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AMBORELLA TRICHOPODA BAILL., A NEW MORPHOLOGICAL TYPE OF VESSELLESS DICOTYLEDON

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With five plates

INTRODUCTION

THE GENUS Amborella is represented by a single species, A. trichopoda Baill., which is endemic to New Caledonia. This remarkable plant was provisionally named and briefly described in a footnote by Baillon (5) in 1869, and was more extensively discussed by him (6) in 1873. Baillon's descriptions were based upon material collected by Vieillard (nos. 32 and 2296) and Balansa (no. 1800) in moist forests in the environs of Balade. The plant is stated to be a shrub of slightly scandent habit which attains a height of from six to eight meters. The best illustrations of its leaf, its male inflorescence, its male flowers, and its fruit are those of Perkins (13); the female flowers are unknown. The only anatomical investigations of the plant are those of Perkins (12), who closely followed Hobein's (8) procedure in the study of monimiaceous genera and focused her attention primarily upon the structure of the leaf and upon the width of the rays in the secondary tissues of the stem. In so doing, she appears to have overlooked the extremely significant fact that the xylem of Amborella is vesselless and resembles that which occurs in young stems of Drimys and of other representatives of the Winteraceae.

Baillon stressed the close similarity of the male flower to that of Hedy-carya and included *Amborella* in the Monimiaceae. Subsequently, Bentham and Hooker (7) placed the genus in the tribe Monimieae of the Monimiaceae, whereas Pax (11), and Perkins and Gilg (14) included it in the tribe Hortonieae of the sub-family Monimioideae of this family.

The fact that a new type of living vesselless dicotyledon should come to light at this late date has many important morphological implications; the eight previously known genera of vesselless dicotyledons were all well known prior to 1900, van Tieghem (16). It seemed advisable, accordingly, to make as comprehensive a morphological study of *Amborella* as possible, the results of which are summarized on succeeding pages.

MATERIAL EXAMINED

The absence of vessels in the xylem of *Amborella trichopoda* Baill. was first detected in a specimen collected by Vieillard (no. 3149), on loan to the Arnold Arboretum from the Gray Herbarium. This observation sub-

sequently was verified by examination of the stems of a series of other specimens. A complete list of the material studied is as follows:

Gray Herbarium

Vieillard 3149, specimen with female flowers and fruits. Balansa 1800, specimen in fruit.

Arnold Arboretum

Vieillard 3149, specimen with immature male flowers.

Museum of Natural History, Paris

(Specimens loaned through the courtesy of Professor H. Humbert, Director).

Vieillard 3149, specimen in fruit.

Vieillard 32, specimen with male flower buds.

Balansa 1800, specimen in fruit.

Pancher, Sept. 1870, specimen in fruit.

Licard, 1879, specimen in fruit.

Herbarium of Royal Botanic Gardens, Kew

Vieillard 3149, two male flowers at anthesis, sent through the kindness of Sir Edward Salisbury, Director.

The *Vieillard 3149* sheet of the Gray Herbarium bears numerous fruits, and, in addition, a few female flowers which unfortunately have been fed upon at some time by insects. However, we have succeeded in reconstructing the form of the previously unknown female flower by a careful study of these fragments.

THE STEM

The largest stem of Amborella (Vieillard 3149, G.H.) of which we have succeeded in obtaining material is seven millimeters in diameter. A transverse section of a smaller stem, 3.5 millimeters in diameter, is illustrated in Fig. 30. The phloem and the collenchymatous outer cortex are considerably compressed owing to contraction in drying, Figs. 30, 31, and 37, but the pith, the primary and the secondary xylem, and the zone of cortical sclerenchyma are well preserved. The pith is relatively homogeneous, being composed of moderately thick-walled, conspicuously pitted parenchyma, and being devoid of idioblasts, nests of stone cells, or sclerenchymatous diaphragms. Vertically elongated strands of parenchyma are confined to the perimedullary region in close proximity to the elements of the primary xylem.

Most of the rays of the secondary xylem are uniseriate or biseriate, as emphasized by Perkins (12). However, broader rays, three to five cells in width, are of not infrequent occurrence, and extend outward from conspicuous interfascicular parts of the eustele, *Fig. 37*. The narrower rays are vertically extensive and are composed of much elongated "erect" cells, *Fig. 38*. The cells of the multiseriate rays tend to become nearly as exextensive radially as vertically. Wood parenchyma strands are few in number and are diffusely distributed.

The tracheids of the vesselless xylem occur in relatively uniform radial seriations, *Fig. 37*. They are long imperforate tracheary cells, *Fig. 38*, and, in the case of the secondary xylem, obviously are formed, as in *Tetra*-

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centron, Trochodendron, and the Winteraceae, by a primitive type of cambium having long fusiform initials with extensively overlapping ends. The inter-tracheary pitting, which is dominantly scalariform in the last-formed tracheids of the metaxylem, fluctuates between scalariform and circular in the secondary xylem, Fig. 39. The conspicuously bordered pits are numerous and tend to be more or less closely crowded in the radial walls of the tracheids, whereas they are smaller and of sporadic occurrence in the tangential walls. The pits between tracheids and parenchymatous cells are small, circular, and bordered.

There are no fibers in the phloem or the cortex of the stem. The sclerenchymatous ring visible in Fig. 30 is composed solely of "hippocrepiform" sclereids, Fig. 31. The parenchymatous cells of the phloem and the outer cortex contain much darkly colored, colloidal, vacuolar material of presumably phenolic composition, Fig. 31.

THE LEAF

The alternately disposed leaves of *Amborelia* fluctuate considerably in size, form, and degree of pilosity even on sheets having the same collection number. Some are oblong with slightly wavy margins, as figured by Perkins (13), whereas others are ovate with conspicuous lobes, *Figs. 1* and 3, or are elliptic-lanceolate with entire or serrate margins, *Fig. 2*. Certain of the leaves, viz. *Vieillard 32* (Paris), *Balansa 1800* (Paris), *Licard*, 1879 (Paris), have numerous hairs on both surfaces, whereas others, i.e. *Vieillard 3149* (G.H.), are glabrous. Whether such differences are due solely to differences in age of the leaves, as has been assumed, appears to us to be somewhat questionable.

The leaf is characterized by having a single broad, arc-shaped strand of vascular tissues in its petiole, Fig. 32, and in the costa of the lamina, Fig. 33. This leaf trace is attached to the eustele of the stem at a typical unilacunar node, Fig. 30. Thus, *Amborella* differs from *Tetracentron* and the Winteraceae, which have prevailingly trilacunar nodes, and from *Trochodendron*, which tends to form multilacunar ones.

The cortical parenchyma of the petiole is collenchymatous, collapses in drying, and does not fully re-expand even when treated with sodium hydroxide, *Fig. 32*. Hippocrepiform sclereids either are absent or develop less precociously in the petiole and the basal part of the costa, compare *Figs. 30, 32*, and *33*. On the contrary, the upper part of the mid-vein, the lateral veins, and the terminal veinlets are completely jacketed by hippocrepiform sclereids. According to Perkins (12), there are no palisade or hypodermal tissues in the lamina of the leaf. However, when leaves are cleared and re-expanded by treatment with sodium hydroxide, there appears to be a well defined hypodermal layer subtending the upper epidermis. The cells of the spongy mesophyll, *Fig. 33*, as in the case of the phloem and the outer cortex of the stem, contain a high ratio of darkly colored vacuolar material, i.e. "Gerbstoffe," Perkins (12).

The stomata are confined to the lower surface of the leaf. They fluctu-

ate considerably in form and the extent to which the guard cells are subtended by parts of adjacent epidermal cells. The stomata may have subsidiary cells that are oriented parallel to the guard cells, *Fig. 6*, or they may be surrounded by a number of ordinary epidermal cells, *Fig. 5*. The stomata are provided with a conspicuous outer cuticular vestibule as illustrated in *Fig. 7*.

The foliar hairs are straight and comparatively short, but are of a thin-walled multicellular type, Fig. 4. These trichomes are jacketed by a thick cuticle which is continuous with that of the outer surface of the leaf. The hair may have a single submerged basal cell or it may be attached to a more or less protuberant, multicellular pedestal.

THE MALE FLOWER

The male flowers of Amborella have been described by a succession of authors, viz. Baillon (6), Bentham and Hooker (7), Pax (11), Perkins and Gilg (14), and have been figured by Perkins (13). Although the concensus of opinion appears to be that the stamens are numerous ("ultra 20"), Perkins and Gilg (14) in their key to the genera of the Monimiaceae differentiate Amborella from Peumus upon the basis of "Stamina 9 eglandulosa, Fl. $\[mathbb{S}$ sine staminodiis," whereas in their description of Amborella they state, in agreement with other writers, "Stamina $\[mathbb{c}$ (ultra 20) ... Fl. $\[mathbb{S}$ ignoti." Subsequently Perkins (13) figured a male flower from Vieillard 3149 (Kew) with 19 stamens. In material examined by us, Vieillard 3149 (Kew) and Vieillard 32 (Paris), the number of stamens varied from 10 to 12.

The stamens are stated to have "filamentis brevissimis" and are figured by Perkins (13) with narrow, short, cylindrical "filaments." In the material of *Vieillard 3149* (Kew), the stamens at anthesis, *Figs. 8* and 9, as in so many other ranalian plants, are broad, flat appendages bearing sporangia. The outer stamens tend to be larger and exhibit a more conspicuous branching of the vascular strand, compare *Figs. 8* and 9. The basal parts of the stamens bear more or less numerous, faintly striated hairs. These hairs commonly are unicellular, but may at times be composed of two cells. The epidermal cells at the apex of the outer stamens tend to differentiate into numerous papillae.

The male flower appears to have incipient perigynous tendencies, i.e. concavity of the torus and concrescence and adnation of parts. However, the vascularization of the flower is still relatively simple. The pedicel contains a ring of discrete vascular bundles and each bracteole is vascularized by a single strand. The vascular bundles increase in number toward the base of the torus and each tepal is vascularized by a single strand. The inner stamens exhibit no evidence of adnation to the base of the tepals and each is vascularized by a single trace from the apex of the torus. On the contrary, the larger outer stamens are vascularized by branches from the trace of the tepal which subtends them.

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The pollen grains of Amborella resemble those of various monimiaceous genera in having a tenuous, finely papillate exine. They fluctuate considerably in form. Those obtained from open flowers of Vieillard 3149 (Kew) have an irregular unthickened area on one polar face, Figs. 18 and 19, whereas pollen from flower buds of Vieillard 32 (Paris) are uniformly thickened and granular appearing on all surfaces. The former pollen grains are circular in polar view, Figs. 18 and 19, having a diameter which averages approximately 27 micra. When viewed at right angles to the presumed polar axis, the pollen grains exhibit the form illustrated in Fig. 20, i.e. broader and flatter on the face opposite the germinal area. This shape of the pollen suggests that the grains may possibly be formed in tetragonal tetrads, and the irregular unthickened area may be on the proximal side of the grain as in certain of the Annonaceae, Bailey and Nast (1).

THE FEMALE FLOWER

The gross external morphology of the female flower, reconstructed from fragments of open flowers of *Vieillard 3149* (G.H.), may be summarized as follows:

Pedicel naked or bearing from one to four bracteoles. Tepals six to eight, slightly connate at the base, in two series, those of the inner more nearly cyclic series broader with expanded membranous margins. Staminode one, or occasionally two, resembling the stamens of the male flower in form, but sterile and basally adnate to a subtending tepal. Carpels five, free, obovoid, borne on the slightly convex center of the torus; stigma oblique, sessile, extensive, with two conspicuous feathery flanges.

In general, the pedicel and the perianth of the female flowers, Figs. 12 and 13, resemble those of the male flowers. Although there is no sharply defined differentiation into calyx and corolla, the five upper tepals commonly are larger, broader, and have a more nearly cyclic orientation. The staminode, Figs. 10, 13, and 14, is broad and basally adnate to a subtending tepal, Fig. 14. It commonly bears a more or less rudimentary anther, with sporangial cavities and more or less extensive endothecial thickening, but is devoid of pollen in the limited number of specimens that we have examined.

The carpel of Amborella appears to exhibit a particular trend of specialization of the primitively conduplicate ranalian carpel, compare Bailey and Nast (2). The basal part of the carpel is sealed, whereas the extensively developed paired stigmatic crests of the upper part of the conduplicate carpel are unfolded, *Figs. 15* and *16*. Each carpel contains a single anatropous ovule which is directly attached to the ventral side of the locule by a short, obliquely oriented raphe. The level of attachment to the carpellary wall fluctuates between one-half and two-thirds of the distance between the base and the apex of the locule. The micropylar end of the ovule points downward at an angle of considerably less than 90 degrees to the axis of the raphe. The ovule is krassinucellate and bitegumentary,

Fig. 11. The inner integument consists uniformly of three layers of cells, whereas the outer one is composed of five to seven layers on the rapheal side.

The primary vascular system of the pedicel of the female flower is typically eustelic, consisting of a ring of discrete bundles, Fig. 22, as in the pedicel of the male flower. Each scale-like bracteole is vascularized by a single strand, Figs. 22 and 23. Just below the level of the perianth, the bundles of the eustele become more diffusely arranged owing to incipient broadening of the torus. The traces of the tepals are clearly differentiated at the level illustrated in Fig. 24. Each tepal has a single trace in its connate base, which subsequently divides into a median and two lateral veins in its lamina. At the levels illustrated in Figs. 25 and 26, there are two concentric circles of vascular strands, an outer one concerned with the tepals and staminode and an inner one of five bundles concerned with the vascularization of the five carpels. At the base of each carpel, its vascular bundle bifurcates into a large dorsal strand and a smaller ventral one, Fig. 27. The dorsal strand develops extensive branches and terminates in an inverted spray of vascular elements, Figs. 15 and 16. The ventral strand bifurcates in its upward course and the vascular supply of the ovule is derived from one of its branches. The concrescence of tepals is clearly indicated in Figs. 26 and 27. The adnation of the staminode to its subtending tepal is still evident at the levels illustrated in Figs. 28 and 29.

THE FRUIT

The drupaceous fruit is obovoid with slightly compressed sides and apex. Vestiges of the stigmatic crests occupy a subterminal position, Fig. 17, due to asymmetrical development of the carpel after fertilization. In the case of dried specimens, the external surface of the fruit appears to be reticulately wrinkled with evenly distributed depressed areas, as illustrated by Perkins (13). However, when the fruit is re-expanded, these depressions disappear and the entire surface of the fruit becomes smooth. The stony endocarp is not a sclerenchymatous tissue of uniform thickness as figured by Perkins (13), but has highly embossed ridges on its outer surface, corresponding with a complex, reticulate system of vascularization of the exocarp. The softer parts of the exocarp, between the embossed ridges of the thick sclerenchymatous layer, appear at times to give rise to cup-shaped lysigenous lacunae, Fig. 34. The unaffected outer laver of the exocarp presents a more or less uniform cellular organization, though the general uniformity may be defaced here and there by the eruption of corky excrescences.

A single seed occupies the entire cavity of the fruit, Fig. 34. Baillon (6) and Willis (17) state that the seed is pendulous and orthotropous, but the orthotropy has been questioned by Pax (11). As we have demonstrated on preceding pages, the ovule is anatropous, Fig. 11. During post-fertilization development, the enlargement of the carpel and seed is such that the lateral attachment of the seed appears to occur at a higher

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level in the locule. At the same time, the originally oblique raphe becomes deflected, as indicated by its vascular strand, into an orientation more nearly at right angles to the long axis of the seed, Fig. 17. In fruits from herbarium specimens, the crushed remains of the two integuments have assumed a membranous texture and constitute the seed coat, Fig. 35. The cells of the outermost layer of the outer integument are conspicuous owing to their content of darkly colored, phenolic, vacuolar material.

The bulk of the seed, Fig. 35, is composed of a compact endosperm whose constituent cells are of relatively uniform size and shape, those at the periphery, however, being smaller and having more darkly stained contents, Fig. 36. The embryo is minute, Figs. 35 and 36, and is situated at the lower apex of the downwardly projecting seed. In fruits from various collections examined by us, the embryo exhibits merely incipient stages of the formation of cotyledonary primordia.

SECRETORY IDIOBLASTS AND CRYSTALS

According to Perkins (12), there are no secretory cells containing ethereal oils or resins in the pith or cortex of the stem, but she states that a few small cells of this type occur in the spongy mesophyll of the leaf. Although we have utilized a variety of special techniques, we have not succeeded in demonstrating the presence of such cells in any tissues of the stem, leaf or floral appendages. Nor have we succeeded in demonstrating the presence of mucilaginous cells, such as occur in the Lauraceae and are considered to differentiate this family from the related Monimiaceae.

The tissues of *Amborella* do not contain druses or large rhombic crystals of calcium oxalate. Nor have we been able to find small acicular crystals which are stated by Solereder (15) to occur so commonly in the Monimiaceae, Lauraceae, and Hernandiaceae. However, entire absence of crystals and of secretory idioblasts cannot be conclusively established until properly preserved material of freshly collected specimens is obtainable.

DISCUSSION

Since the publication of Baillon's (6) description, *Amborella* has consistently been placed in the Monimiaceae, and by Pax (11) and Perkins and Gilg (14) in the Hortonieae, the florally most primitive tribe of the family. The vesselless xylem of *Amborella* raises the question whether the genus actually belongs in the Monimiaceae, and what its relationships to other vesselless genera of the dicotyledons may be.

Relatively few botanists are inclined to follow van Tieghem (16) in segregating vesselless dicotyledons in a special order, the Homoxylées. Indeed, there are grave dangers in basing phylogenetic conclusions and classification upon the study of any *single* organ, tissue, or morphological character. Much of the confusion in past and present botanical literature is due to a failure to recognize that parallel and convergent evolution are of common occurrence in all organs of the vascular plants, and to allow for the fact that morphological specializations rarely, if ever, occur simultane-

ously and at uniform rates in all parts of a plant. Deductions regarding relationships should be based, therefore, upon careful assessment of evidence from all organs, tissues, and parts of the plant.

The totality of morphological evidence indicates that the Winteraceae (*Drimys, Pseudowintera, Bubbia, Belliolum, Exospermum,* and Zygogynum) are at best only remotely related to the Magnoliaceae and other surviving ranalian families, Bailey and Nast (3). Similarly, it demonstrates that, although *Tetracentron* and *Trochodendron* should be placed in close proximity, they bear no close relationship to the Winteraceae or even to such genera as *Euptelea* and *Cercidiphyllum*, Bailey and Nast (4), Nast and Bailey (9 and 10).

The general structural similarity between the vesselless xylem of Amborella and that of comparable young stems of the Winteraceae, taken by itself, provides no cogent evidence for including the genus in that family. Fundamental structural differences in the flowers, in the pollen, in the pith and cortex, and in the vascularization of the leaf, etc., provide a negation of such a possibility. In even greater measure, the totality of evidence excludes any possibility of including Amborella either in the Tetracentraceae or the Trochodendraceae. This leaves unanswered the question whether Amborella should likewise be excluded from the Monimiaceae.

Possible evidences of relationship to the Monimiaceae are (1) incipient perigynous tendencies particularly in the male flower, coupled with unisexuality, (2) form and structure of the pollen, (3) uniovulate carpels, (4) presence of hippocrepiform sclereids, (5) unilacunar nodal anatomy, (6) absence of druses and large rhombic crystals of calcium oxalate, and (7) absence of a combination of special morphological characters indicative of close relationship to any other family. Potentially significant differences are (1) absence of vessels and of septate fibers in the xylem, (2) absence of fibrous sclerenchyma in the pith and cortex of the stem, and in the leaf and other appendages, (3) apparent absence of conspicuous secretory idioblasts containing ethereal oils or resinous contents, and (4) the presence of multicellular hairs; according to Solereder (15) the Monimiaceae are characterized by having unicellular trichomes or variously clustered groups of such hairs.

Whether Amborella should be retained within the Monimiaceae or should be segregated in a new related family must await the results of extensive coöperative investigations that we have undertaken of the various genera of the Monimiaceae. Sufficient progress has already been made, however, to demonstrate that if the present narrow concept of the family is to be retained, other genera in addition to Amborella should be excluded from the Monimiaceae (sensu stricto). For example, Trimenia and Piptocalyx have a fundamentally different type of nodal anatomy, have no hippocrepiform sclereids in the cortex of young stems, and have large mucilaginous cells which have been used as a reliable criterion for differentiating the Monimiaceae (absent) from the Lauraceae (present). On the contrary, if the existing concept of the Monimiaceae is to be broadened to inBAILEY & SWAMY, AMBORELLA TRICHOPODA

clude such genera as Amborella, Trimenia, and Piptocalyx, it should likewise include such genera as *Gomortega* and *Austrobaileva*.

It should be noted in conclusion that the nine surviving genera of vesselless dicotyledons exhibit a wide range of diversified specializations in their floral organs, indicative, as prophesied by van Tieghem (16), that additional morphological types will ultimately be discovered either in living or fossil floras. Of the nine known genera, five (Bubbia, Belliolum, Exospermum, Zygogynum, and Amborella) occur in New Caledonia, and three (Amborella, Exospermum, and Zygogynum) are endemic on that Island.

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EXPLANATION OF PLATES

All plates show Amborella trichopoda Baill.

PLATE I

Figs. 1–3. Balansa 1800 (Paris). Variation in the form of the leaves. $\times \frac{1}{2}$. Fig. 4. The same. Multicellular hair. \times 280. Fig. 5. Vieillard 3149 (G.H.). Surface view of a stoma showing subsidiary epidermal cells. \times 600. Fig. 6. The same. Stoma with subsidiary cells oriented parallel to the guard cells. \times 600. Fig. 7. The same. Transverse section of a stoma, showing the cuticular vestibule. \times 600. Figs. 8 and 9. Vieillard 3149 (Kew). An outer and an inner stamen viewed from their adaxial side. \times 21. Fig. 10. Vieillard 3149 (G.H.). Staminode of a female flower, showing sterile anther. \times 21. Fig. 11. The same. Longitudinal section of a carpel, showing pattern of vascularization and the anatropous ovule. \times 25.

PLATE II

Fig. 12. Vieillard 3149 (G.H.). Reconstruction of a female flower, with one inner tepal removed to show the five carpels. Staminode at the right. \times 10. Fig. 13. The same. Flower oriented to show the breadth of the staminode. \times 10. Fig. 14. The same. Part of a female flower, showing one carpel and the adnation of the basal part of the staminode to its subtending tepal. \times 10. Fig. 15. The same. Lateral view of a cleared carpel, showing pattern of vascularization. \times 33. Fig. 16. The same. Cleared carpel, viewed from its dorsal side. \times 33. Fig. 17. The same. Longitudinally dissected, cleared fruit, showing vascularization and attachment of the seed. \times 8. Figs. 18 and 19. Vieillard 3149 (Kew). Polar views of pollen, showing variation in the size and form of the irregular unthickened areas. \times 800. Fig. 20. The same. Pollen grain viewed at right angles to the polar axis. \times 800.

PLATE III

Figs. 22–29. Vieillard 3149 (G.H.). Diagrammatic transverse sections of a female flower cut at successive levels, as shown in Fig. 21. S, vascular strand of staminode. \times 33.

PLATE IV

Fig. 30. Vieillard 3149 (G.H.). Transverse section of the stem, showing unilacunar node and vesselless xylem. \times 16. Fig. 31. The same. Hippocrepiform sclereids more highly magnified. \times 170. Fig. 32. Balansa 1800 (Paris). Transverse section of the petiole, showing single arc of vascular tissues. \times 33. Fig. 33. The same. Transverse section of the midvein of the lamina. \times 33. Fig. 34. Vieillard 3149 (G.H.). Longitudinal section of the fruit, showing outwardly projecting sclerenchymatous ridges, and lacunae in the outer exocarp. \times 9. Fig. 35. Licard (Paris). Longitudinal section of a seed, showing extensive endosperm and minute embryo. \times 16. Fig. 36. Pancher (Paris). Micropylar region of a seed, showing contracted embryo. \times 170.

PLATE V

Fig. 37. Vieillard 3149 (G.H.). Transverse section of the stem, showing vesselless xylem, uniseriate, biseriate, and multiseriate rays, and hippocrepiform sclereids of the cortex. \times 73. Fig. 38. The same. Tangential longitudinal section of the secondary xylem, showing form of the rays. \times 73. Fig. 39. The same. Radial longitudinal section of the secondary xylem, showing the pitting of the tracheids. \times 340.

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