Comparative Anatomy and Angiosperm Phylogeny

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AN ABSTRACT*

This investigation was a study of some twenty-two families centering about the Moraceae and it had for its purpose the establishment of the phylogenetic relationships of these families. It was based primarily on a comparative anatomical study of the secondary xylem of the plants belonging to these families. Slides representing stems of one hundred and sixty-five genera and four hundred and sixty-five species were examined. In addition, the anatomical evidence derived from a study of the secondary xylem was harmonized with the evidence from floral anatomy, nodal anatomy, floral morphology, and the available evidence from the fields of paleobotany and cytology.

The Moraceae and allied families have been variously placed by the phylogenists who have based their systems for the most part upon floral morphology. Engler and Prantl and Wettstein place these families in the Amentiferae and they consider this collection of families to be the most primitive group among the Dicotyledons. On the other hand, Hutchinson, Bessey, and Hallier feel that the Ranales or Magnoliales are most primitive and therefore they consider the families in the Amentiferae to be rather highly specialized plants which have been derived from various other groups.

Now, on the one hand there are the diverse placements of these groups by the various phylogenists and, on the other hand, through the years the anatomists have worked out an extensive list of lines of specialization in the structures of the plant stele—primarily in the secondary xylem. It is thought by many that these lines or sequences in evolution can be employed in establishing a natural system of phylogeny.

These lines of specialization have been worked out for the evolution of vessel elements, fibrous tracheary elements, rays, wood parenchyma, and other structural features. The lines referred to have been established by Jeffrey, Bailey, Frost, Kribs, Record, Chalk, Sinnott, and some others. Space does not permit a discussion of the evidence upon which these lines of specialization are founded. It can be said, however, that they were established independent of any system of Angiosperm classification. They are not based on any preconceived notion that this or that group of Gymnosperms has given rise to the Angiosperms, or on any preconceived idea that the Ranales or the Amentiferae are primitive.

Now, let us turn to the anatomical descriptions of the various families to see which, if any, of these systems of phylogeny is favored by the anatomical facts.

In the Hamamelidaceae, most of the species have tracheids; vessel distribution is mostly solitary; the vessels are angular and thin-walled; the mean vessel diameter is 32μ; all the species have scalariform perforation plates on the vessel elements; the vessel element end walls are very oblique; the intervascular pitting is scalariform, transitional, and opposite in most of the species; the mean vessel element length is 1089μ; the rays are heterogeneous I or IIA in most; the wood parenchyma is diffuse in most species; and all the woods are diffuse-porous. The secondary xylem of this family is very close in all anatomical details to certain groups in the Magnoliales.

In the Casuarinaceae, the fibrous tracheary elements are tracheids; the pores are solitary for the most part; all the woods are diffuse-porous; the pores are angular in some species and angular to round in others; the vessel walls are thin; the mean vessel diameter is 88μ; most of the species have scalariform and simple perforation plates; the end walls on the vessel elements vary from 15° to 90°; the intervascular pitting is mostly opposite and alternate; the mean vessel element length is 412μ; the rays are heterogeneous IIB; and the xylem parenchyma is metatracheal in most. It is apparent that this family is rather highly specialized anatomically and therefore cannot be regarded as the most primitive, or among the most primitive, of the families of the Angiosperms—as it has often been considered by certain phylogenists.

In the Betulaceae, there are tracheids and fiber-tracheids; the pores are solitary and in multiples; all the genera are diffuse-porous; the vessels are angular in most; the walls of the pores are thin; the mean vessel diameter is 48μ; the perforation plates are exclusively scalariform in most species; some species, however, have simple with some vestigial scalariform plates; vessel end walls vary from 15° to 50°; intervascular pitting is alternate in most genera; the mean vessel element length is 608μ; the rays are heterogeneous IIB or homogeneous I; and the wood parenchyma is diffuse, terminal, metatracheal, vasicentric, or combinations of these. The Betulaceae are clearly on a higher plane of anatomical specialization than the Hamamelidaceae.

The Fagaceae are quite like the Betulaceae except that the former are higher than the latter anatomically.

In the Ulmaceae, there are fiber-tracheids and libriform wood fibers; vessel distribution is a combination of solitary pores, pore multiples, and pore clusters; the woods are diffuse-porous or ring-porous; the pores are angular and round; the walls of the vessels are thin, or in a few cases thick; the mean vessel diameter is 96μ; the vessel elements bear simple perforation plates or vestigial scalariform perforation plates; the vessel element end walls vary from 20° to 90°; the intervascular pitting is opposite and alternate; the mean vessel element length is 286μ; the rays are heterogeneous I, IIA, IIB, or homogeneous I; the wood parenchyma is usually a combination of terminal and vasicentric, or is aliform and confluent, or diffuse and vasicentric; and there is a tendency towards storied structure in a few species. It can be seen that the Ulmaceae are higher anatomically than the Hamamelidaceae. The vestigial scalariform perforation plates would seem to indicate that the Ulmaceae were derived from a family in which there were scalariform perforation plates on the vessel elements.

The Moraceae are anatomically similar, yet more specialized than the Ulmaceae. The Urticaceae are even more highly developed than the Moraceae.

The Rhoipteleaceae do not seem to belong in the Urticales for all the vessel elements are very long and have scalariform perforation plates.

The Eucommiaceae are in many ways intermediate in position between the Hamamelidaceae and the Urticales. The Eucommiaceae have latex, also.

Interpreting the anatomical data given for each family in the light of the lines of specialization in the structures of the plant stele which have been worked out by the anatomists, together with a consideration of the facts from floral and general morphology, the writer has come to the following conclusions concerning the phylogenetic relationships of the various orders and families studied in this investigation: 1. The Hamamelidaceae are derivatives of the Magnoliales. 2. The Casuarinales, the Fagales, and the Urticales are derivatives of the Hamamelidaceae. 3. In the Urticales, the Ulmaceae are most primitive, the Moraceae are less so, and the Urticaceae are least primitive.

In general it may be stated that the above phylogenetic scheme is supported by the greater part of the evidence from the fields of floral morphology, nodal anatomy, cytology, paleobotany, and floral anatomy.

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* A more complete account of this investigation is to be published elsewhere.