

THE FLORAL MORPHOLOGY AND RELATIONSHIPS OF KINGDONIA UNIFLORA

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THE BROAD COMPARATIVE STUDIES of Bailey (1) and his associates have revealed many examples of the combination of primitive and advanced levels of specialization in the vegetative and reproductive structures of woody members of the Ranales. Indeed, certain ranalian genera are the only known dicotyledons which exhibit such primitive characters as monocolpate pollen, vesselless xylem, and "open," styleless, conduplicate carpels. Despite the significant advances in our understanding of the trends of evolutionary specialization in the xylem and in floral organs, the nature of the truly primitive leaf type in angiosperms remains an unsolved problem. The predominance in the woody Ranales of simple leaves with pinnate-reticulate venation is regarded by Eames (8, p. 421) as "strong evidence that this is a primitive leaf type in the Angiosperms." Bailey (2), however, takes a more conservative or skeptical viewpoint and states that the modern angiospermic leaf may have arisen "from one of several diversified forms of potentially ancestral appendages." In full accord with this cautious approach to the problem, I have already raised the question of whether the "closed" reticulate type of venation, so characteristic of living angiosperms, may not have evolved from open dichotomous vasculature (9). This possibility is clearly indicated by the remarkable dichotomously veined leaf of *Kingdonia uniflora*, an herbaceous perennial which is classified at present as a member of the Ranunculaceae (10, 11, 12).

The occurrence of dichotomous foliar venation in a plant of presumed ranalian affinities deserves full consideration in any theory of foliar evolution and emphasizes the need for a comprehensive study of *all* aspects of structure and morphology in *Kingdonia*. For this reason an investigation of the morphology and vasculature of the floral organs of this genus has been undertaken and the results are presented in this paper.

MATERIALS AND METHODS

The flowering specimens used in my study were secured, through the kindness of Professor Yu-Wen Tsui, from the following Shensi collections of *Kingdonia* deposited in the herbarium of the Northwestern Institute of Biology at Wukung, Shensi Province, China, viz.: *Liu & Chun* 1307, collected September 28, 1937, on Taipaishan; *Ho*, s.n., Taipaishan, Fan Yang Szu (Pasturing Sheep Temple); and *Fu* 12296, collected June 7, 1959, on Taipaishan. Grateful acknowledgment is made to Dr. Shiu-ying

Hu, of the Arnold Arboretum, Harvard University, for translating into English the Chinese data included with the Ho collection of *Kingdonia*.

Despite the fragile and desiccated condition of the material, the combined use of cleared specimens and serial microtomed sections made it possible to study many features of floral morphology in considerable detail. All flower buds and flowers were first cleared in 2.5% NaOH and, after thorough washing in water, transferred to cold concentrated chloral hydrate. Specimens cleared in this way proved suitable for drawings of the general organography of the flower and were subsequently dehydrated and lightly stained with safranin. After staining, the individual organs of some of the flowers were dissected from the receptacle and mounted directly in "Piccolyte." Other flowers, as well as the buds, were dehydrated by the tertiary butyl alcohol method, infiltrated with "Histo-wax," sectioned 7–8 μ in thickness, and stained with a combination of safranin and light green.

I wish to thank Mr. Roy L. Taylor for his skillful assistance in all phases of the embedding, sectioning, and staining of the floral material. I am also greatly indebted to my wife who prepared the drawings reproduced in this paper as Figs. 2–7, assembled the photomicrographs and assisted me in proofreading the manuscript. Thanks are also due Mr. Victor Duran for his skill and patience in making the photomicrographs.

GENERAL ORGANOGRAPHY OF THE FLOWER

According to Balfour and Smith's (5) description of the type material collected by F. Kingdon Ward in northwestern Yunnan Province, China, the solitary, apetalous flower of *Kingdonia* is borne on a naked scape 7–10 cm. long and consists of 5 sepals, 10–15 stamens, and 5–7 carpels. My observations, restricted to a study of flowering specimens from a montane area in Shensi Province, differ in several important respects from this description.

In the first place, it seems more appropriate to designate the spirally arranged perianth members as "tepals" rather than as "sepals" (Fig. 1). The latter term implies the former existence of petals in the flower of *Kingdonia*, but no evidence of vestigial petals or their traces was found in either cleared or sectioned flowers. Furthermore, it is obvious even from the limited material examined that the number of perianth members is inconstant. In some flowers five tepals are present (Fig. 1), but flowers with six or seven tepals have also been observed. These fluctuations clearly suggest that a well-defined "calyx," in the formal sense, is not present.

A more serious divergence between Balfour and Smith's description and the present study concerns the nature of the androecium. In all the flowers I have examined, the androecium consists of an outer series of 8–12 spirally arranged staminodia and a more centrally located series of 3–6 stamens, each of which is demarcated into anther and filament (Figs.

1, 8, 10, 11). Although no organs morphologically intermediate in character between staminodia and stamens were observed, the study of a wide range of flowers might reveal such transitions. Whether the larger number of stamens (10–15) cited in Balfour and Smith's description represents a condition peculiar to the material from Yunnan or whether they failed to discriminate between staminodia and stamens must remain open questions for the present.



FIG. 1. Organography of a mature flower with five tepals, numerous staminodia, six stamens, and seven carpels, $\times 14$. (Drawn from a cleared specimen, *Fu 12296*, by Mrs. Emily R. Reid.)

The apocarpous gynoecium of the flower of *Kingdonia* is composed of 5–8 spirally arranged carpels (Figs. 1, 2, 18). Following pollination, the tepals, staminodia, and stamens fall from the receptacle, and the stylar portion of each of the enlarging carpels gradually becomes bent or recurved over the dorsal edge of the ovary (Figs. 2, 21–24). This beaked character of the developing carpel and fruit is highly distinctive of *Kingdonia* and was noted in the brief descriptions of Balfour and Smith (5), Diels (7), and Wang (15).

COMPARATIVE MORPHOLOGY OF FLORAL ORGANS

One of the interesting results of the present study was the discovery of the general similarity in the nodal anatomy of *all* the appendages of the flower. The vascular system of most of the receptacle is a typical eustele in which, as the result of interfascicular cambial activity, a single well-defined gap is associated with the divergence of the vascular supply of each of the tepals, staminodia, stamens, and lower carpels. In contrast, the vasculature of the upper portion of the receptacle consists entirely of the traces of the inner carpels, and no "residual" xylem or phloem strands appear to exist (FIG. 18).



FIG. 2. Form and spiral arrangement of a series of eight carpels of *Kingdonia* (Ho, s.n.) at various stages of enlargement, $\times 8$. Except for a single persistent staminodium (at lower right) all other floral organs have fallen from the prominent receptacle. Note dorsally reflexed styles of three largest carpels at the left.

The following description and interpretation of the form, general structure, and venation of the floral organs of *Kingdonia* is based largely upon the examination of mature flowers. Although much care was devoted to restoring the structure of flower buds, the results in some respects were quite disappointing. As a consequence, many important aspects of floral

morphology, such as the early differentiation of the anther and the structure and vasculature of the ovule, cannot be described until adequate fixed material of all stages in floral development becomes available.

Tepals. A comparison of the cleared and stained tepals revealed interesting variations in both form and venation (Figs. 3–7). Only a single example of a lobed tepal was observed in the present study (Fig. 6). The lamina of this remarkable appendage terminates in two short lobes separated by a deep and clearly defined sinus. Whether or not this form of tepal should be regarded as a rare “anomaly” can, of course, only be determined by a survey of many flowers. It is entirely possible that three- or even five-lobed tepals may occasionally develop. Most commonly, and in agreement with Balfour and Smith’s description of the “sepals,” the tepal of *Kingdonia* is a simple foliar structure consisting of a short petiole and an elliptical-oval, prominently acuminate lamina (Figs. 3–5).

Before describing the venation pattern of the tepals, it is essential to comment briefly on the structure of the tepal traces near their point of divergence from the eustele of the receptacle. A study of thin serial transections of one of the flowers showed that each trace consists of two more or less discrete strands of primary xylem which appear to be independently connected with the receptacle bundles bordering the single gap. However, the limitations of the material prevented a fully satisfactory reconstruction of the exact nature of the subnodal connections and origin of the tepal traces.

The basal portion of each tepal is traversed by the unbranched extension of its double trace, which, in cleared specimens, usually consists of two separate but closely spaced strands of xylem. In the lower region of the tepal lamina, this double bundle gives rise to a midvein and two lateral veins, one or both of which may branch dichotomously (Figs. 4a–6). No evidence of anastomoses or commissural veinlets was found, and hence the tepal venation in *Kingdonia* is simple and “open” in type. However, the exact mode of origin of the midvein and the two main lateral veins from the double bundle fluctuates even among the tepals of one perianth and may be conveniently described under the two following “types.”

TYPE 1. In this very common type, the midvein and one of the lateral veins of the tepal lamina represent respectively the central and outer branches of one of the main xylem strands of the double trace (Figs. 3, 5, 6). However, the level at which divergence and dichotomy of the main strands of the trace occur varies considerably. In many tepals, the single dichotomy which yields the midvein is near or at the level of divergence of both of the lateral veins. But Fig. 3 shows that the dichotomy may take place well above the point of divergence of the other main lateral vein.

TYPE 2. The distinctive feature of this less common type is the dichotomous branching, at approximately the same level, of *each* of the two xylem strands of the double bundle and the union of the central strands

to form the midvein of the tepal (FIG. 4a-b). The two outer strands resulting from these dichotomies constitute the main diverging lateral veins of the lamina. A detailed study, with the aid of dark field illumination, showed that the two central strands which join to form the midvein are relatively slender and often unequal in size (FIGS. 4b, 7).

As FIGS. 3-6 clearly indicate, there is no apparent correlation between these two types of midvein origin and the degree of branching of the main lateral veins. Type 1 may be associated with tepals in which both lateral veins remain unbranched and terminate blindly in the upper half of the lamina, or one or both of the laterals may dichotomize. In the latter case, the *inner branch* very commonly is longer and more highly developed than its sister branch. A striking example of this is shown in the bilobate tepal in which the lateral lobe is vascularized by the stronger inner branch of one of the lateral veins (FIG. 6).

A few comments are appropriate regarding the interesting variations in the amount of xylem differentiated at various levels in the midvein. Near its point of origin, the midvein is relatively slender and comparable in this respect to the main lateral veins. Quite commonly, however, the upper portion of the midvein is conspicuously thicker as the result of the increase in number of tracheary elements. At its point of termination in the apex of the tepal, the midvein is usually dilated, suggesting the possibility that it is associated with a hydathode.

Staminodia and Stamens. As mentioned earlier, the outer members of the androecium are clearly defined staminodia (FIG. 1). Each staminodium consists of an elongated filamentous stalk which terminates abruptly in an apically dilated "knob." The vasculature is represented by a single unbranched vein which extends vertically through the stalk and then curves adaxially into the dilated end of the staminodium (FIG. 8). Although serial transections revealed no traces of rudimentary or abortive microsporangia, the dilated portion of the staminodium is quite comparable in general form and venation with the corresponding sterile region of the anther (compare FIGS. 8 and 11). On the other hand, a definitive character of the staminodial apex is the presence on its adaxial side of a median groove or furrow. As seen in transectional view, the epidermal cells which line the groove occur directly over a tissue comprised of cells which are much smaller and more deeply stained than the bulk of the parenchyma cells of the staminodium (FIG. 9). On the basis of this histological evidence, the groove may be glandular or "nectariferous" and may secrete substances which attract insect visitors to the flowers.

Each of the stamens, like the staminodia, is vascularized by a single unbranched bundle which diverges at the juncture of anther and filament into the broad area of sterile tissue separating the two pairs of microsporangia (FIGS. 10, 11). Although the sporangia are protuberant and superficially may appear "terminal," their position with reference to the anther as a whole and to the plane of dehiscence is more accurately described as "latrorse-extorse." This is shown by FIGS. 10, 11 which re-

spectively depict abaxial and adaxial views of mature, cleared stamens, and illustrate the oblique, more or less abaxial (i.e., extrorse) line of dehiscence between the members of each pair of sporangia.

The tissues of the young stamens of the flower buds which were sectioned were so badly collapsed and distorted that the following description and interpretation of the structure of the microsporangia is necessarily based on the study of mature, dehiscent anthers. FIGURE 12 represents a trans-section of an anther at the time of dehiscence and shows the remains of the partitions which separated the members of each pair of sporangia. The confluent "pollen sacs" contain "normal" pollen grains (see also FIGS. 13-16), small tetrads, and apparently many examples of shrunken abortive cells. At this late stage in maturation it is impossible to describe with any accuracy the cellular structure of the sporangium walls. The dark "lining" of the pollen sacs may correspond to the remains of the tapetum and middle layers of the wall but there is no certainty on this point. In contrast, the endothecium or "fibrous layer" is well preserved and consists of two sharply delimited semicircular layers of cells with bandlike thickenings which jacket the protuberant portions of the confluent sporangia. These strips of endothecium are not continuous across the sterile portion of the anther, nor have cells with similar structure been observed bordering the internal edges of the sporangial cavities.

The taxonomic and phylogenetic interest of information on pollen morphology in *Kingdonia* is emphasized by the present classification of this genus in the Ranunculaceae, a family characterized, according to Bailey and Nast (3), by tricolpate or derived forms of pollen. Because of my extremely limited material, a somewhat "unconventional" technique was employed in securing permanent whole mounts of pollen grains. Following the usual clearing in NaOH and chloral hydrate, the stamens were dehydrated, stained in dilute safranin and the mature anthers "squashed" directly in the "Piccolyte" before adding the cover-glass. Selected examples of pollen processed in this way are shown in FIGS. 13-16.

A comparison of polar and side views clearly indicates that the pollen grain is provided with three longitudinal furrows or colpi (FIGS. 13, 15, 16). Although it has not been possible to study germinating pollen, there is some suggestion that a definable pore or aperture is located in each of the colpi. In the grain shown in median optical view in FIG. 13 the delicate "intine" appears to have evaginated as a short tubular process from the center of each of the furrows. On this basis it would appear justifiable to classify the pollen of *Kingdonia* as tricolporate in type. The exine of mature grains is moderately thick and when seen in surface view exhibits a complex foveate-reticulate structural pattern (FIG. 14).

Carpels. Although the general form and uniovulate nature of the carpels of *Kingdonia* have been described by Balfour and Smith (5) and Diels (7), their accounts are very brief and include no information on early ontogeny or vasculature of these organs. On the basis of the present investigation it is believed that a relatively full description may now be

given of some of the early and critical stages of development and vascularization of the carpel. The most serious gaps in my description and interpretation concern the ontogeny and vasculature of the single pendulous ovule developed in each carpel (FIG. 20). Despite the greatest possible care, the tissues of the ovule appeared collapsed and disorganized at all stages, and the problem can only be solved by the use of adequately fixed and preserved material (see also FIG. 19c).

Before presenting the details of carpel ontogeny it is necessary to describe briefly the general pattern of growth which leads to the adult form of the carpels. At anthesis, the carpel consists of a very short basal stipe, a laterally flattened ovary, and an erect or slightly recurved style with a terminal papillate stigma (FIGS. 1, 21). When the carpels are approximately 2–3 mm. in total length, they contain a single ovule attached to the ventral side of the carpel wall (FIG. 20). As growth continues, the basal stipe elongates, the ovarian region increases conspicuously in length and width and the style becomes reflexed over the upper dorsal edge of the carpel (FIGS. 21–24). According to Wang (15), the mature fruit of *Kingdonia* is a one-seeded achene and exclusive of the recurved “beak” is 8 mm. long and 2.2 mm. wide. A carpel of approximately similar dimensions is shown in FIG. 24.

A transection of the central region of a developing flower bud showing three young carpel primordia is depicted in FIG. 17. At this early stage, the primordia are 200–275 μ in height and throughout most of their length are prominently conduplicate structures. However, because of their spiral arrangement on the receptacle these primordia are not cut at the same level, and the lower primordium in FIG. 17 is represented by a section through the short basal stipe. Comparison of serial sections indicates that the post-genital fusion of the carpel margins to form the closed locule occurs in an acropetal direction. The carpel primordium at the upper right in FIG. 17 shows an early stage in the fusion of the margins, while the primordium at the left has been sectioned at a slightly higher level and exhibits an open conduplicate structure. In both of these carpels a single ovule primordium has arisen distal to the margin of the carpel. Thus the placentation in *Kingdonia* is obviously submarginal in type.

The continued differentiation and enlargement of the carpel is accompanied by the progressive acropetal fusion of the carpel margins and the development of a simple but highly distinctive type of vasculature. A relatively advanced stage in the closure of the carpel is shown in FIGS. 19a–e which represent transections cut at successively higher levels through a carpel approximately 1 mm. in height. Although complete union between the margins and outer adaxial surfaces of the carpel wings has produced a closed locule in the lower portion of the ovary (FIG. 19b, c), the upper third of the carpel, including the style is still unsealed and conduplicate in organization (FIG. 19e). Limitations of material prevented a study of the later and final phases of closure of the carpel, and serial transections of a carpel 6.75 mm. in height showed no evidence, except in the lower adaxial portion of the style, of conduplicate structure.

Each of the spirally arranged carpels of *Kingdonia* is vascularized by a single trace which, in young carpels, consists of a strand of xylem flanked and partially enclosed by two well-defined strands of phloem (FIG. 18). Soon after its extension into the basal region of a carpel, the trace divides tangentially into a dorsal (abaxial) and a ventral (adaxial) bundle. This aspect of carpellary vasculature is shown in the bases of three of the outer carpels in FIG. 18 and is further illustrated in the photographs of the cleared carpels represented by FIGS. 22–24. The structure and course of the dorsal and ventral bundles in a young, apically conduplicate carpel are shown in the transectional views depicted by FIG. 19a–e. The relatively weak development of xylem in the ventral bundle is evident even in sections of the stipe (FIG. 19a). At successively higher levels the ventral bundle appears to consist wholly of phloem, and the strand terminates its development near the point where the carpellary margins are still open and conduplicate (FIG. 19d). In contrast, the dorsal bundle is more robust, and the existence of both phloem and xylem is evident at high levels in the carpel (FIG. 19e). During the further enlargement of the carpel, the dorsal bundle continues its more rapid development and ultimately extends without branching into the lower region of the style. FIGURES 21–24 clearly suggest that xylem development in the dorsal bundle is precocious, acropetal, and continuous, in contrast to the discontinuous and bidirectional pattern of early xylem formation within the ventral bundle.

During the late phases of closure of the upper part of the carpel, the ventral bundle dichotomizes into two slender branches which terminate blindly near the top of the ovary but do not extend into the base of the style (FIG. 24). The point at which the bifurcation of the ventral bundle occurs appears to be below or in the immediate vicinity of the attachment of the ovule to the placenta. The ventral bundle shown in FIG. 19b, for example, although devoid of xylem, appears somewhat “double” in structure. Transections of carpels 6–7 mm. long show that each of the branches of the ventral bundle consists of well-defined phloem and xylem. Unfortunately, however, the ovule in each of these carpels appears abortive and collapsed, and there was no convincing evidence of the derivation of an ovule trace from either of the ventral strands.

A few observations were made of the structure and vasculature of apparently mature fruits. No evidence of *any* venation was seen in the carpel “walls” and it seems clear that the type of vasculature represented in FIG. 24 is typical of both the carpel and the mature achene of *Kingdonia*. During the development of the carpel into a fruit, the dorsal and ventral veins become more or less completely jacketed by sclerenchyma, and the surface cells which line the locule develop remarkable reticulate bands of secondary wall thickening. The prominent beak of the achene is likewise composed largely of sclerenchyma, the initiation of which occurs in the upper region of the styles of comparatively young carpels and proceeds basipetally into the upper portion of the ovary.

DISCUSSION

In the light of current phylogenetic interpretation of floral organs in both woody and herbaceous ranalian plants, the flower of *Kingdonia* appears to show a combination of primitive and advanced levels of specialization. For example, the marked fluctuation in the number of tepals, staminodia, stamens, and carpels, their spiral arrangement on the receptacle, and the absence of fusion between any of these organs point to a rather primitive level of floral organization. On the other hand, the form and vasculature of the stamens and carpels seem decidedly advanced as compared with the foliaceous reproductive structures in the flowers of such woody genera as *Degeneria*, *Austrobaileya*, and *Himantandra*. The following discussion attempts to summarize the anatomical evidence secured by the present study and to evaluate it with particular reference to (a) the phylogenetic significance of the remarkable dichotomously veined leaf of *Kingdonia* and (b) the problem of the systematic affinities of this genus.

The tepals, despite their small size and typically simple form, are the only floral organs in which the vasculature offers points for *direct* comparison with the foliage leaf (Figs. 3-7). The nodal anatomy of the tepal is unilacunar, as in the leaf, and the double trace seems to represent merely a simplification of the system of four traces which vascularizes the foliage leaf. Indirect evidence in support of this interpretation is provided by the cataphylls of *Kingdonia*. These scale leaves occasionally develop a rudimentary lamina, and in such cases they are vascularized by two well-defined traces. Further indication of the fundamental resemblance between the vasculature of tepal and leaf is shown by one of the modes of origin of the tepal midvein. As illustrated in Figs. 4 and 7, this unbranched vein may arise from the union of the two central branches formed by the dichotomy of each of the tepal traces. A similar transition from an even to an odd number of main veins occurs in the base of the median lamina segment of the foliage leaf but results in this case in the formation of three systems of dichotomizing veins (cf. Foster and Arnott 11, Figs. 5, 7). In connection with these comparisons it is interesting to note the marked resemblance between tepal vasculature in *Kingdonia* and certain forms of cotyledonary venation in the angiosperms recently discussed by Bailey (2). The distinctly asymmetrical derivation of the tepal midvein shown in Fig. 3 is matched in certain types of cotyledons which develop an odd number of veins and the venation pattern represented in Fig. 4a, b corresponds very closely to another widespread type of cotyledonary vasculature (cf. Bailey 2, Figs. 2 E, F).

Bailey's (2) comprehensive surveys of the nodal anatomy of cotyledons, foliage leaves, and floral organs provide excellent evidence that the two-trace unilacunar node represents the primitive condition in angiosperms. On the basis of this interpretation, the probable nature of the *complete* vasculature of the primitive leaf type in angiosperms requires careful consideration. Bailey (2) has advanced the suggestion that the "mid-vein

of angiospermic appendages may have evolved by the approximation and fusion of two independent systems of vasculature." This idea implies that the venation of primitive leaves was not "pinnate" in the strict sense of the term but may have resembled certain "pseudo-palmate" or transitional forms of cotyledonary vasculature (Bailey 2, *Fig. 2A, C, G*). In this connection, is it not possible that the leaf of *Kingdonia* — notable for its unilacunar node, its four leaf traces and its palmate system of open dichotomous venation — may typify *one* of the ancient forms of foliar vasculature in the angiosperms? In my opinion, the occurrence of a two-trace and open dichotomous type of vasculature in the tepals of this genus lends additional weight to this theory. Although it may be argued that the persistence of a primitive leaf type is improbable in an herbaceous plant, the family Nymphaeaceae appears to have retained primitive forms of stamens (14), and vessel members with scalariform perforations occur in the xylem of *Paeonia* and *Hydrastis* (8). From these examples there seems to be no *a priori* reason to assume that the dichotomous vasculature of *Kingdonia* must be "specialized" or the result of "reversion" merely because this genus is herbaceous, rather than woody, in habit.

In contrast to the double-trace pattern of vasculature of tepals, each of the stamens of *Kingdonia* is vascularized by a single unbranched bundle (Figs. 10, 11). This fact, coupled with the clear demarcation of anther and filament and the latrorse-extrorse dehiscence of the paired sporangia, indicates a comparatively advanced type of stamen. The morphological and phylogenetic significance of the staminodia, which are likewise unifasciculate appendages, is problematical. However, their inconstant number and their position *below* the stamens suggest an evolutionary origin from fertile microsporophylls.

Like the stamen, the carpel of *Kingdonia* also seems relatively specialized in both form and vasculature, especially when compared with the apparently primitive carpel types which occur in such woody ranalian plants as *Drimys piperita* and *Degeneria* (4). In these species the carpel shows no distinction of an ovary, style, or terminal stigma but is a stipitate, unsealed, conduplicate organ bearing numerous ovules on its inner face between the median and lateral veins. The advanced level of specialization of the stipitate carpel of *Kingdonia* is shown by the clear demarcation between ovary, style and stigma, by the development of a single ovule and by the simple and sparse pattern of vasculature (Figs. 20, 24). Although the conduplicate and open structure of the carpel primordia in *Kingdonia* suggests the persistence of a primitive type of ontogeny, the closure of the carpel occurs relatively early and results in a sealed ovary without a definable ventral suture. The mature vasculature consists of an unbranched dorsal and a forked ventral vein, both derived from the single trace which enters the stipe region of the carpel.

As mentioned earlier in this paper, it proved impossible because of technical difficulties, to determine the nature of the "ovule trace" in *Kingdonia*. The bifurcation of the ventral strand occurs near the point of attachment of the ovule to the inner ventral surface of the carpel and

it is probable that the vasculature of the ovule is derived from one or possibly both of these traces. In this connection, the venation of the carpels of certain members of the Ranunculaceae offers certain points for comparison with the situation in *Kingdonia*. According to Chute (6), the carpel of various species of *Anemone*, *Clematis*, and *Hepatica* is vascularized by a single trace which divides into a dorsal and ventral vein. Near the top of the ovarian cavity, the "fused ventrals" divide into three strands; the median represents the ovule trace, and the two laterals continue into the style. In *Kingdonia*, however, the two branches of the ventral bundle terminate near the base of the style which is vascularized exclusively by the unbranched dorsal bundle (FIG. 24).

In conclusion, it seems appropriate to discuss briefly the bearing of the evidence from leaf and flower on the systematic affinities of *Kingdonia*. As I have recently pointed out (10), the original classification of *Kingdonia* in the Ranunculaceae by Balfour and Smith (5) was accepted without question by Diels (7) and Janchen (13), and the same taxonomic assignment of this genus was later adopted by Wang (15) and Hutchinson (12). Admittedly the herbaceous habit, polymeric flowers and one-seeded achenes of *Kingdonia* are duplicated, at least in a superficial way, in such ranunculaceous genera as *Thalictrum* and *Anemone*. But in my opinion, the *totality* of morphological and anatomical evidence derived from my studies on the leaf and flower strongly indicate that *Kingdonia* is a "relict" genus, without obvious affinity to any ranalian family, including the Ranunculaceae. Prominent among the "unique" and isolated features of *Kingdonia* are the dichotomously veined foliage leaf and the two-trace vascular system of the tepals. Comparable types of foliar vasculature do not occur in any of the genera of Ranunculaceae which I have studied or which have been described anatomically in the literature (10). A similar but less decisive "remoteness" is shown by the pollen grains of *Kingdonia* (FIGS. 13-16). These structures appear to be tricolporate in type and when more thoroughly studied and compared with the pollen of other ranalian plants may support the removal of *Kingdonia* from the Ranunculaceae.

Many important morphological aspects of *Kingdonia* remain for future investigation. These include the determination of the chromosome number, the morphology of the tracheary elements, the study of the seedling (with particular reference to cotyledonary vasculature), and information on the development and structure of the embryo sac, endosperm, and embryo. When these gaps in our present knowledge have been bridged, I suspect that *Kingdonia* will ultimately be treated as the representative of an independent and "relict" family within the Ranales.

LITERATURE CITED

1. BAILEY, I. W. Contributions to plant anatomy. Chronica Botanica Co., Waltham, Mass. 1954.
2. ———. Nodal anatomy in retrospect. Jour. Arnold Arb. 37: 269-287. 1956.

3. ——— and C. G. NAST. The comparative morphology of the Winteraceae. I. Pollen and stamens. Jour. Arnold Arb. **24**: 340–346. 1943.
4. ——— and B. G. L. SWAMY. The conduplicate carpel of dicotyledons and its initial trends of specialization. Am. Jour. Bot. **38**: 373–379. 1951.
5. BALFOUR, I. B., and W. W. SMITH. *Kingdonia uniflora*. In: Diagnoses specierum novarum LI–CII (species Chinenses). Notes Royal Bot. Gard. Edinb. **8**: 191–192. 1914.
6. CHUTE, H. M. The morphology and anatomy of the achene. Am. Jour. Bot. **17**: 703–723. 1930.
7. DIELS, L. *Circaeaster* eine hochgradig reduzierte Ranunculacee. Beih. Bot. Centralbl. **49** (Erg. Bd.): 55–60. 1932.
8. EAMES, A. J. Morphology of the angiosperms. McGraw-Hill Book Co., Inc. New York. 1961.
9. FOSTER, A. S. The phylogenetic significance of dichotomous venation in angiosperms. Proc. IX Int. Bot. Congr. **2**: 119–120. 1959.
10. ———. The morphological and taxonomic significance of dichotomous venation in *Kingdonia uniflora* Balfour f. et W. W. Smith. Notes Royal Bot. Gard. Edinb. **23**: 1–12. 1959.
11. ——— and H. J. ARNOTT. Morphology and dichotomous vasculature of the leaf of *Kingdonia uniflora*. Am. Jour. Bot. **47**: 684–698. 1960.
12. HUTCHINSON, J. The families of flowering plants. Vol. I. Dicotyledons. Ed. 2. Oxford. 1959.
13. JANCHEN, E. Die systematische Gliederung der Ranunculaceen und Berberidaceen. Denkschr. Österr. Akad. Wiss. Math.-Naturwiss. Klasse **108**: 1–82. 1948.
14. MOSELEY, M. F., JR. Morphological studies in the Nymphaeaceae. I. The nature of the stamens. Phytomorphology **8**: 1–29. 1958.
15. WANG, W. T. Notulae de Ranunculaceis sinensibus. Acta Phytotax. Sinica **6**(4): 361–391. 1957.

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EXPLANATION OF PLATES

PLATE I

FIGS. 3–7. FORM AND VENATION PATTERNS OF TEPALS OF *Kingdonia* [*Fu 12296*]. 3, Origin of midvein and lateral vein from dichotomy of one strand of double trace, $\times 7$. 4a, Origin of midvein by union of central branches of both dichotomizing strands, $\times 6$. 4b, Enlargement of region of vein-union represented in 4a, $\times 30$. 5, Tepal showing prominent dichotomous branching of each lateral vein, $\times 6$. 6, Form and vasculature of a bilobed tepal, $\times 7$. 7, A further example of dichotomy of both strands of tepal trace and union of the two short central bundles to form midvein, $\times 30$ — note close approximation of central bundles as compared with 4b. For further explanations, see text.

PLATE II

FIGS. 8–12. STAMENS AND STAMINODIA OF *Kingdonia*. 8, Cleared staminodium [*Ho, s.n.*] showing general form and vasculature, $\times 32.5$. 9, Transection of apical region of staminodium [*Fu 12296*] showing adaxial groove and single vein,

× 135. 10, 11, Cleared stamens [from *Ho, s.n.*], showing vasculature and the orientation and plane of dehiscence of the microsporangia, × 32.5; 10, abaxial view; 11, adaxial view. 12, Transection of dehiscent anther, × 135 — note pollen grains and clearly delimited endothecium.

PLATE III

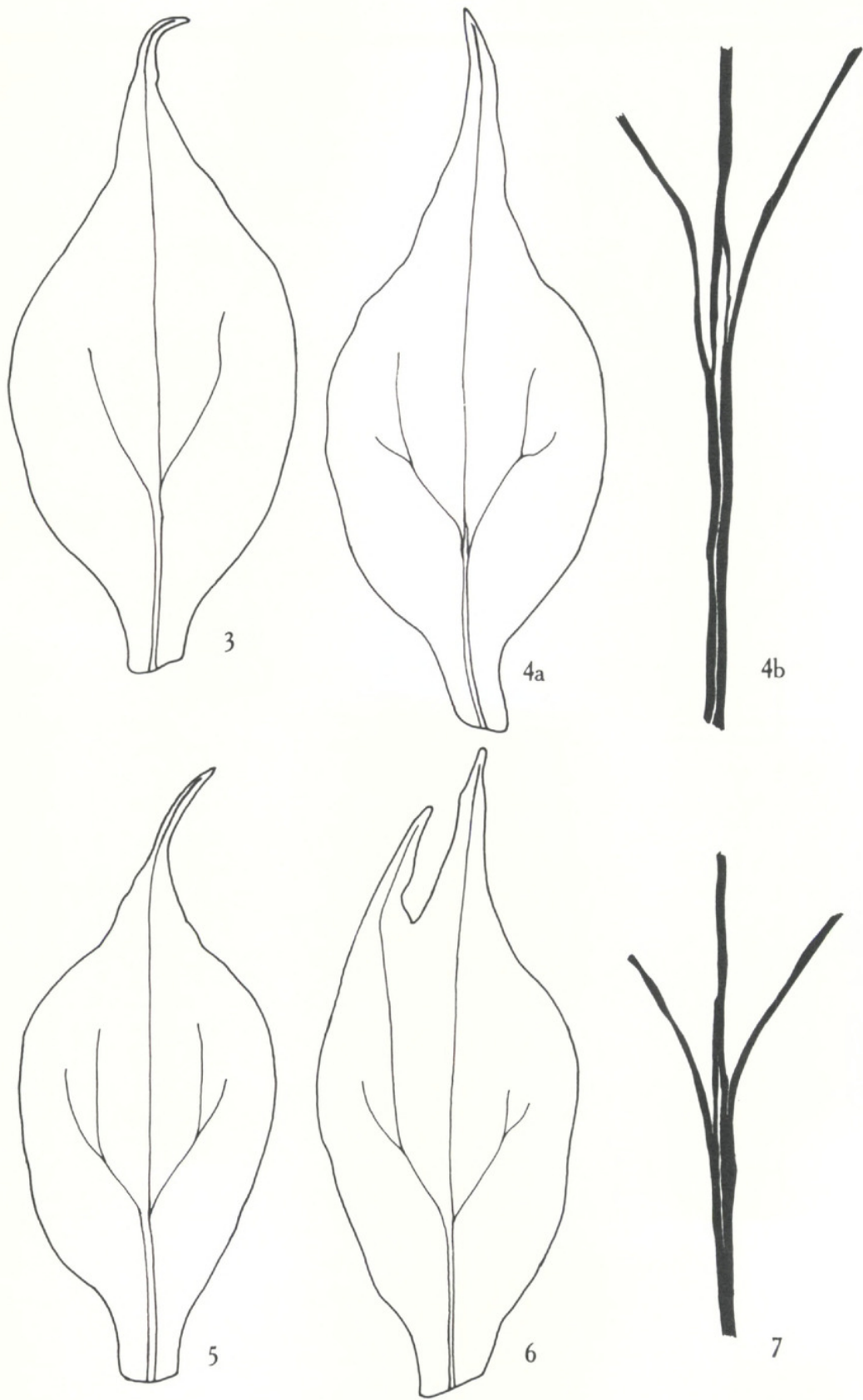
FIGS. 13–17. POLLEN AND CARPELS OF *Kingdonia*. 13–16, Mature pollen grains [from *Fu 12296*], × 1480. 13, Polar view, showing tricolporate structure. 14, Same grain at a higher focal plane, illustrating structural pattern of exine. 15, 16, Side views of pollen grains with longitudinal colpi. 17, Transection of central region of flower bud [*Liu & Chun 1307*] to illustrate young stages of carpel development, × 295. Note conduplicate nature of carpel primordium at left and fused margins of young carpel at upper right.

PLATE IV

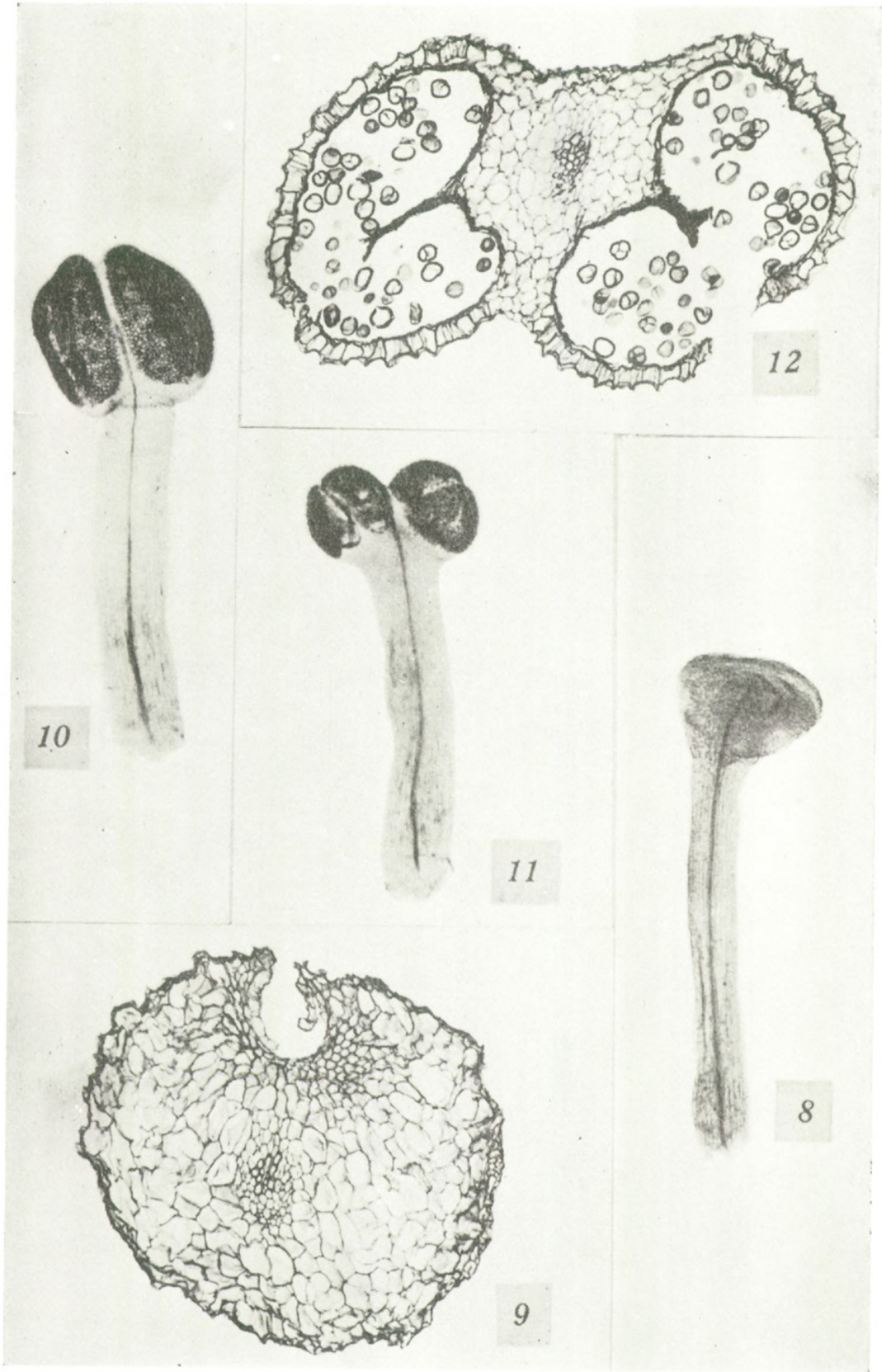
FIGS. 18–20. VASCULATURE AND DEVELOPMENT OF CARPELS. 18, Transection of flower [from *Fu 12296*] with seven carpels, the outer five of which are attached to the receptacle, × 138. Note particularly that each of the traces of the two uppermost carpels consists of a single xylem strand flanked by two phloem strands. 19a–e, Transections, at successively higher levels, of one of the carpels shown in Fig. 18, × 138. 20, Longitudinal section of a carpel about 2 mm. high (exclusive of reflexed style) showing the attachment of the single pendulous ovule to the ventral wall [*Ho, s.n.*], × 22.

PLATE V

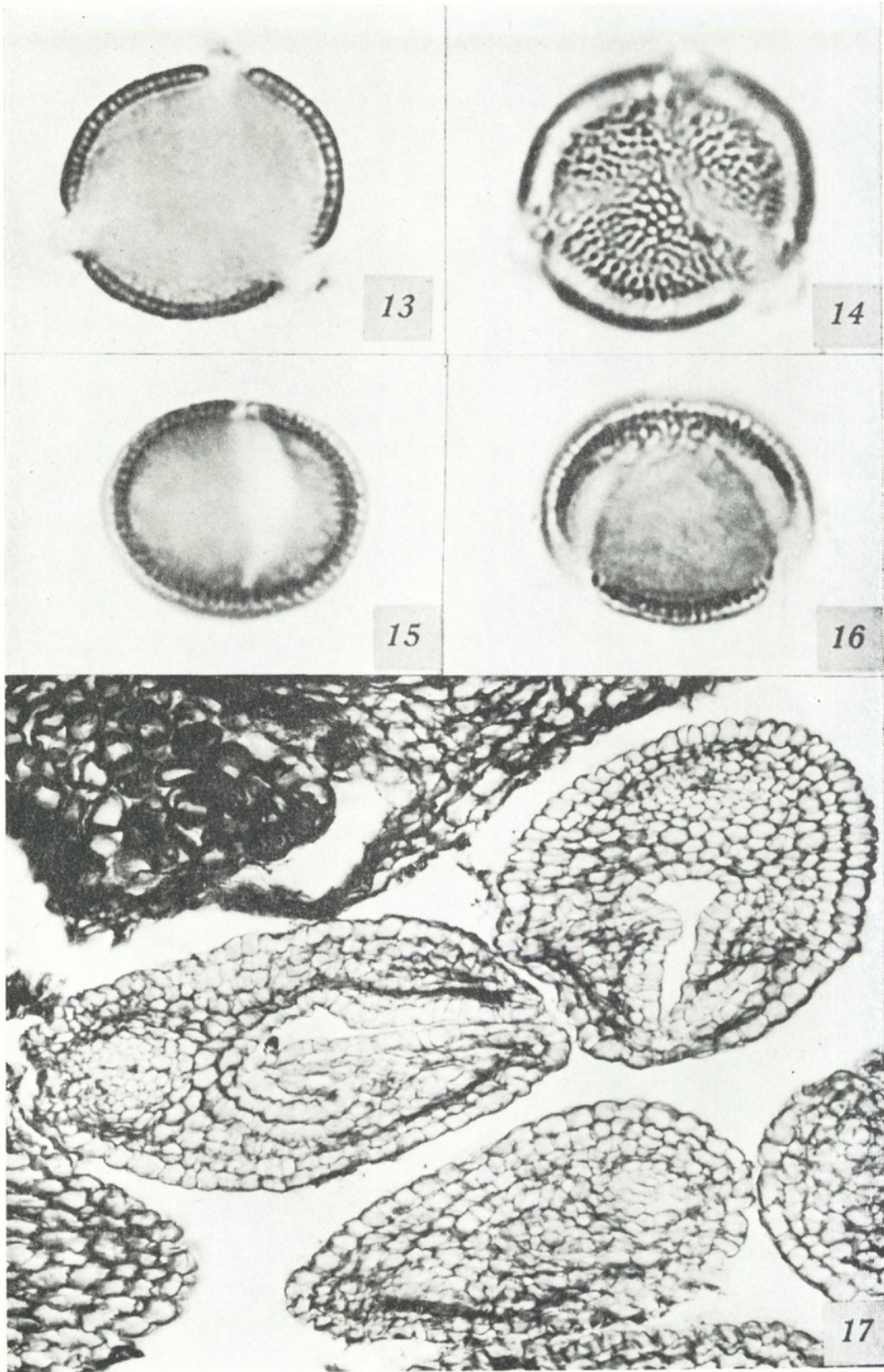
FIGS. 21–24. CLEARED CARPELS, selected from gynoecium [from *Ho, s.n.*] shown in Fig. 2 and photographed with dark-field illumination. 21, Carpel, approximately 2 mm. in height, showing ovary, style, and papillate stigma, × 32.5 — note precocious and acropetal development of xylem in dorsal bundle. 22, Older stage than preceding figure, showing dorsal bundle extending into base of reflexed style and an early phase of xylem development in ventral bundle, × 19. 23, Still later stage illustrating apparent bidirectional and interrupted pattern of xylem differentiation in ventral bundle, × 19. 24, Carpel approximately 7.5 mm. high (exclusive of reflexed style) showing complete vasculature, × 19 — note dichotomy of ventral bundle near top of ovary.



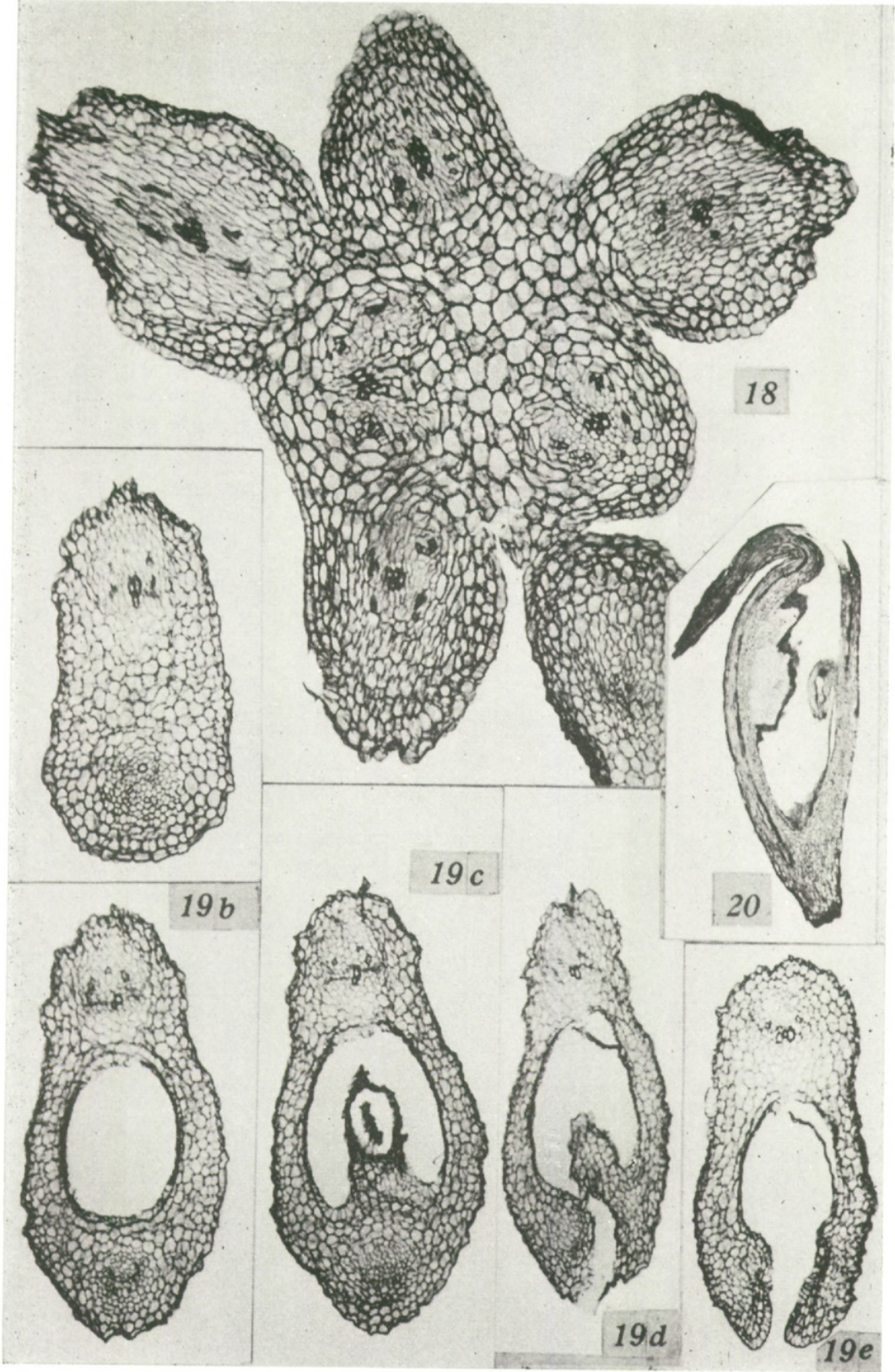
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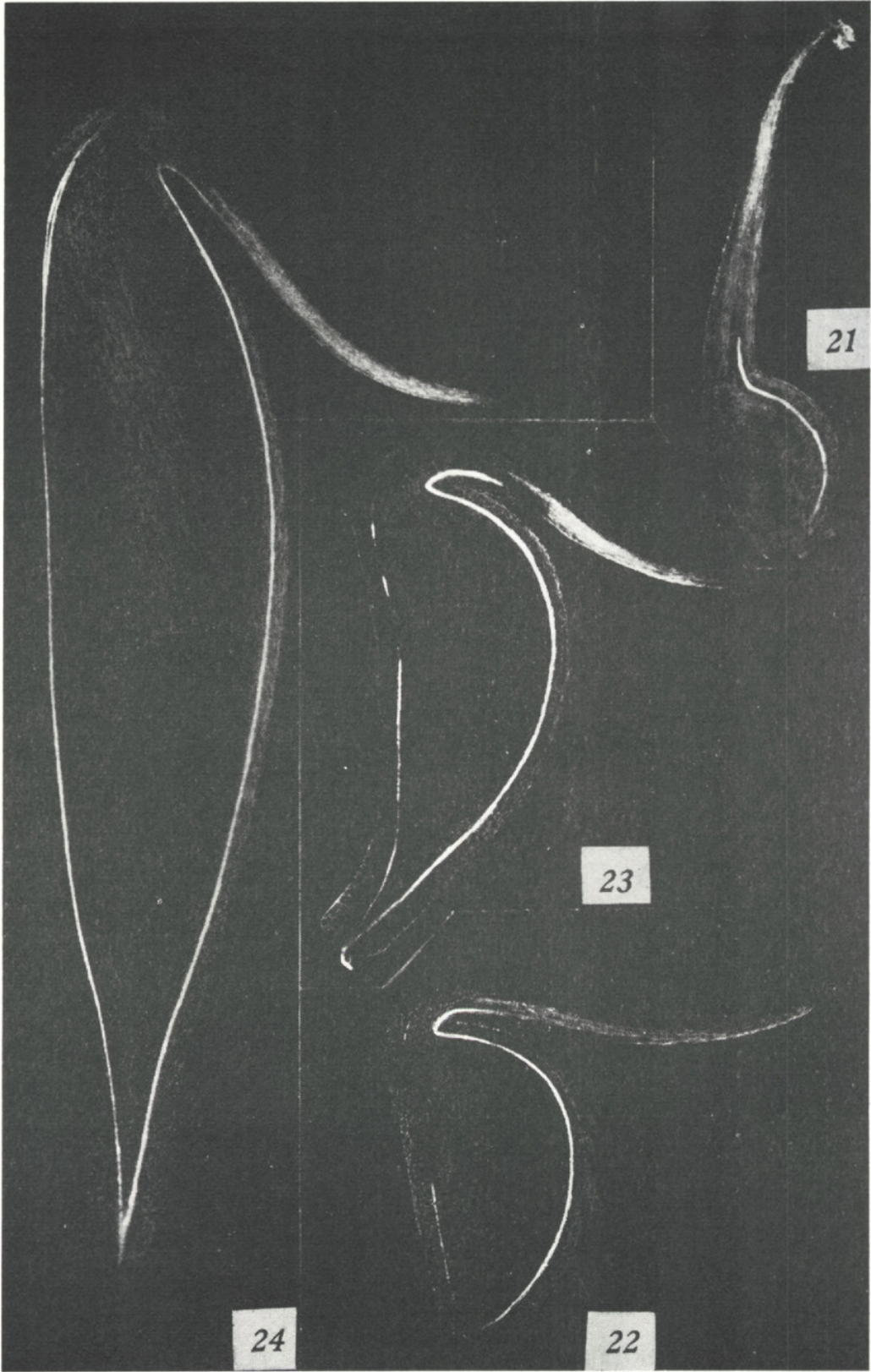
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Foster, Adriance S . 1961. "The Floral Morphology and Relationships of Kingdonia Uniflora." *Journal of the Arnold Arboretum* 42(4), 397–415.
<https://doi.org/10.5962/p.185627>.

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