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THE MORPHOLOGICAL AND TAXONOMIC SIGNIFICANCE OF DICHOTOMOUS VENATION IN KINGDONIA UNIFLORA BALFOUR F. ET W. W. SMITH

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CONTENTS

INTRODUCTION

The purpose of the present article is to present some of the results of a study of the morphology and venation of the leaf of *Kingdonia uniflora*. Although this plant is undoubtedly an angiosperm and was classified by Balfour and Smith (1914) as a monotypic genus in the Ranunculaceae, the venation pattern of its leaf is open dichotomous and strikingly like the venation of the leaves of *Ginkgo biloba* and certain fern genera (Fig. 1–2; Pl. 2). Such specialized foliar organs as bud scales and petals very commonly develop an open dichotomous or dichotomous-reticulate type of venation but authentic examples of open dichotomously-veined foliage leaves in angiosperms are rare and consequently are of unusual interest to the morphologist.

The view is widely held that in the ferns open dichotomous venation represents the primitive type of foliar vasculation and that the varied types of closed or reticulate venation have evolved by the development of anastomoses between the main veins (Goebel 1922; Bower 1935, p. 312–313; Troll 1938). Evidence supporting this theory is derived both from the fossil record as well as from the transitions between dichotomous and reticulate venation which are so beautifully illustrated in the juvenile or even the adult leaves of certain modern genera of ferns. Open dichotomous venation also appears as the prevailing type in many living gymnosperms and is clearly displayed in the foliage leaves of *Ginkgo*, most of the cycads and in certain species of *Agathis*, *Araucaria* and *Podocarpus* (Troll 1938). But in the angiosperms, the reticulate type of venation is virtually universal and is generally recognized as one of the consistent characters of the foliage leaves of this class (Fig. 3–4).

What has been the evolutionary history of the diversified types of reticulate venation patterns in flowering plants? Unfortunately, the fossil record thus far provides no answer to the question and opinions differ sharply as to the phylogenetic significance of those apparently rare cases of dichotomous venation which occur. Some authors (Goebel 1922 and Troll 1938) consider it highly improbable that net venation in the angiosperms has evolved from dichotomous venation. Others, such as Bugnon (1925) maintain that dichotomous venation is an "atavistic tendency" and represents the persistence of an ancestral character. Van der Hammen (1947–48) in particular, has described a number of examples of what he terms "traces of ancient dichotomies" in the main venation systems of foliage leaves and floral organs.

My attention was drawn to the striking dichotomous venation of *Kingdonia* by the brief descriptions of it given by Diels (1932) and Troll (1938). Through the kindness of Dr. H. R. Fletcher, I secured, about a year ago, a portion of the rhizome together with a single leaf and flower stalk from the type specimen of *Kingdonia* which is deposited in the Herbarium of the Royal Botanic Garden in Edinburgh. More recently, with the help of Professor C. Y. Chang of the University of Peking, I have been extremely fortunate in securing additional leaf specimens of three different collections of *Kingdonia* through the generosity of Professor Tsui of the Northwestern Institute of Biology at Wukung, Shensi Province, China. I wish to express my great appreciation to Professor Tsui for donating this material for my study and for providing me with detailed notes regarding the ecology and habitat of *Kingdonia*, and to Professor Chang who personally undertook to send the specimens and notes to me.

The technique used in preparing the herbarium leaf specimens for this study is essentially the same as I have used in my previous investigations on venation patterns (Foster 1953, 1955). The leaves were cleared with the aid of sodium hydroxide followed by chloral hydrate, dehydrated with alcohol, stained with safranin and made into permanent mounts on large glass slides. I am greatly indebted to Mr. Howard J. Arnott for his assistance with the technical aspects of my study and for many helpful suggestions. I also wish to thank my wife for preparing the line drawings illustrating this paper.

GENERAL ORGANOGRAPHY

Kingdonia is an herbaceous perennial with a slender, branching, scaly rhizome. My material is not adequate for an exact description of the annual growth pattern of the shoot system but, as is demonstrated in some of my specimens as well as by the specific name "uniflora", each expanding bud produces a solitary flower accompanied by a single leaf; the foliage leaf consists of a long petiole and a lamina of five major segments (Pl. 1). Balfour and Smith state in their original description that "the habit of the plant is that of a large *Adoxa*" but that "the shape and texture of the leaf recall certain species of *Adiantum*".

Thus far, I have not been successful in obtaining fully developed flowers for study but serial sections have been made of a bud containing a young flower from one of the Shensi collections and ultimately will prove useful especially for the study of the pollen grains and the early stages in development of the carpels. On the basis of the original description, the flower of *Kingdonia* is distinctly "ranalian" in type and consists of 5 sepals, 0 petals, 10–15 stamens and 5–7 uniovulate carpels. Diels (1932) figured and briefly described the carpel of *Kingdonia*, emphasizing that the solitary pendulous ovule is orthotropic and attached to the ventral side of the ovary. Some of the materials sent to me by Professor Tsui included fruits of *Kingdonia* with their distinctively persistent reflexed styles. An anatomical study of these fruits is now in progress.

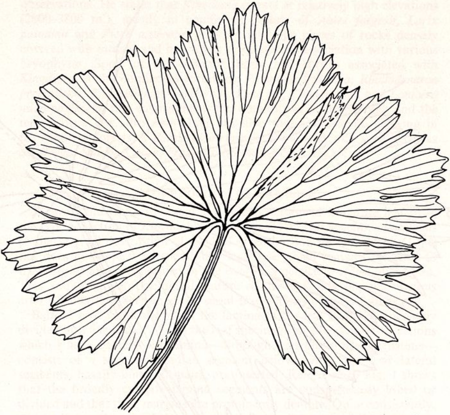

FIG. 1. Form and total venation of a leaf from the type collection of *Kingdonia uniflora* (Ward 734). × 2·5.

DISTRIBUTION AND HABITAT

Kingdonia was discovered by F. Kingdon Ward in 1913 growing at an elevation of 13,000 ft. in Northwestern Yunnan near the borders of China and Tibet, in the neighbourhood of Doker-la (i.e. Atuntzu). Ward's collections formed the basis for the original description of *Kingdonia* made by Balfour and Smith (1914) and, as far as I can determine, the type specimens at Edinburgh represented the only record for many years of this interesting Chinese plant.

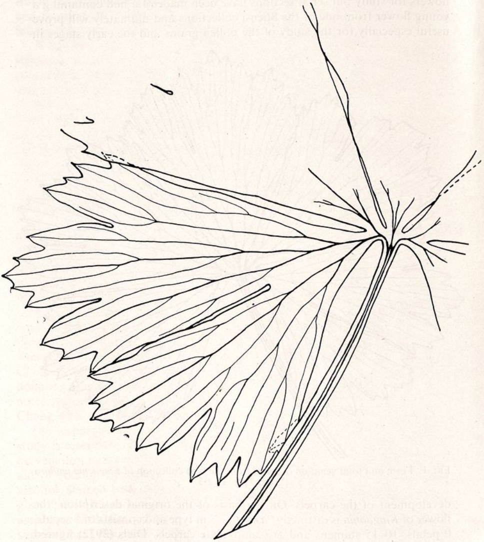

FIG. 2. Enlargement of the petiole and a portion of the lamina of the leaf represented in text Fig. 1, showing details of pattern of vasculation.

The additional material of *Kingdonia* which I have obtained from China stems from three separate and comparatively recent collections, viz: (1) Liu & Chun, No. 1307, collected September 28, 1937 on Taipaishan, Shensi Province; (2) Wang, No. 14552, collected July 25, 1951 near Siku, Kansu Province; and (3) Fu & Wei, No. 10403, collected August 15, 1957 on a mountain "named Western Taipaishan", Shensi Province. These Chinese collections (deposited in the Herbarium of the Northwestern Institute of Biology at Wukung, Shensi) have thus significantly contributed to our still limited knowledge of the actual geographical distribution of *Kingdonia*. Although the late Captain F. Kingdon Ward (personal letter) regarded *Kingdonia* as a rare plant in the Atuntzu region, future botanical surveys may reveal that it is not infrequent throughout the high mountains in Yunnan, Shensi and Kansu Provinces.

Because of the considerable morphological and taxonomic interest of *Kingdonia* I asked Professor Tsui to contribute notes from his own field observations. He states that *Kingdonia* occurs at relatively high elevations (2800–3800 m.), mostly in coniferous forests of *Abies fargesii*, *Larix potaninii* and *Picea asperata*, growing on large pieces of rocks densely covered with mosses and liverworts or on soil in association with various bryophytes. Some of the common herbs and shrubs associated with *Kingdonia* in this coniferous forest are *Potentilla fruticosa*, *Rhododendron przewalskii*, *R. concinnum*, *Sorbus* sp., *Rosa* sp., *Clematis* sp., and *Lonicera microphylla*. In this environment, the humidity is relatively high and the temperature low. Professor Tsui has also found *Kingdonia* growing in the shade of forests of *Betula alba-sinensis*, associated with such herbs as *Saxifraga*, *Sedum*, *Carex*, *Fragaria*, *Bromus*, *Aconitum*, etc.

Morphology of the Leaf

Figure 1 illustrates the form and total venation of a mature leaf from the type collection of *Kingdonia* (Ward, No. 734). This specimen conforms to the original description of the leaf given by Balfour and Smith (1914) but does not depict the sheath-like leaf base which remains attached to the rhizome and is concealed by the overlying persistent scales of the bud. This additional morphological feature of the leaf only became obvious after a study had been made of serial transections of several buds.

Balfour and Smith described the lamina of the leaf as being "pedately divided into five lobes". In all the leaf specimens of the various collections which I have studied, the lamina—although variable in its dimensions—consists of a separate median segment below which the four lateral segments, basally united in pairs, are inserted. Reference to Fig. 1 shows that the broadly cuneate lamina segments are conspicuously lobed or divided and that their margins are prominently dentate. Quite consistently, the median and both of the upper lateral segments are trilobate whereas each of the two lowest segments is characteristically subdivided (often nearly to its base) into two lobes, the upper of which is trilobulate whereas the lower is bilobulate (Fig. 1–2).

In describing the type material of *Kingdonia*, Balfour and Smith state that the petiole is 5–7 cm. long and the lamina 4–4·5 cm. in diameter. Some of my own leaf specimens from Shensi closely approximate these dimensions but it may be of interest to record the range in size of the lamina which I have been able to observe. The smallest lamina studied measured about 3 cm. in width whereas the two largest specimens were respectively 6 and 7 cm. wide. Despite this considerable variation in size, all of the leaves which I have examined rather closely conform to the same general pattern of morphological organization. It would, of course, be extremely interesting in this regard to study the organization of the cotyledons and primary leaves of seedlings of *Kingdonia*. Diels (1932, p. 57) suggests that the juvenile leaves of *Kingdonia* may be simple and comparable in form and dichotomous venation with the adult foliage leave of *Circaeaster agrestis*. I am hopeful that I may ultimately secure from Professor Tsui seedlings and young plants of *Kingdonia* to test this interesting suggestion.

NODAL ANATOMY AND VASCULATION OF THE PETIOLE

An intensive study of the vascular anatomy of the node and petiole of *Kingdonia* is now in progress and the results will be published at a later date. However, a brief preliminary description of the nodal anatomy and the course of the bundles in the petiole is presented here as essential to an understanding of the dichotomous pattern of venation in the lamina.

A study of serial transections shows that four bundles (two of which may appear as double strands) constitute the vascular supply of the foliage leaf. The departure of these traces is associated with a single gap and hence the nodal anatomy of *Kingdonia* is unilacunar in type. At varying distances above the leaf base, the four vascular strands become oriented in such a manner that a pair of adaxial bundles lies directly above the adjacent pair of abaxially oriented bundles. As a result, when cleared leaves are viewed from the adaxial surface, the abaxial bundles are not seen and the petiolar vasculature appears to consist of two parallel closely approximated strands (Fig. 1–2).

At the level of attachment of the lamina segments, the two adaxial petiolar bundles diverge right and left into the common bases of each pair of lateral segments and then dichotomize (Fig. 2). The branches of these dichotomies constitute the beginning of the open dichotomous venation system of the free portions of the lateral segments. As is shown in Fig. 2, the vasculature of the median segment of the lamina is derived from the two abaxial bundles which fuse to form a very short "midvein" in the base of the segment. This midvein promptly trifurcates or dichotomizes and represents the beginning of the dichotomous venation of the median segment and its lobes.

VENATION OF THE LAMINA

Previous descriptions of the venation of *Kingdonia* are extremely brief and are based solely on the study of the type specimen. According to Balfour and Smith (1914) the venation of the lamina segments consists of "veins which diverge from the base, branch without anastomosing and extend longitudinally to the margin". Diels (1932, p. 57) stated that "the veins are dichotomously branched, the forks of the branches extending steeply into the tips of the dentations but always without transverse interconnections". The results of the present study show that the above descriptions, which were apparently based on a study of dry unprocessed herbarium specimens, give a very inadequate and, in part, inaccurate idea of the venation pattern in *Kingdonia*.

In the first place, the number and degree of regularity of vein dichotomies vary not only between leaves from different collections, but even between the lamina segments of the same leaf. In the leaves of some collections, as shown in Pl. 2 the pattern of dichotomous venation tends to be noticeably regular and it closely approaches the isotomous pattern of vein dichotomies in the leaves of certain ferns or in *Ginkgo*. But in other specimens, including the type material studied, the vein dichotomies are much less regular and symmetrical in type (Fig. 1–2).

In the second place, there is considerable variation in behaviour of the ultimate terminations or vein endings in the marginal regions of the lamina segments. Although in all cases the majority of the vein endings extend into the marginal teeth, examples of "blind" vein endings, unrelated to the dentations, were observed in every leaf specimen studied. As is shown in Fig. 2 and Pl. 2, a blind vein ending may represent (1) the termination of one of the branches of a vein dichotomy located near the base of a lamina segment or (2) one of the branches of a vein dichotomy found below or adjacent to a marginal sinus. The total number of these blind vein endings in any particular leaf seems to vary considerably. For example, in the leaf shown in Fig. 1 there occur 128 vein endings, 27 of which are blind and do not extend into marginal teeth. A comparable ratio was found in the leaf of one of the Shensi collections (Liu & Chun 1307) in which 31 out of a total of 166 vein endings were unrelated to marginal teeth. A relatively high percentage of blind vein endings were observed in a large leaf from the Kansu collection (Wang 14552) in which approximately one-fourth of all the vein endings were of the blind type. However, the limited number of leaves available for study makes it impossible to correlate the variations in the number of blind vein endings with either the size or degree of lobing and dentations of the lamina segments.

An additional, and at present unexplained, aspect of leaf venation only revealed by the careful study of cleared and stained specimens is the erratic occurrence of short strands of vascular tissue which are unconnected with the system of dichotomizing veins. In the leaf of the type material, five of such unconnected vascular strands occur (Fig. 1–2). In other collections, however, isolated strands are either very infrequent or entirely absent. As shown in Fig. 2, an isolated vascular strand may occur directly below the sinus between two marginal teeth.

A description of the venation pattern of *Kingdonia* would be incomplete without a few comments on the occurrence of vein anastomoses. My observations on one leaf of the type material from Yunnan agree with the earlier statements of Balfour and Smith (1914) and Diels (1932) that the venation is open and devoid of interconnections. I was, therefore, surprised to discover examples of well-defined and distinctive anastomoses in four of the leaves of the Shensi collections. Only a single anastomosis occurs in each of these leaves and its position is variable. In one of the specimens, the anastomosis is located between two veins near the margin of the median lamina segment whereas in the other three leaves, the single vascular interconnection is restricted to one of the upper lateral segments, and occurs in a central basal position, or in the terminal lobe or near the lower margin (Pl. 2). My interpretation of these apparently infrequent anastomoses is that they represent the fusion of the inner branches of two veins which dichotomize at approximately the same level. The areole which is produced is characteristically elongated and elliptical in form and imparts a very distinctive aspect to the venation pattern (Pl. 2). It would indeed be interesting and instructive to know whether vein anastomoses are actually of rare occurrence in *Kingdonia*. This, however, would require the investigation of a much wider range of leaf material than I have been able to assemble for the present study.

DISCUSSION

Before attempting a discussion of the morphological significance of dichotomous venation in *Kingdonia*, it is necessary to examine critically the taxonomic assignment of this genus to the family Ranunculaceae. Although Balfour and Smith (1914) regarded *Kingdonia* as "a very distinct genus of Ranunculaceae so far monotypic" they expressed considerable doubt as to its relationship with other genera (e.g. *Thalictrum*) in this family. Diels (1932) adopted a similar position and pointed out that the determination of the generic relationships of *Kingdonia* required a better understanding of the other interesting ranunculaceous plants native to the mountains of India and China. On the other hand, Janchen (1948) in his systematic monograph on the Ranunculaceae, classified *Kingdonia* as well as *Circaeaster* as the two genera comprising the subtribe Kingdoniinae under the Tribe Clematideae of the sub-family Ranunculoideae. This extremely precise taxonomic decision regarding *Kingdonia* was made by Janchen largely on the basis of its floral morphology without any knowledge of its reproductive cycle, seed development, xylem structure or pollen morphology and, in my opinion, is open to serious question.

In the light of the present study, the vasculature of the foliage leaf of *Kingdonia* diverges in most respects from descriptions in the literature regarding the nodal anatomy and venation of foliage leaves in members of the Ranunculaceae. According to Müller (1944), for example, the leaves of nearly all genera in the Ranunculaceae are vascularized by three or more traces which are related respectively to trilacunar or multilacunar types of nodes. On this basis, the unilacunar node and the *even* number of leaf traces and petiolar bundles found in *Kingdonia* present a striking contrast to the complex patterns of foliar vascularization characteristic of such ranunculaceous genera as *Anemone*, *Trollius*, *Delphinium*, *Clematis*, and *Aconitum* (see Goffart 1901 and Schrödinger 1914 for extensive descriptions of the vasculature of leaves in the Ranunculaceae). With respect to lamina venation, I have been unable either through personal investigation or a study of the literature to discover any example of open dichotomously veined foliage leaves among genera in the Ranunculaceae. Van der Hammen (1947–48) cites the "dichotomous" venation of the lamina in *Eranthis hiemalis* and *Anemone pulsatilla* but a study of cleared leaves of these species reveals that the venation is of the closed reticulate type. Even the small palmately-lobed primary leaves of *Anemone pulsatilla* are characterized, according to Zimmermann (1939, Fig. 16), by three bundles in the petiole and a pinnate-reticulate type of lamina venation.

It is thus evident that the distinctive nodal anatomy and dichotomous venation of the leaf of *Kingdonia* provide no evidence to support the classification of this genus in the Ranunculaceae. Admittedly, there is considerable danger in over-emphasizing the significance of such a character as foliar vasculature in the solution of problems in systematic botany. But until a more thorough study has been made of its vegetative and reproductive morphology, it seems preferable to recognize *Kingdonia* as an isolated member of the "Ranales" which possibly should be

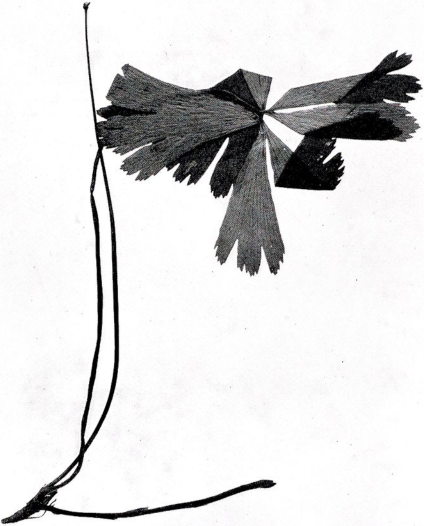

PLATE 1. Herbarium specimen of *Kingdonia uniflora* from Shensi Province (*Fu* & *Wei* 10403), showing portion of branched rhizome (note the scale leaves), the lobed dichotomously-veined segments of the single foliage leaf, and the receptacle and stalk of the solitary flower. ×1.

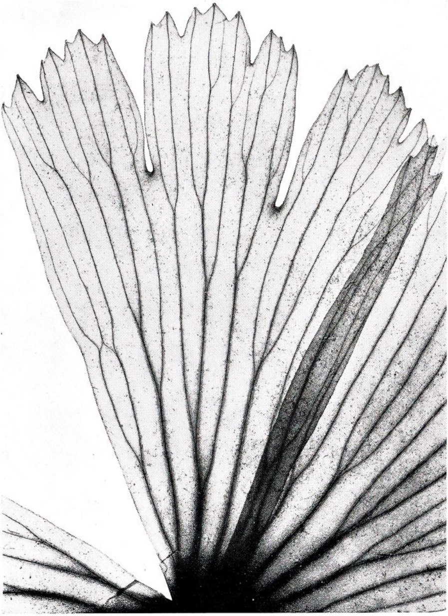

PLATE 2. Photomicrograph showing regular dichotomous venation of a segment of the lamina of *Kingdonia uniflora* (*Liu* & *Chun* 1307). Note conspicuous anastomosis between two veins near the left margin of the segment. ×7.

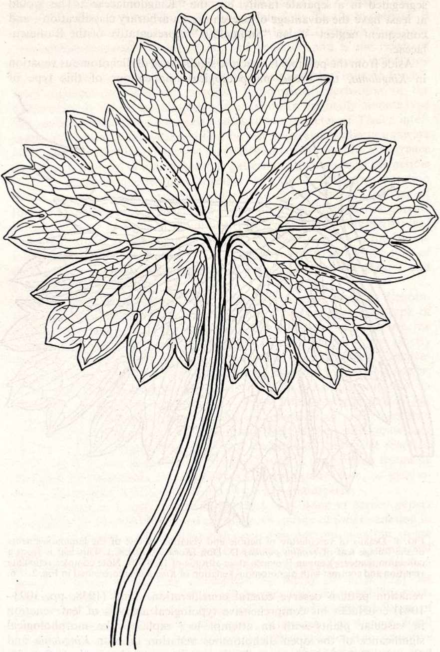

FIG. 3. Foliage leaf of *Trollius pumilus* D. Don (*Forrest* 21228 UC.). This leaf is from a collection made in S.W. Szechuan Province at an altitude of 13–14,000 ft. Contrast reticulate venation of this specimen with open dichotomous venation of *Kingdonia* shown in text Fig. 1. ×7.

segregated in a separate family, e.g. the "Kingdoniaceae". This would at least have the advantage of preventing its arbitrary classification—and consequent neglect—as an "anomalous" representative of the Ranunculaceae.

Aside from the possible taxonomic significance of dichotomous venation in *Kingdonia*, the broad morphological implications of this type of venation pattern deserve careful consideration. Troll (1938, pp. 1093–1094) concludes his comprehensive typological analysis of leaf venation in vascular plants with an attempt to "explain" the morphological significance of the open dichotomous venation of both *Kingdonia* and *Circaeaster*. In the firm conviction that the net venation typical of angiosperm leaves cannot be derived from dichotomous venation, Troll proposes the following series of hypothetical stages in the development of the *Kingdonia* type of venation. Beginning with the dichotomously-branched submerged water-leaf of *Cabomba caroliniana*, he postulates the fusion of the unveined lobes of the median segment of this leaf to an imaginary palmately-lobed and dichotomously veined blade equivalent

FIG. 4. Details of vasculature of petiole and venation of one of the lamina segments of the foliage leaf of *Trollius pumilus* D. Don (*Rock* 23132 UC.). This leaf is from a collection made in Yunnan Province at an altitude of 15,000 ft. Note complex reticulate venation and contrast with dichotomous venation of *Kingdonia* represented in Fig. 2. × 6.

morphologically to the median segment of the lamina of *Kingdonia* and to the entire leaf of *Circaeaster*. To appreciate fully Troll's hypothesis it should be noted that in his view the aquatic leaf of *Cabomba* is actually "pseudodichotomous" in branching and venation and is the result of the equal growth in size of *all* the lateral segments of a ternate leaf during the late phases of ontogeny. In short, by a remarkable "tour de force", Troll attempts to show the possible "typological" derivation of the dichotomously veined lamina of *Kingdonia* from an originally pinnate type of venation. Aside from the highly speculative character of Troll's interpretation, it must be emphasized that he was apparently entirely unaware of the unilacunar nodal anatomy of *Kingdonia* and of the unusual occurrence (for an angiosperm) of a dichotomous pattern of vasculature in the petiole (Fig. 2). These unique features, together with the dichotomous venation of the lamina, make it extremely difficult to regard the *total* pattern of foliar vasculation in *Kingdonia* as a "secondary" modification of pinnate venation. As an example of the difficulty, it seems highly improbable that a "modification" of the complex pinnate reticulate venation of the lamina lobes of such a leaf as that of *Trollius pumilus* would result in the type of dichotomous venation characteristic of *Kingdonia* (compare Figs. 1 and 2 with Figs. 3 and 4).

On the other hand, it is obviously impossible to prove that the dichotomous venation of *Kingdonia* represents the "persistence" of a type of venation characteristic of the ancestors of the angiosperms. However, the absence of vessels in a number of woody ranalian genera shows clearly that the evolutionary development of the xylem is not necessarily synchronized with the various levels of specialization attained by the leaf, flower, and other parts of these plants (Bailey 1954). Is it not possible that, in *Kingdonia*, evolutionary specialization of the foliar vascular system has remained at a primitive level despite the presence of such advanced characters in this species as an herbaceous habit, flowers and uniovulate carpels? It seems evident at any event that if a leaf with the type of venation shown in Pl. 2 were discovered in the fossil record, it probably would be classified by palaeobotanists as part of a pteridosperm, fern, or gymnosperm rather than a foliar organ of a "typical" angiosperm.

In conclusion, I wish to emphasize, as I have done in earlier papers (Foster 1952), the need for broad comparative studies of foliar venation in the angiosperms as a whole. Although open dichotomous venation, in the sense used in this paper, may indeed be a rare condition in the foliage leaf of angiosperms, our present knowledge of venation patterns in this vast group of plants is still very incomplete. As Bailey (1956, p. 272) has recently stated "in the case of the angiospermic leaf, the possibility exists that it may have been derived from one of *several* diversified forms of potentially ancestral foliar appendages". Although the meagre fossil record of the angiosperms offers no clue as to the nature of truly primitive angiosperm leaves, the continued exploration of nodal anatomy and venation patterns in living forms may yield important discoveries which ultimately may aid in a better understanding of the probable evolutionary history of the leaf in modern flowering plants.

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