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FLOWERS, FRUITS, AND PHYLOGENY OF ALANGIACEAE

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PUBLICATIONS ON THE ALANGIACEAE include an excellent monograph (Bloembergen, 1939) and a series of carefully documented anatomical studies (Govindarajalu & Swamy, 1956; Govindarajalu, 1961; 1962 a, b, c), but details of the flower and fruit have never been adequately scrutinized for evolutionary trends or for evidence of extra-familial affinities. This article will emphasize three neglected features that are known to have taxonomic value in many groups of plants: the floral vascular system, the secretory canals, and the stone or endocarp portion of the fruit wall. Species groups within the Alangiaceae differ greatly with respect to these structural features, and some of the differences can be interpreted to show directions of evolutionary change.

Although many older botanical works recognized two genera of Alangiaceae, *Alangium* Lam. and *Marlea* Roxb., Bloembergen's (1939) opinion that *Marlea* deserves only sectional status is now followed in most treatments. Bloembergen's monograph lists 18 species of *Alangium*, all woody, distributed in eastern Asia, Africa, Australia, and islands of the Pacific and Indian Oceans. Japanese botanists accept an additional species, *A. premnifolium* Ohwi (1938, p. 30, 1965, p. 652), considered doubtful by Bloembergen (p. 172, 173). Three species have been described since Bloembergen's monograph appeared. Two of these, *A. chungii* Li (1943, p. 448) and *A. tonkinense* Gagnepain (1950, p. 22), are based on single collections, and their circumscriptions differ so little from those of better known species¹ that an anatomical study need not be concerned with them. The third, *A. grisolleoides* Capuron (1962) is sufficiently distinct to merit a special commentary later in this paper.

Bloembergen distributed the species in four sections, using the number of stamens and characters of style, stigma, and embryo as basis for distinction. Govindarajalu's anatomical observations strongly support the soundness of this distribution. Although I believe the order in which

¹ *Alangium tonkinense* differs from *A. salviifolium* mainly in that its leaves are cuspidate and its filaments not dilated. I have examined the type of *A. chungii* (Chung 82038, A) and I think it belongs to *A. kurzii* Craib. The only fertile material labeled *A. premnifolium* that I have seen, a flowering specimen from Okinawa (Kanashiro 692, A), also belongs to *A. kurzii*.

Bloembergen listed the sections obscures their evolutionary relationships, I follow his delimitation of taxa throughout this paper. I also adhere to his nomenclature and orthography, with two minor exceptions: (1) section *ANGOLUM* Baill., which includes the type species, is herein called section *ALANGIUM* in accordance with Article 22 of the current *International Code of Botanical Nomenclature* (1966), and (2) the specific epithet *salviifolium* is spelled according to Recommendation 73G of the *Code*.

MATERIAL

Cooperating botanists and foresters (see Acknowledgments) supplied the following collections in liquid preservative.

Section *CONOSTIGMA* Bloemb.

- | | |
|------------------------------------|---|
| <i>A. havilandii</i> Bloemb. | SAR S.22767; Sarawak |
| <i>A. ridleyi</i> King | (1) cult., Bogor, VIII. H. 14
(2) cult., Bogor, IX. A. 20. |
| <i>A. javanicum</i> (Bl.) Wangerin | (1) P.P. Sam, s.n. (SAN 36750).
(2) cult., Bogor, VIII. F. 25. |

Section *ALANGIUM*

- | | |
|--|--|
| <i>A. salviifolium</i> (L.f.) Wangerin | (1) <i>Govindarajalu</i> 6840A;
Madras, India
(2) cult., Bogor, Indonesia,
III. G. 41.
(3) cult., Bogor, XVII. C. 136. |
| <i>A. longiflorum</i> Merr. | (1) <i>B. Hernaez</i> 635; Makiling
Natl. Park, Philippines
(2) without voucher; Makiling
Natl. Park |

Section *MARLEA* Baill.

- | | |
|--|---|
| <i>A. platanifolium</i> (S. & Z.) Harms | (1) cult., Bot. Gard. Tohoku Univ.
(2) <i>K. Sohma</i> , s.n., Shiraishi
Pass, Iwate Pref., Japan |
| <i>A. chinense</i> (Lour.) Harms | (1) cult., Tjibodas, Indonesia
(2) without voucher; Makiling
Natl. Park |
| <i>A. rotundifolium</i> (Hassk.) Bloemb. | cult., Tjibodas |

To verify the identifications, I consulted Bloembergen's descriptions and compared the material with herbarium specimens that Bloembergen annotated or cited. Some of the collections are from individual trees that Bloembergen mentioned and that still survive in Indonesian gardens. The infraspecific identity of the specimens seems unimportant to this investigation; so I have not tried to make subspecific or varietal distinctions.

Unable to obtain pickled material of *A. villosum* (Bl.) Wangerin, the

only species in Bloembergen's section RHYTIDANDRA, I removed a few dried flowers from sheets in the U.S. National Herbarium. (Because of Dr. A. C. Smith's field activities, the Herbarium is well supplied with the Fijian variant of *A. villosum*.) My remarks on mature fruits of *Alangium* are drawn mostly from the examination of dried specimens in the U.S. National Herbarium, and in the Gray Herbarium and the Herbarium of the Arnold Arboretum of Harvard University.

Sectioning and staining procedures were routine (Eyde, 1963, 1966), but clearing of flowers required some experimentation. Good results were obtained through Fuchs' (1963) "Method No. 1," with the concentration of NaOH reduced to 5 percent to prevent maceration of tissues. Another successful procedure included the following steps: overnight immersion of the flowers in 5 percent NaOH at 60°C, immersion for several hours in warm "CLP" (Bersier & Bocquet, 1960), transfer through an ethanol series to toluene. In most cases, it was necessary to cut the flowers into thick freehand sections before clearing.

OBSERVATIONS

General. Bloembergen (1939) followed Wangerin (1910) and several earlier authorities in using the relative number of stamens and petals to subdivide *Alangium*. Stamens of Bloembergen's sections MARLEA, RHYTIDANDRA, and CONOSTIGMA — collectively corresponding to subgenus MARLEA of Wangerin's treatment — were said to equal the petals in number. Neither Bloembergen nor Wangerin added that the number of stamens may be one more or one less than the number of petals. I have recorded the following counts for corolla (C) and androecium (A). *A. havilandii*: C4, A4; C5, A5; C6, A5. *A. ridleyi*: C5, A5; C6, A6. *A. javanicum*: C6, A6; C7, A7; C8, A8. *A. grisolleoides*: C4, A3; C5, A5. *A. platanifolium*: C6, A7; C7, A7. *A. chinense*: C7, A7; C8, A8; C8, A9. *A. rotundifolium*: C7, A7; C8, A8. *A. villosum*: C5, A5; C5, A6; C6, A5; C6, A6. For section ALANGIUM ("subgenus Eualangium") Wangerin gave the number as two to four times the number of petals; Bloembergen's description says two to six times the number of petals. My observations, which follow, indicate that Wangerin was more nearly correct. *A. salviifolium*: C5, A12; C5, A17; C6, A15; C6, A26; C7, A26; C7, A28; C8, A30. *A. longiflorum*: C4, A14; C4, A16. With limited material, I have not tried to estimate the frequency with which any of these numbers occur. Not uncommonly, flowers are found in which one petal is "double"; i.e., it is seen as an abnormally broad single appendage when sectioned near its base but as two normal appendages in distal sections. This condition is not restricted to any particular group of species. I also found one flower of *A. grisolleoides* (C4, A3) in which a stamen with six anther sacs and two vascular bundles is clearly a double structure.

Regardless of their number, the stamens are arranged in a single whorl around a prominent pulvinate disc. Dehiscence of the linear anthers is latrorse to somewhat introrse. As Bloembergen emphasized, variations in

the form of the filaments and in the length of their trichomes are important for separating the species. A distinctive character of section *CONOSTIGMA* is the papillose epidermis of the anther.

The microspore mother cells in a developing anther are surrounded by four cell layers: an inner tapetum, an outer epidermis, and two undifferentiated intermediate layers. The subepidermal layer never develops the "fibrous" thickenings of a typical endothecium. Another unusual feature, already reported by Gopinath (1945), is the arrangement of microspore mother cells in a single file in each anther lobe; this is caused by the conversion of primary sporogenous cells into microsporocytes without intervening divisions. Following meiosis, all surrounding layers degenerate except for the thin-walled epidermis, which usually ruptures before the corolla opens. In most species the septa between anther-halves also degenerate before the pollen is released, but anthers of *A. longiflorum* retain four locules at anthesis.

The trichomes and crystal inclusions of *Alangium* flowers are described in detail by Govindarajalu (1962 b, c). My observations agree with his except that I have found druses to be plentiful in floral tissues of section *CONOSTIGMA*, where he found none. Included in my material is one species, *A. havilandii*, that Govindarajalu did not examine: the floral trichomes are

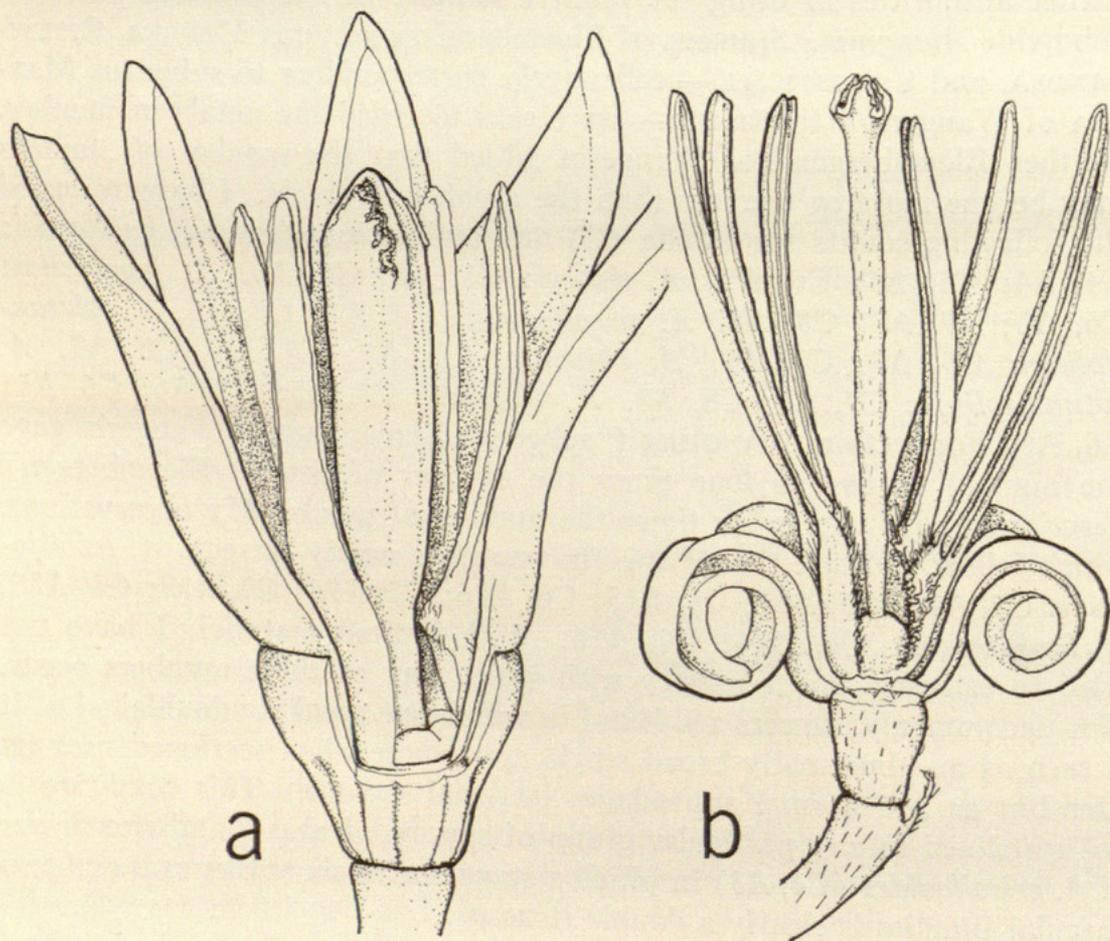


FIG. 1. a, flower of *Alangium ridleyi* (section *CONOSTIGMA*), cult., Bogor, IX.A. 20, $\times 3.5$. b, flower of *A. chinense* (section *MARLEA*), cult., Tjibodas, s.n., $\times 4.3$. Part of each flower has been cut away to show disc.

of the type that he called "stellate-peltate," as could have been predicted from his observations on the other members of section *CONOSTIGMA*.

Sectional differences in the form of the stigmatic area were stressed by Bloembergen. He named section *CONOSTIGMA* for the "conical" termination of the style, but the four stigmatic rays (FIG. 1, a; FIG. 2, a) give it a pyramidal appearance to my eye. In section *MARLEA* (FIG. 1, b) the stigma is capitate and lacks the rays, but is distinctly four-lobed. Section *ALANGIUM* has a capitate stigma that is not four-lobed — here I contradict Bloembergen — but irregularly folded and convoluted (FIG. 2, b). *Alangium villosum* (sect. *RHYTIDANDRA*) is distinguished by two styles, each stigmatic along its ventral surface and slightly bifid at its apex. These are basally united for about half their length (Bloembergen, 1939, *Fig. 7, b, k*) in a stylar column. Microtome sections through the stylar column of *A. villosum* reveal a symmetrically four-lobed stylar canal. When cut about halfway between base and apex, the style in section *CONOSTIGMA* has a similar cross section, but in section *MARLEA* the four-lobed appearance is less symmetrical, and in section *ALANGIUM* the stylar canal is very irregular, often three-lobed. Followed downward through serial sections, the stylar canal of any species loses its lobed appearance, becoming oval or elliptical in outline at its base (Clarke, 1850, *Figs. 4-7*). It is always hollow at anthesis and filled with a mucilaginous exudate.

The ovary, completely inferior throughout the genus, is one-locular in sections *CONOSTIGMA*, *ALANGIUM*, and *RHYTIDANDRA*. In some species of section *MARLEA* two-locular ovaries are common, but the locules are usually unequal, and one of them may be empty (FIG. 5, b). Except for such cases, the ovules are solitary in each locule, pendent and anatropous with the micropyle directed laterally (FIG. 2, c; 5, a).

Vascular system. The most conspicuous sectional differences are in the number of carpel bundles and in the extent of fusion of calyx bundles to bundles supplying petals and stamens. The vascular systems of sections *CONOSTIGMA* and *ALANGIUM* differ somewhat (FIG. 4), but the differences that separate these two groups from sections *MARLEA* and *RHYTIDANDRA* are much greater.

Pedicels in all species of *Alangium* contain a rather compact cylinder of vascular tissue, difficult to resolve into individual strands. At the base of the flower this cylinder expands into a circle of 10 or more major bundles (usually twice the number of petals). In *A. javanicum* and *A. ridleyi* two additional series of bundles diverge radially from the first within the short distance of a few 15μ microtome sections and still below the base of the ovarian cavity. The inner series, containing up to 30 fine strands, comprises the gynoeceal vasculature. The middle series supplies stamens and petals, and the outer series supplies the calyx (FIGS. 2, c, d; 3, a). In *A. havilandii* the two outer series and the middle series are united for a distance; their divergence takes place about halfway up the ovary wall. And in section *ALANGIUM* (FIG. 3, b-d), these two series remain united almost to the insertion of petals and stamens.

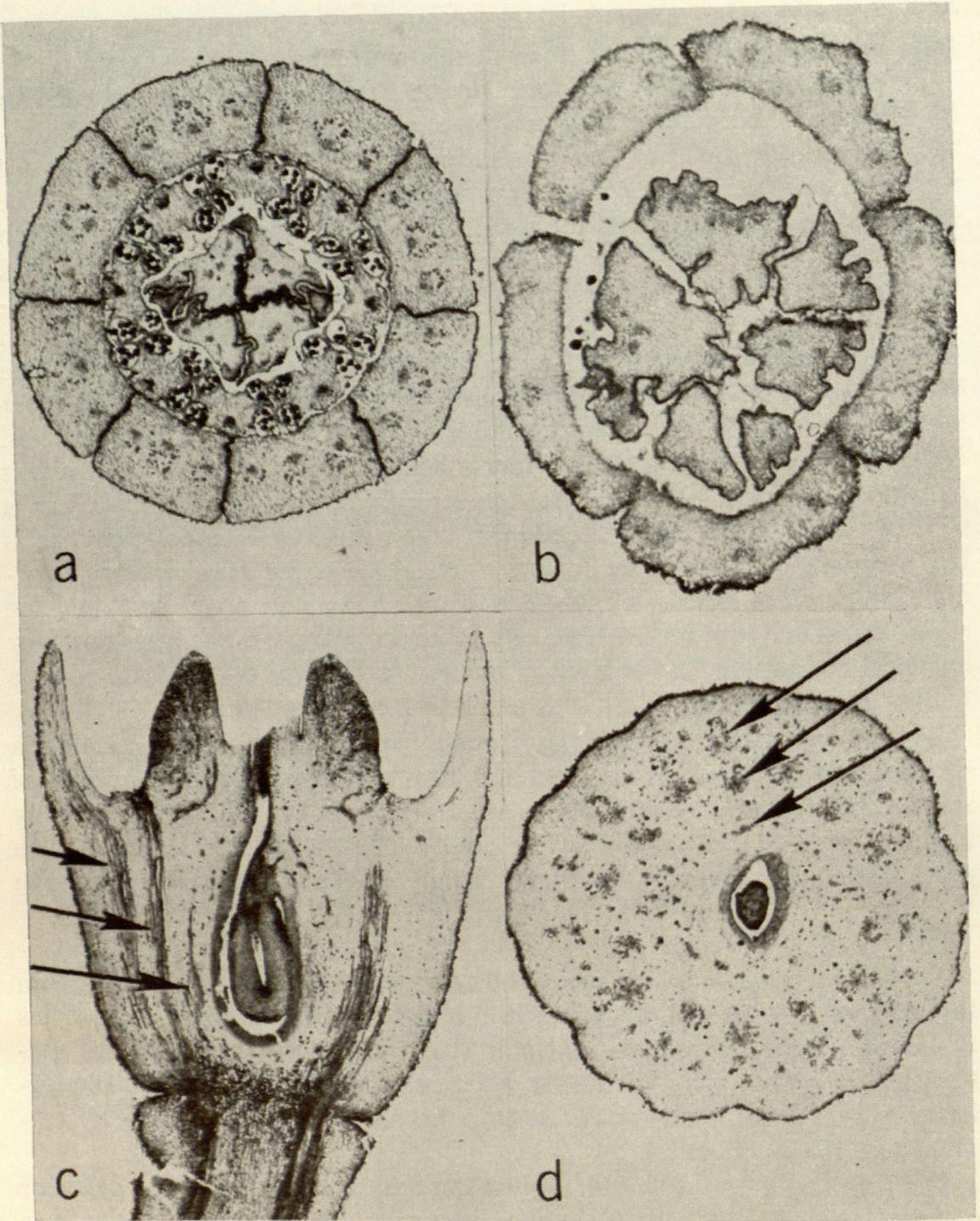


FIG. 2. Flowers of *Alangium*. a, *A. javanicum*, P. P. Sam, s.n.; cross section near apex showing 4 stigmatic rays; $\times 16$. b, *A. longiflorum*, B. Hernaez 635, us; cross section near apex, showing asymmetrical convolutions of stigma; $\times 20$. c, *A. javanicum*, P. P. Sam, s.n., longitudinal section of ovary, showing attachment of ovule; arrows indicate 3 series of vascular bundles; $\times 13$. d, *A. javanicum*, P. P. Sam, s.n., cross section through inferior ovary showing vascular bundles in 3 series (arrows); $\times 17$.

In section CONOSTIGMA there are some heavy tangential and radial strands near the level of insertion of petals and stamens. These interconnect the bundles of the outer and the intermediate series. A special vascular feature in *Alangium javanicum* and *A. ridleyi* is the occurrence of extra longitudinal bundles between the principal strands of the outer

series, bundles that terminate blindly at their basal end, not connecting with any other bundles. At their apical end these join with main bundles of the outer series and with the bundles of the intermediate series in supplying branches to the disc.

The dorsal supply in section *CONOSTIGMA* is peculiar in that a discrete

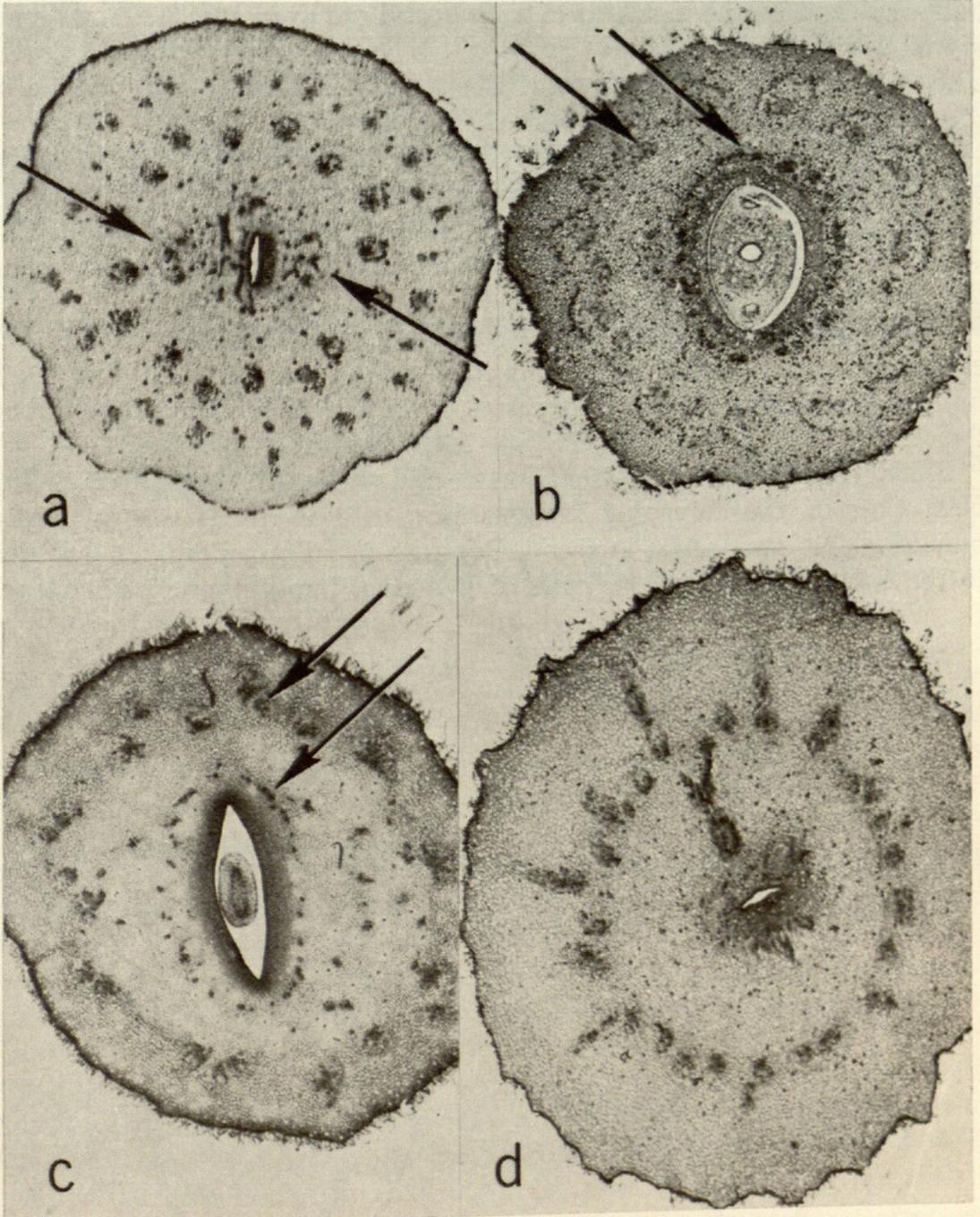


FIG. 3. Gynoecia of *Alangium* in cross section. a, *A. javanicum* (same flower as in FIG. 2, d), placental region; all bundles of inner series except those in the 2 dorsal complexes (arrows) converge on the placenta; $\times 17$. b, *A. salviifolium*, cult., Bogor, XVII.C.136, us; there are only 2 series of vascular bundles (arrows); $\times 18$. c, *A. longiflorum*, B. *Hernaez* 635, us; arrows indicate 2 series of bundles; $\times 17$. d, *A. salviifolium*, *Govindarajalu* 6840A, us; section comparable to that in FIG. 3, a, showing transverse path of one dorsal complex toward base of style (see also FIG. 6, b); $\times 19$.

carpellary midvein is absent from the ovary wall. The position where a single dorsal bundle would be expected is occupied by a group of three or more fine, anastomosing strands, and on the other side of the ovary from this group is a second cluster of fine bundles (FIGS. 2, d; 3, a). Although these two groups of bundles can be considered a part of the inner series, they tend to lie a little to the outside of other members of the series. Followed distally, the members of each dorsal group merge, forming a pair of well defined stylar bundles (FIG. 4, a). The two stylar bundles bifurcate a short distance above the base of the style, and profuse ramification of the resulting four branches supplies the stigma.

Section *ALANGIUM* has a similarly complex dorsal supply, but the component strands separate from the outer series at a higher level, passing transversely across the upper part of the ovary to enter the style (FIG. 4, b). Also, the stylar bundles bifurcate closer to the stigmatic region than they do in section *CONOSTIGMA*.

Ovules receive a similar vascular supply in both of these sections. The entire inner series except the dorsals converges at the placenta (FIG. 3, a), uniting in an ovular bundle that passes down one side of the ovule and up the other.

Floral vasculature of section *MARLEA* and section *RHYTIDANDRA* differs from that in the foregoing sections primarily in the fewer gynoecial bundles. The inner series in section *MARLEA* usually contains, in addition to the two dorsals, only two pairs of gynoecial bundles, one pair at each

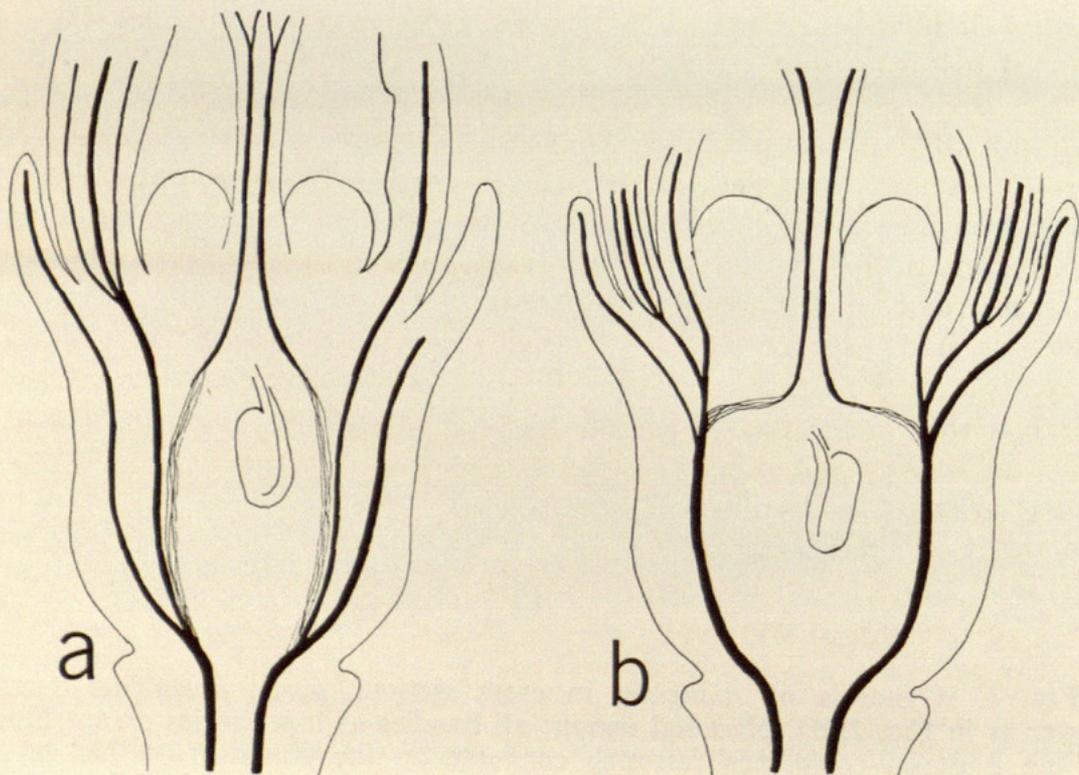


FIG. 4. Dorsal vasculature in section *CONOSTIGMA* (a, based on *Alangium ridleyi*) and section *ALANGIUM* (b, based on *A. longiflorum*). Diagrams represent longitudinal sections cut so as to include both dorsal carpel bundles. For part of their length the dorsals are made up of fine anastomosing strands.

side of the ovarian septum (FIG. 2, b). The paired structure is less evident in some cross sections than others because the two strands of each pair branch and anastomose somewhat; cross sections through the upper part of the ovary are best for showing distinct pairs (Eyde, 1968, *Fig. 13*). I refer to these pairs as ventral bundles, since that term has been used for similarly situated pairs in *Cornus* (Wilkinson, 1944) and *Nyssa* (Eyde, 1963); however, as I have stated in earlier papers, the homology of these bundles to the centrally or marginally located ventrals of other families is uncertain. Paired bundles supplying the ovule or ovules diverge from both sets of ventrals and pass transversely through the summit of the ovary. An unusual feature, never observed in *Cornus* or *Nyssa*, is the occurrence of additional transverse (or oblique) bundles lower in the ovarian septum (FIGS. 5, a; 8, r). These branch at intervals from the ventrals and end blindly in the septum, perhaps indicating the former location of ovules eliminated in the course of evolution. The ventrals in some flowers end abruptly where the ovular strands diverge; in other flowers they end in the base of the style.

A single outer series of prominent bundles supplies the calyx, corolla, and androecium in section MARLEA, as in section ALANGIUM, but in section MARLEA the dorsal bundles (FIG. 5, a, b) are free for most of their length. Furthermore, the dorsal supply in section MARLEA usually consists of single bundles,² unlike the dorsal complexes of sections CONOSTIGMA and ALANGIUM. The two dorsals pass through the style and divide into four strands a little below the stigma.

Dorsal bundles of section RHYTIDANDRA are also discrete, but they are united with the outer bundles to a greater degree than in section MARLEA (also, because there is only one locule, the ventral bundles lie more to one side of the ovary). One of the dorsals diverges a little below the insertion of stamens and petals; the other, always the midvein of the "lost" carpel, is independent for about half the length of the ovary (indicated diagrammatically in FIG. 9). Both dorsals pass into the stylar column as discrete bundles, but they divide below the separation of the two styles; thus the free portions of the styles each receive two bundles.

Petals of *Alangium* species contain three to seven parallel vascular strands that merge basally in the region of insertion. The most common number is five. Where petals are thick (section CONOSTIGMA), additional small strands are often located internal to the others. These are "inverted" bundles, oriented with their xylem toward that of the principal petal bundles. Stamens of *Alangium* species commonly contain only one bundle, but two slender lateral strands flank the principal bundle in *A. ridleyi*.

² Both of my collections of *A. platanifolium* (sect. MARLEA) have fairly discrete dorsal bundles rising through the ovary wall and continuing into the style. But in Horne's (1914, p. 266, 267) material of this species, several small strands form the basal part of the dorsals. This anomaly confused Horne's interpretation of the gynoeical vasculature. He stated that "the so-called dorsal ribs are merely collections of small ovular strands," even though he correctly portrayed their passage into the style (see his *Text-fig. 6, G, H*). Horne worked with very young flowers, which may have contributed to the misinterpretation.

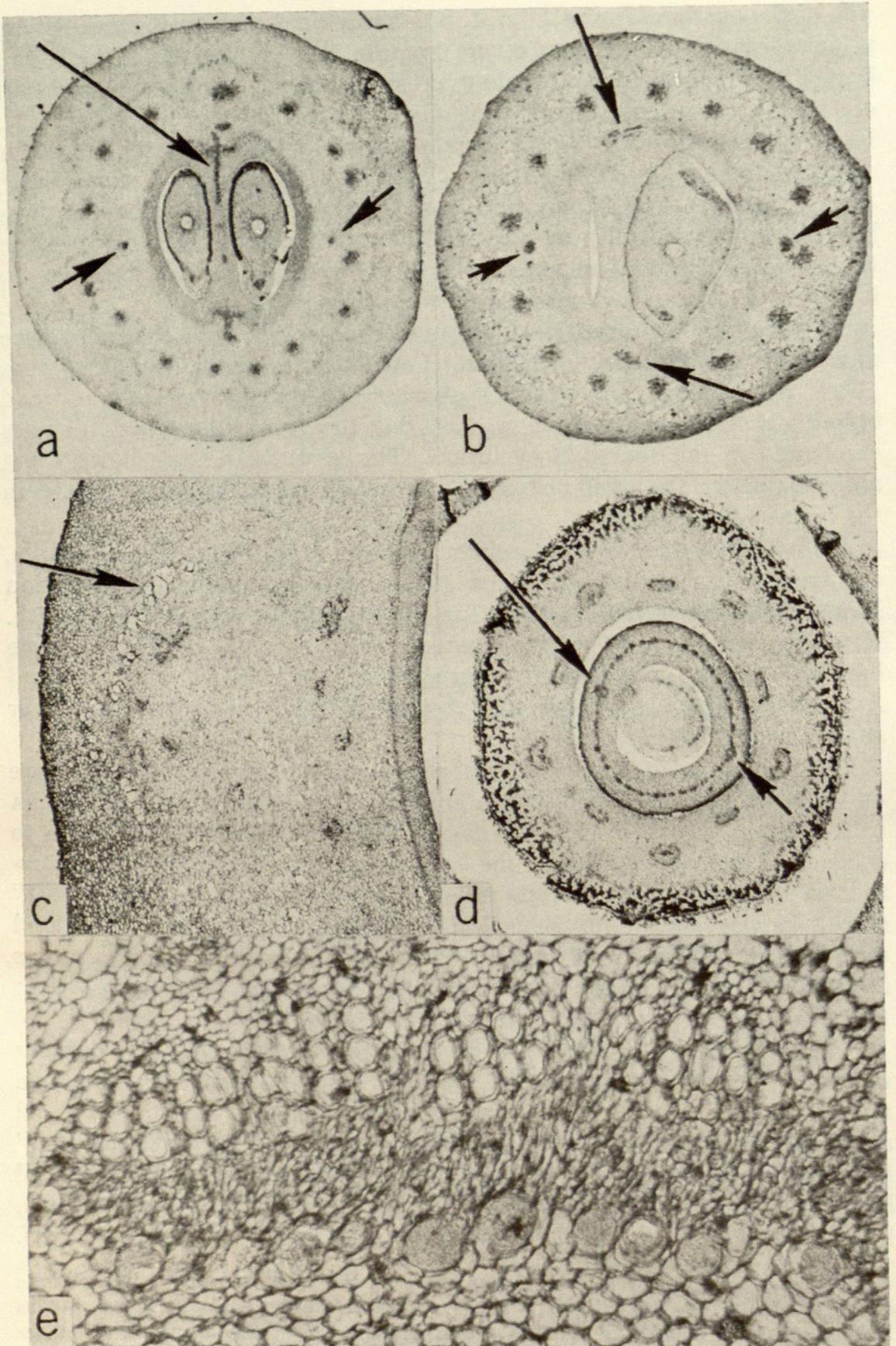


FIG. 5. a, *Alangium chinense*, Makiling Natl. Park; cross section through gynoecium showing subequal carpels, transverse bundle (long arrow) which ends blindly in septum; shorter arrows indicate dorsal bundles; $\times 23$. b, *A. platani-folium*, cult., Tohoku; cross section through gynoecium showing 1 empty, 1 fer-

The filaments of *A. rotundifolium* and *A. chinense* also have some thin "extra" bundles.

The nectariferous disc is thoroughly vascularized in all species of *Alangium*, receiving transverse strands from the bundles that supply calyx, corolla, and androecium. Although the fine vascular ramification within the disc is usually composed of phloem only, as is the case in most dicotyledons (Frei, 1955), I have observed xylem in preparations of *A. chinense* and *A. rotundifolium*; its presence may relate to stage of development. Floral vascular bundles, especially those of the hypanthium and gynoecium, tend to be amphicribal in all species.

Secretory structures. Sertorius (1893, p. 561) recorded the occurrence of "sehr grosse Sekretzellen" in fruits of *Alangium*, and Faure (1924, *Fig. XV, 1, 7*) figured "poches sécrétrices," erroneously providing them with a secretory epithelium of small cells. Schnarf's (1922, *Figs. 1, 3*) drawings of sectioned flowers portray the secretory structures accurately and indicate their proximity to a vascular bundle. None of these authors realized, however, that the structures are articulated laticifers.

The laticifers begin as longitudinal files of elongating parenchyma cells, which enlarge to a diameter several times that of adjacent parenchyma cells and eventually become vessels by the disintegration or rupture of transverse walls. They are usually arranged in an arc around the phloem of floral vascular bundles, and where phloem completely surrounds the xylem of a bundle, a ring of laticifers may surround the phloem. The laticifers do not actually differentiate within the phloem: there are usually three or more parenchyma cells between a laticifer and the nearest sieve tube. In this respect the laticifers of *Alangium* differ from the very similar structures of *Argemone mexicana* (Papaveraceae) figured by Kapoor and Sharma (1963). Laticifers can accompany vascular bundles in any part of the *Alangium* flower with the possible exception of the ovule and the style, but they terminate at the base of the flower or extend only a short distance into the pedicel.

The content of the laticifers stains darkly and usually includes the pellets (Kügelchen) that Schnarf (1922) observed. Laticifers of a maturing ovary often seem to be partially empty when examined in cross section, and the pickled material does not "bleed" when cut, as it should if the contents are under pressure (Esau, 1965, p. 323).

One would not expect laticifers to be abundant in flowers of *Alangium* and to be absent from other parts of the plant. Having at my disposal some pickled leaves of *A. chinense*, I prepared simple freehand sections

tile locule; arrows indicate dorsal and ventral bundles; $\times 27$. c, *A. longiflorum*, B. Hernaez 635, US; cross section of fruit wall showing thin endocarp (right) and empty laticifers (arrow); $\times 11$. d, *Metteniusa nucifera*, Steyermark, Wurdack & Prance 95863, NY; cross section of floral tube and gynoecium; arrows indicate dorsal (short) and ventral (long) bundles; $\times 18$. e, *A. chinense*, Makiling Natl. Park; cross section of petiole showing medullary vascular tissue and accompanying laticifers (bottom); $\times 150$.

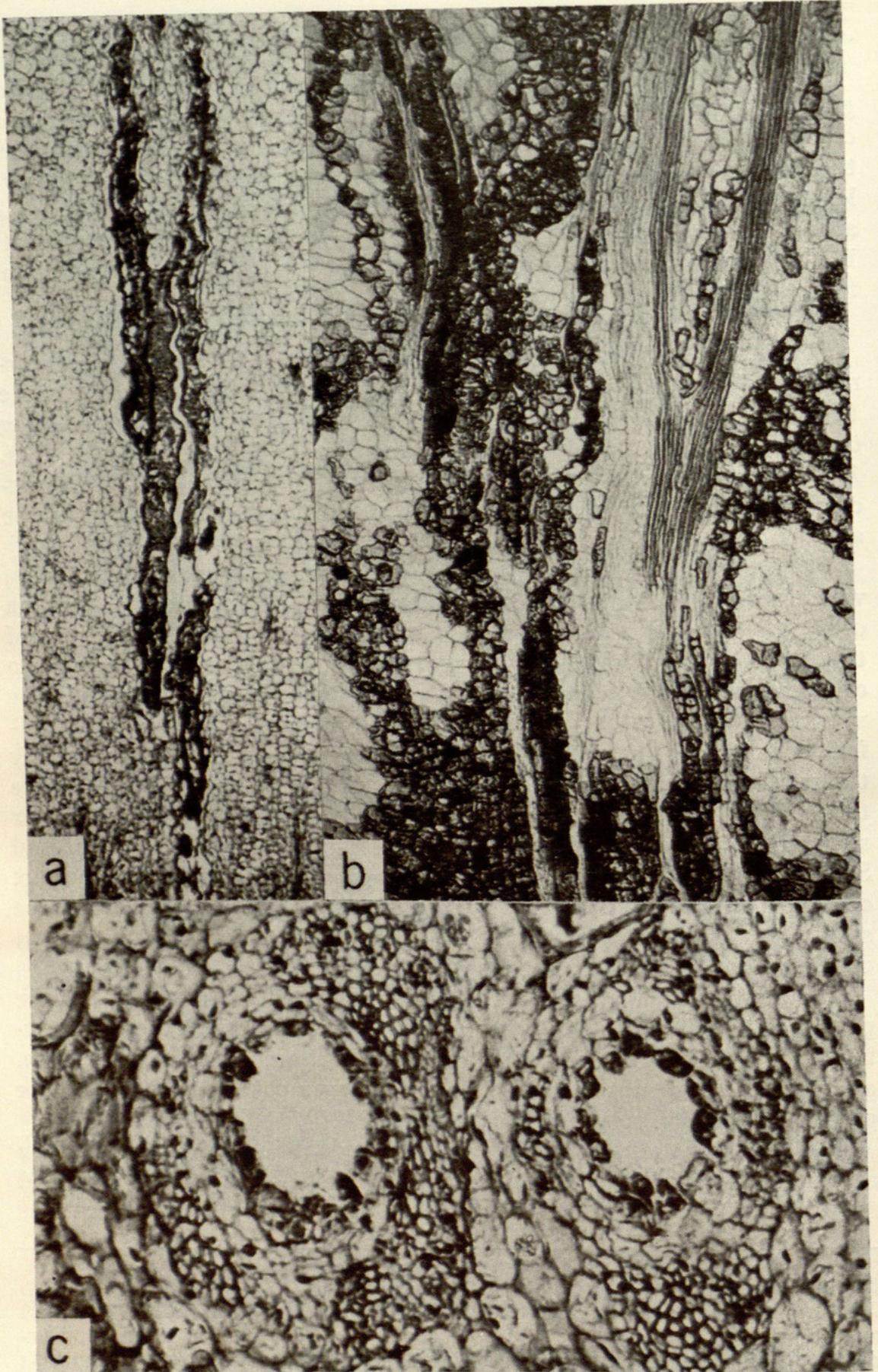


FIG. 6. a, *Alangium javanicum*, P. P. Sam, s.n., inferior part of flower; laticifers in longitudinal section; $\times 75$. b, *A. javanicum*, cult., Bogor, VIII.F.25; fruit;

of a petiole and found laticifers in abundance around the major vascular bundles (FIG. 5, e). It is probable that other anatomists have overlooked the secretory structures in leaves because they were working with dried material. Govindarajalu had living material of *A. salviifolium*, but I have observed that laticifers are inconspicuous or absent in flowers of this species; perhaps they are equally difficult to detect in other parts of the plant.

Latex vessels are plentiful in fruits of section ALANGIUM, although they are hard to find in the flowers. In section MARLEA and in section RHYTIDANDRA, however, laticifers are conspicuous at all stages of flower and fruit. Their arrangement in cross sections creates an attractive "scalloped" effect (FIG. 5, a), which Clarke (1850) showed in his *Fig. 8* and *9*, even though he did not understand the reason for it. Laticifers of sections MARLEA and RHYTIDANDRA expand with the growth of the fruit so that they appear as tangentially elongate cavities in cross sections through the mature fruit wall. Section CONOSTIGMA is peculiar in that the floral laticifers seem to disappear as the fruits develop. My longitudinally sectioned flowers of *A. javanicum* show many latex vessels of large diameter (FIG. 6, a), some of them branching and perhaps anastomosing with neighboring vessels. Fruits of this species, although they contain densely-staining tanniferous cells in great numbers (FIG. 6, b), have no laticifers. Some of the tannin cells are aligned in such a way as to suggest that they have been derived from laticifers through a secondary development of cross walls; i.e., through the reversion of coenocytic laticifers to a cellular condition. I offer this inference cautiously because my flowers and fruits are from different sources. Moreover, I do not know that anyone has ever documented a reappearance of the cellular condition in laticifers.

Endocarp. Fruits of most species contain a thick, woody stone, but the innermost tissue of fruits belonging to section ALANGIUM is thin, leathery, and easily opened with an ordinary razor blade. It is difficult to separate the intact endocarp from outer tissues of such fruits, and when this has been done (by boiling in 5 percent NaOH) the endocarp collapses readily (FIG. 7, f). The endocarp of *A. longiflorum* is so little lignified that satisfactory sections can be prepared by the paraffin method (FIG. 5, c).

The stones of section CONOSTIGMA (FIG. 7, a-e; see also Harms, 1906, *Fig. 16*) are more massive than those of other sections; they are further distinguished by the many fine longitudinal ridges on their surfaces. The ridges may be very faint or fairly conspicuous, straight or undulating. They undoubtedly arise in association with the many fine vascular bundles of the gynoeical series. This can be verified by examining the apex of the

tangential section showing vascular bundles and adjacent tissue. Absence of laticifers may be caused by reversion from coenocytic to cellular condition (see text); $\times 54$. c, *Mastixia* cf. *pentandra*, *Kostermans & Soegeng 920*, us; cross section through wall of young fruit showing two secretory canals with epithelial cells; $\times 210$.

stone, where the bundles converge and pass into the endocarp. No matter how carefully the stone is cleaned, remnants of vascular tissue adhere to the apical end.

Serial sections show that the fleshy outer tissue of the fruit wall in section

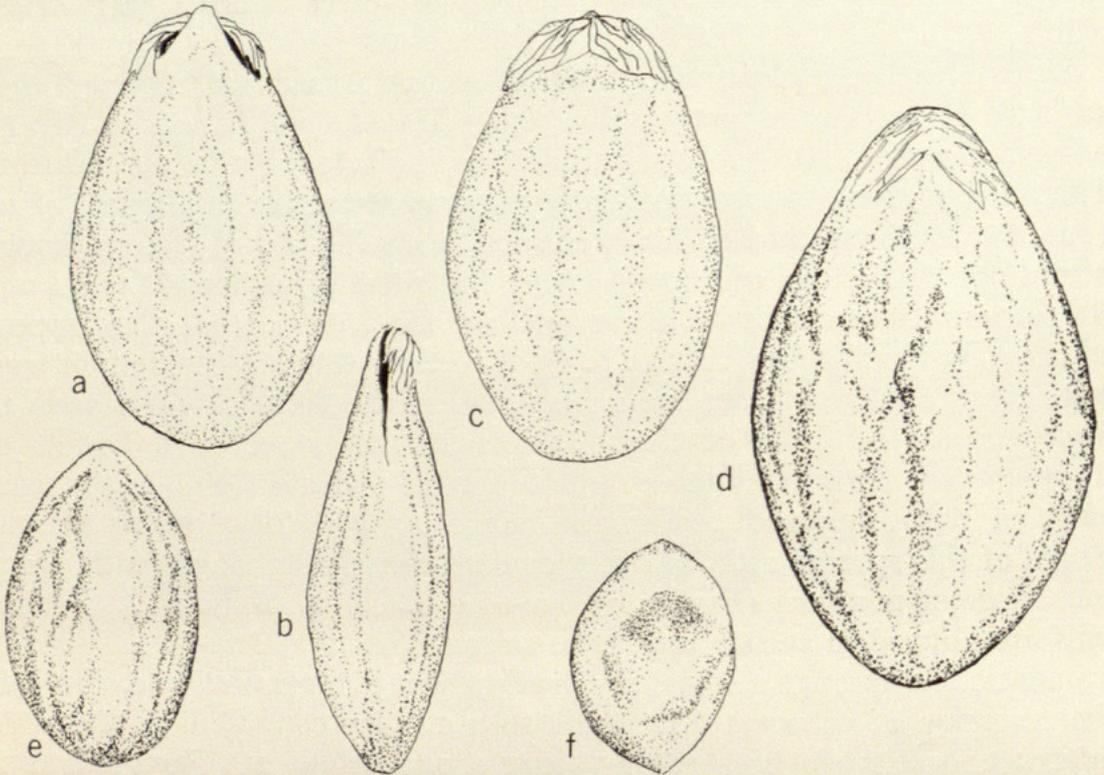


FIG. 7. Stones of section CONOSTIGMA (a-e) and section ALANGIUM (f). a-c, *Alangium javanicum*, cult., Bogor, VIII.F.25, US; 3 views of 1 stone. d, *A. ridleyi*, cult., Bogor, VIII.H.14, US. e, *A. grisolleoides*, Service Forestier 20056-SF, P. f, *A. salviifolium*, Mrs. D. J. Collins 1521, US. All, $\times 2$.

CONOSTIGMA has a broad zone of radially elongate cells immediately peripheral to the stone. In all of my specimens this zone contains large irregular cavities, apparently resulting from tearing of the cells as the fruit wall expands.

Fruits of section MARLEA are often two-carpellate, and stones from different species can be arranged in a sequence to show the gradual loss of one of the carpels. *A. kurzii* (FIG. 8, a-c) commonly has two nearly equal locules in its fruit; therefore, a plane through the septum of the endocarp divides it into roughly identical halves. In *A. chinense* (FIG. 8, p, q), one half is smaller than the other, but both locules can be fertile notwithstanding. Gynoecial asymmetry is more pronounced in *A. platanifolium* (FIG. 8, n, o), *A. alpinum* (FIG. 8, g-i), and *A. rotundifolium* (FIG. 8, m). In stones of these species one of the carpels is reduced to a shield-like prominence, often with a tightly closed abortive locule. *A. griffithii* (FIG. 8, s-u) completes the series; its stones bear no trace of a second carpel. In *A. barbatum* (FIG. 8, d-f, j-l) different collections show marked differences in the degree of reduction of the second carpel.

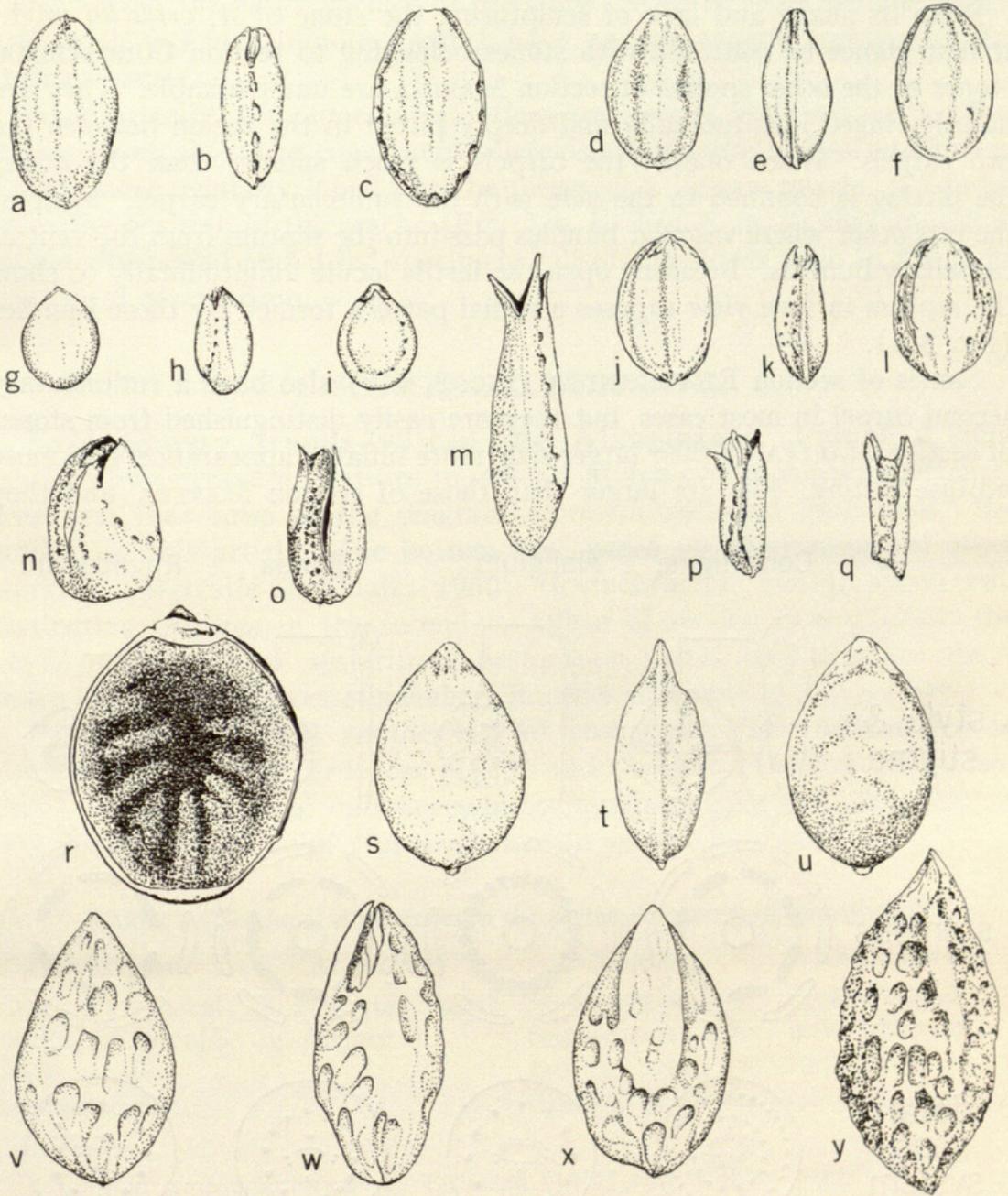


FIG. 8. Stones of section MARLEA (a-u) and section RHYTIDANDRA (v-y). a-c, *Alangium kurzii*, J. & M. S. Clemens 3740, US; 3 stones shown in different views. d-f, *A. barbatum*, C. S. Fan & Y. Y. Li 315, A; 3 views of 1 stone; note subequal 2-carpellate structure. g-i, *A. alpinum*, G. Forrest 27290, US; 3 views of 1 stone. j-l, *A. barbatum*, J. & M. S. Clemens 4200, US; 3 views of one stone; 1 carpel much smaller than other (cf. d-f). m, *A. rotundifolium*, Koorders 25821B, A. n, *A. platanifolium*, E. H. Wilson 142, US; ventral vascular bundles adhere to lateral surface. o, *A. platanifolium*, E. H. Wilson 3272, US; repeated boiling and drying caused longitudinal opening into fertile locule, probably indicating method of germination. p-q, *A. chinense*, C. Y. Chiao, s.n. (*Herb. Univ. Nanking* 14620), US; 2 stones in side view; softer apical tissue of q has been removed by repeated boiling and abrasion. r, *A. platanifolium*, same specimen as o with part of stone split away by forcible enlargement of opening, rotated to show concave ventral wall of locule; ridges appear where vascular bundles pass into septum. s-u, *A. griffithii*, Kepong Field No. 79003, US. v-y, *A. villosum* subsp. *vitiense*. v-x, A. C. Smith 7409, US; 3 views of 1 stone showing large pits in surface, abortive second carpel. y, A. C. Smith 5249, US; orientation is intermediate between that of w and that of x; note absence of second carpel. All $\times 2$ except r, $\times 4$.

From its shape and lack of sculpturing the stone of *A. griffithii* might at first glance be confused with stones belonging to section CONOSTIGMA. Stones of the other species of section MARLEA are unmistakable. They are slightly ridged longitudinally and deeply pitted in the region between the two carpels. When one of the carpels is much smaller than the other, the pitting is confined to the side with the rudimentary carpel. Most of the pits occur where vascular bundles pass into the septum from the ventral carpellary bundles. Breaking open the fertile locule longitudinally to show the septum in face view exposes a radial pattern formed by these bundles (FIG. 8, r).

Stones of section RHYTIDANDRA (FIG. 8, v-y) also have a rudimentary second carpel in most cases, but they are easily distinguished from stones of section MARLEA by their larger size, more inflated appearance, and more profuse pitting. Pits are larger than those of section MARLEA, and they

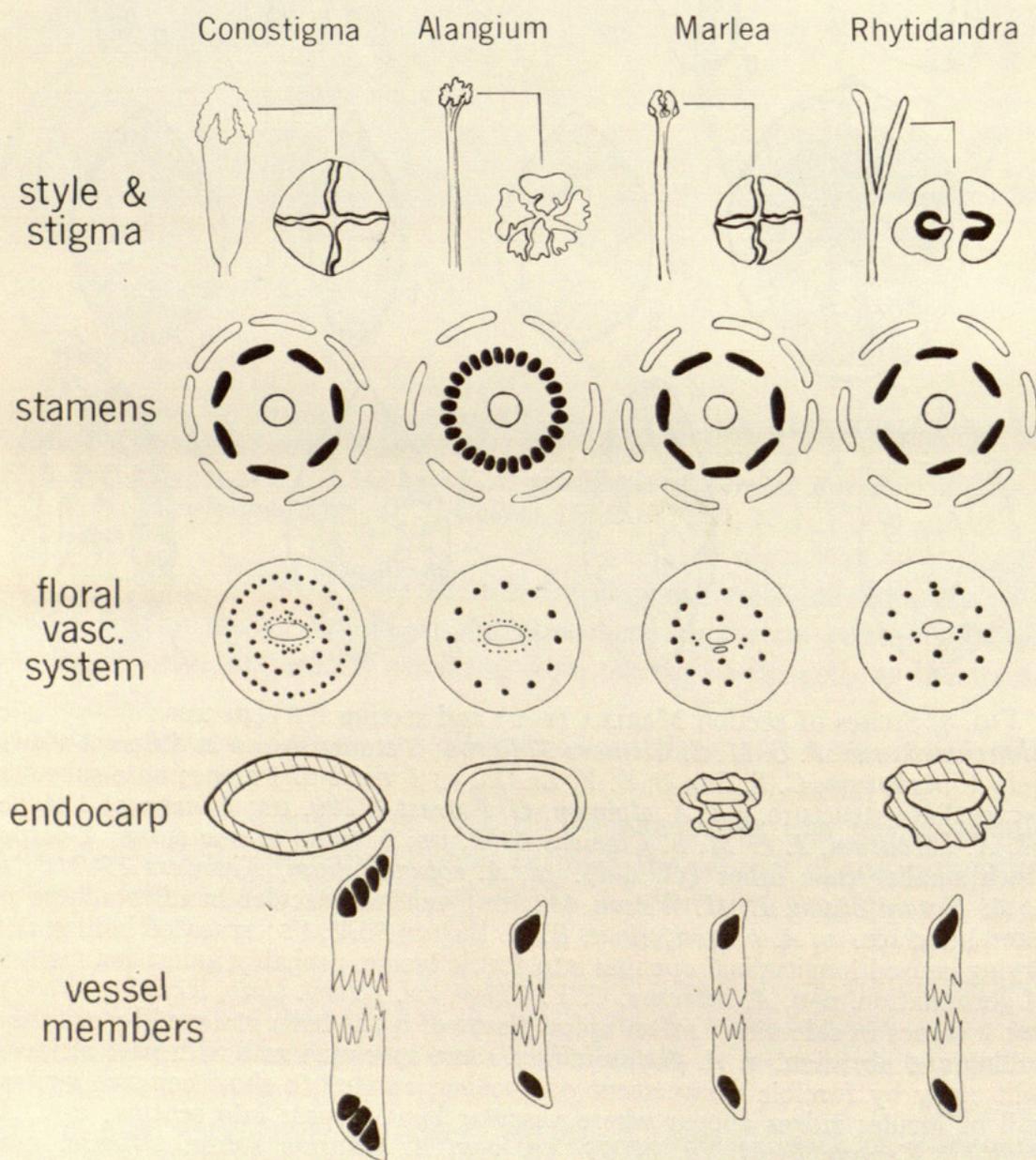


FIG. 9. Some sectional differences in *Alangium*.

cover almost the entire surface of the stone. Most of them are not associated with vascular bundles, and I have no ontogenetic explanation for their presence.

Histologically, the stones of all *Alangium* species are very much alike. Macerations show the component sclereids to be more or less equidimensional and irregularly lobed like the pieces of a jig-saw puzzle. To judge from the position of the cracks (FIG. 7, a, b; FIG. 8, m, o) that appear in repeatedly boiled and dried specimens, all of the stones open in the same manner at germination.

DISCUSSION, CONCLUSIONS

Evolutionary trends within the Alangiaceae. FIGURE 9 summarizes five structural features to which I attach evolutionary importance. The first four rows of the diagram represent sectional differences³ described in this article. The bottom row, based on observations of other workers (Metcalf & Chalk, 1950; Govindarajalu, 1961), shows two distinctive features in the secondary xylem of section CONOSTIGMA: the vessel members have scalariform perforation plates, and they are about twice as large as the vessel members in other sections.

Pollen provides still another set of characters. The information in TABLE 1, taken from Erdtman (1952) and Cookson (1957, *A. javanicum* only), reveals sectional differences in the number of pores, in the presence and distinctness of colpi (furrows), and in surface markings.

TABLE 1. Sectional differences in the pollen characters of *Alangium*.^a

CONOSTIGMA	ALANGIUM	MARLEA	RHYTIDANDRA
(2 -) 3 (-4)-colporate or colpoidorate; small-meshed surface pattern	3-5-porate; warts on surface	3(-4)-colporate or colpoidorate; surface granular, reticulate, or striate	4(-5)-colpoidorate; warts on surface

^a Adapted from descriptions by Erdtman (1952) and Cookson (1957).

FIGURE 10 is an evolutionary diagram that will account for the sectional differences. I visualize members of the ancestral group as having pluricarpellate gynoecea, isomerous androecea, separate bundles to all floral appendages, vessels with scalariform perforations, 3-colporate pollen grains, and multiple styles. Arrows indicate the direction of structural changes, and the size of the lobes roughly indicates the relative number of species in each section.

I assume a direct derivation of section ALANGIUM from section CONOSTIGMA in order to account for the strong similarities between the two and

³ Cytological studies should be undertaken to determine whether each section has its own chromosome number. I know of only two counts for Alangiaceae: $n = 8$ in *A. lamarckii* (= *A. salviiifolium*; Gopinath, 1945) and $2n = 22$ in "*A. begonifolium*" (one or another species of section MARLEA; Wanscher, 1933).

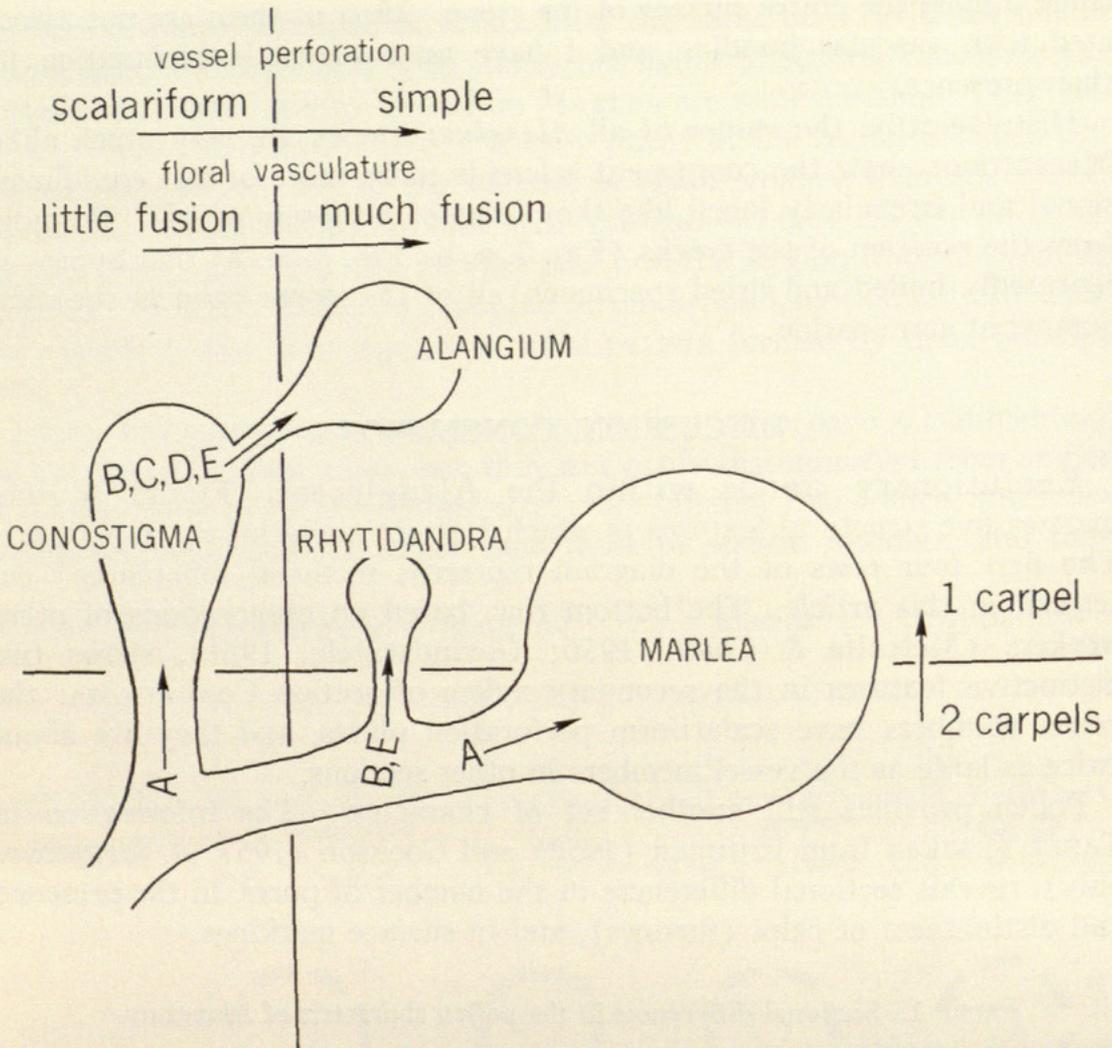


FIG. 10. Evolutionary relationships in *Alangium*. Area of each lobe roughly indicates the relative number of species in the corresponding subgeneric section. Arrows indicate directions of structural change: A, union of styles; B, fusion of dorsal carpel bundles with peripheral bundles (see FIG. 4); C, loss of woody endocarp; D, increase in number of stamens; E, increase in number of pores in pollen. Plants of the hypothetical ancestral group are thought to have had multiple carpels and styles; vessels with scalariform perforation plates; independent bundles to sepals, petals, stamens; isomerous androecium; 3-colporate pollen.

for the concentration of primitive characters in section CONOSTIGMA. Sections RHYTIDANDRA and MARLEA also have many characters in common; I explain this by assuming a close common ancestry. A direct derivation of either one from the other would be unconvincing, because section RHYTIDANDRA retains the more primitive styler characters while some species of section MARLEA retain the more primitive two-locular condition.

This kind of diagram is necessarily speculative, but I have tried to adhere to the most conservative and widely followed concepts of evolutionary morphology. The derivation of simple perforations from scalariform perforations is universally accepted by wood anatomists, and the gradual union of floral structures (in this case, styles and vascular bundles) is

another trend generally recognized as irreversible (Stebbins, 1967, p. 135). That the two-carpellate gynoecium preceded the one-carpellate (pseudomonomerous) gynoecium is unlikely to be challenged because all degrees of reduction can still be seen in section *MARLEA*: it would be difficult to interpret this evolutionary series in the opposite direction without assigning some selective value to the abortive carpels in intermediate forms. My view of evolutionary changes in the pollen is based on the fact that grains of the 3-colporate type occur very early in the fossil record of angiosperms and are retained in many of the less specialized groups of dicotyledons. From this I infer that 3-colporate pollen grains of *Alangium* are more primitive than pollen with four or five pores and with colpi poorly developed (the colpoidorate condition) or absent.

Erdtman (1954, p. 79) has hinted that *Alangium* might be made into two genera on the basis of pollen characters. From his earlier remarks (1952, p. 40), I gather that he would separate the species with porate grains from those with colporate grains, thus requiring the recognition of section *ALANGIUM* as one genus and the three remaining sections as another (a reinstatement of *Marlea* Roxb.).⁴ However, this is not the only arrangement that could be made if only pollen characters were considered: section *ALANGIUM*, lacking colpi, could be allied with section *RHYTIDANDRA*, in which colpi are poorly developed, for these two sections share the warty surface pattern. However, to adopt either of these arrangements would be to ignore all of the other characters discussed in this paper. It seems, therefore, that the same changes — development of a warty exine, increase in the number of pores — have occurred in separate evolutionary lines within the Alangiaceae. If it were necessary to divide *Alangium* into two genera — and I do not see that anything would be gained by doing so — a consideration of all characters would require that section *CONOSTIGMA* and section *ALANGIUM* be put in one genus, section *MARLEA* and section *RHYTIDANDRA* in the other.

The association of many stamens with advanced characters in section *ALANGIUM* will seem unusual to some floral morphologists, for we tend to look for oligomerization of all whorls, including the androecium (Takhtajan, 1959, p. 76; 1964, p. 69). Indeed, the traditional view that evolution favors a change from polystemony to oligostemony was codified a half century ago as Bessey's (1915) 24th dictum. Recently, however, Stebbins (1967, p. 121–123) listed several taxa for which considerations of comparative morphology indicate the opposite trend. The most compelling evidence for adding Alangiaceae to this list is in the vascular supply to the stamens. If flowers with many stamens were primitive, each stamen would have a corresponding vascular strand in the extracarpellary portion of the ovary wall, as is the case in section *CONOSTIGMA*. But section *ALANGIUM* has far fewer bundles in the inferior part of the flower than section *CONO-*

⁴ Yeramian (1967), in a publication that reached me after my manuscript had gone to the editor, explicitly separates the pollen of *Alangium* into two main types, "zonocolporate" and "panporate," corresponding to "subgenus *Marlea*" and "subgenus *Alangium*," respectively. Apparently, Mrs. Yeramian did not consult Bloembergen's monograph before writing her paper.

STIGMA, and the extracarpellary strands are arranged in a single series, each bundle supplying several stamens. Also, the stamens of all *Alangium* species are in a single whorl. This is a clue that *Alangium* is a special case, since taxa in which gradual oligomerization of the androecium has occurred often retain transitional stages in the loss of whorls.

Systematic position of *A. grisolleoides*. By a happy coincidence, Monsieur R. Capuron was working at the herbarium of the Muséum National d'Histoire Naturelle, Paris, when I visited there in 1964, and he kindly gave me a few flowers and fruits from his collections of *A. grisolleoides*. This Madagascan rarity, discovered only a few years ago,⁵ is clearly a member of section CONOSTIGMA, as Capuron (1962) surmised. Although its floral trichomes do not occur in the stellate-peltate pattern, it has the Conostigma type of endocarp (FIG. 7, e) and the characteristic papillose epidermis on anthers and style. It is the only dioecious species of *Alangium*.⁶ I did not get good serial sections from the flowers (all staminate) that Monsieur Capuron gave me, but the preparations were adequate to show a tiny empty locule in the rudimentary ovary. It is noteworthy that this species, with its reduced number of floral appendages, has evolved in the same group that gave rise to the polystemonous section ALANGIUM.

Place of Alangiaceae in the general system. Some of our most influential systematic works place Alangiaceae near Cornaceae (Němejč, 1956; Hutchinson, 1959, 1967; Melchior, 1964; Takhtajan, 1966; Soó, 1967). This concept has a long history (Harms, 1897, and Horne, 1914, review the early opinions), and it has been the prevailing one among those who have worked with the two families. I began my own investigation of Alangiaceae with the belief that *Alangium* is related to *Cornus*, as suggested by embryological studies (Chopra & Kaur, 1965), and to *Nyssa*, as suggested by similarities in the general appearance of the plants⁷ and their pollen grains (Erdtman, 1952). I expected to find an even closer resemblance between *Alangium* and *Mastixia*, the only cornaceous genus with secretory canals. In fact, however, the secretory structures of *Mastixia* are true resin canals with secretory epithelia (FIG. 6, c), not at all like the laticifers of *Alangium*. Furthermore, I have come to realize, con-

⁵ The discovery extended the range for section CONOSTIGMA well beyond the area mapped by Bloembergen (1939, Fig. 8). The known range for section ALANGIUM (Bloembergen's Fig. 2) has also been extended by the addition of *A. salviifolium* to the flora of tropical East Africa (Verdcourt, 1958).

⁶ Bloembergen (1939, p. 195) mentions specimens of *A. griffithii* and *A. salviifolium* with sterile anthers; these may indicate a tendency toward dioecism in section MARLEA and section ALANGIUM.

⁷ Species of *Alangium* can be confused with *Nyssa* in the herbarium. Thus, "*Alangium*" *shweliense* W.W. Sm. is a synonym of *Nyssa sinensis* Oliv. and "*Nyssa*" *hollrungii* Schum. is *Alangium javanicum* (Bloembergen, 1939). Nevertheless, *Alangium* does not resemble *Nyssa*—in floral characters or almost any other characters—as much as *Nyssa* resembles *Cornus*. Consequently, systems that place Alangiaceae and Nyssaceae in Myrtales while placing Cornaceae in Umbelliflorae are manifestly in error.

trary to an earlier assumption (Eyde, 1968), that the gynoecial vasculature of *Alangium* is not exactly like that of *Cornus*. The difference is that *Alangium* has extra (ovular?) bundles ending blindly in the septum. Were such bundles present in the ancestors of *Cornus*, or do they indicate an entirely different origin for the vasculature of *Alangium*? Atypical arrangement of gynoecial vascular bundles must be studied further in other plant families before a confident choice can be made between these two alternatives. It might also be informative to examine the vasculature of a three-locular *Alangium* flower like the one Clarke (1850) figured (I have never seen one). In any case, there now seem to be good reasons for doubting the close affinity of Alangiaceae to Cornaceae and Nyssaceae, and the opposing views therefore deserve careful consideration.

Several modern works link Alangiaceae with Rhizophoraceae and Combretaceae in the Myrtales (Roederer, 1930; Pulle, 1952; Novák, 1954; Vinogradov, 1959). Therefore, I sectioned some flowers of Combretaceae (*Combretum*, *Terminalia*) as a part of this investigation, but I found no structural resemblance to *Alangium*. Flowers of Combretaceae have gamopetalous corollas, biseriate androecia, and unilocular gynoecia with two or more ovules — all points of difference from *Alangium* — and there are corresponding differences in the floral vascular system. Another dissimilarity is that the ovules of Combretaceae have two integuments: there is no trace of a second integument in *Alangium*.⁸ Still another is that the characteristic rudimentary stipules of the Myrtales (Weberling, 1960) are lacking in *Alangium*. Furthermore, the pollen of *Alangium* and Combretaceae are “± different” (Erdtman, 1952, p. 40) and the xylem characters are distinctly different (Janssonius, 1918, p. 707). Finally, the known alkaloids of Rhizophoraceae are quite unlike those of Alangiaceae (Hegnauer, personal communication). In short, all lines of evidence weigh heavily against the alliance of these three families.

Hallier (1905; 1912, p. 221) once considered Olacaceae the closest family to Alangiaceae, although he later (1918, p. 117) modified this opinion. H. K. Airy Shaw, in his revision of Willis' (1966) *Dictionary*, cautiously offers a similar idea. Under Alangiaceae, Shaw says “Relationships obscure; perhaps some connection with Olacaceae and Ehretiaceae.” The suggestion of an affinity with Olacaceae is worthy of further investigation, because many olacaceous genera have non-articulated laticifers (Metcalfe & Chalk, 1967). However, the ventral carpellary vascular system differs from that of *Alangium* in that the bundles rise through the center of the flower (Agarwal, 1963 a, b). The floral structure of *Ehretia* (Johri & Vasil, 1956) is even less like that of *Alangium*.

Shaw adds *Metteniusa* to the Alangiaceae, a change that I do not accept. *Metteniusa* is a genus of uncertain systematic position (Icacinaceae and Olacaceae have been suggested) with epipetalous stamens and a superior

⁸ Mauritzon's (1939, p. 114) comments on *Alangium* are especially pertinent. Observations of other embryologists are reviewed by Johri (1963, p. 424) and Chopra & Kaur (1965). Hutchinson (1967, p. 41), in attributing two integuments to *Alangium*, repeats an error from his 1959 work, despite Takhtajan's (1959, p. 239) effort to correct him.

ovary. A sectioned gynoecium (FIG. 5, d), followed serially from base to style, displays the vascular system and the ventral suture of a single carpel, more like a *Prunus* gynoecium than the complex pluricarpellate or pseudomonomerous gynoecium of *Alangium*.

Recent discovery of the alkaloids emetine, cephaeline, and psychotrine in *Alangium salviifolium* indicates to Hegnauer (1965, p. 245; 1966, p. 219) that the Alangiaceae may be related to the Rubiaceae, the only other family in which these substances are known to occur. Alkaloids are not perfect taxonomic indicators, to be sure, but the suggestion is supported by *Alangium*-like characters in certain rubiaceous flowers. There are rubiaceous taxa (*Oxyanthus natalensis*, *Gardenia resinifera*, *Mussaenda* sp.) in which all or part of the ovular supply passes through the septum. *Guet-tarda speciosa*, like certain species of *Alangium*, has a great many gynoecial bundles around its locules. Furthermore, a vascularized disc is of common occurrence in the Rubiaceae. (Details of floral vasculature are taken from Rao, Ramarethnam, & Iyer, 1964.) Most Rubiaceae are sympetalous, with epipetalous stamens, but in *Synaptantha* free stamens accompany a corolla that is divided almost to its base. Among the many poorly known genera of this large family may be others that are even more like *Alangium* than those I have mentioned.

In conclusion, therefore, I urge other workers to look into the Rubiaceae for the closest allies of Alangiaceae. It is conceivable, as Hegnauer (1965) suggested, that *Alangium* is related both to the Rubiaceae and to the Cornales (sensu Takhtajan, 1966), forming a link between the two groups; however, I do not share that opinion at present.

SUMMARY

Principal observations and conclusions resulting from an anatomical study of flowers and fruits of *Alangium* (the only genus of Alangiaceae) can be summarized as follows:

1. The secretory structures of *Alangium* are non-articulated laticifers.
2. Marked differences in the number of gynoecial vascular bundles separate Bloembergen's section CONOSTIGMA and section ALANGIUM from section MARLEA and section RHYTIDANDRA. In addition, section CONOSTIGMA differs from section ALANGIUM and section MARLEA from section RHYTIDANDRA in the degree to which gynoecial bundles are united with other bundles of the flower.
3. Characters of the endocarp further substantiate Bloembergen's concept of four subgeneric sections. Surface features of the woody stone can be used to separate three of the sections, and the fourth (section ALANGIUM) is distinguished by its poorly lignified endocarp.
4. In section ALANGIUM stamens are much more numerous than petals, but their number is variable and not an exact multiple of the petal number as earlier treatments would lead one to believe. Polystemony is probably an advanced condition in *Alangium*, because it is associated with a reduced gynoecium, an advanced floral vascular system, and advanced characters of the pollen and wood.

5. The prevailing opinion that the Alangiaceae belong to the Cornales is not well supported by anatomical characters of the flower. However, all indications weigh heavily against a close affinity to Combretaceae or Rhizophoraceae, and present evidence is insufficient to prove a relationship with Olacaceae. Similarity in alkaloid content and in certain details of floral structure suggest that the closest allies of Alangiaceae may be found in the Rubiaceae.

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