(4) Evidence is brought forward that is not inconsistent with the idea that salt absorption by storage tissue is dependent on ionic interchange.

(5) So far as it provides an explanation of how the permeability of a plasmatic membrane may be altered, the colloid precipitation theory receives support from this work.

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Perforated Ray Cells.

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(Communicated by R. S. Troup, F.R.S.—Received February 8, 1933.)

In certain woods, whose rays have extensive uniseriate margins, an individual marginal cell may sometimes be modified, by the perforation of its side walls, to connect two vessel segments on opposite sides of the ray. This feature does not appear to have been previously described though it is by no means uncommon; it has been observed by the authors in woods of many widely separated families. It is limited to woods with particular types of ray and vessel structure, but its occurrence seems to be primarily determined by the manner in which the vessels develop.

Large ray cells which appeared to have scalariform perforations in the side walls were first observed by the authors in the wood of *Lacistema aggregatum* (Berg.) Rusby. (Lacistemaceæ); examination of macerated material, fig. 1, has shown that the side walls of these cells are exactly similar to the end walls of the vessel segments, and though it has not been possible to demonstrate the absence of a membrane, the authors are convinced from a careful study of the sections, that these walls are actually perforated, and that each forms a link between two vertical series of vessel segments. The course of the vessel is unusual; instead of continuing up and down between the rays, it periodically passes obliquely through a ray, and continues on the other side. The ray is usually uniseriate at the point at which it is crossed, and the ray cell involved becomes slightly swollen, rather in the manner of an oil or mucilage cell but without visible contents. The lateral walls are perforated, so that the cell resembles a very short vessel segment, and presumably functions as such. From the position and shape of these cells, however, it is clear that they have been derived from ray initials and not from fusiform initials. Attention was first drawn to this phenomenon by the presence of scalariform bars in the

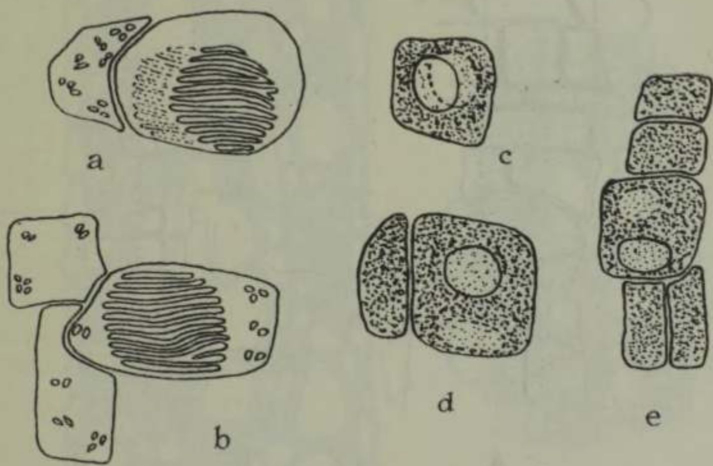


FIG. 1.—*Macerated material.* *a* and *b*, ray cells of *Lacistema aggregatum* Rusby, showing scalariform perforations; *c*, *d* and *e*, *Ptychopetalum anceps* Oliv., with simple perforations. (× 115.)

walls of cells which, from their shape, appeared at first sight to be oil or mucilage cells; simple perforations in such cells are obviously more easily overlooked, and it was not until a special search was made that they were found to be by no means uncommon, and to occur in woods of several different families.

In the following account of these cells, two woods in which they are numerous have been selected for description, *Lacistema aggregatum* (Berg.) Rusby, in which the perforations are scalariform, and *Ptychopetalum anceps* Oliv. (Olacaceæ), in which they are simple. The simple perforations in *Ptychopetalum* are shown in fig. 1, *c*, *d* and *e*; the cells are drawn from slides of macerated material, and the two perforations can be seen on the opposite walls of the cells.

Fig. 2 shows outline drawings of two pieces of tissue from macerated material. The position of a perforated ray cell relative to adjacent vessel segments in *Lacistema* is shown in A. A vessel segment *a* lies over some ray cells, the ray is passed through, and the vertical course of the vessel is continued by the segment *a′* on the other side of the ray; the ray cell *b* shows two scalariform perforations coinciding with those of the vessel segments *a* and *a′*. Fig. 2, B, shows a similar piece of tissue from *Ptychopetalum*; the vessel segment *a* lies

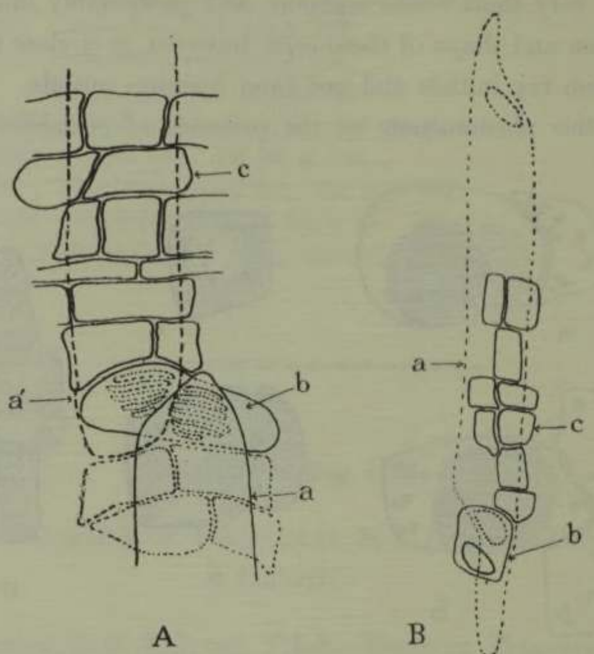


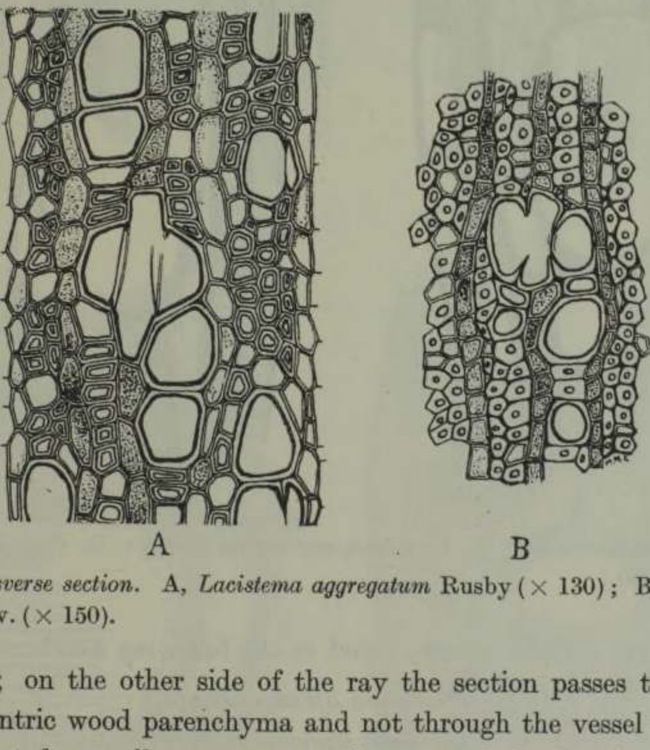
Fig. 2.—*Macerated material.* Groups of unseparated ray cells and vessel segments: A, *Lacistema aggregatum* Rusby; B, *Ptychopetalum anceps* Oliv. (*a*) vessel segment, (*b*) perforated ray cell, (*c*) ordinary ray cells. (× 75.)

under some ray cells *c*, and at *b* there is a ray cell with two simple perforations; the perforation seen at the lower focus of the microscope (shown with a dotted line) coincides with that of the underlying vessel segment.

In macerated material in which the individual elements have not been completely separated, it is often possible to observe the perforated ray cell in position between the two vessel segments, but in longitudinal sections, one or other of the vessel segments is usually missing, and consequently the true nature of the phenomenon may easily be overlooked.

In cross-sections the perforations are not conspicuous but are easily distinguished if a search is made for them. Fig. 3 illustrates cross sections through the wood of *Lacistema* (A) and *Ptychopetalum* (B); the ends of two segments of the same vessel can be seen separated by a perforated ray cell. In fig. 3, A, bars of the scalariform perforations and in B, the rims of the simple perforations are visible. In both drawings it is clear that the perforated ray cells are much larger radially than the normal ray cells, but are only slightly wider tangentially.

The change in the course of a vessel from one side of a ray to the other, and the linking up of the laterally displaced vessel segments by a cell of the ray, are most clearly seen in tangential section, and are illustrated in fig. 4, B. Fig. 4, A, shows a similar lateral displacement of the vessel segments in *Lacistema*, but only one vessel segment and one perforation into the ray cell



A B

FIG. 3.—*Transverse section.* A, *Lacistema aggregatum* Rusby (× 130); B, *Ptychopetalum anceps* Oliv. (× 150).

can be seen; on the other side of the ray the section passes through a cell of the vasicentric wood parenchyma and not through the vessel itself.

The perforated ray cells are most conspicuous, and the details of the perforations most easily seen, on the radial section, but the tangential displacement of the vessel segments usually prevents the inclusion of both segments in the same radial section, and the continuation of the vessel on the opposite side of the ray is consequently seldom evident; it is, however, often possible to see both perforations in the ray cell, fig. 5D.

The perforations of the ray cells are scalariform where the end walls of the vessels have exclusively scalariform or mixed scalariform and simple perforations; where the vessel perforations are simple, those of the ray cells are usually also simple, but may occasionally be scalariform. In both cases the scalariform perforations in the ray cells show a marked tendency to irregularity, of the type shown in fig. 6. This type of perforation is particularly common in association with vessels with simple perforations, for example, in the Rubiaceæ and some of the Euphorbiaceæ.

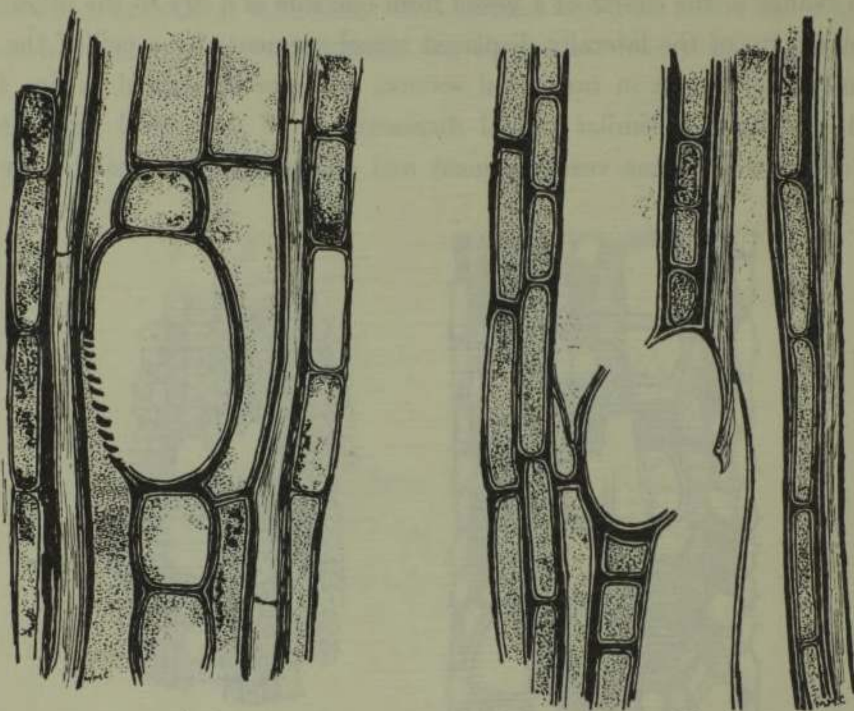


Fig. 4.—*Tangential section.* A, *Lacistema aggregatum* Rusby; B, *Ptychopetalum anceps* Oliv. (× 300.)

Perforated ray cells have been found in the following woods:—

Apocynaceæ	*Funtumia africana* Stapf.†
	Gonioma kamassi E. Mey.
	**Odontadenia speciosa* Benth.†
	**Tabernæmontana citrifolia* L.†
	,, *grandiflora* Jacq.†
Araliaceæ	*Meryta sonchifolia* Linden and André.†
Calycanthaceæ..........	**Calycanthus floridus* L.†
Caprifoliaceæ	*Lonicera* sp.†

* Perforated ray cells extremely common.

† Correlated with herbarium material.

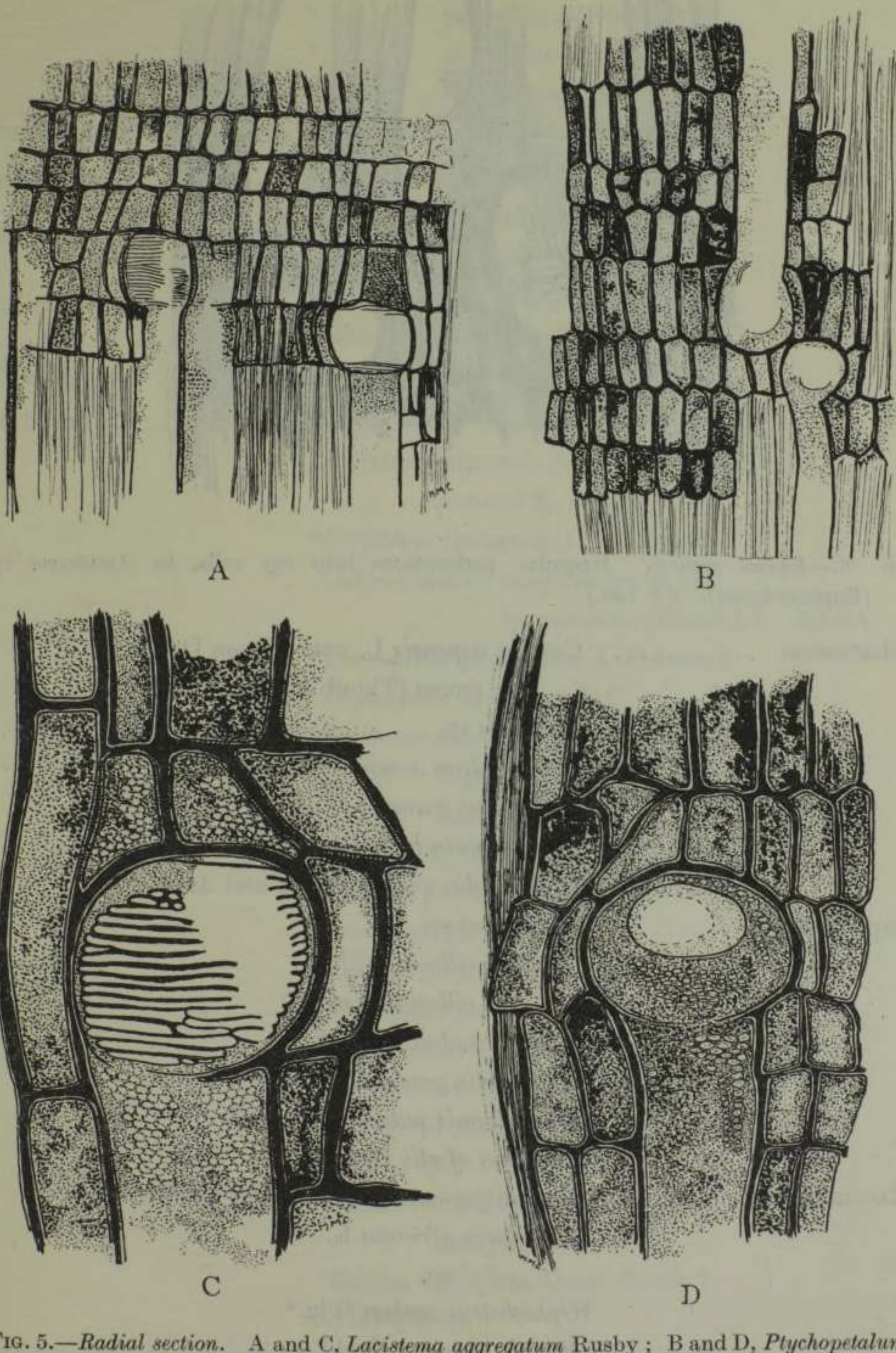


Fig. 5.—*Radial section.* A and C, *Lacistema aggregatum* Rusby; B and D, *Ptychopetalum anceps* Oliv. (A and B, × 150; C and D, × 300.)

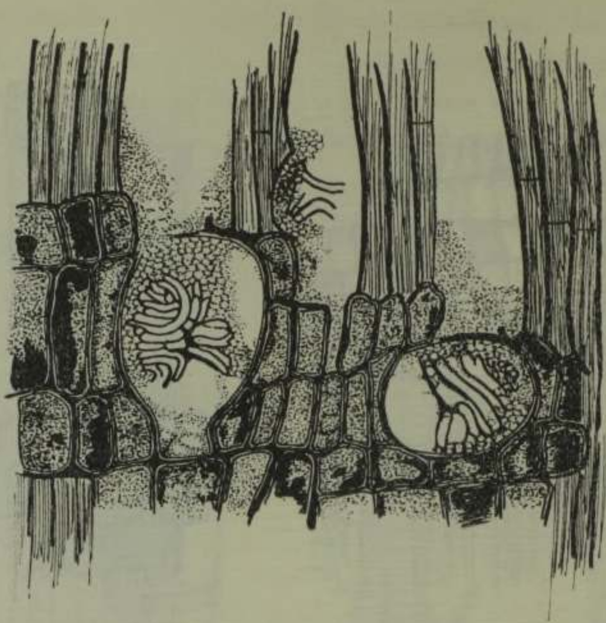


FIG. 6.—*Radial section.* Irregular perforations into ray cells, in *Antidesma* sp. (Euphorbiaceæ). (× 150.)

Celastraceæ	*Cassine capensis* L. var. *colpoon* D.C.
	,, *crocea* (Thunb) O. Kuntze.*
	Celastrus sp.
	†*Elæodendron australe* Vent.
	Euonymus europæus L.*
	Gymnosporia buxifolia Szysz.*
	Pleurostylia wightii Wight and Arn.
Euphorbiaceæ	*Antidesma* sp.
	Aporosa villosa Baill.*
	,, *villosula* Kurtz.*
	†*Blachia umbellata* Baill.
	†*Hemicyclia gardneri* Thwaites.
	Microdesmis pubercula Hook.*
	†*Necepsia afzelii* Prain.*
Flacourtiaceæ	*Erythrospermum phytolaccoides* Gardn.
	Kiggelaria africana L.
	,, sp.
	†*Ophiobotrys zenkeri* Gilg.*
	Ryania speciosa Vahl.*
	Xylosma longifolium Clos.*

* Correlated with herbarium material.

† Perforated ray cells extremely common.

Lacistemaceæ	**Lacistema aggregatum* (Berg.) Rusby.†
	* ,, *pedicellatum* Standl.†
	* ,, *nema* Macbr.†
	* ,, *rosediscum* Macbr.†
Malpighiaceæ	*Byrsonima crassifolia* H.B. and K.†
Olacaceæ	*Coula edulis* Baill.†
	Heisteria macrophylla Oerst.†
	Minquartia guianensis Aubl.†
	**Ptychopetalum anceps* Oliv.†
	**Strombosia javanica* Blume.
Passifloraceæ	*Androsiphonia adesnostegia* Stapf.†
Rubiaceæ	*Antirrhœa bourbonica* Gmel.
	Bertiera guianensis Aubl. †
	,, *racemosa* K. Schum.
	**Canthium ventosum* (L.) S. Moore.
	Calycophyllum candidissimum D.C.
	,, *spruceanum* (Benth.) K. Schum.
	**Corynanthe pachyceras* K. Schum.†
	Diplospora viridiflora D.C.
	Gardenia coronaria Buch.†
	,, *latifolia* Soland.
	,, *sessiliflora* Wall.†
	Guettardia foliacea Standl.†
	**Heinsia pulchella* K. Schum.
	Ixora parviflora Vahl.
	Luculia gratissima Sweet.†
	Mitragyna parviflora Korth.
	Pentagonia macrophylla Benth.
	**Posoqueria latifolia* Roem and Schult.†
	**Psychotria grandis* Sw.†
	Randia sp.†
	**Rondeletia buddleioides* Benth.†
	,, *cooperi* Standl.†
	Rudgea thyrsiflora Donn. Smith.†
	Sickingia sp.†

* Perforated ray cells extremely common.

† Correlared with herbarium material.

Rubiaceæ—(contd.)	**Vangueria griseum* Ridl.
	Vangueriopsis discolor Robyns.†
	Warscewicszia coccinea Klotzsch.†
Samydaceæ	*Casearia dinklagei* Gilg.†
	,, *præcox* Gris.
	* ,, *sylvestris* Sw.†
	Homalium smythei Hutch. and Dalz.†
Saxifragaceæ	*Ribes glaciale* Wall.
Staphyleaceæ	**Turpinia pomifera* D.C.
Symplocaceæ	*Symplocos spicata* Roxb.†
Violaceæ	*Amphirrhox longifolia* Spreng.†

* Perforated ray cells extremely common.
† Correlated with herbarium material.

This list covers a considerable range of families, which are widely separated phylogenetically, and the woods themselves exhibit a corresponding diversity of structure. Even in a single species there may be great differences in the number of perforated ray cells in different specimens, which suggests that the occurrence of this phenomenon is due not so much to constant anatomical features characteristic of the species, but rather to more variable characters such as the orientation of the cambial initials and daughter cells.

Assuming the simultaneous formation of two vessel segments on opposite sides of a ray, it is comparatively easy to visualize the perforation of the ray cell to connect them, but it is extremely difficult to explain why the vessel segments should be so placed. Priestley (1932) has recently shown that in certain trees the differentiation of the vessels proceeds downwards, and it would appear, therefore, that the development of any undifferentiated cell into a vessel segment depends on the presence of a vessel segment above. If the end wall of the lowest differentiated vessel segment happens to be contiguous with a ray cell, it is possible that a perforation will be formed into the ray cell, and that this cell will, in turn, form a perforation on the opposite wall, and so lead to the differentiation of a further vessel segment on the opposite side of the ray.

Although the woods in which this phenomenon occurs are from such widely distributed families and exhibit such a range of structure, it is evident that they must have some common features which are associated with the occurrence of perforated ray cells; such features are to be found in the rays and vessels.

The rays are always high and have uniseriate margins of many cells, and it is amongst these marginal cells that the perforations usually occur ; in only two woods were perforated ray cells observed in multiseriate parts of the ray, fig. 7. In the woods in which the perforated ray cells are most numerous the rays range from 1 to 10 mm. high and are mostly higher than 3 mm. ; where the perforated ray cells are less numerous the rays are usually rather lower. The vessels are mostly small to very small, the tangential diameter of the largest vessels ranging from 50 μ to 100 μ. In a few woods the maximum diameter of the vessels was as high as 130 μ. The end walls of all the vessels are markedly oblique. The marginal cells of the rays are often extremely high, up to 240 μ, but it is noticeable that they are distinctly shorter in the woods where perforated ray cells are less numerous. It would appear, therefore, that the factor of importance in determining the frequency of perforated ray cells is not the actual dimensions of the marginal ray cells or of the vessels, but their relative proportions ; in all the woods it is possible to find ray cells which are higher than the tangential diameter of the largest vessels.

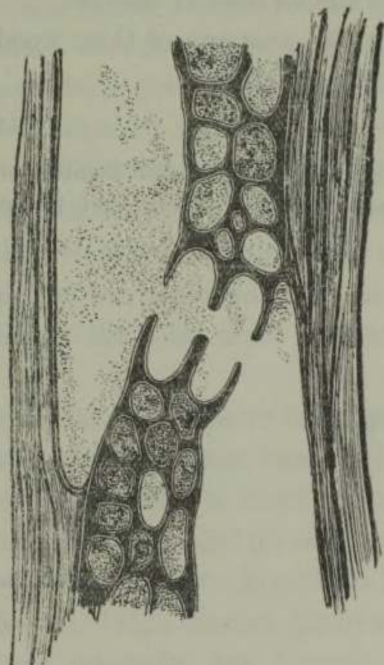


Fig. 7.—*Tangential section.* Vessel segments separated by two perforated ray cells in *Ophiobotrys zenkeri* Gilg. (Flacourtiaceæ). (× 250.)

These features are not confined to any particular systematic group, which may explain the occurrence of the phenomenon amongst such diverse families. The somewhat sporadic occurrence within the families is less easily explained. Though absence of perforated ray cells from many of the genera and species can be accounted for on anatomical grounds their absence from others cannot be so explained, and it would appear that there must be some other factor, which has so far not been observed, which determines the perforation of the ray cells.

It is difficult to show any phylogenetic connection between the families in which this phenomenon occurs, but it is suggestive that most of the woods (47 out of 62 genera) belong to the Celastrales and its offshoots, as suggested by Hutchinson (1926).

Acknowledgments.

Thanks are due to Dr. J. Burtt Davy, who checked the botanical names, and to the Department of Scientific and Industrial Research for a grant to Miss Chattaway.

Summary.

(1) An unusual type of ray cell was first observed in *Lacistema aggregatum*, the side walls being perforated and connecting two vertical series of vessel segments on opposite sides of a ray. Similar cells were subsequently observed in 74 species from 17 families.

(2) The anatomy of these woods is discussed in relation to the occurrence of this type of cell.

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