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SPIRAL THICKENINGS IN THE AXIAL PARENCHYMA OF CHRYSOBALANACEAE*

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SUMMARY

Spiral thickenings in the axial parenchyma, seldom recorded in the secondary xylem of the dicotyledons so far, are described for a number of genera and/or species of Chrysobalanaceae.

In 66 out of 99 samples investigated, representing most genera of the Chrysobalanaceae, spiral thickenings proved to be present. Some genera, such as *Parinari*, lack spirals while others like *Chrysobalanus*, *Exellodendron* and *Hirtella* comprise only species with spiral thickenings. In *Acioa*, *Couepia*, *Cyclandrophora*, *Licania* and *Maranthes* only a part of the species have spirals in their parenchyma cells.

Data on distribution and appearance are given. No connection with tension wood could be demonstrated, neither is the presence related to juvenile wood. Taxonomic value of the spirals in the axial parenchyma is discussed.

1. INTRODUCTION

While studying other anatomical characters in the Chrysobalanaceae my attention was drawn by the casual occurrence of spirals in the parenchyma cells. This phenomenon seemed of sufficient interest to warrant a more intensive search of our material and to consider the taxonomic value of this characteristic. Spiral thickenings, helical ridges on the inner surface of, and part of, the secondary wall (COMMITTEE on Nomenclature of the IAWA, 1964) are formed by deposition of parallel bundles of microfibrils, either as a single helix or as more than one set of coils wound one within the other about the cell axis. Sometimes the bundles are not parallel but branching and anastomosing. The spiral thickenings are usually oriented as an S-helix in the same direction as the microfibrils in the S_3-layer of the secondary wall (PANSHIN & DE ZEEUW 1970). Spiral thickenings have been recorded for gymnosperms as well as angiosperms. Their occurrence in longitudinal tracheids of the gymnosperms is restricted to a few genera: *Torreya* and *Cephalotaxus* (JANE 1970), *Pseudotsuga* and *Taxus* (PHILLIPS 1968) and *Amentotaxus* (MILLER 1973).

More frequently spiral thickenings occur in the secondary wood of angiosperms. In the Anatomy of the Dicotyledons (METCALFE & CHALK 1950) over 100 families are cited with helical spirals in the vessel members of some or all genera. Their occurrence in the fiber tracheids is much more limited: 26 families are listed by METCALFE & CHALK (1950), 19 by RECORD (1936).

In the axial parenchyma spiral thickenings have seldom been noticed. Sporadic occurrence of this type in a single species has been recorded by JANSSONIUS

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(1926), HEIMSCH (1941) and GOTTWALD & PARAMESWARAN (1966). In the Ancistrocladaceae the latter authors (1968) noticed spiral thickenings in all samples investigated.

2. METHODS AND MATERIALS

The Chrysobalanaceae have their greatest extension in the Neotropics. About 80% of the samples investigated are of South American origin, mainly from Surinam. Besides, material of species from Africa and Asia was studied. Although generally the results came from examination of wood blocks with adult secondary xylem, in some cases branchlets from herbarium specimens had to be used. This was necessary in the genera *Afrolicania*[1] and *Kostermanthus* since no wood samples of suitable size were available for these genera.

Almost all herbarium vouchers pertaining to the wood samples were identified by Dr. G. T. Prance (New York Botanical Garden).

Radial sections, 15–20 μm thick, were prepared for microscopical investigations. The sections were bleached, stained with safranin and embedded in Canada balsam. Safranin-fast green was used to demonstrate the possible occurrence of tension wood.

In addition, scanning electron microscopy (SEM) was applied to get better information about the nature of the spiral thickenings in the axial parenchyma.

3. RESULTS

99 Samples comprising 12 genera and 59 species were analysed. The wood of the Chrysobalanaceae is rather uniform in structure and axial parenchyma as apotracheal bands is always present. Parenchyma strands consist of 12–16 cells.

Table 1. Distribution of spiral thickenings in the axial parenchyma of the secondary xylem of 12 genera of Chrysobalanaceae.

Genus	Number of species investigated	Spiral thickenings		
		Present	Probably present	Absent
Acioa	4	2	–	2
Afrolicania	1	–	–	1
Chrysobalanus	1	1	–	–
Couepia	8	4	2	2
Cyclandrophora	2	1	–	1
Exellodendron	1	1	–	–
Hirtella	10	10	–	–
Kostermanthus	1	1	–	–
Licania	20	12	3	5
Maranthes	2	1	–	1
Parastemon	1	–	–	1
Parinari	8	–	–	8

[1] After this manuscript had been presented to the editor, Dr. G. T. Prance informed me that the correct name for the sample collected by Zenker (no. 472) is *Licania elaeosperma* (Mildbr.) Prance & White instead of *Afrolicania* spec.

In the axial parenchyma of 61 samples spiral thickenings are present, their occurrence in 5 samples is doubtful. In 33 samples no spirals were noticed. The occurrence of the spirals in the various genera is shown in *table 1*. For complete results see *table 2*.

Table 2. Occurrence of spiral thickenings in the axial parenchyma of the secondary xylem of Chrysobalanaceae.

Species	Collection	Locality	Spirals*
Acioa barteri (Hook. ex Oliv.) Engl.	Ver/Out. 702	Ivory Coast	+
– *dinklagei* Engl.	Ver/Out. 630	Ivory Coast	+
– *scabrifolia* Hua	Breteler 932	Cameroun	–
– *somnolens* Maguire	Maguire 50490	Amazonia	–
Afrolicania spec.	Zenker 472	Cameroun	–
Chrysobalanus icaco L.	Ver/Out. 143	Ivory Coast	+
– *icaco* L.	Maguire 55915	Surinam	+
Couepia caryophylloides R. Benoist	Lindeman 6743	Surinam	+
– *cognata* (Steud.) Fritsch	Lindeman 4139	Surinam	+
– *edulis* (Prance) Prance	Pr/Ms. 14015	Amazonia	(+)
– *glandulosa* Miquel	Stahel 353	Surinam	–
– *guianensis* Aublet	Stahel 54	Surinam	–
– *guianensis* Aublet	BBS 10880	Surinam	+
– *multiflora* Benth.	A. C. Smith 2502	Guyana	+
– *obovata* Ducke	Maguire 54802	Surinam	+
– *parillo* A. P. de Candolle	Maguire 24782	Surinam	–
Cyclandrophora excelsa (Jack) Kostermans	Kostermans 7044	Borneo	+
– *laurina* (A. Gray) Kostermans	BW 8099	New Guinea	–
Exellodendron barbatum (Ducke) Prance	A. C. Smith 2609	Guyana	+
– *barbatum* (Ducke) Prance	Lindeman 5888	Surinam	+
– *barbatum* (Ducke) Prance	Lindeman 6795	Surinam	+
– *barbatum* (Ducke) Prance	Maguire 55976	Surinam	+
Hirtella bicornis Mart. & Zucc. var. *pubescens* Ducke	Stahel 206[a]	Surinam	+
– *bicornis* Mart. & Zucc. var. *pubescens* Ducke	Heyligers 448	Surinam	+
– *duckei* Huber	A. C. Smith 2999	Brasil	+
– *duckei* Huber	Krukoff 6834	Amazonia	+
– *duckei* Huber	Pr/Ms. 13849	Amazonia	+
– *glandulosa* Sprengel	Schulz 8034	Surinam	+
– *glandulosa* Sprengel	Maguire 51232	Brasil	+
– *glandulosa* Sprengel	Maguire 56100	Brasil	+
– *glandulosa* Sprengel	Maguire 56357	Brasil	+
– *hispidula* Miquel	Schulz 8032	Surinam	+
– *mucronata* Prance	A. C. Smith 2718	Guyana	+
– *obidensis* Ducke	Lindeman 5014	Surinam	+
– *paniculata* Swartz	L. & L. 810	Surinam	+
– *paniculata* Swartz	L. & L. 3048	Surinam	+
– *physophora* Mart. & Zucc.	Wessels Boer 1284	Surinam	+

Table 2. (continued)

Species	Collection	Locality	Spirals*
– *racemosa* Lam. var. *racemosa*	A. C. Smith 3625	Guyana	–
– *racemosa* Lam. var. *racemosa*	Krukoff 6688	Amazonia	+
– *racemosa* Lam. var. *racemosa*	L. & L. 1124	Surinam	+
– *racemosa* Lam. var. *racemosa*	Maguire 55169	Surinam	+
– *racemosa* Lam. var. *racemosa*	Schulz 7403	Surinam	+
– *racemosa* Lam. var. *racemosa*	Breteler 3872	Venezuela	+
– *triandra* Swartz subsp. *triandra*	Maguire 54904	Surinam	+
– *triandra* Swartz subsp. *triandra*	A. C. Smith 3390	Guyana	+
Kostermanthus heteropetala (Scort.) Prance	Kostermans 13630	E-Borneo	+
Licania apetala (E. Mey.) Fritsch var. *apetala*	BBS 1032	Surinam	–
– *apetala* (E. Mey.) Fritsch var. *apetala*	BBS 1033	Surinam	–
– *canescens* R. Benoist	L. & L. 357	Surinam	+
– *canescens* R. Benoist	Schulz 8359	Surinam	+
– *canescens* R. Benoist	Pr/Ms. 14320	Amazonia	+
– *couepifolia* Prance	O.N.S. 1256	Surinam	+
– *densiflora* Kleinhoonte	F.D. 1181	Guyana	–
– *densiflora* Kleinhoonte	BBS 10830	Surinam	+
– *divaricata* Benth.	Stahel 158	Surinam	+
– *elliptica* Standley	Stahel 281	Surinam	+
– *elliptica* Standley	Krukoff 5014	Amazonia	+
– *heteromorpha* Benth. var. *heteromorpha*	Stahel 41	Surinam	+
– *heteromorpha* Benth. var. *heteromorpha*	Krukoff 6898	Brasil	–
– *heteromorpha* Benth. var. *heteromorpha*	Pr/Ms. 13975	Amazonia	–
– *heteromorpha* Benth. var. *heteromorpha*	Krukoff 4796	Amazonia	–
– *hypoleuca* Benth. var. *hypoleuca*	Stahel 150	Surinam	+
– *incana* Aublet	Stahel 141	Surinam	+
– *irwinii* Prance	L. & L. 454	Surinam	+
– *laxiflora* Fritsch	L. & L. 2805	Surinam	+
– *laxiflora* Fritsch	O.N.S. 1179	Surinam	–
– cf. *laxiflora* Fritsch	L. & L. 2472	Surinam	(+)
– *leptostachya* Benth.	L. & L. 895	Surinam	(+)
– *licaniaeflora* (Sagot) Blake	L. & L. 2663	Surinam	–
– *macrophylla* Benth.	Stahel 143	Surinam	+
– *macrophylla* Benth.	BBS 1029	Surinam	+
– *macrophylla* Benth.	BBS 1030	Surinam	+
– *macrophylla* Benth.	BBS 1031	Surinam	+
– *macrophylla* Benth.	Dan/Jonk. 1093	Surinam	+
– *majuscula* Sagot	Schulz 10343	Surinam	+
– *majuscula* Sagot	Maguire 54937	Surinam	(+)
– *octandra* (Hoffm. ex R. &. S.) Kuntze	Heyligers 595	Surinam	–
– *ovalifolia* Kleinhoonte	Burger 21	Surinam	+
– *robusta* Sagot	Stahel 80[a]	Surinam	+
– *rufescens* Klotzsch ex Fritsch	Maguire 24795	Surinam	–
– *splendens* (Korthals) Prance	SAN 75144	Malaya	+
Maranthes corymbosa Blume	F.P.R.I. 326	Philippines	+
– *corymbosa* Blume	Dutton 69	Caroline Isl.	–
– *corymbosa* Blume	Sch/Cr. 4000	Solomon Isl.	(+)

Table 2. (continuated)

Species	Collection	Locality	Spirals*
– *corymbosa* Blume	Jacobs 7754	Philippines	+
– *glabra* Oliv.	Cauwe 3015	Zaïre	–
– *glabra* Oliv.	Corbisier s.n.	Zaïre	–
Parastemon versteeghii Merr. & Perry	BW 12274	New Guinea	–
Parinari campestris Aublet	Stahel 84[a]	Surinam	–
– *campestris* Aublet	BBS 1001	Surinam	–
– *campestris* Aublet	Schulz 8355	Surinam	–
– *curatellifolia* Planch. ex Benth.	Schlieben 457	East Africa	–
– *excelsa* Sabine	Corbisier s.n.	Zaïre	–
– *exselsa* Sabine	Leeuwenberg 2623	Ivory Coast	–
– *nonda* F. v. M. ex Benth.	BW 12462	New Guinea	–
– *nonda* F. v. M. ex Benth.	v. Royen 4843	New Guinea	–
– *oblongifolia* Hook. f.	SAN 20443	North Borneo	–
– *parilis* Macbride	Williams 1113	Peru	–
– *rodolphii* Huber	A. C. Smith 3320	Guyana	–

* : + = present; (+) = probably present; – = not observed

abbreviations used in *table 2:*

BBS	– Bos Beheer Suriname
BW	– Bosch Wezen
Dan/Jonk.	– Daniels & Jonker
F.D.	– Forest Department Guyana
F.P.R.I.	– Forest Product Research Institute
L. & L.	– Lanjouw & Lindeman
O.N.S.	– Oldenburger, Norde & Schulz
Pr/Ms.	– Prance & Maas
SAN	– Sandakan, Sabah
Sch/Cr.	– Schodde & Carven
Ver/Out.	– Versteegh & den Outer

Within a sample the spirals are of sporadic occurrence. Usually the amount of axial parenchyma cells with spirals is less than 1%. A few times the percentage is a little higher but it never exceeds about 3%. Cells with spirals often occur locally. In a certain parenchyma strand never all cells contain spirals. Sometimes the spirals are limited to one parenchyma strand in a section of about 1 cm^2. A few times they are more widespread, especially when the percentage of parenchyma cells with spirals is over 1%. In my opinion a tendency exists towards a more frequent occurrence of spiral thickenings in parenchyma cells in contact with or close to the vessels.

If present, the spirals always occupy the entire cell wall. The angle between cell axis and spiral thickenings varies from 20° to 90°, an angle of 60° to 90° is most frequently found. Towards the ends of the parenchyma cell the angle increases. The angle is also related to the size of the cells. In square parenchyma cells the angle is smaller than in rectangular cells. The spirals are more or less branched especially when bordering pit cavities. Sometimes the ridges are rather

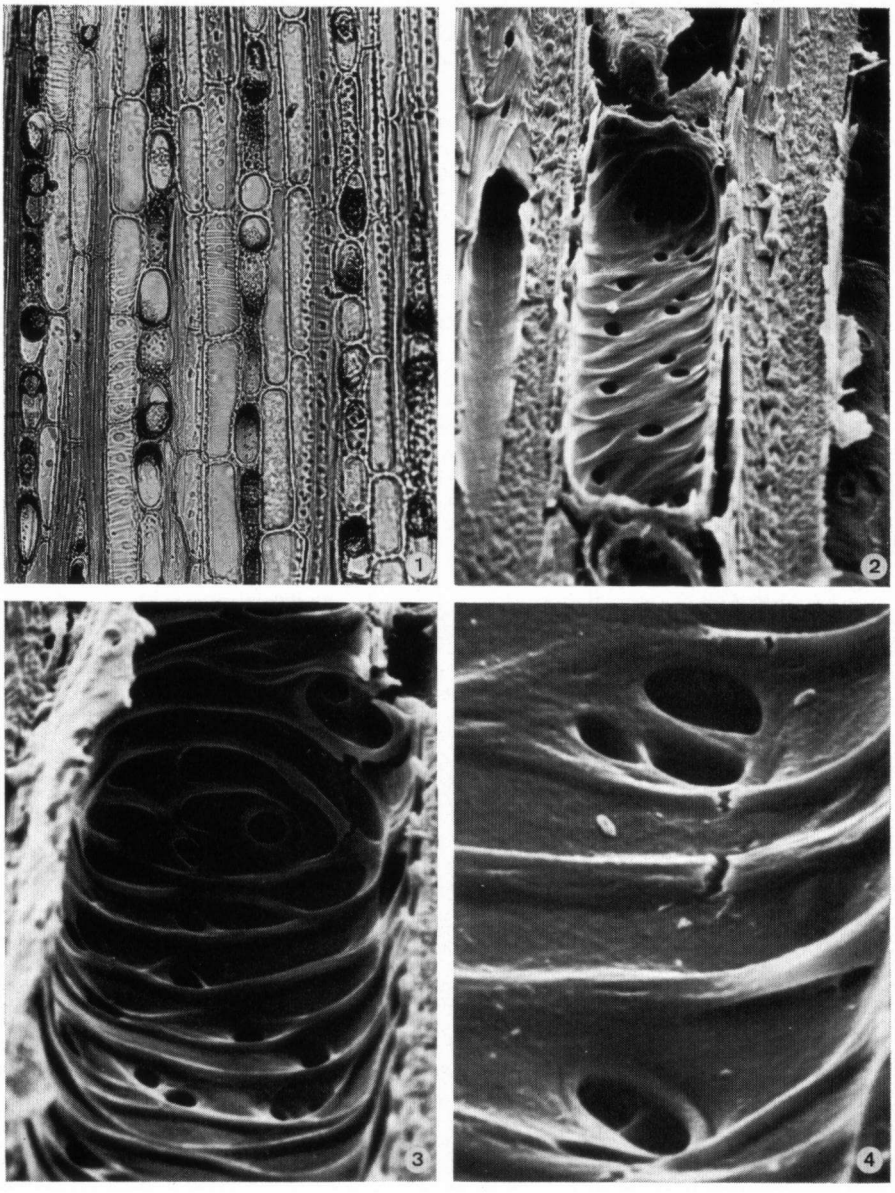

Fig. 1. Tangential section of *Hirtella duckei* Huber (A.C. Smith 2999), showing spiral thickenings in some cells of the axial parenchyma. × 200.
Figs. 2, 3 and 4. SEM photographs of radial sections of the same sample as in *fig. 1* showing the various aspects of the spiral thickenings. Magnification × 850, × 1700 and × 4150 respectively.

flat *(fig. 2)*, in other places in the same sample they are rather sharp *(figs. 3* and *4)*. Using the classification of spiral thickenings proposed by PARHAM & KAUSTINEN (1973) they belong to type 1 (spirals that are closely bound to, and periodically merge with, the lumen surface) and type 2B (very prominent spirals but firmly attached to the wall), though it is difficult to make a satisfactory classification, as intermediate situations also occur.

The nature of the spirals in relation to the cell wall was not investigated. However, it is evident from *figs. 3* and *4* that they are mostly attached to the inner surface of the cell wall. Sometimes they are more or less detached from the cell wall, even openings between the spirals and cell wall occur locally *(fig. 4)*. As the local occurrence of the spirals might be correlated with the presence of tension wood, investigations after this were made in a few samples. Tension wood was absent both in samples with many and in samples without spirals.

4. DISCUSSION

This study demonstrates the occurrence of spiral thickenings in the axial parenchyma of all species investigated of *Chrysobalanus*, *Exellodendron*, *Hirtella* and *Kostermanthus*. I would consider the absence of spirals in one out of 6 samples of *Hirtella racemosa* var. *racemosa* rather as a result of either a wrong determination or incorrect or insufficient search by myself. In *Afrolicania*, *Parastemon* and *Parinari* they are absent. In five genera, *Acioa*, *Couepia*, *Cyclandrophora*, *Licania* and *Maranthes* both species with and without spirals occur. For *Maranthes corymbosa* 4 samples were analysed: two of them contain spirals, in one sample they were absent while the presence of spirals in another sample is doubtful. This inconstant occurrence of spirals should be further investigated. For 20 species more than one sample was analysed: the results were constant for 70% and variable for 30%. In spite of further sections made of other parts of the wood samples the latter percentage could not be brought down.

As so little is known about spiral thickenings in the axial parenchyma, the taxonomic value of this phenomenon is difficult to estimate. GOTTWALD & PARAMESWARAN (1968) consider it as to be characteristic for the monotypical family of Ancistrocladaceae. JANSSONIUS (1926) recorded spirals in the parenchyma of one sample of *Lasianthus purpureus* (Rubiaceae) and states "I have never seen it before". I could confirm his findings in two other species of *Lasianthus* namely *L. rhinocerotis* and *L. stipularis*.

The wood samples of Ancistrocladaceae and of the three species of *Lasianthus* have a small diameter which also applies to the sample of *Trigonia sericea* for which HEIMSCH (1941) stated: In ray and parenchyma cells spiral and reticulate thickenings occur. Thus it might be possible to consider spiral thickenings of parenchyma cells as a feature of juvenile wood. However, since my own investigations were almost restricted to adult secondary xylem the occurrence of spiral thickenings can not be considered as a feature of juvenile wood.

The taxonomic implication of the spirals in the axial parenchyma of the Chrysobalanaceae is not quite clear. The complete absence in *Parinari* and the 100%

presence in *Chrysobalanus*, *Exellodendron* and *Hirtella* seem to indicate a certain taxonomic importance, although not as reliable as METCALF & CHALK (1950), PANSHIN & DE ZEEUW (1970) and BAAS (1973) state for spiral thickenings in vessels and fibers. The results obtained for *Licania* show another interesting feature. PRANCE (1972) divides this genus into three subgenera. In *Parinariopsis* and *Moquilea* the axial parenchyma is without spiral thickenings, while in the third subgenus, *Licania*, species with and without spirals in the axial parenchyma occur. The subgenera *Parinariopsis* and *Moquilea* might be considered as more primitive than the subgenus *Licania*. In *Couepia*, too, the possibly more primitive species lack spirals in the axial parenchyma. This trend however, is not reflected by Prance's generic classification insofar as that is suggested by the numerical sequence in the Flora Neotropica treatment.

In tracheary elements the occurrence of spirals is more frequent in species from temperate zones than in species growing in the tropics (BAAS 1973). This study demonstrates the general, though sporadical, occurrence of spirals in the axial parenchyma of Chrysobalanaceae which are restricted to the tropics. The other species for which spirals in the axial parenchyma are recordered are from tropical origin too. They have even never been described for species from the temperate zones.

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