

# Reduction and Reversion in the North American Salicales.<sup>1</sup>

BY

RUTH HOLDEN,

*Wilby Prize Student of Radcliffe College.*

With Plates **XX** and **XXI**.

IN the accepted classification of the Angiosperms, as presented by Engler and Prantl in 'Die natürlichen Pflanzenfamilien', the Salicales are placed as the third alliance under the Archichlamydeae, the families below them being the Casuarinales and Piperales. A few families above them are the Juglandales and Fagales, with which the Salicales were formerly united to constitute the Amentiferae. The sequence of these orders is based on the development of the perianth and the character of the floral members. On this criterion the Salicales are certainly low in the series, having catkins of flowers which are naked in the axils of bracts. Even on floral structure there is one objection, however, to relegating them to this primitive group, viz. the nectaries of *Salix*. Insect pollination is generally conceded to be characteristic of the higher orders, yet the entomophilous *Salix* is placed below the anemophilous Juglandales and Fagales. Another objection to the existing classification is the fact that the Salicales are porogamous, while the Casuarinales below, the Juglandales and some of the Fagales above, are chalazogamous. Although there is some difference of opinion as to the relative primitiveness of porogamy and chalazogamy, it is a significant fact that chalazogamy is confined to lower families of the Archichlamydeae, while all the higher Dicotyledons and all the Monocotyledons are porogamous. Further, the step from the gymnospermous condition, where the pollen-grains fall on the ovule and burrow through the intervening cells to the archegonia, to chalazogamy is short, but from the gymnospermous condition to porogamy is obviously great.

Granting that insect pollination and porogamy are points against the primitiveness of the Salicales, geological evidence has been cited to prove their antiquity.<sup>2</sup> From the Potomac of Virginia, however, the lowest of the

<sup>1</sup> Contributions from the Phanerogamic Laboratories of Harvard University, No. 44.

<sup>2</sup> Penhallow, D. P.: A Systematic Study of the Salicaceae. American Naturalist, vol. xxxix, No. 464, Aug. 1905, p. 525.

Cretaceous, remains have been discovered not only of *Saliciphyllum* and *Populophyllum*, but also of at least twenty other Angiospermous genera.<sup>1</sup> Until more data are secured, then, it is impossible to prove anything regarding the phylogeny of the Angiosperms from palaeobotanical evidence.

In view of these conflicting standpoints, it seems desirable that something should be said regarding the anatomy of the Salicales. Before doing so it will be well to enumerate some of the principles upon which comparative anatomy rests at the present time. The fundamental one is Haeckel's law of recapitulation. According to this we should look for primitive conditions in the seedling and the first annual ring, as applied to plants. Investigation has shown the soundness of this principle and has added other primitive regions, viz. the tissue about outgoing traces in both root and stem, the reproductive axis, the leaf petiole, &c. Further, experimental work has shown that reversion to a primitive condition often takes place after injury. It is from a study of these regions then, that phylogenetic deductions must be drawn.

Turning now to the Salicales, Figs. 1, 2, and 3 (Pl. XX) represent the wood of a typical poplar, *Populus trichocarpa*, in transverse, radial, and tangential planes respectively. From these it is evident that the rays are one cell in width, or uniseriate, and the parenchyma only at the end of the annual ring, or 'terminal'. Another diagnostic feature of the wood of the Salicales is the end-wall of the vessel, which has one large pore constituting the so-called porous perforation, as opposed to the scalariform perforation characteristic of *Betula*, for example. The type of fibres is obviously not primitive, and the type of vessel-end-wall is likewise high.

*Populus tremuloides* has normally the same wood structure as that of *P. trichocarpa*; Figs. 4 and 5 show, however, transverse and tangential sections through the wood formed after injury. Here the rays are bi- and triseriate, and the parenchyma, instead of being terminal, is present also around the vessels.

Seedlings of *P. tremuloides* were examined and show that, while the rays are always uniseriate, the parenchyma around the vessels, as well as in the terminal position, is common. This is especially true of the transition region between stem and root—in the hypocotylary stem. Above and below, the vasicentric parenchyma tends to die out. In the stem it is always present to a greater or less extent in the first annual ring, while in the root it persists fairly abundantly throughout. Fig. 6 represents a section through the root at some distance from the hypocotylary region and shows most of the vessels with one or two parenchyma cells next their tangential walls. Fig. 7 represents at the same magnification vessels with parenchyma cells, and Fig. 8 represents at a higher magnification another vessel with one cell.

<sup>1</sup> Fontaine : Potomac or Younger Mesozoic Flora. U.S. Geological Survey, vol. xv.

The last section includes the end-wall of the cell, and its simple pits prove conclusively that it is parenchymatous.

The other regions retentive of ancestral characteristics confirm the evidence supplied by the study of wounds. Fig. 9 represents a tangential view of the tissue subtending an outgoing leaf-trace; Fig. 10 an outgoing root-trace. Both show aggregations of bi- and triseriate rays.

Another species, *P. balsamifera*, may now be considered. The normal wood is similar to that of the two species already described, with uniseriate rays and terminal parenchyma. Figs. 11 and 12 are of wounded tissue and show the presence of biseriate rays. As in *P. tremuloides*, the wound also recalls the parenchyma around the vessels. In the former, however, wounds tend to bring back the parenchyma to a much greater extent than in the latter; as regards reversion in the rays, the condition is exactly opposite; i. e. a wound which in *P. tremuloides* would bring multiseriate rays only in the immediate vicinity of the injury, in *P. balsamifera* recalls the rays half-way around the stem. In the root of *P. balsamifera* the parenchyma is mostly terminal, with a slight tendency to the vasicentric condition; a very slight wound, however, suffices to bring it back in abundance around the vessels. Conditions similar to those of *P. tremuloides* were found in the first annual ring of the stem and under the leaf-trace.

*P. nigra* var. *italica* is another species with terminal parenchyma and uniseriate rays. Wounds in stool shoots bring back the parenchyma and rays in a striking way, an interesting feature being that the vasicentric parenchyma extends completely around the stem after a wound, while the multiseriate rays are confined to the immediate vicinity of the injury.

Among other poplars with terminal parenchyma and uniseriate rays are *P. grandidentata* and *P. laurifolia*. On investigation of the latter it was found that a very slight wound in the second annual ring is sufficient to recall the parenchyma to a moderate extent, while a severe wound further out brings back abundant vasicentric parenchyma and multiseriate rays.

*P. deltoides* presents a new condition. In this species the parenchyma is normally around the vessels, but the rays are uniseriate like those species already described. In the first two annual rings of a seedling the rays are practically all biseriate, dwindling thereafter to uniseriate, while vasicentric parenchyma in that region is extremely abundant. Slightly higher in the stem, where the leaf-traces go off, there is a comparatively large amount of parenchymatous tissue above and below each trace. A transverse section slightly above a trace shows a ray ten to twelve cells wide, which runs out for a short distance and then is dissected into multiseriate rays three to four cells wide. The other rays throughout the periphery of the stem are bi- and triseriate. Abundant vasicentric parenchyma is present in the first two annual rings, growing less so in the succeeding years of growth, but a transverse section in the plane of an outgoing trace shows that on

each side of the trace the vessels are surrounded by a jacket of parenchyma. Higher up in the stem biseriate rays disappear entirely except in immediate relation to the leaf-trace, while vasicentric parenchyma is scantily present throughout.

Another poplar with the same type of normal wood is *P. rotundifolia*. Here the wound reactions are what might be expected—multiseriate rays and abundant vasicentric parenchyma, while a moderate amount of ray parenchyma subtends the trace.

One species remains to be mentioned, the cottonwood of California, *P. Fremontii*. The wood of this species, represented in Pl. XXI, Fig. 13, has normally biseriate rays, but the parenchyma is exclusively terminal.

To sum up, the normal wood of the majority of poplars has uniseriate rays and terminal parenchyma. Investigation of regions characterized by ancestral conditions shows that vasicentric parenchyma is retained by the root and seedling and recalled in post-traumatic tissue in the stem. Further, multiseriate rays are retained in the seedling, and in connexion with leaf- and root-traces, and are likewise recalled by wounding.

Conditions in *Salix* are to a large extent similar to those in *Populus*. Figs. 14, 15, and 16 show three planes of *Salix Nuttallii* with uniseriate rays and terminal parenchyma. Fig. 17 represents a radial view demonstrating the vertically elongated 'marginal' cells of the rays. These cells are a perfectly constant diagnostic feature, and serve to differentiate between *Salix* and *Populus*.

Seedlings of various species of *Salix* show more or less abundant vasicentric parenchyma near the pith, but no biseriate rays except in immediate relation to a leaf-trace. Roots show vasicentric parenchyma normally and an abundance of biseriate rays after wounding. Both leaf-trace, Fig. 18, and root-trace, Fig. 19, show abundant subtending multiseriate rays.

Wounds in the stem result in the appearance of parenchyma around the vessels and multiseriate rays. Fig. 20 shows the wood of *S. nigricans* var. *primulifolia* after wounding. Almost every vessel in the field has at least one parenchyma cell on its tangential wall and some have two. Fig. 21 shows a portion of the same under a higher degree of magnification, Fig. 22 under a still higher magnification. This species gives an especially good wound reaction, parenchyma about the vessels being formed to a less extent on the side of the stem opposite the wound.

Young twigs a year old show considerable parenchyma around the vessels opposite the protoxylem clusters. At the node a large medium trace goes off to the bud, and two lateral ones to the leaf. The bud-trace leaves an extensive gap, some distance above and below which are clusters of bi- and triseriate rays. The leaf-traces often have subtending them rays four or five cells wide, which, half-way through the annual ring, are dissected into biseriate rays by the intrusion of vessels.

Leaf petioles and the mid-rib of the leaf itself have such a small amount of vascular tissue that no rays are developed, but the vessels are surrounded with parenchyma.

Other species of *Salix* with terminal parenchyma and uniseriate rays are *S. Hookeriana*, *S. japonica*, and *S. daphnoides*.

There are a number of species with uniseriate rays and vasicentric parenchyma—*S. fluviatilis*, *S. sitchensis*, *S. purpurea*, *S. lutescens*, and *S. viminalis*. Fig. 23 represents a transverse section of *S. fluviatilis*, showing vasicentric parenchyma.

*S. laevigata*, Fig. 24, has biseriate rays and terminal parenchyma normally, while both *S. sessilifolia*, *S. lasiolepis*, and *S. taxifolia* have biseriate rays and vasicentric parenchyma.

To sum up the genus *Salix*—the wood of the majority of species has normally uniseriate rays and terminal parenchyma. Vasicentric parenchyma is recalled after injury and retained in the root, in the seedling, and usually in the first year's growth throughout; multiseriate rays are recalled after injury and retained in connexion with leaf- and root-traces.

Applying then the principles of comparative anatomy as enumerated at the beginning, it is evident that the Salicales were primitively characterized by multiseriate rays and vasicentric parenchyma. A few species retain these features, while others have been reduced and have lost them, except in certain regions especially retentive of ancestral characteristics. In considering the relative position of different species of *Populus* and *Salix*, Penhallow suggests that on the basis of its wide distribution *P. balsamifera* is the most primitive and represents an ancestral type from which many of the localized types have descended. In view, however, of the anatomical considerations, it is evident that such forms as *P. balsamifera*, *P. trichocarpa*, *P. tremuloides*, *Salix Hookeriana*, *S. japonica*, &c., appear to represent reduced types, while such forms as *Populus Fremontii* and *Salix sessilifolia* represent the primitive condition.

Professor Penhallow also regards *Populus* as more primitive than *Salix*, since (p. 808) 'the parenchyma in *Populus* is always terminal' and (p. 813) biseriate rayed forms are more common in *Salix* than in *Populus*. The first statement appears to be a mistake, *P. deltoides* and *P. rotundifolia* having vasicentric parenchyma, but if it were true it would only serve to reinforce the second in showing, not that *Populus* is more primitive, but that it is more reduced and therefore higher than *Salix*. On p. 820 he says that 'the general trend of evidence so far collected, geological, geographical, and anatomical, is all in one direction, and that is to show that the genus *Populus* is essentially the more primitive'. The geographical evidence consists in the fact that the willows are more widely distributed and less localized than the poplars—the latter being supposedly survivors of some ancestral type. This evidence, if unsupported by other more convincing

testimony, is of little weight. The geological evidence consists in the fact that *Populus primaeva* is supposed to be older than any *Salix*, but the finding of both *Saliciphyllum* and *Populiphyllum* in the Potomac discredits any conclusions from fossil evidence. As for the anatomical evidence, there is only one species of *Populus* with biseriata rays, and there are only two with vasicentric parenchyma, as opposed to a dozen or more with terminal parenchyma and uniseriate rays. On the other hand, there are more species of *Salix* with vasicentric than with terminal parenchyma, and almost as many with biseriata as uniseriate rays. Accordingly, since both *Salix* and *Populus*, as shown by comparative anatomical evidence, are descended from forms with multiseriate rays and vasicentric parenchyma, it seems clear that *Populus* is more reduced than *Salix* and consequently higher.

The geographic distribution of the different species is of interest. The three North American species of *Salix* with vasicentric parenchyma and biseriata rays are indigenous west of the Mississippi, and the one species of *Populus* with biseriata rays is a native of California. On the other hand, the more reduced forms with uniseriate rays and terminal parenchyma grow in the eastern as well as the western part of the country. It is not uncommon to find that the western species of the United States are more primitive and less reduced than the eastern. For example, Mr. Bailey has recently investigated the western chestnut, *Castanopsis*, and finds here various structures, present in a greatly reduced form in the eastern *Castanea*.

Having discussed the anatomy of the Salicaceae, it is now desirable to discuss its bearing on their systematic position. Recent investigations in wood structure have shown that the most constant feature for diagnostic purposes is the distribution of the wood parenchyma, and the next best the width of the rays. The evolution of rays in the vascular plant series would be somewhat as follows: most Gymnosperms have uniseriate rays. In the epicotyledonary seedling stem of *Quercus* there are uniseriate rays near the pith which on passing out in certain segments become bi- and triseriate; then by approximation of the rays and elimination of vessels these segments become 'false' rays—the permanent condition in the adult Live Oak. Further on, by the elimination of the intervening tracheides the rays become solidly parenchymatous, as represented in the homogeneous masses of ray parenchyma in the mature wood of North American White and Black Oaks.<sup>1</sup> That rays of this type are made up of compounded multiseriate rays is proved by the wound reaction.<sup>2</sup> In genera slightly higher than *Quercus*, i. e. *Carya*, *Ostrya*, *Fagus*, &c., these rays, solid at the pith, break up as they pass out, until by the intrusion of fibres and vessels in both

<sup>1</sup> Eames, A. J.: On the Origin of the Broad Ray in Oaks. *The Botanical Gazette*, xlix, pp. 161-7, No. 3.

<sup>2</sup> Bailey, I. W.: Reversionary Characters of Traumatic Oak Woods. *The Botanical Gazette*, l, pp. 374-80, No. 5.

horizontal and vertical planes they become the multiseriate rays characteristic of the mature wood of most Dicotyledons.<sup>1</sup> This process can be observed especially well in certain of the Ericaceae and Casuarinaceae, where the compound ray is present only near the leaf-trace. In fact, it has been shown that the leaf-trace has played the chief part in the formation of compound rays.<sup>2</sup> As these multiseriate rays go from the pith, they are apt to dwindle, as seen in the seedling of *Populus deltoides*, for example, until uniseriate rays are formed. This is the condition in the Salicaceae, *Aesculus*, and, as Mr. Bailey has ascertained, in *Castanea*, all of which have uniseriate rays normally in the adult, but multiseriate rays in the primitive regions.

Whether the direct ancestors of the Salicales ever attained compound rays like those of the oak, it is impossible to say. All that comparative anatomical evidence shows is that they are descended from ancestors which possess multiseriate rays, and adequate palaeobotanical evidence on their origin is lacking at present. It is evident, however, that the compounding process must have taken place in very remote geological time, since multiseriate rayed forms are common in the Upper Cretaceous of Japan.<sup>3</sup>

The development of parenchyma is somewhat as follows: In the Abietineae there is no parenchyma in *Pinus*; but in all the other members there is terminal parenchyma. In the Sequoieae and Cupressineae the parenchyma is diffuse, i. e. scattered through the year's growth. Since the Gymnosperms never developed vessels the parenchyma never got beyond the diffuse condition. It is likewise diffuse in the Gnetales and in the lower Angiosperms, as the Casuarinaceae, Betulaceae, Fagaceae, and Juglandaceae; while in the highest Angiosperms it is clustered around the vessels, as in the Oleaceae, Ulmaceae, Leguminosae, &c. Reduction then sets in and the Saliceae and Magnoliaceae have terminal parenchyma in the stem, but vasicentric in primitive regions. It is of interest to note that conditions in the Magnoliaceae are similar to those in the Salicaceae—the Asiatic genus, *Michelia*, has vasicentric parenchyma in the stem, and *Liriodendron tulipifera* has vasicentric parenchyma in traumatic tissue. Another interesting case of reversion is seen in *Osmanthus*, a member of the Oleaceae, where the parenchyma is exclusively terminal.

From this consideration of the evolutionary tendencies in the development of rays and parenchyma, it is evident that the Salicaceae, instead of coming low down among the Dicotyledons, as is assumed by systematic botanists, in reality represent, from the anatomical standpoint at least,

<sup>1</sup> Thompson, W. P.: The Origin of Multiseriate Rays in Dicotyledons. *Annals of Botany*, vol. xxv, 1911, p. 1005.

<sup>2</sup> Bailey, I. W.: The Relation of the Leaf-trace to Compound Rays in the Lower Dicotyledons. *Annals of Botany*, vol. xxv, No. xcvi.

<sup>3</sup> Stopes and Fujii: Studies on the Structure and Affinities of Cretaceous Plants. *Phil. Transactions of Royal Society of London, Series B*, vol. cci.

a condition of reduction from a high type. The evidence for this view may be briefly stated as follows: The primitive distribution of wood parenchyma in the Salicaceae as shown by this investigation is obviously vasicentric or centred around the vessels, a condition uniformly characteristic of such high families as the Compositae, Oleaceae, &c. In ray structure, the Salicaceae are likewise clearly allied with the higher and not the lower Dicotyledons, since their uniseriate rays obviously represent a condition of reduction from the multiseriate type characteristic of the higher woody Angiosperms and not a primitively simple condition as suggested by the late Professor Penhallow.

#### CONCLUSIONS.

1. Most eastern representatives of the North American Salicales are characterized normally by terminal parenchyma and uniseriate rays.
2. In primitive regions vasicentric parenchyma and multiseriate rays are found.
3. Certain western North American representatives of the Salicales have normally vasicentric parenchyma and multiseriate rays.
4. The primitive condition for the wood of the Salicales is vasicentric parenchyma and multiseriate rays.
5. The low position assigned to the Salicales by systematists appears not to be justified.
6. Since their simple structure is due to reduction from a condition originally more complex, the Salicales have a high position in the dicotyledonous series.

In conclusion, I wish to express my thanks to Professor E. C. Jeffrey for his helpful advice and for aid in securing the photomicrographs accompanying this article; to Professor J. G. Jack of the Arnold Arboretum for seedling material he was kind enough to send me; and to Mr. I. W. Bailey for sections of various western species.

#### EXPLANATION OF PLATES XX AND XXI.

Illustrating Miss Holden's paper on Salicales.

##### PLATE XX.

- Fig. 1. *Populus trichocarpa*: transverse section of normal wood, showing uniseriate rays and terminal parenchyma.  $\times 300$ .  
 Fig. 2. Same: radial section, showing terminal parenchyma.  $\times 300$ .  
 Fig. 3. Same: tangential section, showing uniseriate rays.  $\times 300$ .  
 Fig. 4. *P. tremuloides*: transverse section of wounded wood, showing biseriate rays.  $\times 300$ .  
 Fig. 5. Same: tangential section, showing biseriate rays.  $\times 300$ .  
 Fig. 6. Same: transverse section of root, showing vasicentric parenchyma.  $\times 400$ .



Fig. 7. Same.  $\times 400$ .

Fig. 8. Same.  $\times 700$ .

Fig. 9. Same : tangential section of stem, showing multiseriate rays under leaf-trace.  $\times 300$ .

Fig. 10. Same : tangential section of root, showing multiseriate rays under root-trace.  $\times 300$ .

Fig. 11. *P. balsamifera* : transverse section of traumatic wood, showing biseriate rays.  $\times 300$ .

Fig. 12. Same : tangential section of traumatic wood, showing biseriate rays.  $\times 300$ .

PLATE XXI.

Fig. 13. *P. Fremontii* : tangential section of normal wood, showing biseriate rays.  $\times 300$ .

Fig. 14. *Salix Nuttallii* : transverse section of normal wood, showing uniseriate rays and terminal parenchyma.  $\times 300$ .

Fig. 15. Same : tangential section of normal wood, showing uniseriate rays.  $\times 300$ .

Fig. 16. Same : radial section.  $\times 300$ .

Fig. 17. Same : radial section, showing marginal ray cells.  $\times 300$ .

Fig. 18. *Salix* sp. : tangential section of stem, showing multiseriate rays under leaf-trace.  $\times 300$ .

Fig. 19. Same : tangential section of root, showing multiseriate rays under root-trace.  $\times 300$ .

Fig. 20. *S. nigricans* var. *primulifolia* : transverse section of traumatic wood, showing vasicentric parenchyma.  $\times 300$ .

Fig. 21. Same.  $\times 400$ .

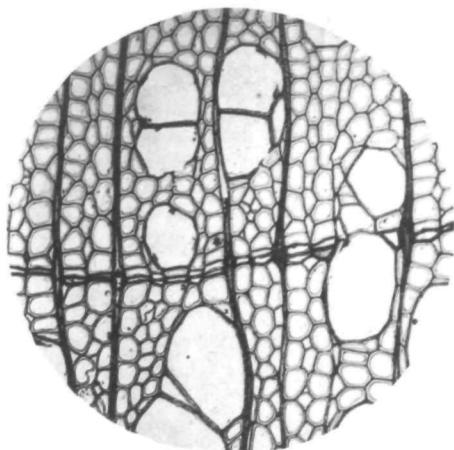
Fig. 22. Same.  $\times 700$ .

Fig. 23. *S. fluviatilis* : transverse section of normal wood, showing vasicentric parenchyma.  $\times 300$ .

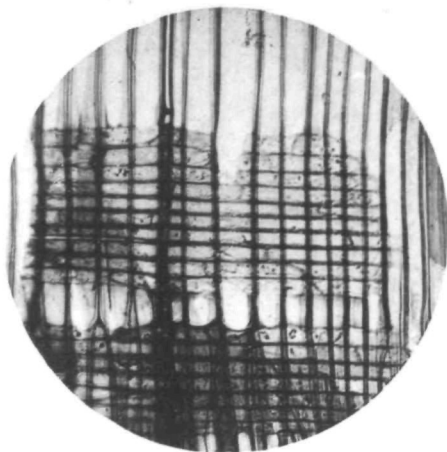
Fig. 24. *S. larvigata* : tangential section of normal wood, showing biseriate rays.  $\times 300$ .







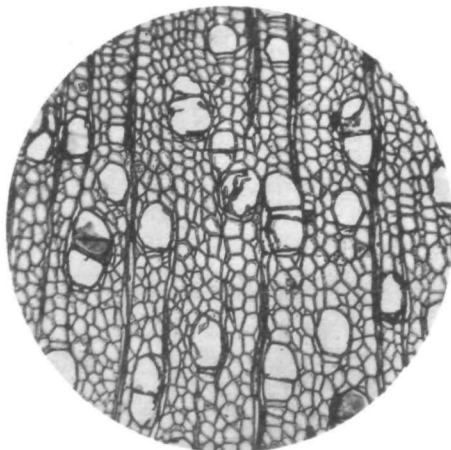
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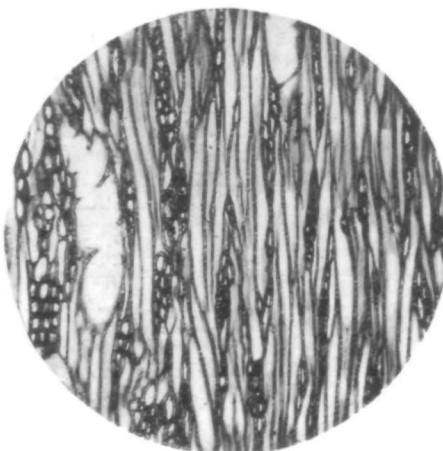
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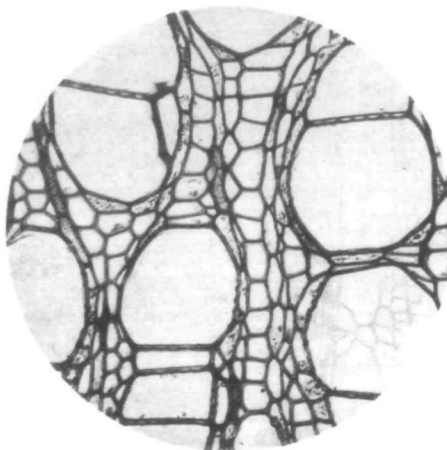
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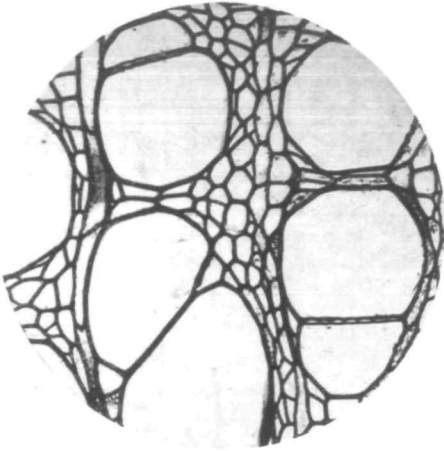


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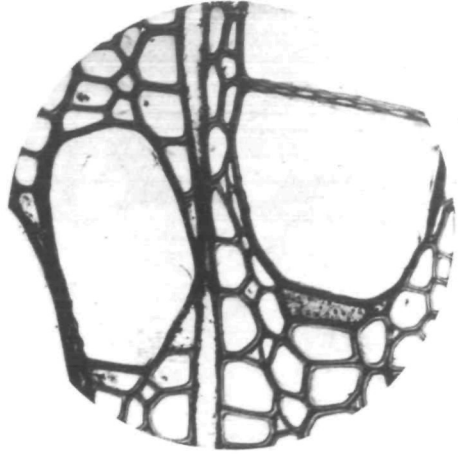


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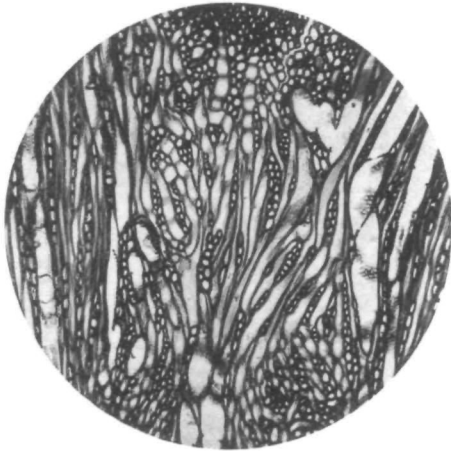
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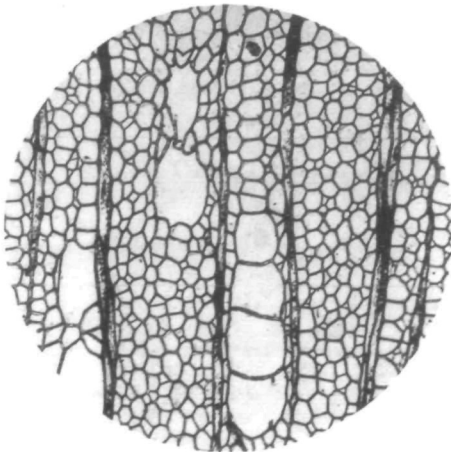
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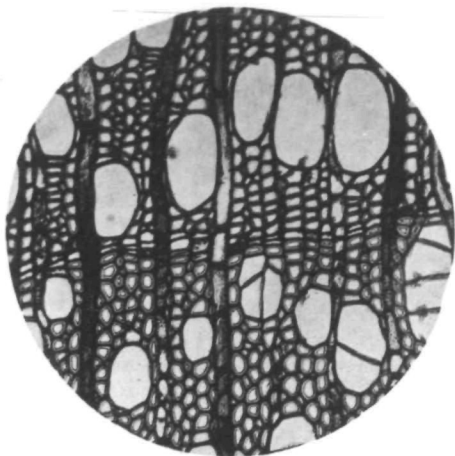
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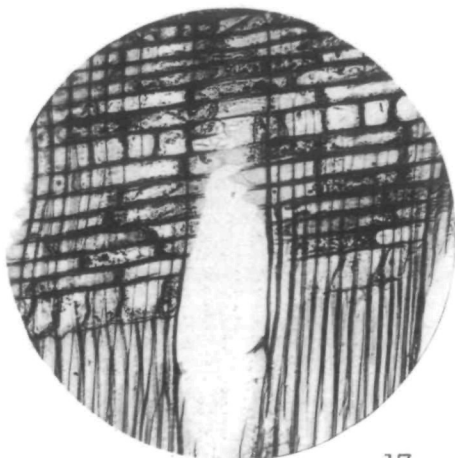
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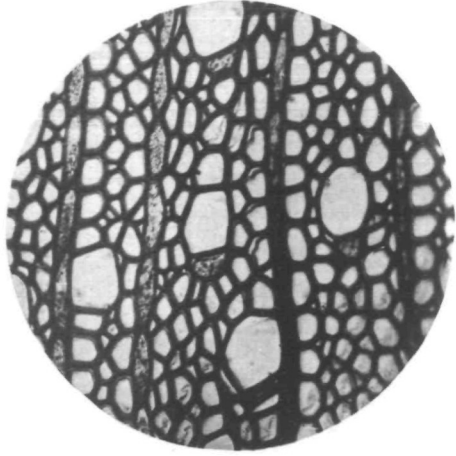
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HOLDEN—SALICALES.

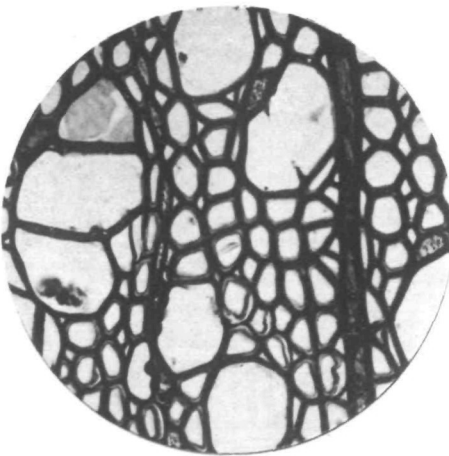




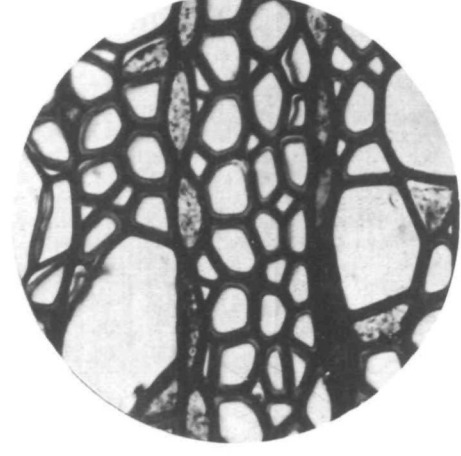
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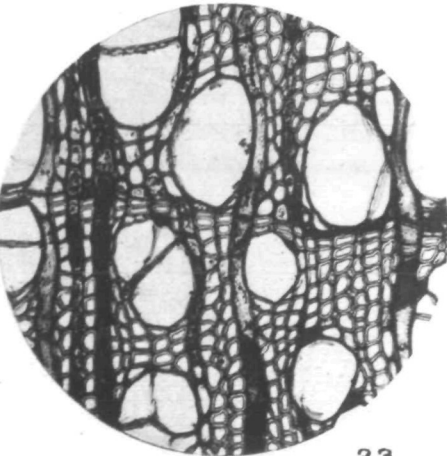
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23.



24.

Huth coll.

