

THE ANATOMY OF BRANCH ABSCISSION LAYERS IN PEREBEA
MOLLIS AND NAUCLEOPSIS GUIANENSIS (CASTILLEAE, MORACEAE)

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Summary. The shedding of branches along a preformed layer is a complex phenomenon in which several types of xylem elements are involved. The abscission layers in *Perebea mollis* and *Naucleopsis guianensis* are distinguished from the normally developed xylem by the presence of shorter unligified fibres with small simple pits. Most of these fibres show large nuclei. In this zone containing abnormal fibres, the vessels, rays and parenchyma are conspicuously different from those of the normal tissue. The transition in anatomy from the main branch to the abscission layer is much more abrupt than that from the abscission layer to the secondary branch. Contrary to what is generally seen in other Moraceae tribes, natural pruning seems to occur in all genera of Olmedieae with the sole exception of the genus *Olmedia*. The correlation with other morphological and anatomical characters and the complexity of the phenomenon of branch abscission seem to justify Berg's decision to use this character in defining the new tribe Castilleae, containing all the genera formerly placed in Olmedieae except *Olmedia*.

INTRODUCTION

Although many studies on the abscission of leaves and fruits have been published, little attention has been paid to either the anatomical or physiological aspects of branch abscission. This is remarkable, because the phenomenon of branch abscission may determine the shape of the tree (Hallé & Oldeman, 1970; van der Pijl, 1952, 1953), and furthermore may influence quality and commercial value of the wood (Millington & Chaney, 1973).

A survey of the literature on the shedding of branches along a preformed abscission layer was given by Millington & Chaney (1973). They reported that data on the microscopic anatomy relating to this phenomenon are available only for *Taxodium distichum*, *Populus grandidentata*, *P. tremula*, and *Agathis australis*. Höster *et al.* (1968) published an extensive study on the morphology and anatomy of branch abscission in *Populus* × *canadensis* Moench 'Robusta', in which they examined the effects of seasonal changes on the process. Finally Licitis-Lindbergs (1956) and Böhlmann (1970) studied the anatomy of abscission layers in respectively *Agathis australis* and *Quercus robur*, and *Populus* section *Aigeiros*.

In this paper we describe the wood anatomical structure of *Perebea mollis* (Poepp. & Endl.) Huber ssp. *rubra* (Tréc.) C. C. Berg (*Mennega & Koek 866*, Brownsberg, Surinam,

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large tree) and of *Naucleopsis guianensis* (Mildbr.) C. C. Berg (*Mennega & Koek 867*, Brownsberg, Surinam, large tree). Our material, contrary to that studied by Höster *et al.* (1968), was taken from a single tree at a single time. The branches of which the abscission zones have been studied were living, apparently healthy, and leaf-bearing. The material available did not allow studies on the influence of time as a variable.

MATERIALS AND METHODS

The wood samples studied were fixed in FAA immediately after collection. Sections, *c.* 15 μm thick, were made without special treatment of the wood. One of the problems of the study was the conical shape of the abscission zone (Plate 1/1–3) and the change in fibre orientation associated with branching. For this reason, true transverse, tangential and radial sections can be made over very short distances only.

The planes in the branch union examined were:

<i>Main branch</i>	<i>Secondary branch</i>
(1) transverse	radial
(2) radial	radial
(3) tangential	transverse
(4) tangential	tangential
(5) as nearly as possible, parallel to the abscission layer.	

Mostly, the sections were stained with safranin, sometimes after treatment with a domestic bleaching agent. Other stains used were a solution of iodine to stain cellulose; safranin and astra blue; safranin and fast green; Sudan III. Two samples of *Perebea mollis* were studied with the scanning electron microscope, one of them being a flattened surface taken through both the main branch and secondary branch in radial plane, and the other one being the basal end of a shed branch.

All quantitative data are based on at least 25 measurements.

MORPHOLOGY

The shed branches had a diameter varying from 1 to 4 cm. The longest of these branches were over 2 m in length and showed about 12 scars of previously shed branches. These scars are concave and the basal end of the shed branches is correspondingly convex. This is in agreement with all data from the literature. On such concave surfaces, the rays can be seen with the naked eye to run in distinct radial lines. The fibre tissue between these appears to be slightly shrunken (Plate 2/8).

As mentioned by Licitis-Lindbergs (1956) for *Agathis australis*, the branches of *Perebea mollis* and *Naucleopsis guianensis* are swollen at the base (Plate 1/1–3). In the latter two species, however, this is not due to the dilatation of the pith, but to the dilata-

tion of the xylem body and to the wrinkling of the bark in the zone of transition from the main branch to the secondary branch (Plate 1/3).

Höster *et al.* (1968) reported, that during the first three years of growth the diameter of the branches in *Populus* × *canadensis* 'Robusta' increases steadily, to about 4.3 mm. After that period the growth almost ceases and the diameter does not exceed 5 mm. The branches to be shed in *Perebea* and *Naucleopsis* reach a much larger diameter (up to 4 cm). We have no data that could indicate whether a decrease in the growth rate also takes place in *Perebea* and *Naucleopsis*.

ANATOMY

As pointed out by Mennega & Lanzing-Vinkenborg (1976) it is very difficult to find characters in the wood anatomy by which the genera of the fairly homogeneous Olmedieae (including the Castilleae sensu Berg as well as *Olmedia*) could be distinguished. They suggest, in a key to the genera, that the differences in the frequency and size of the pores are sufficiently reliable to differentiate between *Perebea* and *Naucleopsis*. The values measured in our specimens are more or less in accordance with these ranges. However, in most other quantitative characters, mean differences between the genera are smaller than the differences within each respective sample. We therefore give one description of the anatomy of the secondary xylem based on the sample of *Perebea mollis*. Deviating data of *Naucleopsis guianensis* are given between brackets.

Anatomy of the main branch

Vessels 7–16–20 (25–30–40) per square mm, diffuse, solitary and in radial multiples of 2–6 (2–8) cells, tangential diameter 40–160 (50–100) μm , vessel member length 340–493–700 (175–394–575) μm , inter-vessel pits alternate, round to slightly angular, 7.5–10 (5–7.5) μm , vessel-ray pitting oval, 16–24 μ . Perforations simple in horizontal to slightly oblique end walls, with or without short tails. *Vascular tracheids* present, 500–600 μm long. *Fibres* mostly septate, 730–1116–1600 μm long, lumen 15 μm in diameter, cell walls 3 μm thick, with small, simple pits confined to the radial walls; part of the fibres gelatinous, arranged in tangential bands. *Rays* 6–8–9 per mm, heterogeneous, of two distinct sizes, uniseriate of up to 13 square to upright cells, up to 20 μm wide, up to 630 μm high; 2–4-seriate mainly composed of procumbent cells, mingled with some square to upright cells and with margins of 1–8 upright cells, up to 45 μm wide and up to 46 cells or 960 μm high; sometimes two multiseriate parts connected by some uniseriate rows of square and upright cells. Many rays with latex tubes, in tangential view of about the same size as the procumbent ray cells. Ray cells with brown granular contents. Rhombic crystals infrequent in the ray cells. *Parenchyma* aliform, frequently to confluent, strands of 4–7 cells, up to 720 μm long; cells often with brown granular contents, as in the ray cells.

Differences between the anatomy of the main branch and the anatomy of the abscission layer

Vessels and fibres diverge from their axial alignment in passing from the main branch into the secondary branch and run perpendicular to the abscission layer (Plate 1/3, light zone between main branch and abscission layer indicated by the dark line). The transition from the normally developed xylem tissue to the abscission layer is abrupt. The vessels are less numerous and much smaller in diameter (up to $20\ \mu\text{m}$) than in the xylem of the main branch. Some of them end in the abscission layer with a non-perforated end wall, others continue into the secondary branch. The vessel members are short ($52\text{--}101\text{--}184\ \mu\text{m}$), often of more or less irregular shape, sometimes nearly isodiametric. The vessel walls show ridges between which elongated pits transitional between scalariform and opposite (up to $52\ \mu\text{m}$) occur, see Plate 2/7. The rays are less wide (1–3 seriate) and less high (up to 14 cells, $240\ \mu\text{m}$, see Plate 1/6). The cell walls are slightly thinner than those in the main branch. Part of the ray tissue is not lignified; lignified ray cells occur both isolated and in radial series. Rather frequently trabeculae occur in radial series of ray cells. This is quite remarkable, when we consider the very few reports of trabeculae in hardwoods (Butterfield & Meylan, 1972; Meylan & Butterfield, 1973). The vessel–ray pits are more irregular in outline and arrangement in comparison with those of the normal tissue, but are of about similar size (up to $25\ \mu\text{m}$). In the sample of *Naucleopsis guianensis* rhombic crystals comparable in size to those which occur in the pith outside the abscission zone are frequently present in the ray cells. *Perebea mollis* shows only few crystals in the ray cells in the abscission zone. The *parenchyma*, rather abundant in the main branch, is very scarce in the abscission zone, where only isolated paratracheal strands occur. The most conspicuous difference is to be found in the *fibre tissue*: the fibres pass into a band of unlignified tissue of about 8 cells wide in the centre of the abscission zone. The absence of lignin can be demonstrated when staining the sections with a solution of iodine or with safranin and astra blue. Under the SEM an abrupt transition of cell wall structure probably corresponding to this absence of lignification was observed (Plate 2/10). Cells thought to be unlignified also showed a rippled cell wall texture. There is, however, a possibility that this rippling is an artefact of specimen preparation. In contrast with the fibres of the normal xylem, there are large nuclei ($3\text{--}4\ \mu\text{m}$) in all fibres of the abscission zone. The tips of the fibres vary from the normal tapering type to blunt. Some fibres show one or more septa. In sections pits are nearly invisible. In the macerations the fibres show simple pits, about $4\ \mu\text{m}$ in diameter. The fibres in the abscission layer and those in the normal secondary xylem are of about the same diameter (lumen about $12\ \mu\text{m}$) and show more or less the same cell wall thickness ($2.5\text{--}3\ \mu\text{m}$). The length of the fibres in the abscission layer is, however, $152\text{--}265\text{--}368\ \mu\text{m}$, which is much shorter than in the normal wood.

Anatomy of the secondary branch

The transition in wood anatomy from the abscission layer to the secondary branch is much more gradual than that from the main branch to the abscission layer. The absence

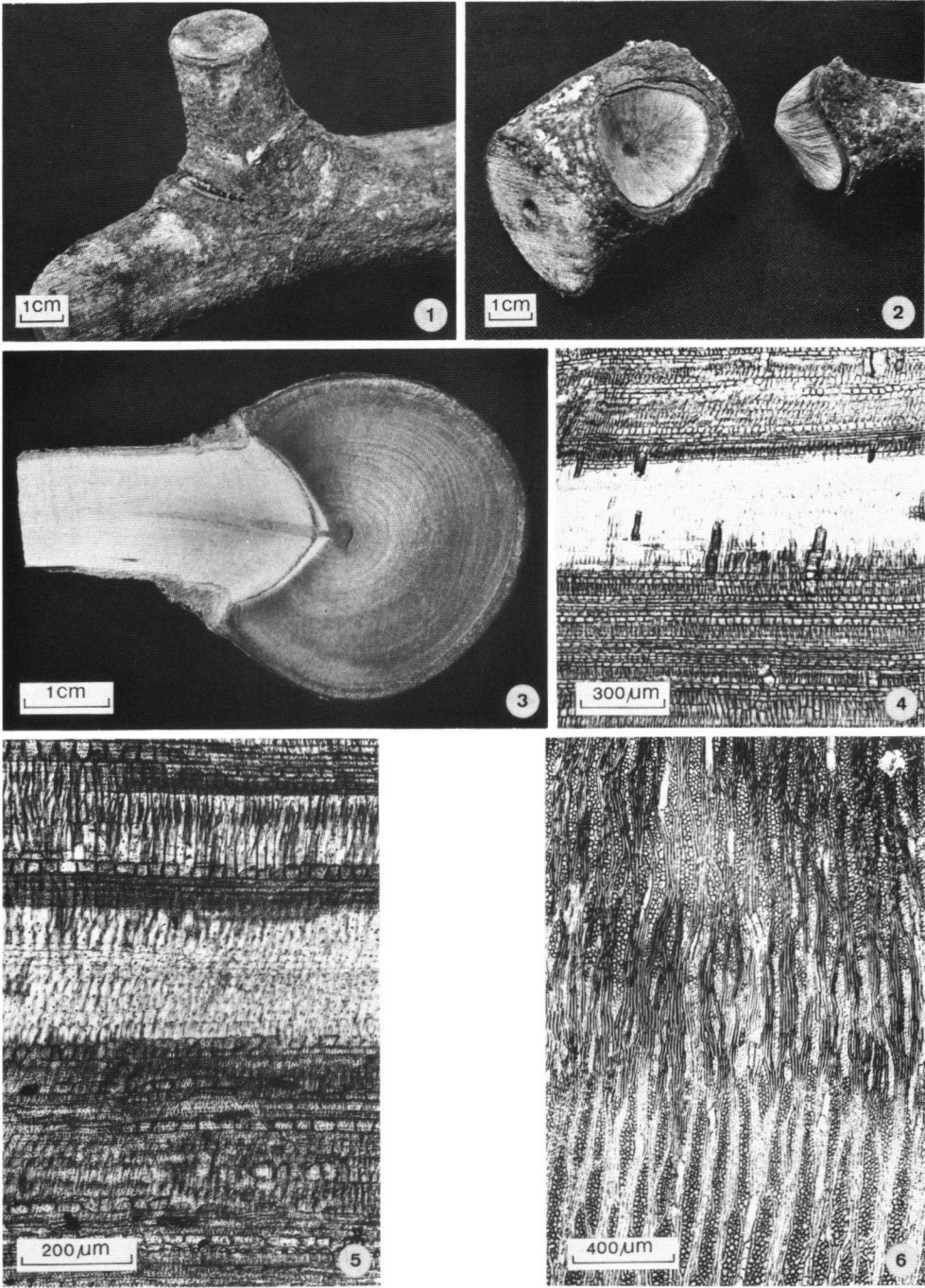


Plate 1.—1–2, *Perebea mollis*. Branch-connection before and after shedding; 3, *Naucleopsis guianensis*. Main branch in transverse view; secondary branch in radial view; 4–5, *Perebea mollis*. Sections through abscission layer. Note nuclei in fibres of 5; 6, *Naucleopsis guianensis*. Tangential section \pm parallel to abscission layer, showing changes in ray structure (dark central zone).

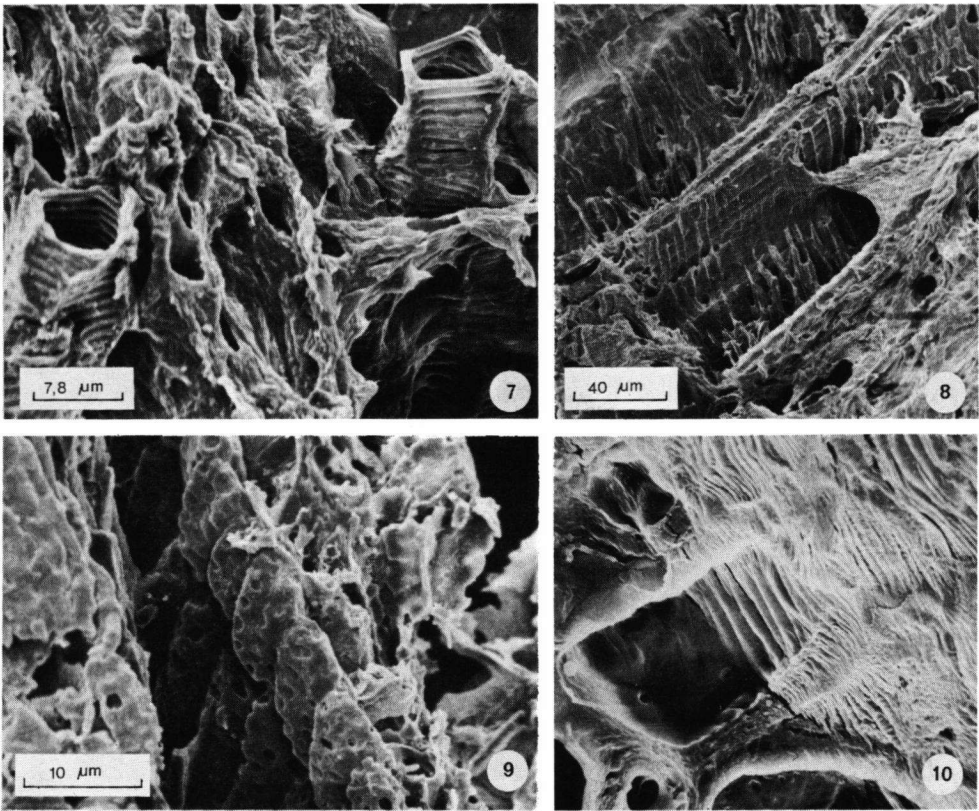


Plate 2—*Perebea mollis*. 7–9, Basal part of shed branch (SEM); 7, Solitary vessels; 8–9, Rays between shrunken fibre tissue; 10, Transition from lignified (left) to unligified (right) cell wall of fibre, $\times 1500$.

of fibre lignification (as indicated by staining with safranin and fast green) persists for about 10 mm. Over the same distance the vessels, still relatively scarce, retain the distinguishing characters of abscission zone vessel elements: short length, long ridges, and elongated pits transitional between scalariform and opposite. Gradually the rays become lignified and all elements revert to the same structure as those in the main branch.

DISCUSSION

The most obvious difference between the 'normal' xylem and the abscission layer is to be found in the fibre tissue, which passes through an unligified zone.

The material studied does not allow us to conclude what happens with the fibres during the process of shedding: Plate 2/8–9, shows rays on the basal part of a branch

after shedding. In Plate 2/8 we see that parts of fibre cell walls remain attached to the ray cells. Plate 2/9, on the contrary, shows 'clean' ray parenchyma cells.

In the zone in which the fibres show an abnormal structure, the other elements are different from those of the normal xylem as well. The shorter vessel elements and the long ridges between which the elongated pits are features which have been noted by other workers (Höster *et al.*, 1968; Böhlmann, 1970) as has the occurrence of numerous crystals in the abscission zone (in our material in the ray cells). In the present study the volume of the ray tissue and the axial parenchyma was observed to diminish in the abscission zone. This can be contrasted with the findings of Höster *et al.* (1968) and Böhlmann (1970) in *Populus* and *Quercus*, that the proportion of parenchymatous cells increases in the abscission zone.

Both anatomically and physiologically the phenomenon of shedding of branches has been very incompletely investigated. In taxonomic studies it is often mentioned only incidentally (see for instance Berg, 1976). Yet Berg states that natural pruning is a characteristic feature of genera of Olmedieae (to which *Perebea* and *Naucleopsis* belong), with the sole exception of the genus *Olmedia*. Berg thus uses the phenomenon of natural pruning, together with other morphological and anatomical characters, to define his new tribe Castilleae. All genera of this tribe show shedding of branches.

Though very incomplete, this incidental study of abscission layers indicates that changes in many aspects of xylem anatomy are associated with shedding of branches along a preformed abscission layer. Berg's use of this complex phenomenon, highly alike in two species of different genera, therefore seems to be justified.

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