THE MUSTARDS AND RELATED PLANT FAMILIES IN EASTERN TENNESSEE[1]

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INTRODUCTION

EXTENT OF THE ORDER AND TERRITORY INCLUDED

The Papaveraceae, Cruciferae, Fumariaceae, Capparidaceae, Resedaceae and Moringaceae are a group of naturally and closely related families comprising the plant order, Papaverales. In Eastern Tennessee, representatives of only the first four of these families occur. Eastern Tennessee, in this case, shall consist of the sixty-three counties east of and including Sumner, Davidson, Williamson, Maury, and Lawrence (Fig. 1). It will be seen that the political boundary between "Middle" and "East" Tennessee practically halves this territory.

Within the territory is a variety of elevations and rock formations. The region at the western boundary is known as the Nashville limestone basin, or bluegrass region. It is composed of fossiliferous limestone and calcareous shales. The average elevation of the basin is about 500 feet. It is in this region that two endemic species of the Papaverales, *Lesquerella Lescurii* and *Leavenworthia stylosa* are found. A few other species noted in the paper occur only in this Middle Tennessee region.

East of the limestone basin is the Cumberland Plateau, a flat tableland deeply cut by many streams. The Plateau is mainly underlain by sandstones and sandy shales. There is an altitudinal range of from 1,800 feet at Signal Mountain, near Chattanooga, to 3,000 feet at Cumberland Gap.

East of and parallel to the Plateau is the Valley of the Tennessee River. Geologically, it is composed chiefly of Knox dolomite (a magnesium limestone) and calcareous shales. In elevation, it varies from 700 feet at Chattanooga to 1,500 feet near the Tennessee-Virginia line. The Plateau and Valley form a belt 60 to 80 miles in width from northeast to southwest across the state. Neither region has a peculiar flora for the order concerned.

The Southern Appalachians occur at the eastern boundary of the territory. They are composed mostly of Cambrian rocks: quartzites,

[1]This study of the Papaverales which has extended over a two-year period (1930-1932) would have been impossible had it not been for the financial aid of a Sigma Xi research grant. For such assistance the writer is extremely grateful. The able direction and constant encouragement of Dr. H. M. Jennison, of the University Botany Department, throughout the term of study are also sincerely appreciated. Collections of all the members of the Botany Staff have helped make the report complete.

sandstones, shales and slates. In this area the altitude varies from around 1,000 feet to above 6,000 feet. Most of the area is wooded. Here are found remnants of the primeval forests of America. Over 100,000 acres of virgin timber stand undisturbed. Mountain forms such as *Cardamine clematitis, Dicentra eximia,* and *Adlumia fungosa* are found nowhere else in Tennessee.

It is readily seen that the territory included offers a wide range of elevation and a variety of soil composition allowing abundant floral variations (Fig. 1).

EARLIER RELEVANT STUDIES

Previous investigations of the mustards and their nearest relatives in this region have been incidental to general floral surveys. Locally, no study has been confined to this natural group.

Dr. Augustin Gattinger became acquainted with the flora of the state as a whole probably better than any other man. A physician by

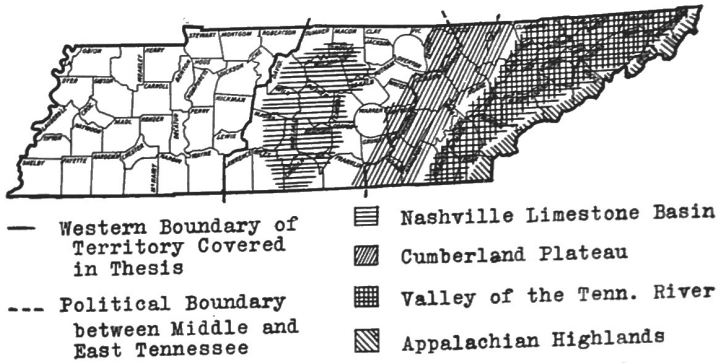


Fig. 1. Tennessee showing the areas involved in this study.

profession, a philosopher by nature, and a botanist at heart, he dedicated to the citizens of Tennessee, in 1901, his *Flora of Tennessee.* In this volume he has listed seventy-five species within the Papaverales known to occur in the state, chiefly in Middle Tennessee. In his list were included many species known to be recent escapes from local gardens, *e. g., Papaver somniferum* L. and *Capparis spinosa* L. His collecting was done mostly in and about the vicinity of Nashville, in the western limit of our territory. His entire collection of flowering plants, now incorporated in the University of Tennessee herbarium, has been the most extensive of any single investigator in the state. His specimens of the Papaverales, especially those from the Nashville region, have been invaluable in the completion of this study.

Albert Ruth, a citizen of Knoxville and East Tennessee for over thirty years, made extensive collections of the flora in general. Many

of his specimens, now in possession of the University, are species within the order under discussion. His studies, like Gattinger's, were confined to no one group.

J. K. Small, whose *Flora of the Southeastern United States* (1913) has been used, together with other manuals, in identifying the specimens here described, once visited the northeastern portion of the state. His sojourn was so cursory as to have had little significance in contributing to our knowledge of the flora of Tennessee in particular.

F. Lamson-Scribner, T. H. Kearney, Jr., and S. M. Bain have likewise made important additions to the University herbarium. Their collections, too, were extensive and general, though Scribner was especially intent on the grasses. Kearney (1897), incidentally, was the first to note the partial duplication of the Atlantic Coastal Plain flora in the highlands of the Southern Appalachians.

The check list compiled by Jennison (1929) and based on collections and records at the University of Tennessee Department of Botany has been most helpful. Both this list and that of Gattinger (1901) have been enlarged in the present paper and the terminology corrected as accurately as possible.

Objects of This Paper

With the investigations of all of these botanists as a background, the present paper was undertaken with the intention of studying the Papaverales in particular. More specifically, the objects of the study were: (1) To clarify the problem of the relationship of the order in the Plant Kingdom, (2) to furnish descriptions and means of identification for species growing wild in Eastern Tennessee, and (3) to note the distribution, time of blooming, and distinguishing ecological factors for the species described.

Part I. Phylogeny

The ordinal name (Papaverales) is an adaptation of the family name, Papaveraceae, which is derived directly from the classic Latin name of the poppy, *Papaver*. "Rhoeadales" is used in older works as the ordinal name for the same group of families.

The Papaveraceae include the poppies, the Fumariaceae (Fumitory family) include the bleeding hearts and Dutchman's breeches, the Cruciferae, the Mustards, and the Capparidaceae, the Capers. The Resedaceae, of which the garden mignonette is a type, is a family of herbs confined to the Old World except when cultivated. This family and the Dipsacaceae are the only two families of Europe which do not have species native also in America. The Moringaceae is entirely tropical and arborescent. The roots of the Horse-radish Tree (*Moringa pterigosperma* Gaertn.) are ground and the pulp is used as an acrid and piquant condiment. Seeds of this same tree are called ben-nuts. From them is pressed the fine oil of ben used in extracting perfumes and in lubricating delicate machinery.

Since members of the Resedaceae and Moringaceae do not occur in Tennessee, the present study includes only species of the four groups (the Poppy, Fumitory, Mustard, and Caper families).

Perhaps one would not guess that a bouquet of bleeding hearts, mustards, poppies, and spider flowers contained such closely related genera as to be confined to a single order. Yet they are all relatively simple types having characteristics in common which naturally unite them. What is the relationship of these plants to the other orders of the Plant Kingdom?

Phylogeny in General

The prevailing opinion among present-day plant taxonomists is that up to this time no single system of classification adequately portrays phylogeny. The objects of the Engler and Prantl system (1887-1909), so universally used, are chiefly descriptive and analytical. For nearly half a century phylogenetic taxonomy has been based on this classification. Many taxonomists with the intention of perfecting a phylogenetic scheme of nomenclature, paradoxically, have founded their hopes in the traditional system.

Recently, however, three systems have been advocated whose authors pretend to use phylogeny as their bases. These are the systems presented by Bessey in 1915; Wettstein, whose latest revised volume appeared in 1924; and Hutchinson in 1926. The order with which this paper is concerned is here placed in the Plant Kingdom according to Wettstein's classification. A brief review of the three recent arrangements, and justification of the use of Wettstein's, are expedient, especially since the German text accompanying the latter system may not be available to many students.

In the first place, why is phylogeny so perplexing? Perhaps it is because we must approach the problem more as philosophers than as scientists! Examination of fossils and a study of comparative morphology furnish the only evidence upon which scientists may draw. Accurate and decisive experimentation, to which the scientist is accustomed, is impractical if not impossible. With the immense modern specialized flora in the foreground and scattered fragments of the flora of past millions of years in the background, our cleverest conclusions can be but speculative. At the outset, then, the taxonomist knows that he will never attain his purpose, but only hopes to approach his goal. He would construct a "tree" from a bundle of clipped twigs and a few naked branches.

Bessey tried it, and gave us a "tree," indeed. His conclusions were published in 1915 and have remained essentially the same since then. However one may apprize his final solution, he must admit the value of at least two features of his system: (1) The enumeration of the criteria ("dicta") by which relationships could evidently be judged; and (2) his graphic illustration of the relationships of the plant orders

as he saw them (Fig. 2).[2] The criteria have been used in more or less modified form by all subsequent taxonomists, and the "tree" has provoked other attempts at such delineation. If not accepted as fixed perceptions, then, both of the distinctive features may serve as tentative guideposts.

Bessey's criteria may be examined in full in the original paper (1915). It will be sufficient here to survey the "tree" based upon the criteria (Fig. 2). The horizontal lines in the plate imposed upon Bessey's original chart are according to Pool (1929). The most striking aspect of the "tree" is its monophyletic nature, indicating that all modern plant orders are derived more or less directly from one recent phylum, the Ranales. It seems most likely from recently uncovered fossil evidence that the modern flora of the world must be derived, as far as traceable, from several parallel stocks rather than from a definite common order still intact such as the Ranales. If, as far back as there is evidence, there were several diverging stocks, flowering plants are said to have had a polyphyletic origin.

Of course there must have been a remote common ancestor. But, considering the numberless ages during which the flora have been changing, it is not logical to assume that all of the existing angiosperms claim more or less direct descent from the modern Ranales. This is implied in Bessey's "tree."

The most acceptable opinion is that definite and divergent lines of descent were already established at the time that the early Ranalean types are known to have existed. Else how can we explain the abundant Cretaceous amentiferous fossils, contemporaneous with fossil Ranaleans? Other examples may be cited, all of which point to a polyphyletic development of the present flora (Campbell, 1928).

With special reference to the problem at hand, the mustards and their close relatives are seen to have a direct relationship with the Ranales without intervening types. Together with the Malvales, Geraniales, Guttiferales, and Caryophyllales; the Papaverales (Rhoeadales) claim the Ranales as their immediate progenitors. Inventive Ranaleans! One more thing should be noted before passing to the next system. Bessey agrees with Hutchinson and many other taxonomists that whatever their ancestry the mustards and their kin have been productive of no new types. They were the end of their "line." Wettstein believes that from the Papaverales development was continued through such families as the Violaceae, Cucurbitaceae, and Compositae.

Hutchinson's system is not given since its monophyletic nature discredits it at the outset. This system, like Bessey's, introduces the Apetalae as late derivatives from Ranalean ancestors; whereas these

[2]The order Papaverales appears on both charts as "Rhoeadales." In modifying or formulating the charts, it was thought not wise to change the authors' terminology, lest confusion result on consultation of the originals.

forms are known to be at least as old as the Ranales. Until some revisions are made, Hutchinson's system may not be widely accepted.

An adaptation of Wettstein's scheme in graphic form is introduced here also (Fig. 3). It exhibits the acceptable polyphyletic scheme of phylogeny. The whole framework of the system rests upon the three

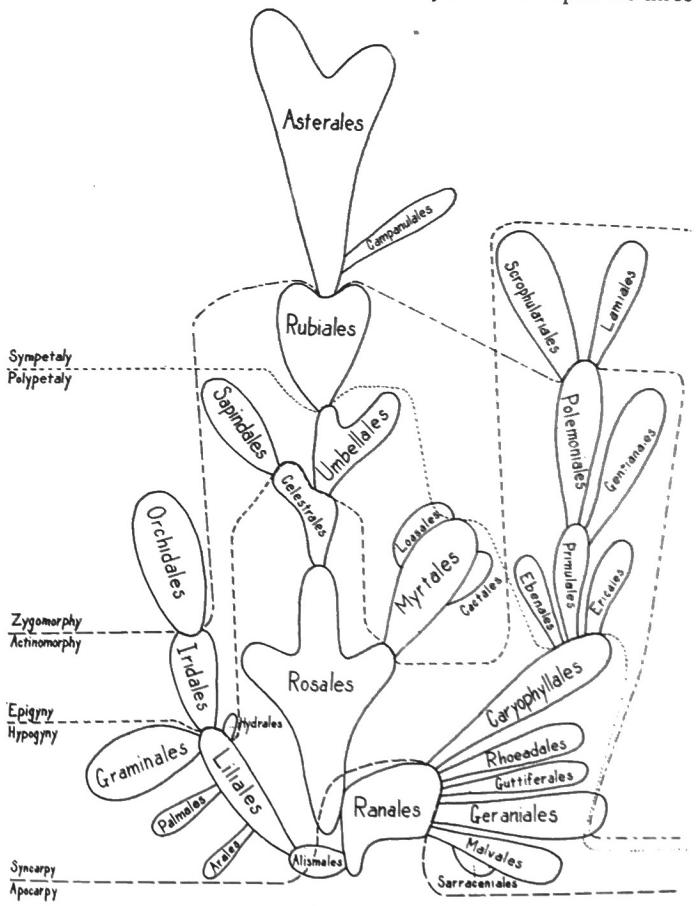
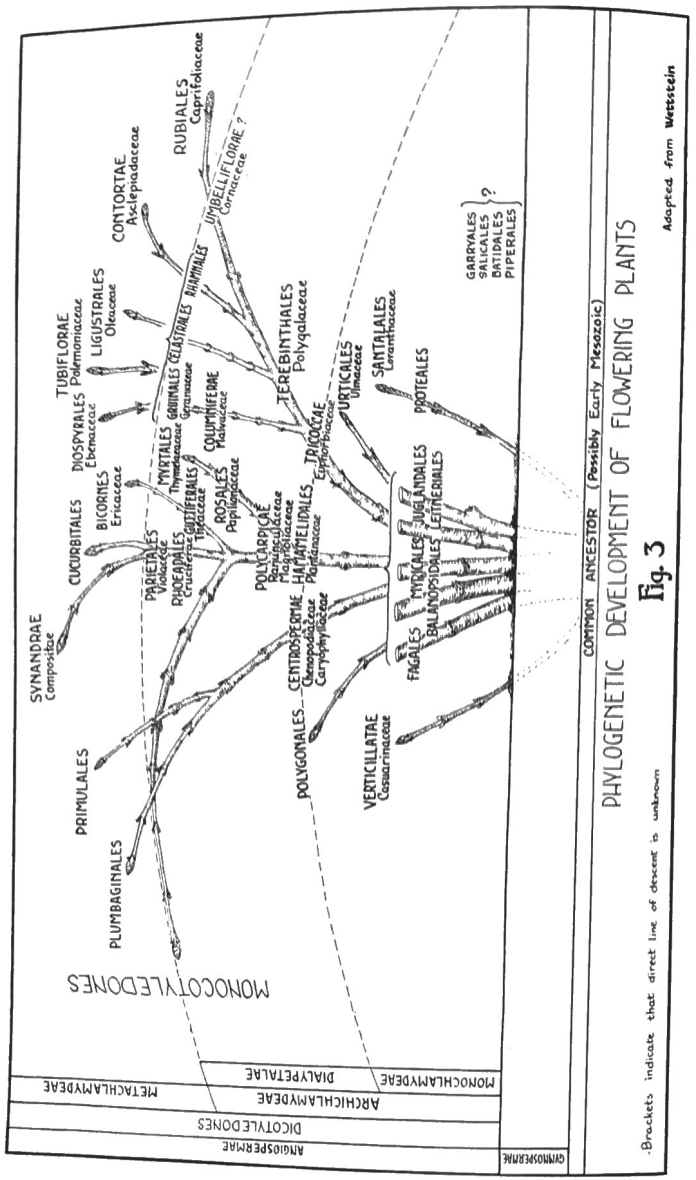


Fig. 2. The Phylogenetic Tree. After Bessey.

foundational and parallel branches proceeding from antiquity and at length giving rise to our modern dicot and monocot flora. Paleobotany, plant geography, and comparative morphology all furnish criteria of relationships that attest the plausibility of this system. Wettstein's system will serve as a basis for determining the ancestry of the mustard group. Since Wettstein's system is the only poly-



phyletic one of the three, one might inquire the reasons for choosing it as the basis of classification.

If it is agreed with Bessey and Hutchinson that the monophyletic origin of the angiosperms is true, the one phylum from which the recent orders were derived is the Ranales. Then the common ancestral flower must have resembled the modern magnolia or the buttercup flower. It would at least have been anemophilous, and monoecious, and have had separate carpels and a petaloid perianth. From this type, the apetalous and diclinous orders must have been reduced, and therefore must have appeared much later in plant history than their ancestors. But when we examine all known fossil evidence, what do we find? Knowlton (Campbell, 1928) believes that the oldest unquestionable angiosperms are represented in the lower Cretaceous Patapsco formations of Maryland and Virginia. According to Bessey and Hutchinson, they should be anemophilous, petaloideous, monoecious, and apocarpous types. But actually, of the sixteen families represented, all have apetalous or at least insignificant flowers, often dioecious, and certainly wind-pollinated. The flower-visiting insects of the Lepidoptera, Diptera, and Hymenoptera are unknown from the Jurassic and lower Cretaceous (Campbell, 1928).

According to Bessey and Hutchinson, such orders as the Fagales and Salicales (the Apetalae) must be "recent" derivatives reduced from petaloideous ancestors. The primitive Ranaleans, especially the woody ones, presumably would fossilize as readily as the amentiferous forms; but fossil magnolias have not been found until the early upper Cretaceous (Swingle, 1928, p. 9). So, until magnolias are found which are undoubtedly older than the oldest known Amentiferae, it cannot possibly be assumed that the Ranales are the progenitors of the latter, but the reverse might easily be postulated in the light of the above evidence.

Wettstein does so postulate, and proposes that the Apetalae emerged as a closely related group from an ancestor as yet unknown. The possible relationship to the gymnosperms is indicated by dotted lines in the chart. From this apetalous group, then, most of the higher plant orders probably have descended. Several gaps, where the trend of evolution is obscure, are unavoidable because of the scant number of fossils and the long ages of time intervening. If the line of descent is questionable, brackets are used in the diagram to indicate the period of uncertainty.

In addition to the five parallel and closely related apetalous groups, two other races extend from early ancestors: One the Proteales, also from an unknown type, and the other from the tropical Verticillatae. This last order, judging from the vegetative structure and the anatomy of the reproductive organs, is very closely related to the gymnosperms (Wettstein, 1924, p. 541). The unbroken line indicates nearness of relationship.

Upon surveying the whole diagram, one sees a shrub-like arrangement because of the probable polyphyletic origin of the angiosperms, and not a "tree" implying monophyletic origin. In the presence of all available evidence, it seems more judicious to accept this system of Wettstein. Thus, it is assumed that already in Jurassic times, an ancestral complex of plant phyla was present, and that therefore the modern dicotyledons had a polyphyletic origin.

Position of the Papaverales in the Plant Kingdom

Exactly where in this polyphyletic scheme is the Papaverales located? What were its ancestors, and what its descendants? From the direction of the ancient Apetalae, the Hamamelidales, partly petalous and partly apetalous, seem to be derived. Then appeared the Ranales (Reihe Polycarpicae, according to Wettstein). Among the descendants of this large order are the mustards and their close relatives (Reihe Rhoeadales). Development continued supposedly from this order until the violets, curcurbits and composites were evolved.

Evolution Through and Beyond the Papaverales

As mentioned before, Wettstein is in disagreement with many taxonomists in proposing that development was continued through and beyond the Rhoeadales. Undoubtedly the Cruciferae are specialized to no particular advantage, and have likely given rise to no more complex types. The Moringaceae, too, are a fixed group and insignificant. The other families, the Papaveraceae, Fumariaceae, Capparidaceae, and Resedaceae contain more flexible forms. Within these four families are herbaceous to woody types with actinomorphic to zygomorphic flowers composed of indefinite numbers of floral parts. This combination seems ideal for modification. Therefore, if descent was continued through the Papaverales, it must have been through the Papaveraceae, Fumariaceae, Resedaceae, and Capparidaceae rather than through the Cruciferae and Moringaceae.

(*Continued in the October number*)