

THE  
BOTANICAL GAZETTE

JUNE 1919

STRUCTURE, DEVELOPMENT, AND DISTRIBUTION  
OF SO-CALLED RIMS OR BARS OF SANIO

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(WITH PLATES XIII-XV)

Introduction

In recent years a number of botanists and paleobotanists have given considerable attention to the study of the distribution of certain bandlike thickenings of the middle lamella, so-called rims or bars of Sanio, in the gymnosperms, and their significance in discussion concerning the relative antiquity of the Abietae and Araucarieae.<sup>1</sup> Before considering the distribution of these bandlike thickenings of the middle lamella, it is desirable to outline the conclusions of various investigators concerning their structure and development. The work of SANIO is particularly significant in this connection, as it is also in a discussion of the controversy that has arisen in regard to the true meaning of the term "bars of Sanio."

Historical

STRUCTURE AND DEVELOPMENT OF SANIO'S QUERLEISTEN.—It was stated by SANIO (13), in his comprehensive paper upon the anatomy of *Pinus silvestris* Linn., that in the cambium of young stems the radial and tangential partitions separating adjacent protoplasts are of equal or nearly equal thickness, but in that of

<sup>1</sup> The terminology of ENGLER and GILG (2) is used in this paper.



old stems the radial walls are considerably thicker. He showed that each of these thick radial partitions is distinctly stratified, and consists of a central cellulose septum, *Zwischensubstanz*, overlaid by cellulose layers belonging to the protoplasts on either side of the wall. Furthermore, he believed that at an early stage in the development of tracheids thin spots appear in the radial primary walls; and that, as the tracheids increase in size, these areas become larger, the *Zwischensubstanz* is gradually absorbed, and the outer layers of the wall are fused together and stretched to form a thin, more or less homogeneous membrane. Inasmuch as bordered pits are subsequently laid down over portions of these attenuated areas, SANIO considered them to be *Primordiale Tupfeln*. He described them as follows (p. 74):

Während diese Verdünnungen in der Membran seitlich, d. h., in horizontaler Richtung allmählich in den stärker verdickten Theil übergehen grenzen sie sich Oben und Unten scharf ab, und erscheinen hier sogar zuletzt mit doppelten Umrissen. Häufig liegen diese Verdünnungen so nahe an einander, dass die sie trennenden verdickten Stellen als Querleisten erscheinen. Untersucht man diese Bildung in Tangentialschnitte, so erscheinen diese Querleisten als knotenförmige Verdickungen der Membran zweier Nachbarzellen, während die Verdünnungen als zarte Scheidwände sich ausweisen.

It is evident from SANIO's figures and descriptions that he considered the primary pit areas, *Primordiale Tupfeln*, to be separated by others in which the *Zwischensubstanz* is not entirely absorbed, and in which the outer cellulose layers are less attenuated. It should be emphasized, in this connection, that SANIO used the word *Querleisten*, cross-pieces or cleats, in referring to transverse thicker strips of the middle lamella between closely approximated primary pit areas, and the word *Umrissen*, contours, in referring to the upper and lower outlines of these areas. It is difficult to determine with certainty whether SANIO understood the real significance of the *doppelten Umrissen*, which partially surround the more isolated primary pit areas in certain of his drawings. That he probably considered them to be contours, outlining the top and bottom of a sloping surface or escarpment, is indicated by his illustration (pl. 10, fig. 2) of a tangential section of a young tracheid of *Pinus silvestris*. I have found no conclusive evidence in his text or figures



to indicate that he considered these parallel curved lines as outlines of a heavily embossed or thickened rim.

STRASBURGER (15) showed very clearly that in *Pinus* and *Larix* SANIO'S *doppelten Umrissen* may be the outlines of embossed portions of the middle lamella. In other words, he made it evident that when the primary pit areas are close together they are separated by a single transverse thickening, but that when they are not closely approximated there may be two curved thickened strips, separated by a less heavily embossed area, between them (fig. 5).

MISS GERRY (3), in discussing the distribution of bandlike thickenings of the middle lamella in the Gymnospermae, referred to them as follows (p. 119):

The "bars" or "folds" of cellulose which when stained with haematoxylin are especially obvious as horizontal or more or less semicircular markings in the tracheide walls of a radial section from such a conifer as *Pinus silvestris* L. were described by SANIO in 1872. . . . These structures were named "Bars of Sanio" from him. . . .

GROOM and RUSHTON (5), who have studied the structure and chemical composition of the bandlike thickenings of the middle lamella in Indian species of *Pinus*, state:

According to SANIO'S work it is these unoccupied margins of the primary areas that coincide in position with the above-mentioned bands that are seen in radial section. Consequently the name "Sanio's rims" may be given to the structures causing the bandlike appearance. . . . When the primary pit areas are in contact, the two contiguous Sanio's rims are naturally "fused" and form a band that is transverse and single, except possibly at the two lateral edges where the natural curvature of each original boundary of the area causes the band to fork. . . . In *radial* sections with iodine and sulphuric acid the "rims" stain yellow; with ordinary haematoxylin they remain unstained; leaving sections in cupra-ammonium to dissolve out any cellulose, their staining properties are not changed materially. They are not composed of cellulose. . . . When young the actual marginal portion of the primary pit area does not thicken by deposits of lignified wall as soon as it does elsewhere (except on the pit-closing membrane), but thickens by successive deposits of pectic substance until a stage is reached when lignified wall-substance is deposited even over the now thickened rims of the primary pit area. Sanio's rims represent a system of rodlike or bandlike pectic thickenings of the middle lamella running transversely in the radial walls and linked here and there by slightly



curved longitudinal bandlike similar thickenings (representing the lateral margins of the primary pit areas). . . . C. MÜLLER (1890) was the author of the name "Sanio's Bars" and, as he explicitly stated, he coined the term to designate these structures,<sup>2</sup> as first discovered by SANIO in *Pinus silvestris* (1873-74).

JEFFREY (7), however, still maintains that the bandlike thickenings of the middle lamella in the Ginkgoales, Abietae, Taxoideae, Cupresseae, and Taxaceae are typical "bars of Sanio." SIFTON (14) considers that the rims of neighboring primary pit areas unite to form bars and uses the latter term in referring to bandlike thickenings of the middle lamella that occur in *Araucaria* and *Cycas*.

BARS OF SANIO VS. TRABECULAE.—The fact that the term bars of Sanio is used by certain investigators in referring to trabeculae and by others in describing entirely different structures is unfortunate and likely to lead to considerable confusion. In a paper, published in 1863, SANIO (12, p. 17) described trabeculae as: "Querbalkens quer durch den Zellenraum von einer Wandung zur andern verlaufen." In 1890, MÜLLER (9) referred to these structures as *Sanio'sche Balken*; and later PENHALLOW (10) called them Sanio's bands. It is evident that SANIO and MÜLLER used the word *Balken* (beams) to designate rodlike structures that are attached at their ends and cross the lumens of cells. In view of this fact, and that SANIO used the word *Querleisten* (cross-pieces or cleats) in referring to bandlike thickenings of the middle lamella, the terms "bars of Sanio" and *Sanio'sche Balken* are not necessarily synonymous. As has been pointed out by GROOM and RUSHTON, however, JEFFREY and his students were undoubtedly mistaken in supposing that the bandlike thickenings of the middle lamella had been named after SANIO. This conclusion is strengthened by the fact that the phrase "diese scheibenförmige Verdickung der Scheidewand ist bisher übersehen" (used by SANIO [13, p. 78] in referring to the torus) was interpreted as indicating that SANIO considered himself the discoverer of the bandlike thickenings of the middle lamella; whereas, as a matter of fact, he expressly stated (13, p. 74) that "Deartige Bildungen hat bereits Unger gesehen, aber nicht zu deuten gewusst."

Although the use of the term "bars of Sanio" was undoubtedly unfortunate, JEFFREY and his students do not appear ever to have

<sup>2</sup> Trabeculae.



actually confused SANIO's *Querleisten* with trabeculae. Furthermore, it is to be emphasized that GROOM and RUSHTON consider the rodlike thickenings, between closely approximated primary pit areas, as fusions of two thickened rims. The word rims, therefore, is not an entirely satisfactory substitute for the word bars in referring to SANIO's *Querleisten*.

DISTRIBUTION AND SUPPOSED PHYLOGENETIC SIGNIFICANCE OF SANIO'S QUERLEISTEN IN CONIFERAE.—There are considerable differences of opinion among various investigators concerning the distribution and phylogenetic significance of these bandlike thickenings of the middle lamella. JEFFREY (7) and his students (3, 6) maintain that they are conspicuously developed in the older wood of *Ginkgo* and all of the Coniferae except the Araucarieae. GOTHAN (4) assumes that they are absent in the Araucarieae because the pits are so closely packed together that there is no room for such structure. THOMSON (16), on the other hand, considers that they are present in rudimentary form in the Araucarieae, and are closely applied to the margins of the bordered pits.

Whatever view is taken in regard to the relative antiquity of the Abietae and Araucarieae, it must be admitted that there is a very striking difference between the older wood of the Araucarieae and that of the Abietae, Taxodieae, Cupresseae, Taxaceae, and *Ginkgo*. "Alternate" pitting (fig. 13) is stereotyped in the Araucarieae; whereas "opposite" pitting and *Querleisten* (pl. XV) are firmly fixed in the Abietae, Taxodieae, Cupresseae, and Taxaceae. There appear to be no true transitional series between these two types of secondary xylems that may be considered to indicate conclusively that the latter type of pitting is a modification of the former.

In so far as tracheary pitting is concerned, the principal arguments in favor of deriving the Abietae and Taxaceae from the Cordaitales or Araucarieae are based upon the anatomy of the young wood of seedlings, cone axes, and the first annual rings of stems and roots, so-called conservative regions. Thus JEFFREY (7) maintains that the presence of alternate pitting and the absence of bandlike cellulose thickenings of the middle lamella in the young wood of reproductive axes, leaf strands, and the first annual rings of *Ginkgo*



and *Pinus*, are evidences of the Cordaitean ancestry of these genera. He considers the opposite pitting and thickenings of the middle lamella which occur in the cone axes of Araucarians to indicate that the Araucarieae are descended from forms resembling *Ginkgo* and *Pinus*. Furthermore, although admitting that "bars of Sanio" are absent or "evanescent" in the young wood of seedlings and the first annual rings of the stems and roots of Araucarieae, he interprets the absence of approximation and consequent flattening of the bordered pits in such tissue as evidence for deriving the Araucarians from pinelike ancestors.

The accuracy of these conclusions has been questioned by THOMSON (16) and SIFTON (14), who have figured and described bandlike thickenings of the middle lamella in the tracheids of the petiole of *Cycas* and the cone axes, seedlings, and first formed secondary xylem of the stems and roots of *Pinus* and other Abietaeae. THOMSON (16) interprets the rimlike thickenings and alternate pitting that occur at times in the cone axes and first annual rings of stems and roots of *Pinus* as indicating that the Abietaeae are descended from the Araucarieae.

It is to be emphasized, in this connection, that in dealing with other structural characters JEFFREY interprets the anatomy of selected conservative regions or organs of the Abietaeae and Araucarieae as indicating that the latter are descended from the former; whereas THOMSON, by applying the same laws to similar material, proves the reverse to be true.

Such discrepancies as these suggest that there may be a considerable element of danger in placing too much emphasis upon "laws" of recapitulation, reversion, and retention in arguments concerning the phylogeny of plants. Even the most ardent advocates of these doctrines admit, in certain cases at least, that cenogenetic characters do occur in seedlings, roots, traumatic tissue, cone axes, etc. So long as this is acknowledged to be so, it must be extremely difficult, in the absence of reliable collateral evidence, to determine with certainty whether a given structure in a given region is palingenetic or cenogenetic. In other words, even if it should be proven, by means of careful statistical and experimental investigations, that certain organs or regions of plants are inherently



somewhat more conservative or slower to change than others, considerable difficulty must inevitably be encountered in formulating such facts as these into laws for use as "short cuts" in the study of phylogeny.

That this is likely to be the case in dealing with the Ginkgoales and Coniferae is indicated by a number of facts in the comparative anatomy and ecology of the Pteridophyta and Gymnospermae. In the evolution of these groups the primary, as well as the secondary, tissues appear to have been considerably modified. For example, the more primitive vascular plants were characterized by having relatively wide zones of primary xylem; whereas the Coniferae have usually only a relatively limited amount of this tissue, which is correspondingly specialized in structure.

#### **Structure and distribution of bandlike thickenings of middle lamella in Pteridophyta, Gymnospermae, and Angiospermae**

In view of the fact that much emphasis has been placed upon bars of Sanio in the identification of fossil woods of the Mesozoic, and that these structures have been used as the basis for important but conflicting generalizations in regard to the phylogeny of the Coniferae and the relative conservatism of different organs or regions of plants, the structure and distribution of bandlike thickenings of the middle lamella in the Pteridophyta, Gymnospermae, and Angiospermae deserve more careful consideration than they have received heretofore.

As is well known, the metaxylem of most Filicales is composed largely of scalariform tracheids. The bordered pits in these tracheary elements are much elongated horizontally, at right angles to the long axis of the tracheids, and are closely approximated in vertical series (fig. 2). The elongated bordering areas of the secondary walls are exactly superimposed over attenuated areas of the middle lamella; and the outlines of these areas are more or less effectively concealed by the margins of the bordering areas. The primary pit areas are separated by narrow, bandlike, thicker portions of the middle lamella, which, in carefully stained<sup>3</sup> longitudinal sections of the xylem, appear as fine dark lines between the

<sup>3</sup> Haidenhain's iron-haematoxylin and safranin.



bordered pits. Owing to the approximation of the bordered pits and the thickness of the secondary walls, however, these *Querleisten* are usually more conspicuous when seen in section (fig. 19) than in surface view.

This scalariform type of tracheary pitting becomes at times considerably modified. Thus the elongated bordering areas of the secondary wall may be replaced by two or more shorter elongated or oval bordering areas (fig. 2). Under these circumstances the primary wall frequently retains its typical scalariform pitting after the secondary wall has lost it; that is to say, each horizontal row of smaller bordering areas is laid down over a single elongated primary pit area (fig. 6). In other cases the elongated bordered pits of the secondary walls may become contracted to form smaller bordered areas which cover only a portion of the surface of the elongated primary pits, and the *Querleisten* project beyond the outlines of the bordering areas. This process of reduction in the pitting of the secondary wall may even be carried to a point where the primary pit areas have no superimposed bordered pits; or the primary pit areas become less closely approximated, of oval or circular outlines, and separated by relatively wide biconcave thickenings with forking ends (fig. 7).

Scalariform pitting also grades into types in which there is less unconformity between the primary and secondary walls. The elongated bordered pits become replaced by vertical rows of smaller pits which are staggered so that the pits in one row alternate with those in the next series. These pits are usually superimposed over nearly the whole surface of similar primary pit areas, and the thicker portions of the middle lamella tend to anastomose or form a reticulum, as is shown in fig. 6a.

Such transitions between scalariform and derived types of tracheary pitting occur in other groups of vascular plants. In certain of the paleozoic and lower mesozoic plants, which had "open" bundles, the metaxylem and secondary wood were composed of scalariform tracheids; whereas, in others, the scalariform bordered pits were more or less completely replaced by horizontal or diagonal rows of smaller pits, except in the tracheids of the younger wood of the stele. In the latter types, in passing from the



younger to the older metaxylem or secondary wood, there were transitions between typical scalariform and opposite and alternate multiseriate pitting. Such transitional stages between scalariform and multiseriate pitting have been observed in a number of Sphenophyllales, Calamariales, Cycadofilicales, Cordaitales, and Bennettitales. In *Protopitys*, *Cycadeoidea Dartoni* (Coulter and Chamberlain) Wiel. (figs. 14, 20), and other forms whose secondary xylems show indications of zonation, such transitions occur periodically in the older wood of the stem, as they do in the stems and roots of the vesselless angiosperms, *Tetracentron* and *Trochodendron* (figs. 15, 16). In these transitional regions the elongated primary pit areas and *Querleisten* that underlie the scalariform secondary walls tend to persist in tracheids having horizontal rows of bordering areas.

It is such transitional types of tracheary pitting that have been figured by JEFFREY in the cone axes of Araucarians, and by SIFTON in the petioles of *Cycas*. In *Araucaria Bidwillii* Hook., owing to the fact that the middle lamella is often relatively thick and the pits not closely approximated, the *Querleisten* are frequently broad and conspicuous. In transitional tracheids they may break into fragments which cling to the margins of the bordered pits, even after the latter have shifted to the alternate arrangement. Eventually, however, the more or less circular primary pit areas of the older tracheids appear to become surrounded on all sides by equally thickened portions of the middle lamella.

Scalariform and transitional types of bordered pitting occur in the lateral walls of the vessels of many dicotyledons. In fig. 3 is illustrated the typical scalariform bordered pitting that occurs in the radial and tangential walls of the vessels of certain Magnoliineae. This type of pitting is in marked contrast to the multiseriate pitting shown in figs. 4 and 9. As these figures indicate, the bordered pits which form the horizontal rows may be closely packed together and have flattened sides, or they may be more loosely arranged and have oval outlines. Transitional stages, between these typical scalariform and multiseriate types of pitting, are of frequent occurrence in the vessels of certain of the Magnoliineae (figs. 4, 11).

In photomicrographs of carefully stained sections there are thin dark colored lines between the elongated or scalariform



bordered pits. These transverse strips are deeply stained portions of the middle lamella that stand out in sharp contrast to the thin pit membranes. They are, in fact, very narrow, bandlike thickenings (*Querleisten*) which separate the elongated primary pit areas. In the case of vessels with multiseriate pitting, these transverse ridges or *Querleisten* tend to occur between the elongated primary pit areas that underlie the horizontal rows of bordered pits. In other words, a single elongated bordered pit may be laid down over the whole surface of the elongated primary pit area, or one or more smaller bordered pits may be laid down over portions of its surface. Under the latter circumstances, the outlines (*Umrissen*) of the primary pit areas become more conspicuous (figs. 4, 9, 11). In certain cases these *Querleisten* become more or less completely divided into shorter, rodlike thickenings, which lie between the upper and lower margins of contiguous bordered pits of the vertical series.

It was shown by STRASBURGER (15) that bordered pits are not laid down over all the primary pit areas in the tracheids of *Pinus* and *Larix*. In the Magnoliineae and other dicotyledons the lateral primary walls of the vessels frequently have elongated attenuated areas, which have no bordered pits superimposed over them, or only a comparatively limited part of their surface so covered (figs. 1, 8, 12).

In the Magnoliineae, Trochodendrineae, and other groups of dicotyledons there is much evidence to indicate that scalariform pitting is a relatively primitive feature in the structure of vessels. That is to say, those vessel segments which most closely resemble tracheids in general form and structure tend to have scalariform or scalariform and opposite multiseriate pitting; whereas the larger and more specialized conducting passageways are characterized by having alternate multiseriate pitting in their lateral walls (fig. 10).

In the evolution of larger and more specialized vessels the modification of the primary walls does not appear, in many cases, to have kept pace with that of the secondary walls. Thus in primitive types of vessel segments the elongated bordered pits are exactly superimposed over similar elongated primary pit areas, but in more



specialized types the primary wall (the first formed portion of the vessel member) tends to retain its primitive elongated type of primary pit areas after the scalariform bordered pits have become locally constricted (fig. 4), or divided into horizontal rows of smaller pits (fig. 9). Similarly, in those walls where there is a tendency to eliminate the bordered pits, the elongated primary pit areas persist after the bordered pits have partially or completely disappeared (figs. 1, 8, 9).

In the highly specialized vessels of the Anonaceae and Lauraceae (fig. 10) there are numerous circular or oval bordered pits in the lateral walls of the vessels. Usually they appear to be laid down over similar circular primary pit areas. In other words, in the most highly specialized types of vessels, in which the bordered pits are not arranged in horizontal rows, even the elongated primary pit areas are more or less completely obliterated, and replaced by attenuated areas with circular outlines. Vestiges of *Querleisten*, however, are sometimes present near the upper and lower margins of the bordering areas.

In the dicotyledons, with increasing specialization of the vessels, there is a corresponding reduction in the pitting of the remaining tracheary elements. Thus typical tracheids are replaced by fiber tracheids, which are in turn replaced by libriform fibers. The fiber tracheids of certain dicotyledons have elongated or oval primary pit areas that are separated by wide dark colored bands. Furthermore, it is not uncommon to find that many of the attenuated areas of the middle lamella have no superimposed bordered pits (fig. 22).

Unconformity of the type that occurs in the tracheids of various primitive vascular plants, and in the vessels of certain dicotyledons, has been observed in the wood of *Ginkgo*, and certain of the Abietae and Taxodieae. Fig. 23 illustrates a type of tracheary pitting that is of frequent occurrence in the older secondary wood of vigorous mature specimens of *Ginkgo* and *Taxodium*. It is most characteristically developed in large thin-walled tracheids of the so-called spring wood. The numerous, uniformly narrow, elongated primary pit areas and thin, straight, narrow *Querleisten* are typically scalariform in structure. Each primary pit area has superimposed



over it 2-4 bordered pits. The latter are somewhat elongated in many cases, and frequently are so closely approximated as to be flattened by mutual contact and to cover nearly the whole of the primary pit areas. This type of tracheary pitting grades into a second type in which the surfaces of the elongated primary pit areas are only partially covered by circular bordered pits (figs. 24, 25). The latter type, in turn, grades into a third type in which the primary pit areas are not typically scalariform in structure. Certain of the attenuated areas appear to increase in size at the expense of intervening areas, which are either eliminated entirely or persist as constricted areas that are not overlaid by bordered pits (figs. 26, 29, 30). By this process of specialization certain of the primary pit areas become oval or biconvex and less closely approximated. Certain of the *Querleisten* tend to widen and to become biconcave with forking ends; whereas others are crowded together and appear to fuse to form similar biconcave thickenings (figs. 26, 29, 31). This type of pitting grades into others in which the attenuated areas that are overlaid by bordered pits become more circular and more widely separated, the intervening primary pit areas and *Querleisten* (except the curved bands that commonly persist above and below the bordered pits) becoming vestigial or obliterated (figs. 27, 28). In certain cases the portions of the middle lamella between widely separated primary pit areas may be uniformly thickened so that the pits appear to be separated by a single, wide dark colored band. In other cases, for example, in the thick-walled fiber-like cells of the so-called summer wood, and in the small tracheids which occur in seedlings and the first annual rings of stems and roots, the bordered pits frequently tend to be superimposed over nearly the whole surface of the circular primary pit areas, and the curved *Querleisten* cling to the upper and lower margins of the bordering areas, or are completely obliterated.

Such transitions in tracheary pitting have been observed in *Larix*, *Pinus*, *Abies*, *Sequoia*, and other genera of the Abietae and Taxodieae, as well as in *Taxodium* and *Ginkgo*. The more elongated primary pit areas and the narrower, straighter *Querleisten* tend to occur in the larger, thinner-walled, heavily pitted tracheids; and are therefore most characteristically developed in the first formed



portions of the growth rings of the older secondary xylem. The particular types of unconformity and bandlike thickenings of the middle lamella which occur in a given species vary considerably in plants grown under different environmental influences and in different organs or regions of a single plant. This is as true of the first formed as the older secondary xylem.

### Discussion

It is evident that bandlike thickenings<sup>4</sup> of the middle lamella, separating more or less elongated primary pit areas, are not confined to the tracheids of certain Coniferae, but are widely distributed among the Pteridophyta, Gymnospermae, and Angiospermae.<sup>5</sup> Any interpretation of the so-called rims or bars of Sanio in the Coniferae, therefore, should be in general harmony with the structure and distribution of these bandlike thickenings in other groups of vascular plants.

Since bandlike thickenings of the middle lamella and transitions between scalariform and "alternate" and "opposite" multiseriate pitting are of common occurrence in the younger xylem of many paleozoic and mesozoic (as well as less primitive) plants, the occurrence of opposite (as well as alternate) pitting and more or less rudimentary *Querleisten* in the transitional tracheids of the cone axes of Araucarians does not indicate conclusively that the Araucarieae are descended from the Abietae. Similarly, the more or less sporadic occurrence of alternate pitting, as well as opposite pitting and "bars of Sanio," does not indicate necessarily that the secondary xylem of the Ginkgoales, Abietae, Taxodieae, Cupressae, and Taxaceae is a modification of that which occurs in the Araucarieae or Cordaitales.

Furthermore, there are a number of facts in the comparative anatomy and ecology of the Pteridophyta, Gymnospermae, and Angiospermae which suggest that unconformity between the pits in the primary and secondary walls of tracheids and vessels may be

<sup>4</sup> Which stain dark blue in sections treated with Haidenhain's iron-haematoxylin.

<sup>5</sup> The bandlike thickenings are usually inconspicuous in surface views of the facets of tracheary elements owing to the fact that they are concealed by the thick, superimposed secondary walls.



a phenomenon that is concomitant of processes of modification or reduction in tracheary pitting. In the metaxylem of ferns and in the secondary xylem of a number of primitive vascular plants, the primary wall frequently tends to retain its scalariform structure after the scalariform bordered pits in the secondary wall have been replaced by horizontal rows of smaller pits. It may even retain its elongated pit areas and bandlike thickenings after the bordering areas of the secondary wall have been considerably contracted, or have disappeared entirely from certain portions of a facet. On the other hand, when scalariform pitting is replaced by alternate multiseriate pitting, the bandlike thickenings of the middle lamella tend to anastomose and form a reticulum.

Similar phenomena occur in the metaxylem of many of the higher vascular plants, in the tracheids of the secondary xylem of the vesselless dicotyledons *Tetracentron*, *Trochodendron*, and *Drimys*, and in the lateral walls of the vessels of many of the angiosperms.

This general tendency for the persistence of scalariform pitting in the middle lamella, after it has disappeared more or less completely from the secondary wall, raises an interesting question in regard to the probable significance of the scalariform pitting which occurs so commonly in the middle lamellae of certain of the Abietaceae, Taxodiaceae, Taxaceae, Cupressaceae, and *Ginkgo*, but appears to be entirely absent in the later formed secondary tracheids of the Araucariaceae.

It is important to note in this connection that the more primitive vascular plants, which possessed relatively wide zones of primary xylem, were characterized by having numerous closely approximated pits in the radial facets of their relatively large tracheids. In the evolution of the Ginkgoales and Coniferae there appears to have been a more or less pronounced reduction in the amount of primary xylem, in the size of the first formed secondary tracheids of the stele, and in the number of bordered pits in the walls of the tracheary elements.

The large, thin-walled, heavily pitted tracheids which occur in the spring wood of the older secondary xylem of mesophytic Coniferae, resemble the primitive types of tracheids more closely than do the thick-walled, highly specialized elements of the summer wood,



or the relatively small tracheids of the first formed portion of the secondary xylem. It is in these larger thin-walled tracheids that the most typical scalariform primary pit areas tend to occur. Occasionally, where the tracheary pitting is very strongly developed, scalariform bordering areas of the secondary wall are superimposed over portions of these elongated primary pit areas (fig. 23). This is likely to occur in *Taxodium* and *Ginkgo* and roots of certain of the Abietae. As has previously been shown, the scalariform structure of the middle lamella and narrow straight *Querleisten* become gradually modified with increasing reduction in the number of bordered pits. Furthermore, it has been shown that a similar widening of the bandlike thickenings of the middle lamella may occur in certain of the Pteridophyta, as well as the Angiospermae, when the bordered pits tend to become more or less isolated.

The occurrence of these interesting structures in the Abietae, Taxodieae, Cupresseae, Taxaceae, and *Ginkgo*, and their absence in the secondary wood of Araucarieae, are difficult to explain upon the assumption that the former groups are descended from ancestors having "alternate multiseriate" pitting. On the other hand, from analogy with similar phenomena in other groups of vascular plants, their occurrence is easily accounted for if the microphyllous and relatively xerophytic Coniferae are descended from forms having scalariform tracheary pitting.

#### Primary pit areas of cambium and their relation to the pitting of xylem and phloem

The important observations of DE BARY, JANCZEWSKI, RUSSOW, STRASBURGER, KIENITZ-GERLOFF, KRÜGER, and others upon the occurrence of bandlike thickenings of the middle lamella in the cells of the cambium, and their relation to similar structures in the elements of the xylem and phloem, have been overlooked entirely in discussions concerning the phylogenetic significance of the so-called rims or bars of Sanio. KRÜGER (8) found that, in the cambia of all plants (stems and roots of gymnosperms, dicotyledons, monocotyledons, including trees, shrubs, herbs, and succulents) investigated by him, there were *leistenformige Verdickungen* in the radial partitions (figs. 17, 18). These ridgelike thickenings separated roundish



thin spots or pit areas and were more conspicuous in the winter than in the spring and summer, a fact previously noted by DE BARY (1). Furthermore, KRÜGER traced these structures to the "procambial strands" and through the developing daughter cells of the cambium to the highly differentiated cells of the xylem and phloem. They appeared to be least modified in the walls of phloem parenchyma. In the development of tracheids, vessels, and sieve tubes, owing to increase in the size of the individual cells, they tended to become more or less modified. KRÜGER concluded, however, that the thin spots became enlarged and modified to form sieve plates (fig. 21), and to form the primary pit areas of tracheary elements. He noted that during this process the ridgelike thickenings tended to become more or less modified in shape. RUSSOW (11) and STRASBURGER (15) emphasized the fact that in the Abietae many of the pit areas become more or less obliterated in the development of tracheids and sieve tubes; that is to say, many of the primary pit areas become vestigial, since they have no superimposed bordered pits or do not become modified to form sieve plates.

It is evident, therefore, that not only are bandlike thickenings of the middle lamella of frequent occurrence in the tracheary elements of Pteridophyta, Gymnospermae, and Angiospermae, but also in the cells of the cambium and phloem. In discussing the phylogenetic significance of the bandlike thickenings of the middle lamella in tracheids of Coniferae, therefore, it is essential, not only to compare these structures with similar structures which occur in other types of cells and other groups of plants, but also to contrast the various stages in their development. This must inevitably be the case, since there is a considerable element of danger in basing generalizations concerning relationships upon comparisons between the structure of end products. Of course similar structures may be attained through entirely different developmental stages. Unfortunately, comparatively little is known in regard to the detailed structure of the cambium and the various stages in the development of tracheary pitting in different groups of vascular plants. It is to be hoped that this gap will be filled in the near future, since information of this character promises to throw con-



siderable light upon a number of interesting problems, especially upon the structure and true significance of the so-called rims or bars of Sanio.

### Summary

1. Bandlike thickenings of the middle lamella and scalariform primary pit areas are characteristic of tracheids which have scalariform bordered pits. They are widely distributed among the Pteridophyta, Gymnospermae, and Angiospermae.

2. The middle lamella frequently retains its typical scalariform structure after the secondary wall has lost it.

3. In the Gymnospermae, as well as in the Pteridophyta and Angiospermae, there appear to be transitions between primary membranes of this type and others in which the scalariform structure is profoundly modified.

4. The comparative anatomy and ecology of the Pteridophyta, Gymnospermae, and Angiospermae afford considerable evidence which suggests that the types of unconformity and peculiar bandlike thickenings of the middle lamella (so-called bars or rims of Sanio) which occur in certain Pteridophyta and Angiospermae, as well as in many Gymnospermae, are concomitants of processes of modification or reduction in tracheary pitting.

5. The structure of the walls of the cambium and the development of the pitting in the elements of the xylem and phloem in Pteridophyta, Gymnospermae, and Angiospermae deserve more careful consideration in discussions concerning the phylogenetic significance of the so-called rims or bars of Sanio, than they have received heretofore.

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## EXPLANATION OF PLATES XIII-XV

### PLATE XIII

FIG. 1.—*Magnolia acuminata* Linn.: pitting in facet of small vessel segment, showing scalariform primary pit areas and isolated circular bordered pits;  $\times 300$ .

FIG. 2.—*Todea hymenophylloides* A. Rich.: pitting in lateral facet of tracheid, showing typical scalariform and transitional types of pitting;  $\times 300$ .

FIG. 3.—*Magnolia acuminata*: scalariform pitting in lateral facet of vessel segment;  $\times 400$ .

FIG. 4.—*Magnolia acuminata*: pitting in lateral facet of vessel segment, showing scalariform and transitional types of pitting;  $\times 450$ .

FIG. 5.—*Pinus Strobus* Linn.: tangential longitudinal section, showing *knotenformige* thickenings of middle lamella;  $\times 500$ .

FIG. 6.—*Todea hymenophylloides*: pitting in lateral facet of tracheid, showing pairs of elongated bordering areas superimposed over single scalariform



primary pit areas; portions of bandlike thickenings of middle lamella visible between rows of bordered pits;  $\times 300$ .

FIG. 6a.—*Todea hymenophylloides*: showing alternating arrangement of bordered pits and anastomosing of bandlike thickenings of middle lamella;  $\times 300$ .

FIG. 7.—*Acrostichum sorbifolium* Linn.: lateral facet of tracheid, showing small, circular, bordered pits and biconcave thickening of middle lamella, latter somewhat indistinct owing to thickness of superimposed secondary wall;  $\times 800$ .

FIG. 8.—*Cercidiphyllum japonicum* Sieb. and Zucc.: lateral facet of vessel segment, showing persistence of scalariform primary pit-areas after more or less complete disappearance of bordered pits;  $\times 300$ .

FIG. 9.—*Magnolia macrophylla* Michx.: lateral facet of vessel segment, showing unconformity between primary and secondary pitting.

FIG. 10.—*Asimina triloba* (Linn) Dun.: lateral facet of vessel segment, showing alternate multiseriate pitting;  $\times 300$ .

FIG. 11.—*Cercidiphyllum japonicum*: lateral facet of vessel segment, showing transitional types of bordered pitting and unconformity between primary and secondary walls;  $\times 400$ .

FIG. 12.—*Cercidiphyllum japonicum*: lateral facet of vessel segment, showing unconformity between pitting of primary and secondary walls;  $\times 400$ .

#### PLATE XIV

FIG. 13.—*Agathis australis* Steud.: pitting in radial facet of tracheid, showing "alternating" type of arrangement;  $\times 350$ .

FIG. 14.—*Cycadeoidea Dartoni* (Coult. and Chamb.) Wiel.: radial longitudinal section of secondary xylem, showing transitional types of pitting;  $\times 100$ .

FIG. 15.—*Trochodendron aralioides* Sieb. and Zucc.: radial facets of 2 tracheids, showing transitions between scalariform and opposite bordered pitting; *Querleisten* appear as narrow dark lines separating scalariform pits or pairs of smaller bordered pits;  $\times 350$ .

FIG. 16.—*Trochodendron aralioides*: radial longitudinal section of secondary xylem, showing transitional types of pitting and (right) persistence of scalariform primary pit areas with reduction in number of bordered pits;  $\times 200$ .

FIG. 17.—*Ulmus americana* Linn.: tangential longitudinal section of cambium (winter condition), showing *knotenformige* thickenings of middle lamella;  $\times 230$ .

FIG. 18.—*Ulmus americana*: radial longitudinal section of cambium and young phloem cells, showing sculpture of middle lamella;  $\times 200$ .

FIG. 19.—*Pteris aquilina* Linn.: adjacent walls of 2 tracheids in sectional view, showing *knotenformige* thickenings ("bars of Sanio") of middle lamella;  $\times 300$ .



FIG. 20.—*Cycadeoidea Dartoni*: radial longitudinal section of secondary xylem, showing transitions between scalariform and opposite and alternate pitting;  $\times 100$ .

FIG. 21.—*Juglans nigra* Linn.: radial longitudinal section through cambium (left) and young phloem (right), showing relation between sieve plates and primary pit areas;  $\times 180$ .

FIG. 22.—*Kayea paniculata* Merrill: radial longitudinal section of secondary xylem, showing primary pit areas and "bars of Sanio";  $\times 200$ .

PLATE XV

FIG. 23.—*Taxodium distichum* (Linn.) Richard: radial facet of tracheid, showing scalariform structure of primary wall and crowded bordered pits;  $\times 400$ .

FIG. 24.—*Larix occidentalis* Nutt.: radial facets of 3 tracheids, showing scalariform structure of primary wall;  $\times 350$ .

FIG. 25.—*Taxodium distichum*: radial facet of tracheid, showing scalariform structure of primary wall and less crowded bordered pits than fig. 23;  $\times 400$ .

FIG. 26.—*Larix occidentalis*: radial facets of 2 tracheids, showing numerous primary pit areas having no superimposed bordered pits;  $\times 220$ .

FIG. 27.—*Pinus Strobus*: radial facets of 3 tracheids, showing modified types of primary wall structure;  $\times 220$ .

FIG. 28.—*Pinus Strobus*: radial facets of 3 tracheids, showing reduction in bordered pitting and persistence of primary pit areas;  $\times 220$ .

FIG. 29.—*Larix occidentalis*: radial facet of tracheid, showing curving and fusing (or widening) of bandlike thickenings of middle lamella;  $\times 240$ .

FIG. 30.—*Pinus Strobus*: radial facets of several tracheids, showing scalariform structure of primary wall;  $\times 220$ .

FIG. 31.—*Taxodium distichum*: radial facet of tracheid, showing curving of bandlike thickenings of middle lamella with reduction in number of bordered pits;  $\times 400$ .

FIGS. 14, 17, 18, 20, and 21 were made from sections loaned to the writer by Drs. G. R. WIELAND and L. H. MACDANIELS.





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<https://doi.org/10.1086/332499>.

**View This Item Online:** <https://www.biodiversitylibrary.org/item/27477>

**DOI:** <https://doi.org/10.1086/332499>

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