

THE SIGNIFICANCE OF THE REDUCTION OF VESSELS IN THE CACTACEAE

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SINCE THE EXTENSIVE SURVEY OF Bailey and Tupper (1918), broadly based summations of evidence from the vascular land plants, as a whole, demonstrate that vessels have developed in angiosperms by dissolution of membranes in scalariformly pitted tracheids, as they did in *Pteridium* among ferns. The major trends of specialization of such vessels in secondary xylem of numerous dicotyledonous families have been comprehensively investigated by various anatomists during the last 40 years, as they have in the primary xylem of monocotyledons by Cheadle (e.g. 1942, 1944). Thus, it is possible at present to arrange the vessels of both dicotyledons and monocotyledons in major trends of phylogenetic specialization. This can be done independently of the various systems of classifying angiosperms, thereby avoiding circular arguments based upon assumptions regarding the primitive or specialized character of plants in which the vessels occur. In other words, primitive vessels can be distinguished from specialized ones solely upon their own structural differences without dependence upon controversial taxonomic systems of classifying dicotyledons and monocotyledons.

In the secondary xylem of dicotyledons, the major trends of specialization in vessels are closely correlated with changes in the cytology of the cambium. The most significant modifications of the cambium and its tracheary derivatives appear to be largely unidirectional and are extensively irreversible. From a genetic point of view, it seems that, if mutations leading to prolonged reversals arise, they must in general be selectively disadvantageous since the adaptive specializations of vessels are concomitants of more or less profound changes in other cells and tissues and of physiological activities concerned in the survival of plants in which they occur.

It should be noted in this connection, however, that localized aberrations from the major trends of specialization in vessels do occur at times in vines, lianas, and other plants of divergent habits of growth. For example as shown by Carlquist (1962), the phenomenon of paedomorphosis leads to an extension during ontogenetic development of anatomical features of primary xylem into secondary xylem formed by the cambium. According to him, the phenomenon occurs in such anatomically highly specialized families as the Begoniaceae, Caricaceae, Compositae,

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Crassulaceae, Goodeniaceae, Piperaceae, Portulacaceae, and Umbelliferae, particularly in certain herbs, stem succulents, and in "rosette shrubs" and "rosette trees." In the case of plants where the specialization of vessels in primary xylem lags behind that in secondary xylem, paedomorphosis may lead to the development of less specialized appearing vessels in the secondary xylem. But such divergent, superimposed aberrations do not result in extensive reversals to a primitive vesselless condition.

In discussions with botanists who are unfamiliar with the significance of anatomical evidence now available, one still meets individuals who argue that such primitively vesselless dicotyledons as the Winteraceae, *Tetracentron*, *Trochodendron*, *Amborella* and *Sarcandra* may once have possessed vessels and subsequently lost them. Similar arguments are advanced by taxonomists who wish to derive monocotyledons from herbaceous dicotyledons, the structure of the xylem in stems of arboreal Agavaceae being due, by implication, to evolutionary reversion to a primitive appearing vesselless condition. As a last resource in such arguments, the Cactaceae are cited as exhibiting a phylogenetic reversal to a vesselless condition.

Fortunately the Cactaceae provide unusually comprehensive and favorable evidence in the study of highly divergent trends of morphological specializations. These are so bizarre and so closely correlated, from ecological and physiological points of view, with adaptations for survival in excessively arid environments, as to leave few uncertainties regarding the directions in which phylogenetic changes are progressing. Furthermore, an unusually comprehensive and adequate record of the divergent trends of specializations is preserved in surviving representatives of the family. It is not essential to speculate, as one sometimes must in other families, regarding missing links in the major evolutionary sequences.

Morphological evidence indicates that the most primitive surviving representatives of the Cactaceae occur in the genus *Pereskia*. Such better known species as *P. sacharosa* Griseb., *P. bleo* DC., and *P. grandifolia* Haw., with their large thin leaves, have long been recognized by taxonomists as having a habit of growth and absence of succulence characteristic of many typically woody dicotyledonous trees and large shrubs. The internal structures of these species demonstrate that ancestral Cactaceae attained a high level of anatomical specialization in their cambium and vessels prior to the development of incipient succulence. Successive stages of accentuating succulence occur in other species of *Pereskia* and particularly in the leaf-bearing genera *Peresklopsis* and *Quiabentia*.²

In the most primitive surviving Cactaceae, the fusiform initials of the cambium are much reduced in length and tend to be arranged in a stratified or "storied" condition such as occurs in dicotyledonous families that have attained a structurally advanced level of specialization. The vessel members formed by the fusiform cambial initials are correspondingly short and have simple porous perforations, whereas the libriform fibers

² For detailed illustrations of the anatomy of these genera see fifteen papers by Bailey published in the *Journal of the Arnold Arboretum*, volumes 41 to 46.

formed by the cambial initials elongate markedly during tissue differentiation and are of the highly specialized non-septate or septate, starch-storing modification.

In contrast to some families of the dicotyledons, vessels with highly specialized simple porous perforations have worked backward (phylogenetically) in the primitive Cactaceae throughout the primary xylem, occurring even in the first formed tracheary cells having annular and helical thickenings.

The tall, broader, more massively succulent representatives of the subfamilies Opuntioideae K. Sch. and Cereoideae K. Sch. commonly tend to retain more or less numerous vessels in their xylem. More conspicuous evidences of modification and reduction of vessels occur in the smaller more lowly forms of excessively xerophilous species, e.g. the mamillarias. In these plants, short, imperforate cells with annular and helical thickenings become increasingly abundant in the primary xylem and, by pedomorphosis, in the secondary xylem. Simultaneously fibers and vessels with bordered pits may be reduced in number or eliminated. Such structural aberrations were described and illustrated by Schleiden (1845) and Darbishire (1904) in their pioneering investigations.

Although more comprehensive and reliable investigations are needed to determine with accuracy whether vessels are ever completely eliminated throughout all parts of any of the Cactaceae, there is ample evidence available at present that the end-products of super-specialization in the xylem of the family in no way resemble the structure of such primitive vesselless dicotyledons as the Winteraceae, *Trochodendron*, *Tetracentron*, *Amborella*, and *Sarcandra*. The reduction of vessels in some representatives of the Cactaceae cannot be cited as evidence in favor of unsupported assumptions of an evolutionary reversal to a primitive vesselless condition.

It should be emphasized here, that in future investigations of anatomical differences in plants of divergent habits of growth more attention should be devoted to ecological and physiological influences in the habitats in which plants normally grow. This was recognized by Preston (1900, 1901) in his early investigation of certain cacti and has recently been stressed by Carlquist (1966) in connection with his extensive investigations of the xylem in Compositae.

Significant and reliable correlations between anatomy and physiological and ecological influences in specific habitats are more easily attainable in xerophilous plants where water-relations play a dominating role in survival. Cacti of the growth forms investigated by Preston have an extensive system of superficially located water-absorbing and -conducting roots and mechanically stronger, deeply penetrating anchoring roots. Reduction and elimination of fibers in the xylem tends to be conspicuous in the superficially located root system in contrast to the xylem of anchoring roots where vessels may be reduced in number. Thus from functional ecological points of view, in environments where temporary rains are of infrequent occurrence, the extensive superficial root system appears to

be an adaptation for rapidly absorbing and transporting water for storage above ground in succulent stems. The structure of the xylem in other growth forms of excessively xerophilous cacti merits detailed future investigation, e.g. in those forming massive succulent anchoring roots with less extensive lateral roots. In addition, it remains to determine from a reliable physiological point of view whether the curious short cells with broadened annular and helical thickenings which attracted so much attention and discussion by earlier investigators of cacti, function primarily in storage of water, in strengthening excessively succulent tissues, or in both capacities, rather than fundamentally in translocation of sap.

Cheadle's numerous and comprehensive investigations (e.g. 1942, 1944) have demonstrated that in monocotyledons, in contrast to dicotyledons, vessels developed first in roots and subsequently became extended into their aërial parts. In the case of arboreal representatives of the Agavaceae, growing in arid environments, there is significant ecological evidence of why this should be. Their extensive superficial system of roots provides an essential adaptation, when rains occur, for absorption and rapid transportation of water for retention in their massive vesselless stems where concomitant adaptations for reduced evaporation can develop. The occurrence of primitive vesselless xylem in stems of such plants cannot be accounted for by assumptions of extensive anatomical reversals from highly specialized herbaceous dicotyledons.

In conclusion, it is advisable to comment upon the significance and utility of wood anatomy in the taxonomy and classification of angiosperms. As I emphasized in an earlier publication (1957), the major trends of specialization in xylem, when considered by themselves, are reliable in *negations*, owing to inherent difficulties in deriving a taxon with primitive xylem from one exhibiting a uniformly high level of anatomical specialization. Unfortunately, due to the frequent occurrence of parallel and convergent evolution, wood anatomy cannot be utilized by itself in reliable *positive* assertion without corroborative evidence from other parts of a taxon, e.g. the reproductive ones. In most families, morphological changes in different parts of the plants are not closely synchronized, some being precocious when others are markedly retarded. Assertions that anatomical characters are inherently more conservative than reproductive ones (some anatomists) and vice versa (many taxonomists), are no longer cogently reliable in view of extensive data now available. Since evidence from all organs and parts of plants must be harmonized if a natural classification of angiosperms is to be attained, data from wood anatomy should be given due consideration in taxonomy.

Anatomical evidence negates any possibility of deriving the primitive vesselless xylem of such relics as the Winteraceae, *Trochodendron*, *Tetracentron*, and *Amborella* from ancestors with vessels. However, wood anatomy, by itself, does not provide conclusive evidence that the Degeneriaceae, Magnoliaceae and other ranalian families were derived directly from the Winteraceae. Furthermore, although the anatomy of *Sarcandra* negates any possibility of deriving this genus from vessel-bearing genera

of the Chloranthaceae, xylem anatomy alone does not provide reliable evidence for concluding that the latter genera were derived from *Sarcandra* rather than from now extinct vesselless ancestors.

In the case of monocotyledons, xylem anatomy negates a derivation in the Agavaceae of primitive vesselless stems from vessel-containing ones, and particularly from those of herbaceous dicotyledons. But, it is not possible at present to determine which monocotyledonous families may have been derived from the Agavaceae. The retention of more primitive forms of vessels in the roots of some families, e.g. Amaryllidaceae, negates their derivation from existing Agavaceae. Of course, the possibility exists that such families may have diverged from ancestral Agavaceae, or plants of comparable form, prior to excessive specialization in their roots and reproductive organs.

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