The Relationships of the Different Types of Angiospermic Vessels.

BY

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With eleven Figures in the Text.

IT was recently demonstrated that in some angiosperms the simple or 'porous' perforation of the vessel has been evolved by the loss of bars from the scalariform type. At the same time it was pointed out that the scalariform type itself may either represent a retention and slight modification of the primitive scalariform pitting of the older gymnosperms and pteridophytes or may have been secondarily evolved by the fusion of circular bordered pits. Subsequently Miss Bliss (1) has called attention to the fact that in some cases the simple perforation seems to have been formed by the haphazard fusion of circular perforations derived from bordered pits after the manner which I had described as occurring in Gnetales (5). She considers that in some cases circular bordered pits have fused in horizontal rows to form scalariform pits which by a slight modification have become scalariform perforations, and these by a further fusion have become simple, while in other cases the circular bordered pits have fused haphazardly to produce simple perforations. The two methods are simply variations of the same fusion process. Brown (2), on the other hand, maintains that scalariform pits and perforations are not secondarily derived by pit fusions, but are retentions of the primitive scalariform pitting, and that the circular pits of angiosperms, as of lower plants, have been formed by the breaking up of scalariform pits through a reticulate condition.

It was therefore desirable that a comprehensive survey of angiospermic vessels be made to determine how the vessel had been evolved in each group, how commonly haphazard fusions had occurred, their significance in the general evolution of the angiospermic vessel, and their relationship to the process described for Gnetales. In this survey it became clear that the existence of certain other types of perforations required emphasis.

THE WIDESPREAD OCCURRENCE OF TRANSITIONS BETWEEN SCALARIFORM AND SIMPLE PERFORATIONS.

Transitions between scalariform and simple perforations (Fig. 1) are present in a great many species belonging to many different families. In a considerable number of species both scalariform and simple perforations may be found in the adult wood, and almost invariably these woods also show transitions between the two types. In many species simple perforations only are found in the adult wood but scalariform ones are present next to the pith, and these species generally show beautiful stages in the loss of scalariform bars in the region just outside the scalariform vessels. In almost every family in which species are found characterized by simple

perforations and others characterized by scalariform ones, species may also be found showing the intermediate stages.

FIG. 1. A-D. Transitions between scalariform and simple perforations in the vessels of *Symphoricarpos occidentalis*.

While on the whole the transitions are commoner in the lower families they can be found even among families placed very high systematically. In the Caprifoliaceae, for example, beautiful cases are quite common. In Fig. 1 a group of transitional perforations are shown as seen in *Symphoricarpos occidentalis* (Hook.). For the details of the

process the reader is referred to my earlier paper (5). Altogether I have noted such transitions in many species distributed among twenty-eight families from Casuarinaceae to Compositae. It may be concluded that at least in the great majority of angiosperms the uniperforate vessel has been evolved from the scalariform type by the loss of bars from the latter.

VESSELS WITH RETICULATE PERFORATIONS.

In some species there are perforations which are neither simple nor purely scalariform but which are in some degree reticulate. The reticulations are of several different sorts. The simplest kind is that which is not uncommonly associated with the scalariform type. Wherever scalariform pits or perforations are found, from ferns to angiosperms, there is a tendency for contiguous bars to be joined occasionally, either by a more or less definite cross-piece or as a result of their being not quite parallel. In some cases these connexions between contiguous bars become fairly frequent, and a more or less intricate net results. But the essential

scalariform nature of such perforations is evident. Particularly intricate examples are found in some Compositae (Fig. 2) and Ericaceae, in *Sauraja*, *Myrothalamus*, *Tetracera*, *Alsodeia*, *Cornus*, and *Tropaeolum* (Fig. 5). They are of the same nature as the reticulate pitting which frequently accompanies the scalariform pits of the side walls. It is well known that in the older vascular plants, at least, the multiseriate circular pits have been derived from scalariform pits through such reticulate conditions.

Another kind of reticulate perforation is found in a few species. We may take as examples of these the vessels of *Cordia* illustrated in Fig. 3. Here the perforation is in the form of a rather regular uniform net. The individual openings in the net are approximately isodiametric and about the same size as, or slightly larger than, the bordered pits on the side walls of the same vessel. The whole net is about the same size as the simple per-

FIG. 2. A, B. Reticulate perforations in *Helianthus* sp.

FIG. 3. A, Reticulate perforation from *Cordia myxa*. B and C, from *Cordia suaveolens*.

foration of other types. In many cases the net sags down at the centre into the vessel-segment below it. This is shown in face-view, Fig. 3, B, and in section in Fig. 3, C. In these perforations there is no indication whatever of the scalariform condition or of the fusion of pits to form the individual openings. In fact these openings are little larger than the bordered pits of the side wall, and appear to have been formed by the loss of the membranes of the pits accompanied by a slight amount of enlargement.

These reticulate perforations have been observed in several species of *Cordia* (Boraginaceae), *Tecoma radicans* (Fig. 4, A) (Bignoniaceae), *Vitex alata* (Verbenaceae), *Bougainvillea speciosa* (Fig. 4, B) (Nyctaginaceae), and *Boerhaavia* sp. (Nyctaginaceae). They never occur to the exclusion of other types. In fact in every case observed the great majority of perforations are of the simple type, though examples of the reticulate type are present in most sections. Their occurrence is very sporadic. I have carefully examined many other species in the families to which the above-mentioned forms belong without finding any trace of them. They occur in forms where the great majority of perforations are simple.

Reticulate perforations of this type appear to be quite different from those described above as frequently accompanying the scalariform type. They show no trace of the scalariform condition. It is, of course, conceivable that they are of the same nature as those previously described, and that the reticulation of the latter has gone much farther and the individual pores rounded up. In *Tropaeolum* one sometimes finds perforations approaching the *Cordia* type along with more numerous ones which are nearly scalariform-

FIG. 4. A, Vessel from *Tecoma radicans*. B and C, from *Bougainvillea speciosa*.

FIG. 5. A-D. Scalariform-reticulate perforations from *Tropaeolum*.

FIG. 6. Vessels from *Cordia callacosa*, A showing evidence of the loss of reticulations.

FIG. 7. A-F. Stages in the disappearance of reticulate perforations in *Potentilla monspeliensis*.

form (Fig. 5). But the origin and relationships of the different types will be discussed in later paragraphs.

In some cases there is evidence that the reticulate perforations of the *Cordia* type have disappeared and given the simple type. Appearances such as Fig. 6, A, are common next to the pith in *Cordia callacosa*. The scalloped edge of the perforation appears to be the result of the loss of a net. A similar perforation is shown in Fig. 4, C, drawn from *Bougainvillea speciosa*. In these forms I have never seen any evidence of the individual pores of the net fusing; apparently the whole net is lost at once.

In some species a very irregular net appears to be associated with a fusion of perforations, as pointed out by Miss Bliss. Such conditions may be found in certain members of the Rosaceae, and are illustrated in Fig. 7 from *Potentilla monspeliensis*, and in Fig. 8 from *Cydonia*. Somewhat

similar conditions have been observed in *Tropaeolum* (Fig. 9), and in *Pelargonium paeclargium* collected at Cape Town. From these figures it seems clear that small perforations are fusing irregularly and producing large simple perforations. In many vessels in the region where this fusion is proceeding the perforations are scalariform or nearly so (Fig. 8), while in

FIG. 8. A-F. Scalariform-reticulate perforations and their fusion in *Cydonia*.

FIG. 9. A and B. Loss of reticulations in vessels of *Tropaeolum*.

FIG. 10. A-C. Perforations in *Epacris coriacea*.

FIG. 11. A and B. Perforations in *Epacris coriacea*.

other vessels the reticulate condition which frequently accompanies the scalariform is evident. Such fusions are relatively rare and are usually found in herbs.

Still another type approaching a net is figured by Solereder (4) for *Epacris*. In this case there are peculiar clusters of perforations as shown in Fig. 10, A. Careful examination of many vessels shows, however, that these are really due to scalariform bars inclined at different angles on the two sides of the wall as seen in Fig. 10, B and C, and Fig. 11, A. Frequently the bars on one side are larger and farther apart than those on the other side. Sometimes the finer bars can be traced right across the larger ones, but in other preparations they cannot be so traced. In some cases (Fig. 11, B) the bars on one side disappear, while those on the other side remain.

DISCUSSION.

The significance of these reticulate perforations in regard to the evolution of the vessel depends on their relation to the scalariform type, and this in turn depends on the origin of that type. I pointed out in an earlier paper that the scalariform perforation may have originated in two ways: it may represent a slight modification of the primitive scalariform pitting, or may have been derived by the fusion in horizontal rows of circular pits.

Miss Bliss has presented evidence that the scalariform pit and perforation in angiosperms have originated in the second way—by the fusion of circular pits. It is necessary to assume, on this view, that the circular pits were originally formed from the scalariform ones by the reticulation of the latter, and that in angiosperms the reverse process has occurred, and the circular pits gone back again to scalariform by a fusion process. She believes also that the irregular nets, as seen in *Rosaceae*, &c., are simply a variation in this fusion process.

Brown (2), on the other hand, holds that the scalariform condition is primitive in angiosperms, being a survival of the exactly similar pitting of the older gymnosperms and not a most remarkable instance of reversed evolution. The scalariform pit is being discarded for the circular one. It is first discarded on the side walls because, since these walls are in contact with a variety of cells differing in shape, size, &c., the scalariform pit loses its alinement. Under these conditions the circular pit is more adaptable and comes to prevail. On the end walls, however, which are in contact with walls like themselves, the scalariform type remains and becomes the scalariform perforation.

Miss Bliss's chief argument is the occurrence of intermediate stages between multiseriate and scalariform pits. Admittedly there are abundant examples of these transitions in angiosperms. But obviously the transitions may be read in either direction. Bliss reads them from circular to scalariform and Brown from scalariform to circular. The decision must be made on other evidence.

Brown states that in conservative regions the scalariform pit prevails, and that the multiseriate circular type characterizes the more specialized parts, while Bliss contends that the reverse is true. I am bound to state that in my experience with a large number of species Brown is correct. The order from the pith outwards as I find it is the familiar one of lower plants, spiral, scalariform, reticulate, multiseriate. And in a large number of species the scalariform pitting persists through the secondary wood with or without the circular type. It is, of course, possible in some forms to find scalariform pits in the older wood and compare them with carefully selected circular pits near the pith somewhere else. It is necessary to take into

consideration differences in the rate at which the transformation of one type into another takes place. In one radial row it may take place more rapidly than in another. Also the first vascular elements of one row may be farther out than those of another. Therefore sections which are slightly oblique and include more than one row may give very deceptive appearances. When the transitions are studied carefully in a single row of cells it is found that the scalariform pitting appears first, is succeeded by the reticulate type, and this in turn by the multiseriate circular type, just as in ferns and gymnosperms, and that in many forms the scalariform type persists through the secondary wood.

Moreover, adequate comparisons of the secondary wood of specialized and primitive families shows that scalariform pitting when it occurs is generally in the latter (such as Piperaceae, Monimiaceae, Cupuliferae, Magnoliaceae, Bruniaceae). As in other cases, the different tendencies in the evolution of wood structures are expressed in different degrees in different cases. But in general highly specialized woods show multiseriate and not scalariform pitting on the side walls.

Miss Bliss also argues that since in some cases in ferns the end walls are reticulate while the side walls are scalariform, therefore the end wall is more specialized than the side wall. Consequently in those angiosperms which show the scalariform condition on the end wall and multiseriate pits on the side wall, the scalariform must represent the more advanced condition. It seems to be stretching the doctrine of conservative regions rather far to say that one side of a cell must in all cases be more conservative than another side. Moreover, as a matter of fact there are plenty of reticulate side walls in ferns and many dicotyledons with scalariform side walls. The true explanation of the occurrence of multiseriate pits on the side walls and scalariform perforations on the end walls of the same segments appears to be that the scalariform pit is being discarded for the multiseriate, that since the side walls in dicotyledons are in contact with a great variety of smaller cells the scalariform pits loses its alinement and quickly becomes broken up, and that since the end wall is in contact with a similar end wall the scalariform condition tends to remain in this position.

The view that the scalariform pit is primitive in angiosperms and not derived secondarily by the fusion of multiseriate circular pits is then supported by (1) the extreme improbability of such a remarkable example of reversed evolution, (2) the succession of vessels with the different types of pitting and transitions in the first-formed wood, and (3) the occurrence of the scalariform type in primitive families and the nearly universal occurrence of the multiseriate type in highly specialized families.

If the scalariform perforation is primitive in angiosperms, being a retention and slight modification of the scalariform pitting of primitive gymnosperms and pteridophytes, there has been no fusion process in its

production, and consequently the various reticulate conditions cannot represent a variation of such a fusion process. Reticulate perforations of the type found in Compositae, Ericaceae, &c., appear to be modified reticulate pitting which is commonly associated with scalariform, and which in some cases is derived from the latter as a passing phase in the production of multiseriate pitting.

The uniform nets of *Cordia*, *Tecoma*, &c., are relatively very rare and sporadic, and occur in highly specialized families (Borraginaceae, Bignoniaceae, Verbenaceae), so that they appear to have no significance in the evolution of the vessel as a whole. Moreover, there is no evidence of pit fusions in these cases. The individual pores are of the same size or only slightly larger than bordered pits. The whole net appears to drop out at once. They are found in only a few of the vessels. It seems probable that they represent a special condition. Apparently the vessel-segments start to form alternate pitting on all walls, and then the membranes drop out at the ends. In some cases the net seems to be due to the fact that the end of one vessel-segment abuts on the side wall of another overlapping segment. The end becomes perforated, but the side on the other element retains its alternate pitting, in many cases losing the membranes. Sometimes two adjoining vessels have lateral communications, and it is not unnatural that in such conditions the reticulate condition derived from alternating pits should occur.

As for the fusions in *Cydonia*, *Potentilla*, &c., in some cases at least they appear to be due to the loss of reticulations in the same way as the bars disappear from scalariform perforations. It is to be noted that frequently both scalariform and reticulate conditions are found in the same perforated area which is breaking down to form the simple perforation. The scalariform pit has been transformed into the multiseriate through the reticulate condition, and there appears no reason why this transformation could not have begun in occasional forms before the pits became perforate. At any rate the reticulate condition frequently accompanies the scalariform, and may break down to produce the simple perforation in the same way that the scalariform does. But even if we grant that they are real fusions of multiseriate bordered pits, it seems that they could have little significance. They are of such rare and sporadic occurrence, and are found in such specialized forms (chiefly herbs), that their existence can be of little real importance, in view of the evidence that the scalariform type is primitive and the widespread occurrence of transitions between scalariform and simple perforations.

It is undoubtedly true that in the great majority of angiosperms the uniperforate vessel has been derived from the scalariform by the loss of the bars, and the balance of the evidence shows that the scalariform perforations are the result of a slight modification of the primitive scalariform

pits. These latter have also on the side walls become broken up to form multiseriate circular pits through a reticulate condition. The reticulate end-wall perforations are associated with this, or in some cases may represent special anomalies.

In Gnetales, on the other hand, the uniperforate vessel has undoubtedly been produced by the fusion of smaller perforations derived from circular bordered pits (5). There is no scalariform or reticulate condition in the secondary wood. Occasionally, since the pits are haphazardly arranged, two perforations derived from bordered pits may, in specially selected places, stand on the same horizontal level. But to use such specially chosen portions of an end wall as examples of the scalariform condition, as MacDuffie (3) has done, is to use the term scalariform in a sense quite different from that which it has always conveyed.

SUMMARY.

1. Transitions between scalariform and simple perforations are found in the vessels of numerous species of angiosperms belonging to many different families from the lowest to the highest.

2. In a few species reticulate perforations accompany the other types. In some cases they are like the reticulate pitting which frequently accompanies scalariform pits; in other cases a regular net with isodiametric individual openings is found. In the former the individual openings may fuse irregularly and produce simple perforations; in the latter the net appears to be lost as a whole.

3. The evidence, which is reviewed, indicates that the scalariform *pitting* of angiosperms is a retention of the primitive scalariform pitting of the older gymnosperms and pteridophytes, and is not produced secondarily by the fusion of circular multiseriate pits. On the other hand, it has given rise to the circular pits of the side walls through a reticulate condition. It has also given rise to the scalariform *perforations* of the end walls.

4. Since the scalariform perforations are not the result of a fusion, the reticulate perforations are not the result of a variation in this fusion. They represent rather a special or abnormal condition generally found in specialized forms.

5. The perforations of Gnetales are not genetically related to any of the types found in angiosperms.

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