THE OCCURRENCE OF AXIAL LATEX TUBES IN THE SECONDARY XYLEM OF SOME SPECIES OF ARTOCARPUS J. R. & G. FORSTER (MORACEAE)

by

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Summary

In a number of species of *Artocarpus* J.R. & G. Forster (Moraceae) laticifers were not only observed as radial tubes, enclosed in the ray tissue, but also as axial tubes, enclosed in the fibre tissue. Both types of latex tubes are connected and considered as one branched laticiferous system. A detailed description of the individual latex tubes and the whole system, based on light microscopic and scanning electron microscopic observation, is presented.

Introduction

The present investigation is part of a detailed, comparative wood anatomical study of the Moraceae.

Until now latex tubes in the secondary xylem of Moraceae and in general have been observed only in the rays. Consequently a latex tube in the secondary xylem has been defined by the Committee of Nomenclature of the IAWA (1964) as 'a laticifer enclosed in a ray'. In our search of the literature we found two exceptions but both authors considered them as an exception of the rule: Tippo (1938) remarks that some of the radial latex tubes of *Craterogyne kameruniana* (Engl.) Lanj. (= *Dorstenia*, Berg, 1978), are 'outside of the ray' and Vreede (1949) gives an example of a radial latex tube that 'does not lie in a ray'. As far as known to us, *axial* latex tubes have never been reported for the secondary xylem.

Materials

Only dried material was used for this investigation. The material was partly present in the Utrecht wood collection and was partly obtained by the kind cooperation of the curators of the wood collections of the Rijksherbarium Leiden, the Royal Tropical Institute Amsterdam, TNO Houtinstituut Delft and the Musée Royal de l'Afrique Centrale Tervuren. The genus *Artocarpus* is represented by the following species. An asterisk indicates the absence or uncertainty about the existence of herbarium vouchers. The abbreviations used are according to the Index Herbariorum (Holmgren & Keuken, 1974) and the Index Xylariorum (Stern, 1978).

A. anisophyllus Miq.: Sabah, Uw 24213, SAN 50567; Indonesia, Uw 24607 (RTIw, IND coll. 2307), BO 1778; S.E. Asia, Uw 24308, BO Pfeiffer E 952. – *A. blancoi* (Elmer) Merr.: Philippines, Uw 24214, Tw Rojo 262*. – *A. communis* Forst.: New Guinea, Uw 24325, L BW 1465 (sterile); Uw 24603, L BW 4219; Uw 24600, L BW 1269; Uw 24602, L BW 2904; Uw 24326, L BW 2541; Samoa, Uw 16632, US coll. L.S. Dutton nr. 8; Philippines, Uw 24310, BO Pfeiffer 3113 TS*. – *A. elasticus* Reinw. ex Blume: Java, Uw 24421, BO Koorders coll. 1026c/22031b; Uw 24422, BO Koorders coll. 1621m*; Sabah, Uw 24215, SAN 18656. – *A. fretessii* T. & B. in Hassk.: New Guinea, Uw 18112, Lw BW 9871*; Uw 24318, Dw Fokkinga 2175*; Uw 24316, L BW 2133. – *A. integer* (Thunb.) Merr.: New Guinea, Uw 24319, L BW 5659; Philippines, Uw 24323, BO Pfeiffer 385*. – *A. kemando* Miq.: Sumatra, Uw 24324, L Endert & v.d. Zwaan nr. 90, R.R.I. 755; Indonesia, Uw 24605 (RTIw IND coll. 3590)*; Malaya, Uw 24608, FHOw 4536, Desch FMS 28853*. – *A. lakoocha* Roxb.: E. Pakistan, Uw 18033, MADw 24487. – *A. lanceifolius* Roxb.: Moluccas, Uw 24609, L De Vriese & Teysmann 20; Sabah, Uw 24216, SAN 59079; Indonesia, Uw 24604 (RTIw IND coll. 2200), BO 1682; Uw 24606 (RTIw IND coll. 4027)*; S.E. Asia, Uw 24328, Dw Pfeiffer 6891*. – *A. nitidus* Tréc.: Sabah, Uw 24217, SAN 25510. – *A. sepicanus* Diels: New Guinea, Uw 24329, Dw Fokkinga 7822*. – *A. sericicarpus* Jarrett: Sabah, Uw 24218, SAN 50586. – *A. tamaran* Jarrett: Sabah, Uw 24219, SAN 25581. – *A. teysmannii* Miq.: New Guinea, Uw 24330, L BW 1204.

The available slides in our institute and in the Rijksherbarium Leiden have been used in search of axial latex tubes in other genera of Moraceae. The numbers between brackets indicate the number of species studied: *Antiaris (10); Bagassa (3); Batocarpus (4); Bosqueiopsis (1); Brosimum (12); Broussonetia (3); Castilla (6); Chlorophora (7); Clarisia (3); Cudrania (3); Dorstenia (1); Ficus (5); Helianthostylis (2); Helicostylis (9); Maclura (1); Maquira (7); Morus (3); Naucleopsis (7); Olmedia (2); Parartocarpus (2); Perebea (3); Plecospermum (1);*

Prainea (2); Pseudolmedia (5); Sorocea (3); Sparattosyce (1); Streblus (3); Treculia (1); Trilepisium (2); Trophis (2); and Trymatococcus (3).

Methods

Sudan III was used for staining latex as recommended by Vreede (1949). The scanning electron microscope, used in this investigation was a Cambridge Stereoscan S 604. Photographs were made at 7.5 Kvolt. Microtome sections of about 20 microns thick were first photographed with the aid of the light microscope. Afterwards they were air dried, sputter coated with gold and studied with the SEM. This enabled us to compare light micrographs and SEM observations, and thus facilitated the detection of the axial latex tubes among the fibres with the scanning electron microscope.

Results

The occurrence of axial and radial latex tubes – In agreement with data from the literature (Solereder, 1885; Janssonius, 1934 as 'radiál laufende Elemente'; Metcalfe & Chalk, 1950; Brazier & Franklin, 1961; Sharma, 1962; Burgess, 1966; Kribs, 1968; Purkayastha et al., 1976) radial latex tubes were observed in a number of species of the large genus *Artocarpus*, consisting of 52 species (Jarrett, 1977). In the secondary xylem of seven out of the fourteen species (see Table 1) latex tubes occur not only in the rays, as they usually do, but also in axial direction in the fibre tissue. Not all specimens of these seven species showed axial latex tubes. Neither have axial latex tubes been observed until now in the other listed species studied of *Artocarpus*, nor in any other moraceous genus.

Radial latex tubes on the other hand have been recorded for specimens of all *Artocarpus* species studied.

The position of the latex tubes in the secondary xylem – In *Artocarpus* radial latex tubes are always surrounded by ray parenchyma. The axial latex tubes lay scattered in the fibre tissue and are consequently surrounded by fibres (Fig. 1). They only make lateral contact with the rays in their course through the fibres. The lumina of the axial latex tubes are only slightly larger than the lumina of the largest fibres and of the parenchyma cells which makes them barely recognizable in cross sections (Fig. 1). However, at high magnifications, the differences in size, wall thickness and cell contents are quite striking.

Frequency of the occurrence of the latex tubes – The frequency of occurrence of the axial latex tubes is rather low. Although exact figures are not available a rough estimate is here given: in a cross section of about one square centimeter one may expect 0–6 latex tubes. Radial latex tubes occur generally more frequently but sometimes they are as rare as axial latex tubes or not present at all (Table 1). All wood samples with axial latex tubes also showed radial latex tubes.

The contents of the latex tubes – The contents are yellowish brown, often granular, resembling the dark cell contents of many parenchyma cells. Upon staining with Sudan III the latex in the latex tubes turns into orange red, and the contents of the parenchyma cells become purplish red.

Table 1. Presence (+) or absence (–) of axial (a.l.t.) and radial latex tubes (r.l.t.) in the *Artocarpus* material studied.

	Sample	a.l.t.	r.l.t.
A. anisophyllus	Uw 24213	+	+
"	Uw 24607	+	+
"	Uw 24308	–	+
A. communis	Uw 24325	+	+
"	Uw 24603	+	+
"	Uw 24310	+	+
"	Uw 24600	–	–
"	Uw 24602	–	–
"	Uw 24326	–	–
"	Uw 16632	–	–
A. integer	Uw 24319	+	+
"	Uw 24323	–	–
A. kemando	Uw 24324	+	+
"	Uw 24605	+	+
"	Uw 24608	–	+
A. lanceifolius	Uw 24609	+	+
"	Uw 24606	+	+
"	Uw 24604	+	+
"	Uw 24328	+	+
"	Uw 24216	–	+
A. sericicarpus	Uw 24218	+	+
A. teysmannii	Uw 24330	+	+
A. blancoi	Uw 24214	–	+
A. elasticus	Uw 24421	–	–
"	Uw 24422	–	–
"	Uw 24215	–	+
A. fretessii	Uw 18112	–	+
"	Uw 24318	–	+
"	Uw 24316	–	+
A. lakoocha	Uw 18033	–	+
A. nitidus	Uw 24217	–	+
A. sepicanus	Uw 24329	–	+
A. tamaran	Uw 24219	–	+

The constitution of the wall of the latex tubes – The walls of the laticifers are difficult to observe when they are filled with latex. However, often the tubes are partly empty or the latex is removed during sectioning. Both with the light microscope and the SEM the existence of a thin wall is most obvious in those places where it is locally ruptured during sectioning (Fig. 2 & 3), or as happened once during the observation with the SEM, where two blind pits were blown up as a result of local gas production (Fig. 4). The walls of the laticifers, although distinct, are extremely thin, less than 0.5 micron thick (Fig. 2 & 3). Pits were found neither in radial, nor in axial latex tubes. Radial latex tubes show often blind pits to contiguous parenchyma cells (Fig. 4). In macerations no traces of latex tubes have been found. This is possibly due to the fact that they have only primary walls (see discussion).

Only in one sample, Uw 24324 (*A. kemando* Miq.) there is an indication that these laticifers are 'articulated' (see discussion). A radial section of this sample (Fig. 5) shows a structure in a radial latex tube which might be interpreted as a transverse cell wall. In other samples the walls are smooth and without any cross wall or a perforated remainder of it. This is also true for the 'connections' between axial and radial latex tubes.

The use of the SEM provided no additional information about the wall properties but confirmed the observations obtained with the light microscope.

The structure of the laticifer system – Without implying any ontogenetic process the entire laticifer system can be described as branched. It exists of radial components, following the rays and of axial parts which, in striking contrast to the straight course of the radial parts, show a rather capricious course through the fibre tissue (Fig. 6) and are even branched themselves (Fig. 7). Different connections between radial and axial latex tubes have been observed (Fig. 8 to 12).

Discussion

Articulated or nonarticulated laticifers – Already David (1872) distinguished between articulated (Milchsaftgefässe) and nonarticulated (Milchsaftschläuche) laticifers. The tubular laticifers of the Moraceae are commonly considered as nonarticulated laticifers, comparable with those in the Euphorbiaceae, Asclepiadaceae, Apocynaceae and Urticaceae (David, 1872; Schaffstein, 1932; Vreede, 1949). However, Dippel (1865) and Milanez (1954) defended the 'articulated' point of view, based upon studies of *Ficus*. We are inclined to consider the latex tubes of *Artocarpus* as 'nonarticulated' because no cross walls or perforated cross walls could be found. Some caution remains necessary as we observed with the light microscope one structure very much resembling a cross wall (Fig. 5).

Taxonomic value – The value of axial latex tubes for identification purposes seems to be restricted, as will be clear from Table 1.

The genus *Artocarpus* is subdivided (Jarrett, 1959) in two subgenera: *Artocarpus* and *Pseudojaca*, both with about the same number of species. Only three species of the subgenus *Pseudojaca* have been studied. All species with axial latex tubes belong to the other subgenus, *Artocarpus*, but several species of this subgenus lack them so that no taxonomic conclusions can be attached to the distribution of axial laticifers.

The distribution of axial and radial latex tubes over the samples of *Artocarpus communis* Forst. suggests that within this species two taxa can be distinguished. This is in agreement with the existing doubt about the homogeneity of this species (Jarrett, 1959).

Wall properties – The walls of laticifers are primary, rich in pectic substances and nonlignified (Frey-Wyssling, 1926; Moor, 1959; Esau, 1965; Fahn, 1967). This may explain why we never succeeded in finding latex tubes in macerations as primary walls are easily desintegrated by the macerating agents. This is contradictory to Dippel (1865), who recorded

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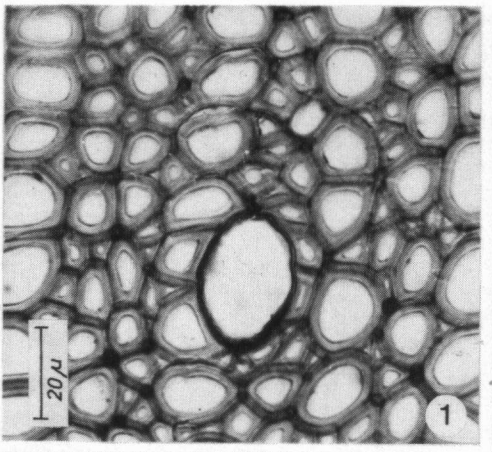
Fig. 1–12. Latex tubes in *Artocarpus*. – 1: *A. lanceifolius*. Cross section. – 2: *A. lanceifolius*. Radial section. SEM photograph showing an axial latex tube with a smooth, thin, locally ruptured (arrow) wall without pits. – 3: *A. communis*. Tangential section. Connection between radial and axial latex tube; thin wall locally ruptured (arrow). – 4: *A. kemando*. Radial section. SEM photograph showing blind pits in a radial latex tube; two of them ruptured (arrow). – 5: *A. kemando*. Radial section. Structure in a radial latex tube resembling a cross wall (arrow). – 6: *A. communis*. Tangential section, showing the rather capricious course of the axial latex tubes through the fibre tissue.

7: *A. communis*. Radial section. Axial latex tube, with a V-shaped furcation. – 8–12: Connections between axial and radial latex tubes in the secondary xylem of *A. kemando* (8 & 9) and *A. lanceifolius* (10, 11 & 12); radial sections except figure 12, which shows a tangential section.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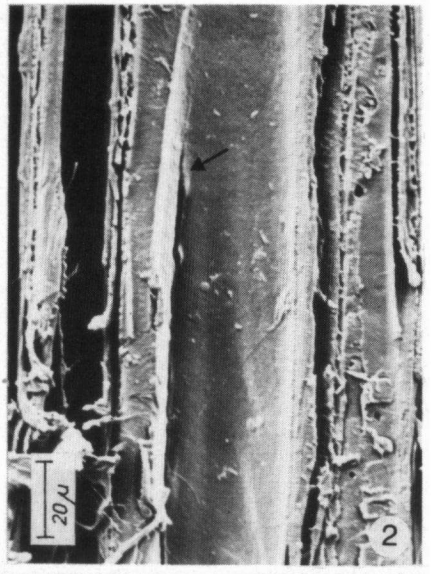
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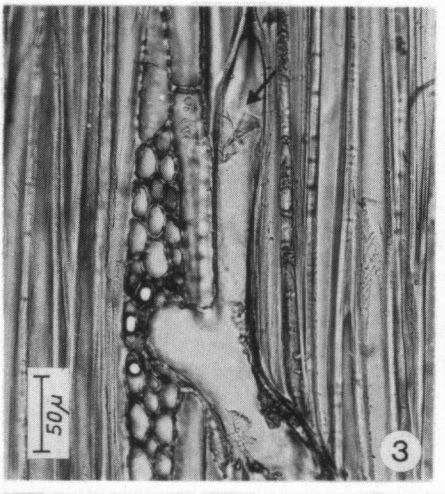
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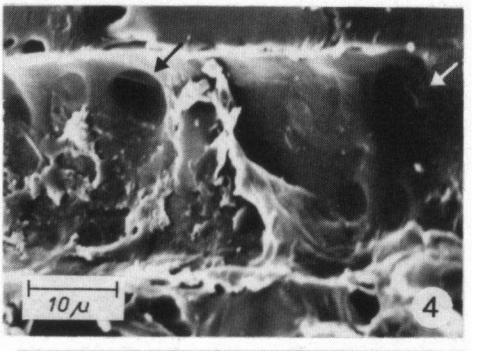
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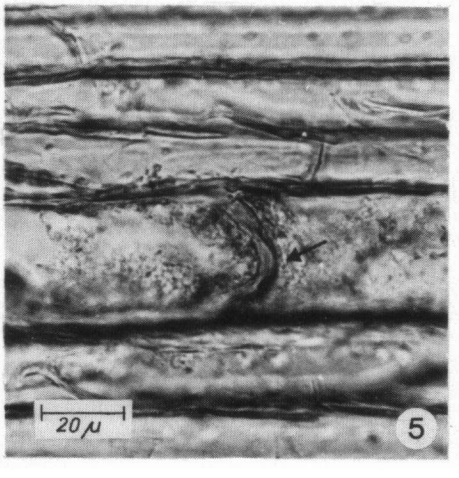
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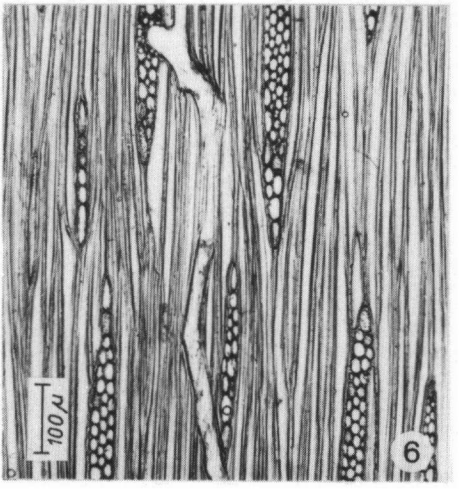
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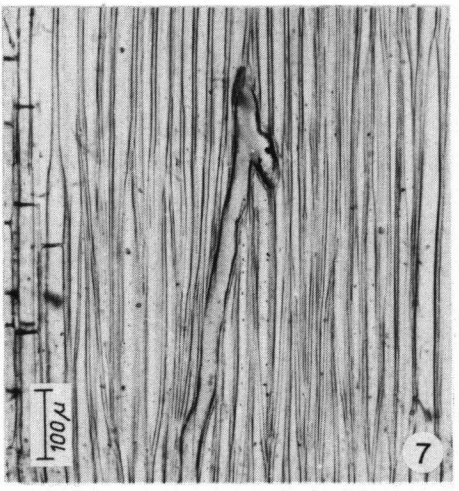
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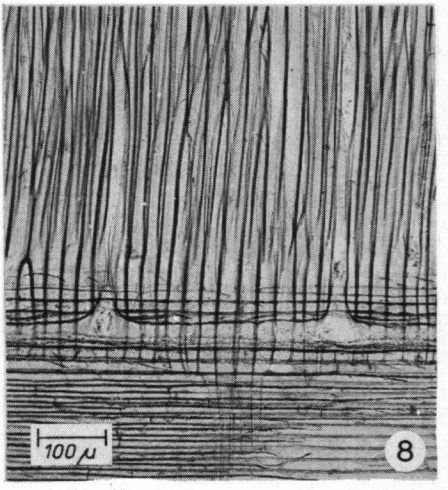
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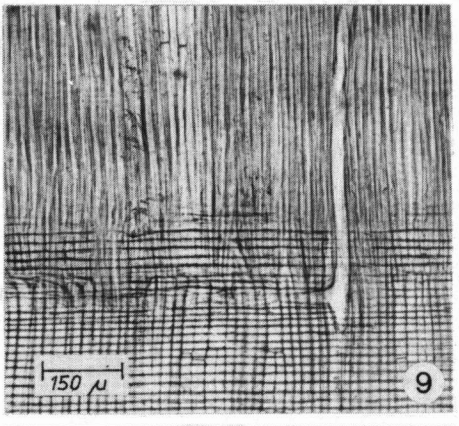
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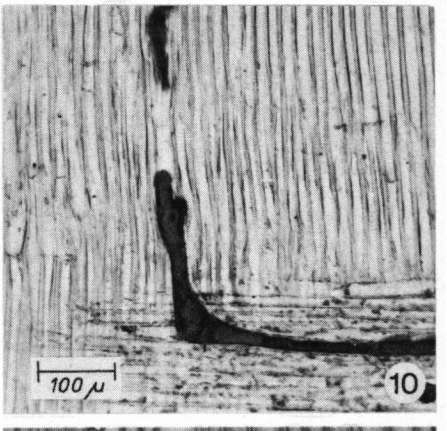
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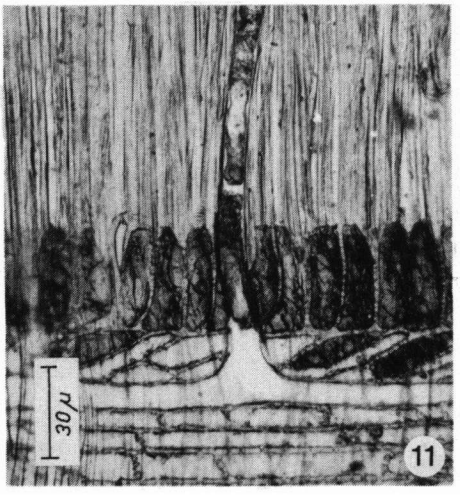
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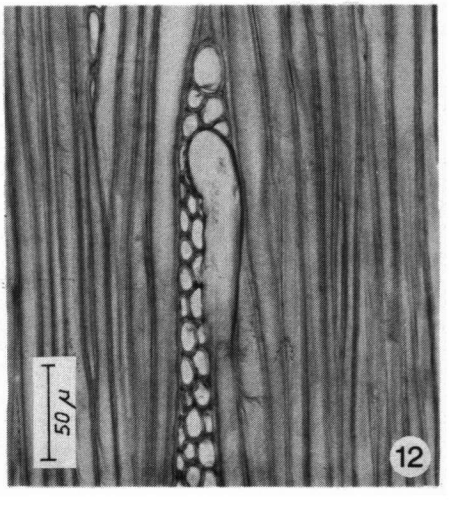
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12

latex tubes in macerations of *Ficus*. Vreede (1949), Esau (1965) and Fahn (1967) state that primary pit fields (= pits in primary cell walls) are rare. This is also in full agreement with our observations. We only found blind pits where latex tubes and parenchyma cells are contiguous.

Origin and growth of latex tubes – Nonarticulated, branched laticifers in secondary tissues grow by means of intercalary growth (Artschwager, 1946), keeping pace with the subsequent growth of tissues from the cambium and resulting in continuous tubes (Vreede, 1949). This explains the existence of the radial latex tubes and their straight course.

The occurrence of axial latex tubes and their often capricious course asks for another explanation. In other plant parts nonarticulated latex tubes are known to originate as single cells in the embryo and develop by way of a combination of apical and intrusive growth, comparable with the growth of hyphae of successful intercellular fungal parasites (Esau, 1967). This may also explain their course in the secondary xylem. Probably the radial latex tubes give off side branches in the direct vicinity of the cambium which by means of intrusive growth enter the young, not yet lignified, fibre tissue. Elucidation of this problem requires an investigation of the cambial region.

Addendum

During the preparation of this paper axial latex tubes were also found in another taxon of the Moraceae, viz. *Bagassa guianensis* Aubl.

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