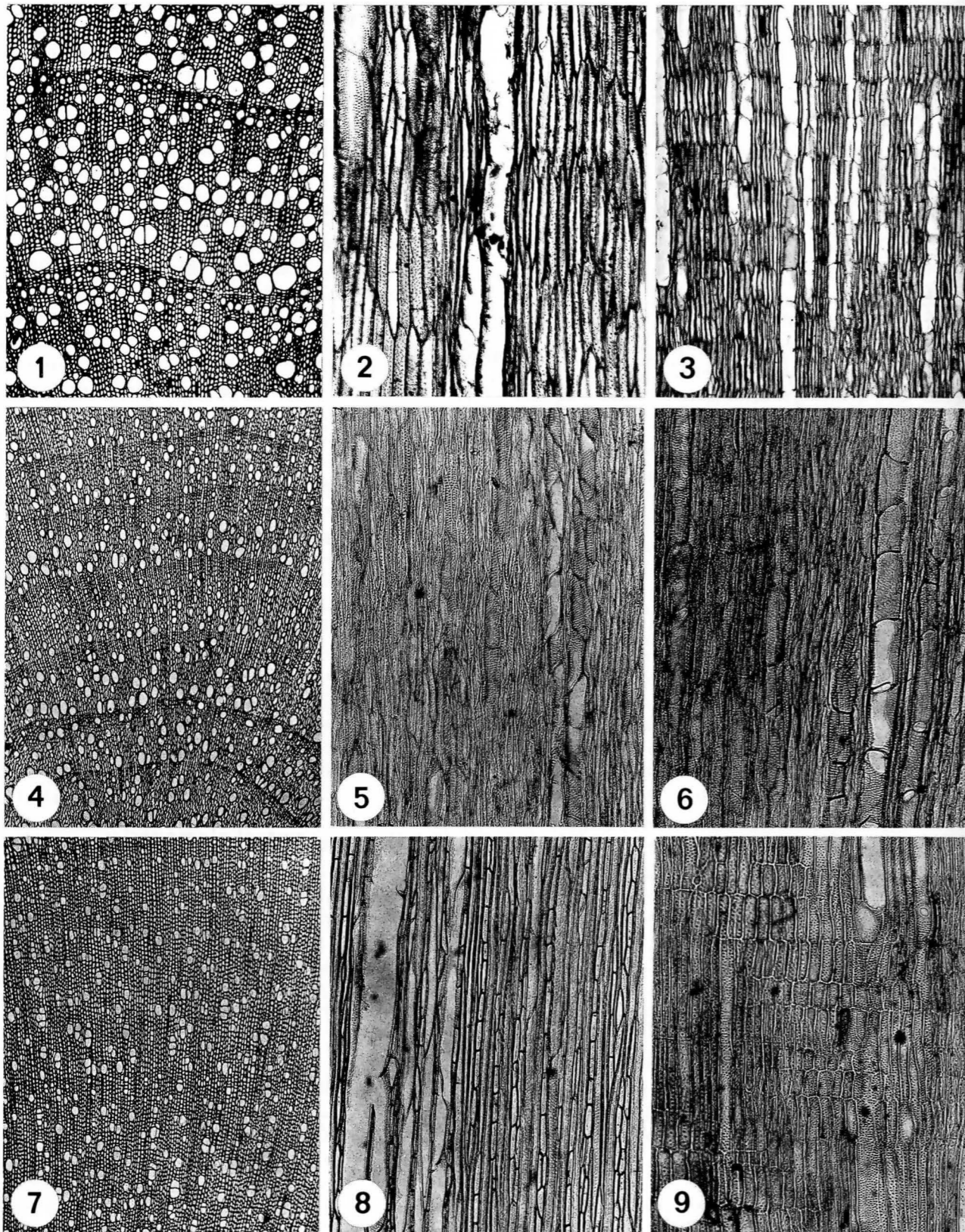


Figure 1. Length-on-age graphs for longitudinal xylem elements of *Rubia fruticosa* and *Diodia brasiliensis*. Age is indicated by distance from pith. Lengths are mean values out of at least 15 measurements, except lengths of vessel elements of primary xylem, which are based on 10 measurements.

Legends

Plate I:

1—3, *Rubia fruticosa* Ait. (Ridsdale and Baas 5); 1. transv. sect. × 41; 2. tang. sect. × 97; 3. rad. sect. × 41.
 4—6, *Galium eriocarpum* Bartl. ex DC (Zollner 5020); 4. transv. sect. × 41; 5. tang. sect. × 97; 6. rad. sect. × 97.
 7—9, *Diodia brasiliensis* Spr. (Kirkbride 1746); 7. transv. sect. × 41; 8. tang. sect. × 87; 9. rad. sect. × 97.



ASSOCIATION AFFAIRS

New Membership Directory

Thanks to a considerable increase of our Membership, the 1975 directory (*IAWA Bulletin* 1975/2) is out of date, and a new directory is needed. Dr. Ken Bamber (Sydney, Australia), has suggested that the new version should also contain information on current research projects of the individual members, in order to provide a better basis for communication within the IAWA. This suggestion has been warmly welcomed, the more so because Dr. Bamber, who is a member of the IAWA council, has offered to carry out the considerable task of collecting this information and collating the new directory. May we ask your collaboration in returning promptly the questionnaire which will reach you shortly, so that one of the major aims of the Association: stimulating research through direct contact between members, will be best served?

New Members

Full Members

Mr. F. W. Addo-Ashong
 Forest Products Research Institute
 University
 P.O. Box 63
 Kumasi, Ghana

Dr. Daniel Cassens
 LSU Cooperative Extension Service
 Knapp Hall
 Baton Rouge, Louisiana 70803
 USA

Dr. W. Höll
 Institut für Botanik
 Technische Hochschule München
 Arcisstrasse 21
 8 München 2, West Germany

Dr. Donald R. Kaplan
 Department of Botany
 University of California
 Berkeley, California 94720
 USA

Dr. Jette Dahl Møller
 Institute of Plant Anatomy and Cytology
 Solvgade 93
 1307 Copenhagen, Denmark

Dr. Philip R. Morey
 Department of Biological Sciences
 P.O. Box 4149
 Texas Tech. University
 Lubbock, Texas 79409
 USA

Mr. P. O. Olesen
 Skovbrugsinstituttet
 Thorvaldsensvej 57
 1871 Copenhagen, Denmark

Professor Rudolf Schmid
 Department of Botany
 University of California
 Berkeley, California 94720
 USA

Dr. Erak Staka
 Zavod za tehnologiju drveta
 71 000 Sarajevo
 Omladinsko setaliste, 12
 Yugoslavia

Dr. Elisabeth A. Wheeler
 North Carolina State University
 Division of University Studies
 P.O. Box 5971
 Raleigh, North Carolina 27607
 USA

Associate Members

Mr. Stephen Clark Taylor
 P.O. Box 3803
 Mississippi State
 State College, Mississippi 39762
 USA

Mr. David Wheat
 The Biological Laboratories
 Harvard University
 16 Divinity Avenue
 Cambridge, Massachusetts 02138
 USA

Replacement of Membership

Dr. Gunilla Smedman
 MoDoCell Research and Development
 S-891 00 Ornskoldsvik, Sweden

Changes of Address

Dr. Donald R. Bissing
 Department of Botany
 Southern Illinois University
 Carbondale, Illinois 62901
 USA

Miss Dorothy M. Catling
 Metropolitan Police Forensic
 Science Laboratories
 109 Lambeth Road
 London SE 1, England

Dr. L. Chalk
38 Ritchie Court
380 Banbury Road
Oxford OX2 7 PW
England

Mr. Walter J. Hayden
3424 Tulane Drive, #34
Hyattsville, Maryland 20783
USA

Dr. Zoltan Koran
Département d'Ingénierie
Université du Québec à Trois-Rivieres
Case Postale 500
Trois-Rivières, Québec
Canada G9A 5H7

Resignation

Mr. J. F. Hughes
Commonwealth Forestry Institute
University of Oxford
Oxford, England

WOOD ANATOMY ACTIVITIES AROUND THE WORLD

Request For Wood Samples

For his current wood anatomical survey of the Combretaceae, Mr. G.J.C.M. van Vliet (Rijksherbarium, Schelpenkade 6, Leiden, The Netherlands) wishes to complement his research materials with samples of the genera *Calopyxis* Lam. (Madagascar), *Finetia* Gagnep. (Indo-China), *Meiostemon* Exell & Stace (syn. *Combretum humbertii* & *Combretum tetrandrum*, Zambia, Rhodesia, Madagascar), and *Thiloa* Eichl. (South America).

Sixteenth World Congress of IUFRO

From June 20-26 the International Union of Forest Research Organizations (IUFRO) held its 16th world congress in Oslo, Norway. Although the major divisions of IUFRO are concerned with forestry and aspects of forest products which are beyond the scope of our Association, a short report for wood anatomists seems appropriate. IUFRO aims at coordinating and stimulating applied research, and it was therefore all the more gratifying to note the strong awareness of the value of fundamental wood structural knowledge amongst the participants of the Wood Quality, the Wood Protection and the Xylem Physiology group symposia. Several members of the IAWA contributed to these symposia with elegant wood anatomical papers. In order to secure that future IUFRO meetings with an emphasis on the structure-property relationship or on other anatomical aspects should not escape the attention of IAWA members, a permanent form of contact between IUFRO-division V and IAWA is now being discussed. Our Bulletin can also serve to announce some of the activities of IUFRO which are of interest to the whole of our membership. Thanks to our Norwegian hosts the IAWA held a meeting to discuss Association Affairs. This meeting was attended by 12 members and about the same number of interested non-members. During this meeting the support was sought and obtained for a slight increase in dues, for a campaign to increase the number of library subscriptions and of members, and for amending the constitution. Future plans were also discussed.

P. Baas