

DISTRIBUTION AND DEVELOPMENT OF SECRETORY DUCTS IN TRICHOSCYPHA (ANACARDIACEAE)

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SUMMARY

Distribution and development of three different secretory ducts systems were studied in leaves, stems and roots of several *Trichoscypha* species (Anacardiaceae) from west tropical Africa. One primary three-dimensional network occurs in the pith and the cortex of the stem and mesophyll of the leaves. A second primary system of mainly longitudinal orientated, hardly ramifying, secretory ducts is found in the metaphloem of leaves, stem and roots while a secondary three-dimensional system is detected in the secondary phloem of leaves, stem and roots. In the stem and roots, the last system is continuous with the secondary xylem via horizontal secretory ducts in both secondary phloem- and xylem rays. The three systems are separated from one another.

Ducts initiate schizogenously and develop further lysigenously in the primary phloem of the root, in the secondary phloem of the stem and sometimes also in the wood rays. In other parts of the plant the ducts develop entirely lysigenously.

1. INTRODUCTION

Secretory ducts have considerable taxonomic importance and are characteristic of a small number of dicotyledon families (METCALFE 1983). Their products are sometimes of economic significance. When present in Anacardiaceae, secretory ducts will always be found in the stem. In several species secretory ducts are not only confined to the stem, but are also present in leaf, root, flower or fruit.

There is much confusion in literature concerning the mode of origin of the canals; do they originate schizogenously, lysigenously or schizo-lysigenously? This may be dependent on the species or even within a species on the considered tissue (GIBSON 1981; VENKAI AH & SHAH 1984). Also the chemical nature of the deposits in secretory canals caused much discussion (FAHN 1979; FAHN & EVERT 1974).

In the Anacardiaceae more or less longitudinal secretory ducts are particularly common in the phloem, cortex and pith of the stem, but they also occur in both phloem- and wood rays in numerous genera (METCALFE 1983). Whether this is also the case in the genus *Trichoscypha* Hook. f. that comprises about 75 species, all trees and shrubs, is not known or only partly described. The genus occurs in tropical and south Africa, however it is absent on Madagascar (PERRIER DE LA BATHIE 1946).

The present paper describes the duct system in six *Trichoscypha* species from

the Ivory Coast and Liberia which are treated in the flora of west tropical Africa (HUTCHINSON & DALZIEL 1954).

2. MATERIALS AND METHODS

Samples used comprise the following *Trichoscypha* species:

- *T. arborea* (A. Chev.) A. Chev. (Versteegh & Den Outer 659, Ivory Coast, 1969, large tree, dbh 30 cm, stem and leaf; Versteegh & Jansen 778, Liberia, 1969, large tree, dbh 40 cm, root, stem and leaf; De Koning 3571, Ivory Coast, 1974, seedlings);
- *T. beguei* Aubrev. et Pellegr. (Versteegh & Den Outer 648, Ivory Coast, 1969, small tree, dbh 15 cm, stem and leaf; Versteegh & Jansen 794, Liberia, 1969, small tree, dbh 20 cm, stem and leaf);
- *T. chevalieri* Aubrev. et Pellegr. (Versteegh & Den Outer 571, Ivory Coast, 1969, shrub, dbh 6 cm, stem and leaf);
- *T. mannii* Hook. f. (Versteegh & Den Outer 739, Ivory Coast, 1969, shrub, dbh 6 cm, stem and leaf);
- *T. oba* Aubrev. et Pellegr. (Oldeman 443, Ivory Coast, 1963, small tree, dbh 10 cm, root, stem and leaf);
- *T. yapoensis* Aubrev. et Pellegr. (Versteegh & Jansen 758, Liberia, 1969, small tree, dbh 10 cm, stem and leaf).

Samples of *T. arborea*, *T. mannii* and especially those of *T. oba* were used most frequently in the present study. Stem samples containing bark attached to wood, were collected at breast height and immediately fixed in FAA. All the material of *T. oba* was collected from a living tree raised from seed (Oldeman 443) in the greenhouse at Wageningen and cut freshly. The collection is housed at the Department of Plant Cytology and Morphology, the accompanying herbarium vouchers at the Department of Plant Taxonomy, Agricultural University, Wageningen. Anatomical features were studied in transverse, radial and tangential serial sections, which were unstained or stained with sudan III (staining fatty substances, latex), iodine (starch stain) or toluidine blue (contrast, cytoplasmic stain), but also with sudan IV (fatty substances, latex stain), phloroglucin-hydrochloric acid (staining lignin), eosine (cytoplasmic stain), zinc chloride-iodine (cellulose stain), aceto-carmine (according to Heitz; staining the nucleus), nitric acid (Xanthoprotein reaction; protein stain) and sulfuric acid (reaction of Raspail; protein stain, but also staining glucosids, alkaloids) (JOHANSEN 1940).

Some material was impregnated with technovit 7100 before sectioning with a rotary microtome. All sections were embedded in Kaisers gelatin-glycerin (JOHANSEN 1940).

3. RESULTS

3.1. Distribution of the secretory ducts

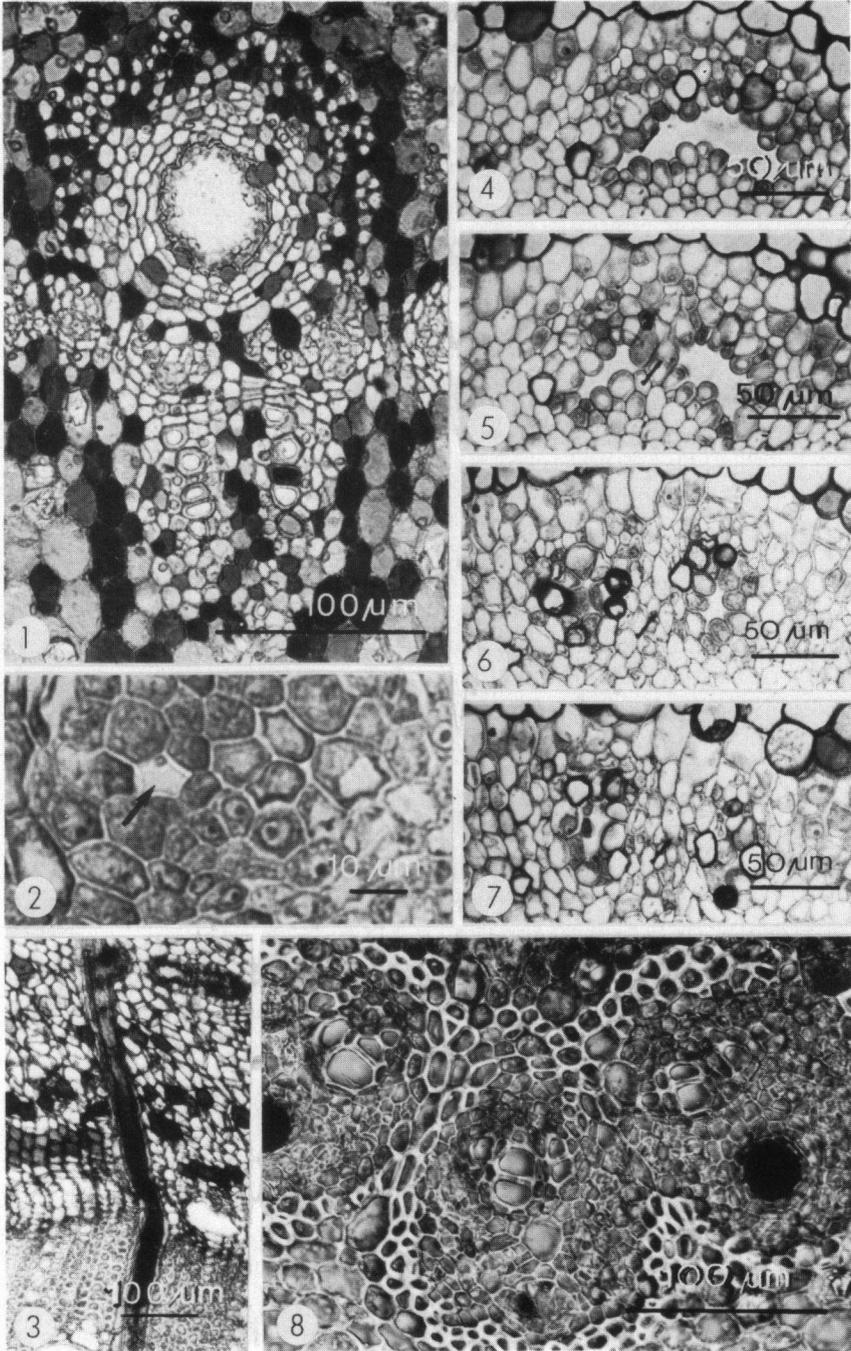
In the stem of the investigated *Trichoscypha* species longitudinal secretory ducts are present in the cortex, primary (meta-)phloem, secondary phloem and pith as is summarized in *table 1*. Horizontal (radial) ones are present both in the secondary phloem- and wood rays. The longitudinal ducts in the cortex and pith are branched, anastomose and form a three-dimensional network; both networks are in contact with each other via semi-vertical ducts in the leaf gaps and constitute in this way one continuous primary system. The very wide, longitudinal secretory ducts formed in the meta-phloem of the vascular bundles (*fig. 1*), are protected on the outside by arcs of sclerenchyma fibres of the pericycle. They are unbranched and in contact with each other only in the nodes. This second primary system is separated from the first one. The longitudinal ducts in the secondary phloem which are arranged in more or less concentric rings show ramifications and anastomosis and form also a three-dimensional network together with the horizontal (radial) ducts in the phloem rays. These horizontal ducts pass the cambium and continue their course in the secondary xylem rays (*fig. 3*). In the secondary xylem vertical ducts are absent. This secondary duct system is not connected with the two primary systems mentioned above.

In the root longitudinal secretory ducts are present in the primary (meta-) phloem (*fig. 2*) and secondary phloem; horizontal (radial) ones occur in the secondary phloem- and wood rays. These ducts are arranged, branched and/or fused in the same way as in the stem (*figs. 4-7*). But in contrast to the trunk here the first primary system is absent, since the central part of the root is com-

Table 1. Distribution and development of secretory ducts in root, stem and leaf of the investigated *Trichoscypha* species.

type duct system	presence in tissue	orientation	root	stem	leaf
prim. system one	cortex parenchyma	ir	-	l	-
	pith parenchyma	ir	-	l	-
	mesophyll parenchyma	ir	-	-	l*
prim. system two	prim. phloem	lg	s-l	l	l
		rd	-	-	-
	prim. xylem	lg	-	-	-
		rd	-	-	-
sec. system	sec. phloem	lg	l	s-l	l
		rd	l	l	-
	sec. xylem	lg	-	-	-
		rd	-	s-l	-
				also l	

Legends: * = no ducts present in the mesophyll of the leaflet outside the surroundings of the midvein; - = ducts absent; + = present; ? = not reported; hor = more or less horizontal; ir = irregular, in all directions; l = lysigenous; lg = longitudinal; prim. = primary; rd = radial; s = schizogenous; sec. = secondary; s-l = initiation schizogenously but lysisigeny occurs in later stages of development; tg = tangential.



posed of metaxylem and no ducts were found in the cortex. The two remaining systems constitute two continuous systems separated from each other, but connected with the corresponding systems of the stem.

The leaves are compound, imparipinnate, alternate and estipulate. Only longitudinal ducts were found. They are present in the mesophyll, primary (meta-) and secondary phloem (when produced) of the leaf primordium, petiole, rachis, petiolule and midvein of the leaflet (*fig. 8*); furthermore also in the primary (meta-)phloem of the lateral veins in the leaflet. Each of the three duct systems of the stem, though separated from one another, form a continuous system with the corresponding ones in the leaf; yet in the leaf the secondary system is limited.

Fruits and flowers were not investigated.

3.2. Development of the secretory ducts

Secretory ducts initiate schizogenously but lysigeny occurs in later stages in the primary phloem of the root, in the secondary phloem of the stem and sometimes also in the xylem rays. Ducts found in all other tissues (see for instance initiation in the leaf primordium, *figs. 9–16* and *17–20*) including the greater part of the wood rays, initiate and develop entirely lysigenously (see *table 1*). The secretory ducts are lined with epithelial cells. In general a schizogenous duct has a sharp boundary of epithelial cells (*figs. 4–7*), whereas in a lysigenous duct the epithelial cells are ruptured and so the boundary is not well defined (*fig. 1* and *8*). In developing schizogenously initiated ducts the epithelial cells eventually disintegrate after secretion of substances into the duct cavity and neighbouring cells become the new epithelial cells. So here the boundary of the ducts is also ill defined.

Often in older ducts like in the secondary phloem, epithelial cells with or without their neighbouring cells undergo several periclinal divisions. This causes a duct surrounded by some layers of tangentially flattened sheath cells, arranged in radial rows.

Plate I. *Trichoscypha* species. Transverse sections

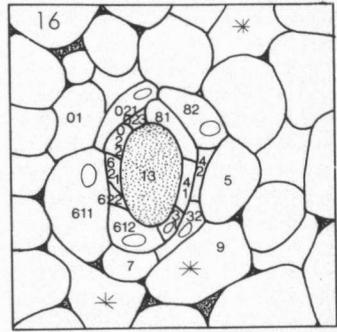
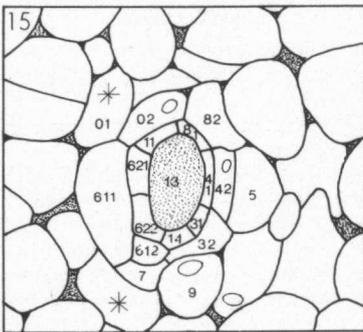
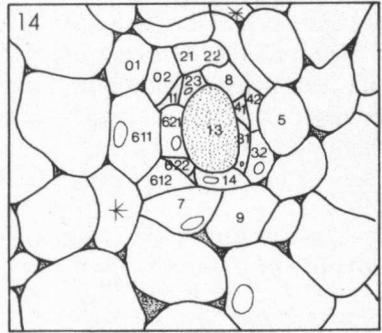
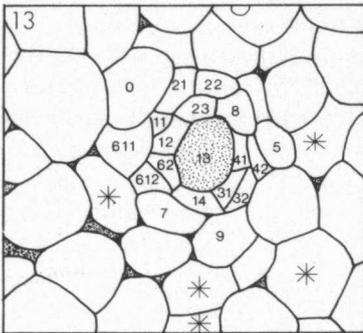
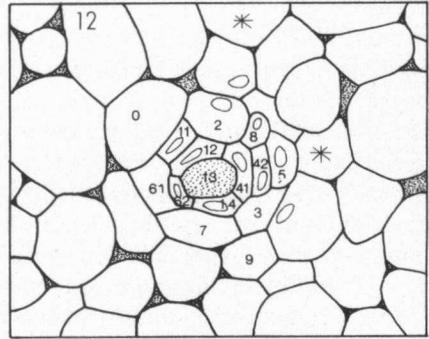
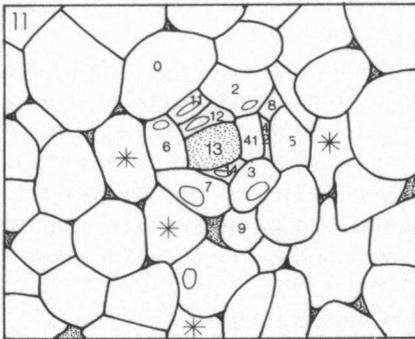
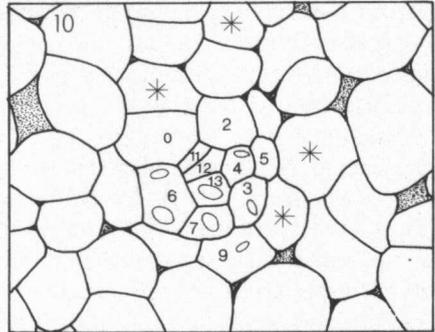
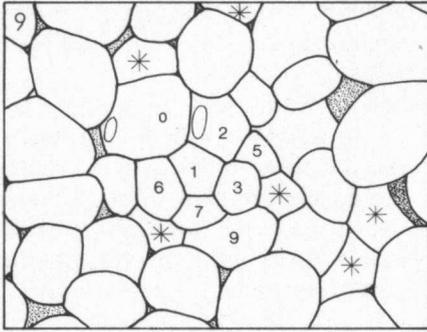
Fig. 1. T. oba, shoot, 6 mm from apex. One of the vascular bundles with beginning secondary growth. Note the large secretory duct in the metaphloem.

Fig. 2. T. oba, root, 700 μm from calyptra apex. Endodermis on left hand side; note sieve tube of the protophloem (arrow). Secretory duct in the metaphloem (right hand side) not yet differentiated.

Fig. 3. T. yapoensis, stem, secondary phloem (upper two-third of the photograph) and secondary xylem (lower one-third of the photograph). A radial secretory duct in a wood ray crosses the cambial zone (bend) and continues in the phloem ray. In the secondary phloem there is contact with a vertical duct (middle top part of the photograph).

Figs. 4–7. T. oba, root, dividing secretory duct in the metaphloem, respectively 2770, 2810, 3120 and 3200 μm from the calyptra apex. Endodermis with dark coloured cell walls, partly visible in upper margin of the photograph.

Fig. 8. T. oba, midvein of leaflet, 3 mm below apex. The three vascular bundles of the midrib are surrounded by a sheath of sklerenchyma fibres; sometimes this sheath produces intrusions and thereby separates the bundles from each other. Note the large secretory ducts in the metaphloem, the outer most with dark coloured substances.



10 μ m

3.3. Contents of the secretory ducts

Handmade sections from freshly collected stem material stained with sudan III, showed that only in the cortex and primary phloem the secretory duct lumen stained red, not those in the secondary phloem and the pith. The ground substance in the duct contained droplets, which were stained red more intensively. Furthermore the same red colouring was present in some vessels of the primary and secondary xylem and in some parenchyma cells of the pith. Stainings with sudan IV, phloroglucin-hydrochloric acid, eosine, zinc chloride-iodine, acetocarmine, nitric acid and sulfuric acid caused no visible reactions in the secretory ducts different from those in the surrounding tissues.

4. DISCUSSION

The investigated species of the genus *Trichoscypha* share the general anatomical feature of the axis of all Anacardiaceae, viz. the occurrence of gum-resin ducts (ENGLER 1896), or resin canals, resin ducts, laticiferous canals or secretory ducts in the phloem (VENNING 1948, METCALFE & CHALK 1950, METCALFE 1983, FAHN & EVERT 1984). They are universally present in the primary phloem immediately on the inside of the arcs of sclerenchyma fibres of the pericycle and in the secondary phloem. In numerous genera secretory ducts were also reported in rays but much less frequent in the cortex.

In *Trichoscypha* medullary resin canals and intercellular canals occurring in the rays are reported (METCALFE & CHALK 1950). Reports on the distribution of these ducts throughout the whole plant body within a specific species or genus in Anacardiaceae are scarce. This holds also for information on network formation by means of anastomosis and the connection of this network with the horizontal radial duct system. So intergeneric anatomical comparisons within the Anacardiaceae are difficult to make. There are however at least two papers of more elaborately investigated anacardiacean species viz. *Lannea coromandelica* (Houtt.) Merril (VENKAIHAH & SHAH 1984), an important gum yielding plant, and *Pachycormus discolor* (Bentham) Coville (GIBSON 1981), the elephant tree. A comparison between the reported presence of gum ducts in *Lannea coromandelica* (table 2) and our findings concerning *Trichoscypha* species (table 1), shows that in the first mentioned species no ducts are reported in the cortex of the stem and the whole root; we did not investigate the phelloderm. So the first primary duct system of *Lannea coromandelica* is little developed, but the other two systems are probably constructed in a comparable way as in *Trichoscypha*,

Plate II. *Trichoscypha oba*. Transverse sections

Fig. 9-16. Leaf primordium. Secretory duct differentiating lysigenously, about four cell layers inwards from the lower epidermis. Fig. 9 is drawn from a section 1 mm below the apex of the primordium; each following drawing is made from a section cut 10 μ m below the previous one. Equal marks in different drawings indicate the same cell or a cell of the same longitudinal strand. If cell 6 divides into two daughter cells, they are indicated as 61 and 62 respectively; if cell 62 divides, the daughter cells are marked 621 and 622 etc. Dotted areas are intercellular spaces, except in cell 13 which indicates the duct cavity; * = a druse crystal; small ovals are nuclei.

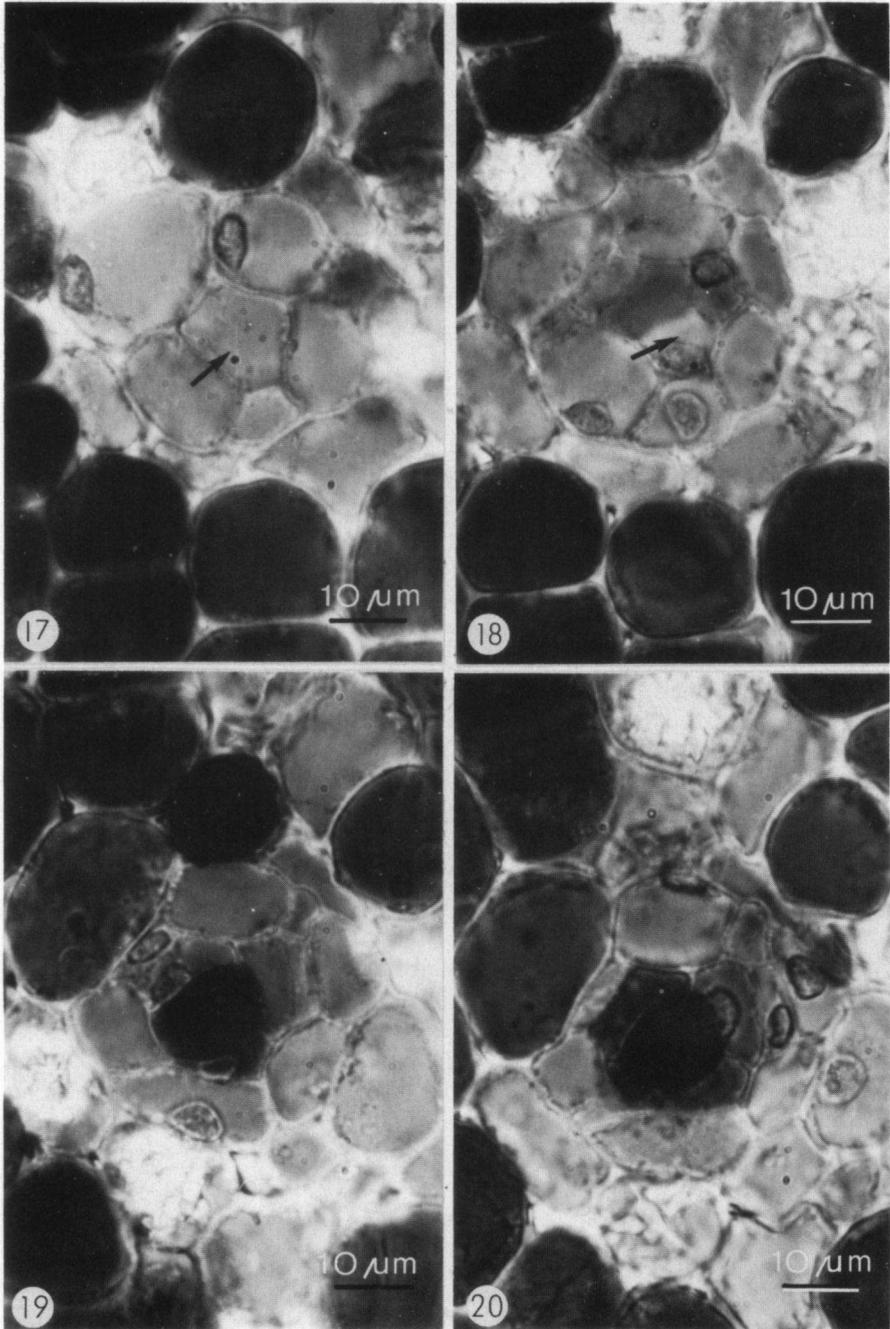


Table 2. Distribution and orientation of secretory ducts in *Lansea coromandelica* (Houtt.) Merrill (VENKAI AH & SHAH 1984) and *Pachycormus discolor* (Bentham) Coville (GIBSON 1981) compared with those in the investigated *Trichoscypha* species; legends see table 1.

tissue		orientation		
		<i>Lansea</i>	<i>Pachycormus</i>	<i>Trichoscypha</i>
Stem	phelloderm	ir	ir	?
	cortex	?	?	ir
	prim. phloem	lg	ir	lg
	sec. phloem	lg, hor (tg and rd)	lg, hor (tg)	lg, hor (tg and rd)
	sec. xylem	hor (rd)	?	hor (rd)
	prim. xylem	?	?	-
	pith	lg	?	ir
Leaf	mesophyll of midvein	+	?	ir
	prim. phloem	lg	+	lg
	sec. phloem	+	?	lg
Root	cortex	?	?	-
	phelloderm	-	ir	?
	prim. phloem	-	ir	lg
	sec. phloem	-	lg, hor (tg)	lg, hor (tg and rd)
	sec. xylem	-	?	-
	prim. xylem	-	?	-
Fruit	mesocarp	+	?	?
Flower		?	?	?

especially the secondary integrated ramifying duct system in the bark of the trunk. In *Lansea coromandelica* at some places radial ducts in the phloem rays are continuous with xylem ray ducts (VENKAI AH & SHAH 1984).

A similar comparison between *Pachycormus discolor* (table 2) and *Trichoscypha* species (table 1), reveals that in *Pachycormus discolor* the first primary system is entirely absent, whereas the arrangement of the ducts in the two other systems is different from that in *Trichoscypha*. In *Pachycormus discolor* extremely large ducts in the primary phloem, more often horizontal than vertical, form a three dimensional network. Annual layers of the secondary phloem are marked by a ring of longitudinally elongated secretory ducts. Within a ring the ducts fuse tangentially but there is no fusion between those of successive layers. This situation in the secondary phloem of *Pachycormus discolor* is also described for *Rhus glabra* L. (FAHN & EVERT 1974). Furthermore in *Pachycormus discolor* no duct contact is reported via rays with the secondary xylem. In the phelloderm, produced by a single phellogen which is persistent during the lifetime of this arborescent desert perennial, a cylindrical network of ducts exists.

Whereas in *Pachycormus discolor* all ducts develop schizogenously, in *Lansea coromandelica* they either arise schizogenously like in the primary phloem, pith and xylem rays, or lysigenously in the secondary phloem and phelloderm (see also table 3). Also in the investigated *Trichoscypha* species the development of the secretory ducts is not identical in all tissues (see table 1). Within the Anacardiaceae ENGLER (1896) reported all secretory ducts to develop schizogenously. Later on several authors described within Anacardiaceae secretory ducts of schizogenous, lysigenous and schizo-lysigenous origin depending on the plant organ

Table 3. Development of secretory ducts in some anacardiacean species; legends see *table 1*

Species	authors of the various reports	secretory ducts				
		stem	leaf	root	fruit	flower
<i>Anacardium occidentale</i> L.	SIECK 1895	s-l	s-l		s-l	
<i>Anacardium occidentale</i> L.	VARGHESE & PUNDIR 1964				l	
<i>Lannea coromandelica</i> (Houtt.) Merril	VENKALIAH & SHAH 1984	l, also s	l, also s			
<i>Mangifera indica</i> L.	VENNING 1948	s-l	s-l		s	l
<i>Mangifera indica</i> L.	JOEL & FAHN 1980a and b	l			l	
<i>Pachycormus discolor</i> (Bentham) Coville	GIBSON 1981	s	s	s		
<i>Rhus glabra</i> L.	FAHN & EVERT 1974	s				
<i>Schinus terebinthifolius</i> Raddi	VENNING 1948	s	s			
<i>Spondias dulcis</i> Forst.	VENNING 1948	s-l	s-l			
<i>Trichoscypha</i> species investigated		s-l, also l	l		s-l, also l	

and the considered species (see *table 3*). For some anacardiacean species it is suggested that the ducts which originate schizogenously, in a later stage become lysigenous because cells lining the duct swell, become mucilaginous, desintegrate and are freed from their neighbouring cells (SIECK 1895, VENKALIAH & SHAH 1984) as is likely the case in some tissues of *Trichoscypha*.

In *Rhus glabra* L. the ducts in the secondary phloem were investigated ultra-structurally; they were found to develop and expand schizogenously (FAHN & EVERT 1974). These investigators suppose that their electron microscopic observations explain the view of several previous authors of schizo-lysigenous development of the duct lumina in the Anacardiaceae. In *Trichoscypha* however, at least in some tissues, secretory ducts develop and expand lysigenously, like those of the shoot of *Mangifera indica* L., demonstrated in also a detailed electron microscopical study by JOEL & FAHN (1980a). Within the large genus *Mammillaria* belonging to the family Cactaceae, it is suggested that schizo-lysigenous ducts are ancestral to strict lysigenous ones (WITTLER & MAUSETH 1984). If a similar phylogenetical sequence is also present within genera of the Anacardiaceae, for instance *Trichoscypha*, is an interesting intermediate.

According to FAHN (1979) the secreted substance into the duct lumen of Anacardiaceae, contains terpenes and polysaccharides. In *Rhus glabra* L. (FAHN & EVERT 1974) there were small lipophilic droplets present. Their findings were based on stainings with sudan IV and Ruthenium red. We also found a red staining not with sudan IV but with sudan III. Probably the duct contents in *Trichoscypha* is comparable with that in *Rhus glabra* L. and contains the basic substances (gum-resin) present in all anacardiacean ducts. Since stress situations like transpirational stress or drought during a long period, induce abundant gum-resin production (GREENWOOD & MOREY 1979) an absence of these environmental factors, like in the greenhouse, might be the cause of the minute quantities secreted substances in the secondary phloem ducts (hardly any staining) found in *Trichoscypha oba*.

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