

FLORAL MORPHOLOGY AND VASCULAR ANATOMY  
OF THE HAMAMELIDACEAE:  
THE APETALOUS GENERA OF HAMAMELIDOIDEAE

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THE HAMAMELIDACEAE ARE A FAMILY of twenty-seven genera and possibly 100 species distributed in the tropical, subtropical, and temperate regions of both the New World and the Old. The genera are small, fourteen are monotypic, six contain only two to three species, while seven comprise from five to fourteen species. Most of the genera are narrow endemics or very restricted in their distribution, only two (*Hamamelis*, *Liquidambar*) being present in both Asia and North America. The genera are morphologically diverse, ranging from huge evergreen trees to low deciduous, rhizomatous shrubs. Their leaves vary from palmately lobed and veined to elliptic-oblong and pinnately veined and may be spirally arranged, two-ranked, or opposite. They are stipulate in all genera except one (*Rhodoleia*). Inflorescences vary from simple racemes to panicles, spikes, heads, or densely congested and fused, complex, capitate flowering branch-systems. The flowers may be showy or inconspicuous, petaliferous, apetalous or naked, bisexual or unisexual, with few to numerous stamens, many ovules to only one, and few winged seeds per carpel to mostly a single wingless seed. Perhaps the one unifying morphological feature of the family is in its characteristic 2(-3)-carpelled, septicidal (and sometimes partially loculicidal as well) woody, capsular fruits.

The morphological, systematic, and phyletic relationships of the Hamamelidaceae were last reviewed in detail forty years ago (Harms 1930). Many of the problems encountered then concerning morphological interpretations and systematic or phylogenetic affinities have remained unresolved up to the present time. Furthermore, in the intervening years, the concept of the family has been expanded through the discovery or recognition of new genera which have increased its diversity, rather than bridged its internal gaps. Indeed, the diversity of the family is such that some consider two or more families to be represented, rather than one. The limits of some tribes, or the tribal affinities of a few genera are uncertain, while the morphological nature of certain floral organs has evaded satisfactory interpretation in some cases, or has been widely misinterpreted in others. These problems have prompted several workers, in recent years, to point out the need for more detailed study of the group. Foremost among the areas in need of examination is that of floral vascular anatomy, which has only recently come under scrutiny (Bogle 1967, 1968, 1969; Endress 1967; Horne 1914). Evidence from such studies in other groups has been very valuable in the interpretation of difficult problems of floral morphology, which is among the principal bases on which systematic and phylogenetic relationships may be established.



This paper is the first in a series which will provide a detailed comparative account of the floral vascular anatomy, coupled with other observations on floral and inflorescence morphology, for each of the 27 known genera of the family. The ultimate purpose of this work is the clarification of the morphological homologies of the organs of the hamamelidaceous "flower," and of the phylogenetic trends among the divergent floral types within the family. Such information, along with evidence from other lines of research, should then permit a re-evaluation of the interfamilial and phylogentic relationships of the Hamamelidaceae. The opinions expressed in the literature concerning this family differ widely. It has been thought to be 1), related to several extant magnolialian families, or directly derived from a magnolialian or proto-magnolialian stock (Solereeder 1899; Hallier 1903, 1912; Tippe 1938; Tang 1943; Chang 1961; Cronquist 1968; Takhtajan 1969); or 2), derived from a rosalian or proto-rosalian stock, with close affinity to the extant Rosaceae, Saxifragaceae, or more especially the Cunoniaceae (Bentham & Hooker 1865; Baillon 1871, 1874; Eichler 1875; Reinsch 1889; Niedenzu 1891; Bessey 1915; Hutchinson 1926, 1959; Tong 1930; Harms 1930; Melchoir 1964; Endress 1967; Jay 1968); or 3), to be derived from an amentiferous ancestral stock (Wettstein 1935; Croizat 1960, 1964). On the other hand, many of the authors cited above derive from a proto-hamamelidalian stock the highly specialized and advanced group of families included in the "Amentiferae" (particularly the Betulaceae, cf. Endress 1967) which are characterized by greatly condensed inflorescences and reduced, typically unisexual, monochlamydeous, wind-pollinated flowers. The authors mentioned above who view the "Amentiferae" as primitive, however, consider the Hamamelidaceae and its allies transitional to the more advanced Polycarpicae, Rosales, or Cornales, with dichlamydeous, bisexual flowers, but this view receives little support from current workers.

#### MATERIALS AND METHODS

All of the specimens collected in the field in Southeast Asia and Mexico for anatomical study were preserved in fluid. Fresh specimens were preserved in formalin-acetic acid-alcohol (F.A.A.) for the most part, or in 70 per cent ethyl alcohol. With collections in Hong Kong, however, a reasonable preservation was achieved with a makeshift solution consisting of equal parts of Rectified Spirits of Wine B.P., and distilled white vinegar, giving concentrations of about 50 per cent ethyl alcohol and 2.5 per cent acetic acid. These specimens were later transferred to F.A.A. Flowers from herbarium specimens have been used for a few genera, but were often found to be unsatisfactory for anatomical purposes due to distortion and rupturing of the tissues caused by pressing, drying, and re-expansion. Flowers at both anthesis and post-anthesis stage were sectioned when available, since the ovary and its vasculature are poorly developed in some genera at flowering time.

Cleared and uncleared whole flowers, hand sections, and serial microtome



sections were utilized according to the nature of the material to be examined. Flowers from herbarium specimens were softened and re-expanded, using the modified Juel method described by Tillson & Bamford (1938), and then treated as fresh material.

Specimens to be cleared were first soaked in water to remove excess F.A.A., then bleached to near-whiteness at room temperature in a solution consisting of nine parts 2.5 per cent sodium hydroxide to one part 5 per cent sodium hypochlorite or commercial Clorox. The bleaching solution was rinsed out thoroughly with water before gradual dehydration followed by clearing in xylene, chloral hydrate, or paraffin oil. Where necessary and possible, pubescence was removed from floral surfaces after clearing in xylene, when the brittle epidermis lifts off easily.

Flowers to be sectioned were of necessity bleached and softened. Untreated flowers proved generally unsatisfactory for sectioning and staining due to 1), tearing of the sections caused by the hardness of the lignified, often dense epidermal pubescence, or hard internal tissues such as the developing bony endocarp, or 2), the presence of densely staining organelles or intracellular substances of undetermined nature with a particular affinity for safranin, which often obscure the vasculature. A distinct disadvantage of this harsh process is the collapse of cells that it may cause in delicate parenchymatous epidermal surfaces, as in young ovules, or the transmitting tissues of the stylar canal, etc. After bleaching, the flowers were dehydrated in a normal-butyl or tertiary-butyl alcohol series, embedded in "Paraplast," and sectioned at 10, 15, or 20 micra, depending on the size of the flower.

Various stain combinations were tried, including erythrosin and crystal violet, safranin and anilin blue, safranin and fast green, and Foster's tannic acid-iron chloride (Johansen 1940). The last two methods gave the most satisfactory results for tracing vasculature, and were used almost exclusively. Polarized light was frequently used to aid in tracing small vascular bundles.

Drawings were made with the aid of the drawing attachments designed for the Wild M-20 and M-5 microscopes. The floral pubescence so obscures the outlines of the floral organs in many genera that it has been omitted in most of the figures for the sake of clarity.

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#### GENERAL CONSIDERATIONS

For the purposes of this work the genera of the family will be considered as comprising three fairly natural groups. The apetalous tribes and genera of the Hamamelidoideae (Distylieae: *Distylium*, *Sycopsis*, *Matudaea*, *Molinadendron*; Fothergilleae: *Parrotia*, *Parrotiopsis*, *Fothergilla*) will be



considered here, followed later by the petaliferous Hamamelidoideae (tribes Hamamelideae, Eustigmateae, Corylopsideae), and finally the four small and distinct tribes Liquidambaroideae, Rhodoleioideae, Disanthoideae, and Symingtonioideae. The order of consideration of the genera here differs somewhat from that given in the system of Harms (1930, as revised by Melchior, 1964, and with four tentatively placed genera included), which is the most comprehensive available.

The tribe Distylieae Hallier (1903) originally contained only *Distylium* Sieb. & Zucc. and *Sycopsis* Oliv. and was characterized by Hallier (op. cit., p. 255) as follows: Leaves leathery, entire or toothed, evergreen, with small lanceolate stipules, spicular cells, two-layered palisade tissues, and small single crystals. Inflorescences pedunculate, solitary, of axillary heads or racemes; bracts small; flowers monoecious or andromonoecious, lacking petals; anthers oblong, narrowed below to a short filament and above into a short point, dehiscing by two lateral, longitudinal, simple slits.

The Central American genus *Matudaea* Lundell (Lundell 1940) was considered by Walker (1944) to conform in most respects with Hallier's description of the tribe, and has been tentatively included in it. Walker also maintained two Central American species of *Distylium* which, with a third species since described, were recently and rightfully removed as the segregate genus *Molinadendron* Endress (Endress 1969). Endress considers *Molinadendron* misplaced in the Distylieae, and closer to *Fothergilla* and *Parrotiopsis* (*Fothergilleae*) or to *Fortunearia* and *Sinowilsonia* (Corylopsideae). The genus *Sinowilsonia* Hemsl. (Hemsley 1907) was added to the Distylieae (Harms 1930) but later removed to the Corylopsideae (Schulze-Menz 1964). I shall describe it with the petaliferous Hamamelidoideae.

Leaf venation in the Distylieae is pinnate. In *Molinadendron* the veins terminate in the distal, marginal teeth, but in the other three genera the veins are, for the most part, curved-anastomosing (camptodromous type) well within the margins, or in a few species basally triplinerved (*Matudaea*, *Sycopsis laurifolia*) and approaching a camptodromous condition.

The tribe Fothergilleae DC. (1830) contained only *Fothergilla* L. Niedenzu (1891), however, recognized a tribe Parrotieae which combined the apetalous genera *Distylium*, *Parrotia* C. A. Mey., and *Fothergilla* (including *Parrotiopsis*) with the petaliferous *Corylopsis* (*Sycopsis* was placed in the tribe Hamamelideae between *Eustigma* and *Hamamelis*). The tribe Fothergilleae in Harms's system (1930) contains *Fothergilla*, *Parrotia*, and *Parrotiopsis* (Niedenzu) Schneid., and is characterized in his key to the family (op. cit., p. 315) as having flowers perfect, in congested spikes or small heads. Petals lacking. Stigma punctiform or capitate. Number of floral parts irregular. Stamens often more than five. Anthers dehiscing by longitudinal slits or valves.

The leaves of the three genera of Fothergilleae are membranous, stipulate and deciduous, with ascending, often more or less parallel pinnate veins which terminate in the distal lobes of the sinuate-dentate to coarsely toothed margins (craspedodromous type).



The structure of the ovary is rather uniform within the Hamamelidoideae. Therefore, a general description is provided at this point in order to avoid repetition in the generic descriptions below. The trends of vascular specialization will be discussed later for the entire subfamily.

The gynoecium consists of two, or not infrequently three, involute carpels. The carpel margins are fused below, and the carpels united adaxially through the length of the ovary, forming an incompletely septate, essentially bilocular capsule. The two locules become confluent above, just below the level of ovule insertion near the apex of the locules, as the opposing fused adjacent carpel margins incorporated in the septum separate to form the parietal placentae. Above the ovules the ovarian cavity continues upward as a narrow, elongated canal which opens to the outside through the style bases. Above the ovary the carpels are free, in the Distylieae and Fothergilleae terminating in exserted, linear-subulate styles which are often recurved, and sometimes slightly expanded, bearing extensive exposed or included papillate stigmatic surfaces along their ventral faces. One or occasionally two, pendent, anatropous ovules may occur in each carpel, inserted on both margins, but usually only one of these (occasionally two) is functional.

Each carpel is supplied with five bundles: the dorsal midvein, two submarginal lateral bundles, and two marginal ventral bundles. In the syncarpous ovary the lateral bundles or adjacent fused carpel walls are incorporated in discrete or diffuse compound lateral bundles (the synlaterals of Endress, 1967; lateral bundles of Horne, 1914) which ascend at each edge of the septum. The compound laterals may dichotomize to form individual lateral bundles well below the level of ovule insertion, or remain united almost to the top of the ovary, where they fuse with the ventral bundles. With few exceptions the ventral bundles arise in the septum from a narrow, largely procambial remnant of the receptacular cylinder (the inner series of Horne, 1914), which enters the base of the septum before consolidating as a single axial bundle (the synventralmedian of Endress, 1967) and dividing to form two compound ventral bundles (the synventrals of Endress, the septal or placental bundles of Horne). The ascending compound ventrals may also divide to form distinct ventral bundles well below the level of ovule insertion, or remain united to the level of fusion with the lateral bundles near the top of the ovary. After fusing with the lateral bundles the ventrals continue upward into the margins of the style. Each functional ovule receives a single trace from the adjacent ventral or compound ventral bundle. No traces have been observed to supply abortive ovules. Within the ovary walls the dorsal and lateral bundles supply lateral branches to the vascular network of the carpels. At anthesis this network is poorly developed and mainly procambial, but in the fruit it forms a coarse reticulum of thickened bundles over the surface of the bony endocarp. Above the locules the dorsal bundles pass upward as the major bundle to the style bases, where they may remain distinct, or unite with the ventrals as a single broad vascular arc.



In the following descriptions the general morphology of the inflorescence and flowers of each genus is discussed, followed by a description of the vascular anatomy. Abbreviations for various organs and anatomical features illustrated in the figures are introduced as necessary in the text. In the absence of petals, and due to the uncertain morphological origin of the perianth in some genera, the terms *perigon* and *tepal* are used, rather than calyx and sepal. An appendicular hypanthium consisting of fused sepal, stamen, and petal bases is present in the petaliferous genera of Hamamelidoideae, but is absent in certain apetalous genera (*Distylium*, *Molinadendron*, *Matudaea*), or is replaced by an analogous structure, possibly consisting of foliar, axial, and floral tissues united in a cup around an ovary. This structure, which has not previously been investigated, is here referred to as a *hypanthium* for the sake of simplicity. But, as seen in *Sycopsis dunnii*, staminate flowers may occur at various levels on its outer wall or on its rim, in which case the term "hypanthodium"<sup>1</sup> in the sense of Emerson & Emerson (1960) might be more appropriate. The shallow floral cups in the flowers of *Parrotia*, *Fothergilla*, and *Parrotiopsis* may be of similar origin, although this is not known for certain, and they are also termed *hypanthia*. The term *stèle* is used here in a general sense with reference to the vascular system of the peduncle, pedicel, and receptacle, and may include both primary and secondary tissues. The terms *bundle*, *trace*, and *strand* are used interchangeably. The term *trunk bundle* is applied to those vascular bundles which traverse the hypanthium longitudinally, and branch distally to supply traces to the perianth and androecium.

#### OBSERVATIONS AND INTERPRETATIONS

1. *Distylium* Siebold & Zuccarini, Fl. Jap. 1: 178. t. 94. 1841.

FIGURES 1-3, 4A-D.

The widespread but poorly understood Asian genus *Distylium* contains about 11 species of evergreen shrubs and trees distributed in temperate, subtropical, and tropical regions from Japan and southern Korea southward to Taiwan, eastern and southeastern China, westward in the Himalaya to Assam, and southward through Burma, Indo-China, and Malaya to Java and Sumatra (Walker 1944; Airy-Shaw 1963; distribution map in Balgooy, 1966). Three Central American species originally ascribed to this genus were recently segregated as the genus *Molinadendron* Endress (1969).

The complexities associated with the variation and reduction of flower and inflorescence in *Distylium* are such that it is difficult to consider one without the other, for it is often difficult to distinguish between flower (euanthium) and inflorescence (pseudanthium), or between vegetative

<sup>1</sup>Eames (1961, p. 249) notes that the term hypanthium has been loosely used to cover "complex and varied" morphological structures. Jackson (1928) lists both hypanthium and hypanthodium, with the definition "an enlargement or development of the torus under the calyx; a syconium." Emerson & Emerson define hypanthodium as "an inflorescence with concave capitulum on whose walls the flowers are arranged."



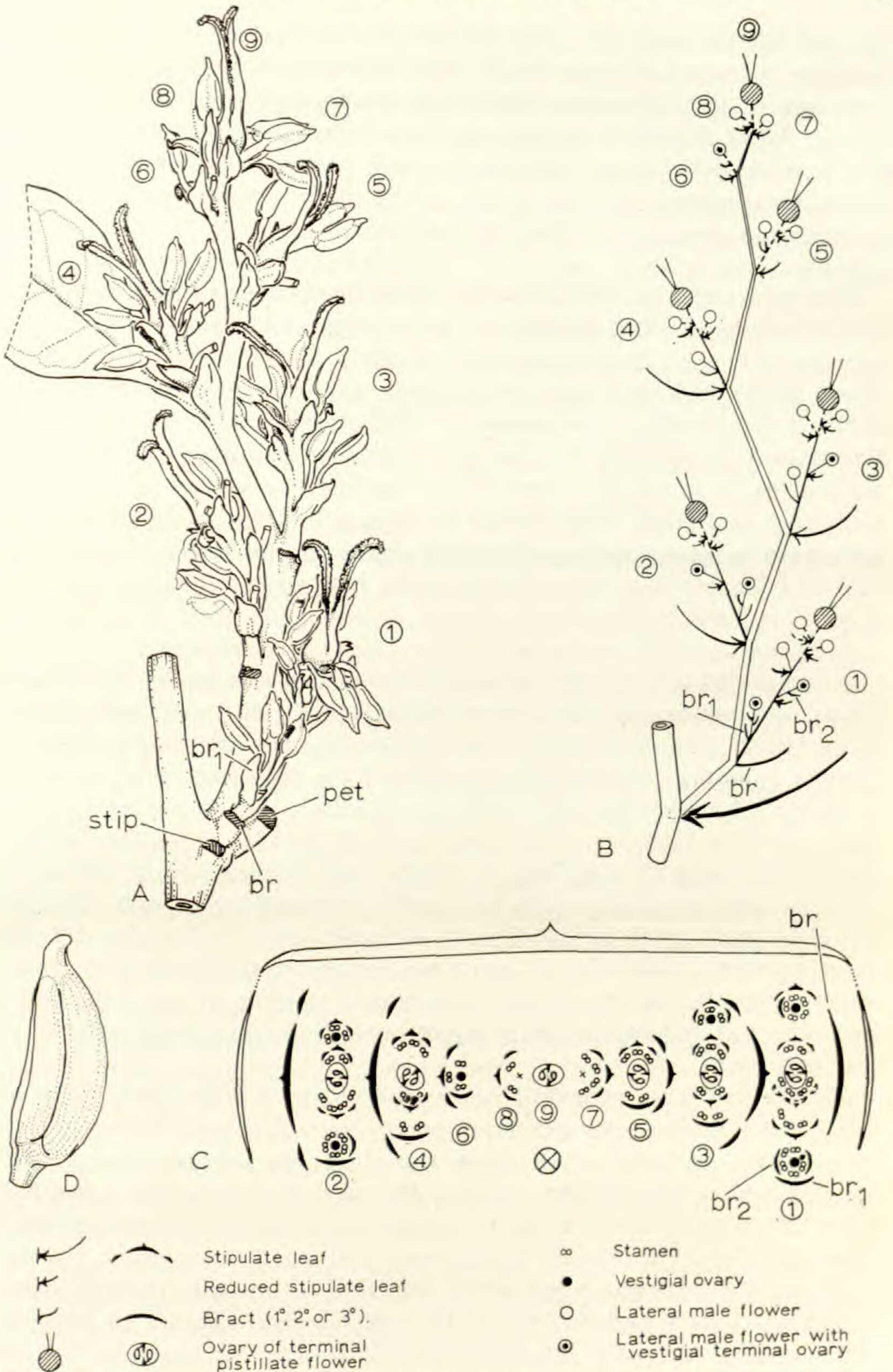


FIGURE 1. *Distylium racemosum*: A-C, structure of a complex inflorescence, showing stages of reduction in leaves, bracts, and lateral inflorescence units. Each unit is designated by the same number in all three figures; A, inflorescence at anthesis, some bracts and anthers removed — note terminal position of functional ovary in each unit; B, diagrammatic representation of A; C, inflorescence diagram of A; D, anther — solid line marks path of dehiscence.



axis and inflorescence axis. The inflorescence of *Distylium racemosum* is, therefore, discussed in some detail. The following descriptions and interpretations of the inflorescence and floral morphology are based primarily on material of *Distylium racemosum* Sieb. & Zucc., *D. gracile* Nakai, and *D. stellare* O. Ktze. in my collections, but I have also examined available herbarium specimens of other species of the genus, and find no morphological evidence to contradict the interpretation.

**MORPHOLOGY:** The inflorescences of *Distylium* are small, bracteate, axillary or terminal spikes, racemes, or panicles, produced from a bud of the previous or current growth season (FIGURES 1, 4). The flowers are naked (Vink 1957) and unisexual, but through aggregation of staminate and pistillate flowers often appear bisexual, with a functional or abortive ovary. The stamens at maturity are strongly exserted, with oblong to ovate, dark-red anthers in which the connective is produced as a short apiculus, and dehiscence is slightly dorsi-lateral by means of longitudinal slits which are simple in some species and basally subvalvate in others (FIGURE 1D). The functional ovaries are terminal on the inflorescence axes and are very small at anthesis, with exserted, straight to recurved styles. A hypanthium such as that found in most genera of the family is never present.

A compound inflorescence of *Distylium racemosum* ( $n = 12$ , Sugiura 1936), containing several axillary inflorescence units arranged along a short lateral axis, is illustrated in FIGURE 1A, and diagrammatically in FIGURE 1B and C. Examination of each of the inflorescence units reveals a variety of vegetative and floral modifications and reductions such as those noted by Hemsley (1907) and by Vink (1957), as follows: inflorescence unit number 1 is axillary to a large bract (br, excised in FIGURE 1A, but scar area hatched); units 2, 3, and 4 are axillary to well developed stipulate leaves, such as that figured with unit 4 (excised at 2 and 3, scar areas hatched); units 5, 6, 7, and 8 are axillary to trimerous bract groups which continue the two-ranked phyllotactic pattern of the lower nodes and represent reduced stipulate leaves; unit 9 is represented only by the terminal ovary.

Within unit 1, in ascending order: the proximal node bears a primary bract which encloses two secondary bracts inserted oppositely in the transverse plane, flanking a male flower containing six stamens (one of them sterile) and a tiny abortive ovary; the second node bears a trimerous bract group to which is axillary a small, transversely inserted secondary bract, a flower consisting of five stamens, and an abortive ovary; the third node bears a trimerous bract group with three stamens in the axil, but no secondary bracts and no ovary; the inflorescence appears to terminate with a set of trimerous bracts unilaterally inserted at the base of a well developed, functional ovary which is surrounded basally by a cycle of six irregularly inserted stamens, two of which are more or less axillary to the bracts, while the other four are inserted on the receptacle around the naked side of the ovary. In the systematic literature this terminal group of bracts, stamens, and ovary would be interpreted as a bisexual flower with



three sepals, but morphological and anatomical evidence indicate that the bract group and its associated stamens represent a fourth node, that the remainder of the stamens represent a fifth node at which the bracts have failed to develop, and that the ovary represents a terminal, naked pistillate flower. Bracts such as those which I interpret as abortive at node five (indicated by dashed symbols in FIGURE 1B-1, C-1) are actually present at the tips of inflorescence units 2, 3, and 4. In the material available, all stages of reduction of such bracts can be found, down to three abortive primordial protrusions on the receptacle on the naked side of the ovary. The interpretation of the ovary as a terminal, naked, pistillate flower is based on vestigial vasculature in its base (described below), which suggests the former presence of a hypanthium or floral envelope of some sort in the recent phylogenetic history of the genus.

Each higher inflorescence unit is progressively more reduced than unit 1, with fewer bracts and flowers. Unit 5, for example, is axillary to a trimerous bract group and consists of a functional ovary surrounded by five hypogynous stamens and four bracts of varying size. But one of the bracts is obviously larger, is inserted opposite and morphologically lower than the other three in the transverse plane, and bears two fertile stamens in its axil, while three stamens are associated with the opposing bract group. This inflorescence would also be described as a bisexual flower, but actually consists of two lateral, naked staminate flowers and a terminal, naked pistillate flower. Unit 6 consists of single primary bract and three fertile stamens, representing a naked staminate flower associated with an abortive terminal ovary. Units 7, 8, and 9 are aggregated as a terminal group of six bracts, six "hypogynous" stamens, and a terminal functional ovary. But three of the bracts, with four associated stamens, morphologically lower and opposite the others on the axis, represent an inflorescence (unit 7) reduced to a naked staminate flower axillary to a bracteate stipulate leaf. Unit 8 is similarly reduced to two stamens axillary to the three higher bracts, and the ovary, designated as unit 9, represents a terminal, naked pistillate flower. Units 7, 8, and 9 thus duplicate the condition apparent at the tips of units 2, 3, and 4, with six bracts, five or six stamens, and a functional ovary forming what has generally been considered an incomplete, bisexual flower, a condition brought about by the reduction of leaves and distal internodes of the inflorescence axes, resulting in the aggregation of naked unisexual flowers and their associated subtending bracts to form a bisexual pseudanthium.

More complicated flowering branch systems have been seen in which the lateral axis illustrated in FIGURE 1A would represent only one of numerous progressively reduced units arranged along an axis which terminates in a similar pseudanthium. In such a system branches to the fourth order are involved, each terminating in a pseudanthium, each pseudanthium incorporating elements of two orders of branching.

The terminal position of the functional ovaries and the reduction of subterminal units are more clearly demonstrated in FIGURES 4A-D, of *Distylium racemosum*. FIGURE 4A illustrates an axillary, paniculate in-



florescence bearing seven maturing terminal ovaries subtended by trimerous bract groups. The stamens have fallen away from all the lateral staminate flowers, in some cases, revealing abortive ovaries. A subterminal ovary reduced to one carpel and an abortive bicarpellary ovary (ab ov) are shown in FIGURE 4B and C, while a tricarpellary ovary with an abortive organ protruding from its side is illustrated in FIGURE 4D. The protruding organ is probably a stamen which has become adnate to the ovary and developed a small stigma-like structure terminally. I have found, in my material, several isolated examples of such monstrous stamens consisting of part anther and part stigma, associated with terminal ovaries.

In inflorescences from flowering specimens of *Distylium buxifolium* (Hance) Merr. (*E. H. Wilson 115, 3537, [A]*) the inflorescence units were found to be spirally arranged rather than two-ranked as in *D. racemosum*, and much reduced from the condition seen in the latter, with shorter, more congested primary axes, fewer nodes and lateral flowers, considerable modification and fusion of the primary and secondary bracts, and pseudanthial complexes containing from 4 to 10 bracts (for the most part in obvious groups of three, and representing the reduced stipulate leaves of possibly 2 to 4 subterminal nodes) surrounding the subterminal staminate and terminal pistillate flowers. An abortive subterminal ovary may be present among the stamens axillary to the morphologically lowest group of bracts in the terminal complex.

ANATOMY: The vascular supply to the petiole of the foliage leaf and to the inflorescence bracts of *Distylium racemosum* and *D. gracile* consists of three traces derived from three gaps in the stele, with a single trace provided to each stipule from the adjacent lateral leaf trace (FIGURE 2A).

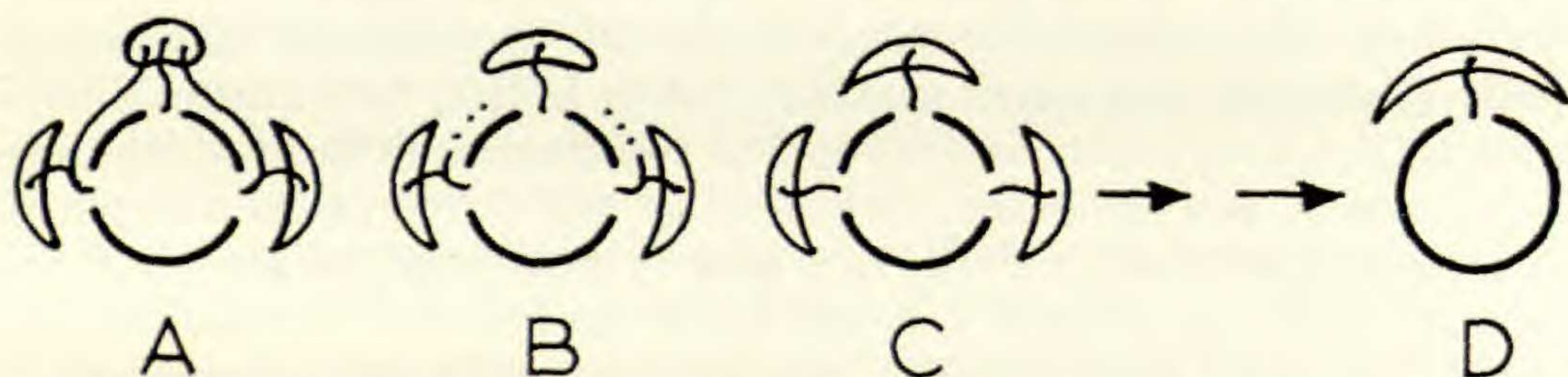


FIGURE 2. Steps in the reduction of the vascular supply to the inflorescence bracts of *Distylium racemosum* and *Sycopsis dunnii*: A, typical three trace, trilacunar node of the stipulate leaf; B, lateral traces to petiole vestigial; C, lateral traces absent, only the stipules supplied from the lateral gaps; D, stipulate leaf reduced to a single bract receiving one trace from one gap.

Within the flowering branch system reduction of the leaf blade is accompanied by a corresponding reduction in the vascular supply to the petiole. Reduction of the lamina results first in the failure of the lateral traces to the petiole to develop fully, as indicated in FIGURE 2B, where the lateral traces supply traces to the stipules, then end blindly as vestigial stubs in the cortex near the petiole base. The petiole then receives only a single median trace. Further reduction of the lamina results in the loss of the vestigial stubs, so that only the stipules receive traces from the



lateral gaps in the stele (FIGURE 2C). The bracteate blade may fuse with the stipules to form a single broad, trifid bract, or the leaf blade may be lost and the persistent stipules may fuse into a single bifid bract. The penultimate stage of reduction is a single bract supplied by one trace from one gap. The latter condition is encountered most frequently at the base of an axis (FIGURE 2D).

In view of the great variation in the flowers of *Distylium* I have based the following anatomical description on a selected specimen which I think exhibits the general morphological and anatomical features of the species which were available for anatomical study. FIGURE 3A illustrates the tip of an inflorescence of *D. racemosum* which is similar to those described above except that here the leaf blades at the subterminal nodes are fully developed rather than bracteate. Group 1 consists of a naked staminate flower of four stamens axillary to a leaf. Group 2 looks like a terminal bisexual flower, but consists of two or three stamens axillary to the distal leaf, while the remaining stamens inserted on the naked side of the receptacle (one with a partially laminar anther) are interpreted as referable to a third node (not numbered), the bracts of which have failed to develop. The axis terminates in the terminal ovary.

At the base of group 1, in the wake of the departing leaf traces (lf tr), a small axillary stele (ax 2) is pinched off from the main axis to supply the base of the sessile staminate flower. At anthesis this stele is largely procambial, with scattered protoxylem elements apparent only in polarized light. As the stele ascends in the receptacle four large collateral bundles (st) organize (FIGURE 3C, D, E). Scattered protoxylem strands lying between these bundles in the stele gradually die out, leaving only procambial arcs (stippled) which die out as the four stamen traces depart.

At the base of the distal complex, after the departure of the leaf traces, the stele consists of a ring of numerous collateral bundles. Five more or less equally spaced stamen traces (st) differentiate, then arch outward to enter the bases of the filaments (FIGURE 3F-H). The gaps left by the traces are shortly repaired as the stele consolidates in the receptacle. Although the stamens are inserted at the base of the ovary morphologically, their traces originate well down in the axis anatomically, as much as 500 micra below the ovary base. In longitudinal sections and cleared specimens the ovary appears to be subtended by a relatively long vascular cylinder or stipe (stp in FIGURE 3O, stamen traces and scars not shown in the receptacle).

In the base of the ovary, at a level slightly above the insertion of the filaments, the tips of numerous small, recurved, procambial strands (peri) are encountered in the cortex. When followed upward these can be seen to branch or anastomose to a slight extent before connecting with conspicuous large reflexed bundles which originate from the receptacular stele at the base of the gynoecial supply (FIGURE 3G-I). Although most of this peripheral system appears in the base of the ovary below the locules, some branches of it continue upward and end blindly in the ovary walls above the level of the locule bases (FIGURE 3J-L, O).



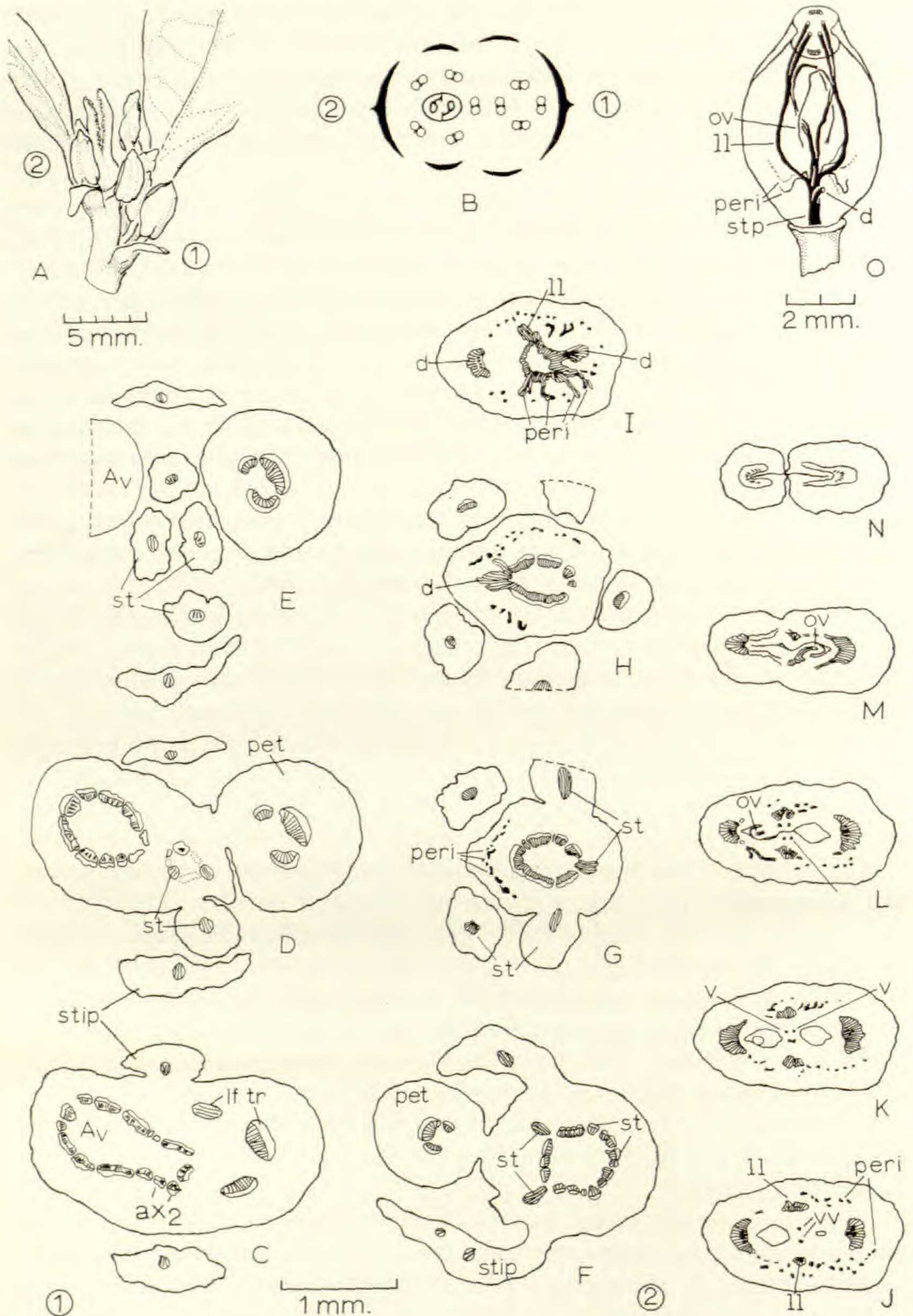


FIGURE 3. *Distylium racemosum*: A, tip of an inflorescence — group 1 is a subterminal staminate flower, group 2 a terminal bisexual pseudanthium — note the stipulate leaves subtending each “flower”; B, diagrammatic representation of A; C-E, transverse sections through group 1 (slightly oblique); C, departing leaf and stipule traces — secondary axis developing; D, stamen traces developing in and departing from the secondary axis; E, stamen filaments in axil of leaf;



In the base of the ovary the receptacular stele is slightly elliptic in transverse sections, with its long axis in the plane of the dorsal bundles. From the median sides of the ellipse broad dorsal carpel bundles (d) depart, along with adjacent bundles of the peripheral system (FIGURE 3H, I). At a slightly higher level two compound lateral bundles (ll) organize on opposite sides of the stele in the transverse plane and diverge slightly toward the periphery (FIGURE 3I, J). The stele then constricts to form a narrow procambial cylinder at the base of the locules, which divides in the median plane to form two procambial compound ventral bundles (vv) in the base of the septum.

The dorsal bundles ascend in the ovary as broad vascular arcs. The compound laterals dichotomize transversely at about the level of ovule insertion near the top of the locules. The compound ventral bundles are not entirely developed at anthesis, and those portions which are present are entirely procambial. They appear to die out as they ascend in the base of the septum, but reappear at a slightly higher level as four individual ventral bundles (v, FIGURE 3J-L). This discontinuity in their development suggests that their differentiation proceeds both acropetally and basipetally in the developing septum. Near the top of the locules the ventrals approach and fuse with their adjacent lateral bundles (l), but the ventral bundle of each fertile margin branches just prior to fusion to provide a trace to the solitary ovule (ov).

The most striking features in the floral apparatus of *Distylium* are the extreme variation in the external morphology of the inflorescences and flowers, the foliar nature of the inflorescence bracts, the development of bisexual pseudanthia, and the curious system of vestigial vascular bundles, here referred to as the peripheral system, in the base of the ovary. The flowers of the genus have not previously been studied anatomically, but have been variously interpreted by systematic workers as polygamous, or as unisexual and monoecious, or as andromonoecious, with a variable number (0-6) of free and unequal sepals (or bracts, or bracteoles) inserted at different levels, an irregular number (2-8) of hypogynous stamens, and a superior ovary (Bentham & Hooker 1865; Baillon 1874; Niedenzu 1891; Harms 1930; Walker 1944; Vink 1957). The gynoecium of *Distylium* has long been considered a prime example of the superior ovary in a family generally characterized by half-inferior ovaries.

Hemsley (1907) described each of several flowers from two inflorescences of *Distylium chinense* Hemsl. in detail, and could find no uniformity in their organization, nor any way to differentiate between the various "bracteoles" and "sepals." He concluded that the flowers of

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F-N, transverse sections (slightly oblique) through group 2; F, stamen traces departing the stele; G, stamens separating — vestigial peripheral bundles appearing in the base of the ovary; H, carpel dorsal bundle and adjacent peripheral bundle departing the receptacular stele; I, several peripheral bundles and second dorsal bundle departing from the stele; J, base of locules — some peripheral bundles still evident; K, ovary — individual ventral bundles appearing; L-M, insertion of ovules; N, style bases; O, gynoecial vasculature as seen in a cleared ovary (semi-diagrammatic).



the genus are functionally either male or female, but never hermaphrodite. Walker (1944) states that "the variations in the floral parts between one species and another are so little, or so inconsistently variable that they are of scant use in differentiating species . . ." "It is often difficult to determine whether flowers are unisexual or bisexual, because there may be found stamens and pistils of all degrees of development even in the same inflorescence."

Vink (1957) noted that the floral bracts of *Distylium stellare* most often occurred in threes and sixes, and that the middle bract of a group of three sometimes was leaf-like in appearance, while the two lateral bracts were always more or less lanceolate in shape. Since the leaves of the genus are stipulate, he interpreted the bracts as reduced stipulate leaves, and concluded that the flowers of *Distylium* are asepalous, as well as apetalous. His is the only interpretation of the inflorescence bracts which is supported by the anatomical evidence. He also observed that distal flowers are often merged in twos, forming "twin flowers" at the tips of the inflorescences.

Croizat (1960, 1964) rejects any conventional explanation for the inflorescence bracts and floral organization of *Distylium*, considering the flowers of the genus exemplary of his proposed transitional stage of "flower making" between a unisexual amentiferous inflorescence and a bisexual angiospermous flower. He considers the unisexual flower and inflorescence primitive, and derives the bisexual flower through the "sexualization into maleness" of pistillate flowers by the *de novo* origin of stamens on scales (the "sepals," "bracts," "bracteoles" of *Distylium*) subtending the pistils. These stamens supposedly assume the functions of the male inflorescences which are then suppressed. However, I find no evidence in my material of a unisexual staminate inflorescence of the type figured by Croizat (1960, p. 296, *fig. 36A*). The "twin flowers" mentioned by Vink are interpreted by Croizat (1960) as "Scales ("carpels") originally arranged to establish two separate floral structures . . . here rearranged to establish one only, thus factually marking the final transformation of an inflorescence into a single flower." Morphologically and anatomically, "twin flowers" are nothing more than two bisexual pseudanthia, one terminal the other subterminal, closely associated at the tip of an inflorescence. Each is subtended by a trimerous bract group, stamens of both are inserted between the two pistils, and vestigial peripheral bundles are present in both ovaries. Although Croizat was correct in his interpretation of the pseudanthial nature of some "flowers" in *Distylium*, the evidence now available contradicts his views concerning the method of their derivation.

2. *Sycopsis* D. Oliver.<sup>2</sup> Trans. Linn. Soc. London 23: 83. 1860.

FIGURES 4E-F, 5, 6.

An Asian genus of evergreen shrubs or trees containing about nine species ranging in distribution from Assam through Southeast Asia and

<sup>2</sup> The generic name is derived from the Greek *sykos*, for fig, and *opsis*, meaning



the Malay Archipelago to New Guinea. *Sycopsis sinensis* Oliv. has the most northerly distribution, occupying a broad east-west band across seven provinces of central China, while *Sycopsis dunnii* Hemsl. has a very broad southern distribution from southern China southward to Sumatra and eastward to the Philippines and New Guinea. The other seven species have relatively restricted distributions. Prominent among them are *S. griffithiana* Oliv. in Assam and possibly Yunnan, *S. laurifolia* Hemsl. in Yunnan, *S. tutcheri* Hemsl. in Kwangtung (Hong Kong) and Hainan, and *S. salicifolia* H.-L. Li in Walker, in Hainan.

Only *Sycopsis sinensis* is well known in cultivation, and it has recently been shown to be interfertile with *Parrotia persica*, although the hybrid,  $\times$  *Sycoparrotia semidecidua*, is apparently sterile (Endress & Anliker 1968).

The following descriptions are based primarily on flowers and inflorescences from cultivated plants of *Sycopsis sinensis*, and from herbarium specimens of *S. dunnii* and *S. laurifolia*, but available specimens of the several other species were also examined morphologically.

**MORPHOLOGY:** The inflorescences of *Sycopsis* are short, axillary or terminal panicles, spikes or heads. The congested spikes or heads of *Sycopsis sinensis* (FIGURE 6N) and *S. griffithiana*, with each flower enclosed by a broad, densely dark-brown-hirsute primary bract, differ significantly from the short open spikes or racemes of *S. dunnii* and related species, with flowers subtended by unilaterally inserted trimerous groups of small bracts (see FIGURE 4E-H). Secondary bracts are generally absent in the inflorescences, but one or two may occur flanking a basal flower, either free or partially adnate to the hypanthium.

The axillary or terminal flowers are sessile to subsessile, asepalous (Vink 1957) and apetalous, and appear to be andromonoecious (I have found no evidence of strictly pistillate flowers that would substantiate the interpretation of polygamous inflorescences encountered in the systematic literature). Staminate flowers contain 3 to 7 stamens in *Sycopsis dunnii*, and (5-)7 to 10 in *S. sinensis*, inserted perigynously in a single cycle on the rim of a rudimentary, hirsute, naked (*S. dunnii*) or irregularly toothed and lobed (*S. sinensis*, FIGURE 7A) hypanthium, around a minute abortive ovary. At anthesis the stamens become strongly exerted, with elliptic to ovate (*S. dunnii*, *S. laurifolia*) to distinctly oblong (*S. sinensis*), 2-celled anthers containing four pollen-sacs, and dehiscing by means of lateral longitudinal slits which are simple above, but ventrally subvalvate below. The anther connective is produced as a short, blunt point. Bisexual flowers contain a 2(-3)-carpellary, superior to slightly semi-inferior ovary, surrounded by an urceolate to subglobose hypanthium which, in *Sycopsis dunnii* and related species, bears irregular bracts or bract groups (the bracteoles and sepals of most authors) in-

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likeness (Rehder 1954). Oliver (1860, p. 83), in his original description, states that "the young subobovate fruits, narrowed and (from drying?) more or less sulcate below, together with the general appearance of the plant, recall some of the narrower-leaved species of East Indian *Fici*."





FIGURE 4. *Distylium racemosum* and *Sycopsis dunnii*: A-C, *Distylium racemosum*; A, maturing inflorescence, stamens absent — note terminal functional ovaries and a few axillary abortive ovaries; B, pistil of subterminal pseudanthium re-



served unilaterally at its base, at various levels on its outer surface, and on its often oblique rim. But in *S. sinensis* and *S. griffithiana* there are no unilaterally inserted bract groups, and the level to oblique hypanthium rim bears a single cycle of (4–)5 to 7 irregularly lobed to incised tepals which are basally connate into a tube above the rim (cf. FIGURES 5A and 6A). Three to seven stamens are present in the bisexual flowers of *S. dunnii*, while 8 to 9 stamen scars could be counted on the hypanthium in the post-anthesis flowers of *S. sinensis* which I examined. The long styles are spreading (*S. dunnii*) to spirally curved (*S. sinensis*). A single ovule or seed occupies each locule. In inflorescences of *Sycopsis dunnii* and *S. laurifolia* it appears to me that only the terminal ovary (i.e., in the terminal bisexual flower) on each inflorescence axis is functional. The lateral and subterminal flowers on each axis are staminate through reduction of the ovary. A staminate flower, or an abortive sterile flower, is usually axillary to the bract group at the base of the terminal flower, and stamens may also be axillary to the bract group inserted at mid-height on the hypanthium (FIGURES 4E–H, 5A, C). In *S. sinensis* the ovary of each bisexual flower in the spike may be functional.

The morphological differences between *Sycopsis dunnii* and *S. sinensis* are sufficient to place their congeneric relationship in question. Consequently, the vascular anatomy of both species is considered here.

**ANATOMY OF SYCOPSIS DUNNII:** Terminal flowers with functional ovaries, associated bracts, and in some cases abortive subterminal flowers, taken from herbarium specimens (*Steward & Cheo*, 165, 170, 199[A]; also *S. laurifolia*, *A. Henry*, 11365[A]), were sectioned or cleared. The flowers are variable in their organization with regard to the level of insertion of the bracts, and in the number of bracts (0–2) and stamens on the rim. Relatively few flowers of either species were available for sectioning, and the vascular organization of individual flowers differs with their morphological organization. The flowers of *S. laurifolia* appear to agree in general with those of *S. dunnii*.

The vascular supply to the trimerous bract groups subtending the lateral staminate flowers and the terminal bisexual flowers is similar to the nodal anatomy typical of the foliage leaf, i.e., three traces derived from three gaps, supplying the central reduced leaf blade, with a trace supplied to each stipule by the adjacent lateral leaf trace. The vascular supply to the three bracts mounted on the side of the hypanthium may be similar to the typical pattern or represent a reduced modification of it, ultimately consisting of three separate traces, each of which supplies only one bract. The modifications of the vascular supply to the bracts are similar to those described above (FIGURE 2) for *Distylium*. The

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duced to a single carpel; c, subterminal pistil abortive; d, three-carpelled terminal pistil — note protruding adnate organ. E–H, *Sycopsis dunnii*; E, maturing inflorescence, stamens absent — note trimerous bract groups on flanks of hypanthia; F, subterminal flower almost fully developed, probably functionally staminate; G, subterminal flower abortive and sterile; H, subterminal flower reduced to a bristle-like appendage (ab fl) adnate to the hypanthium.



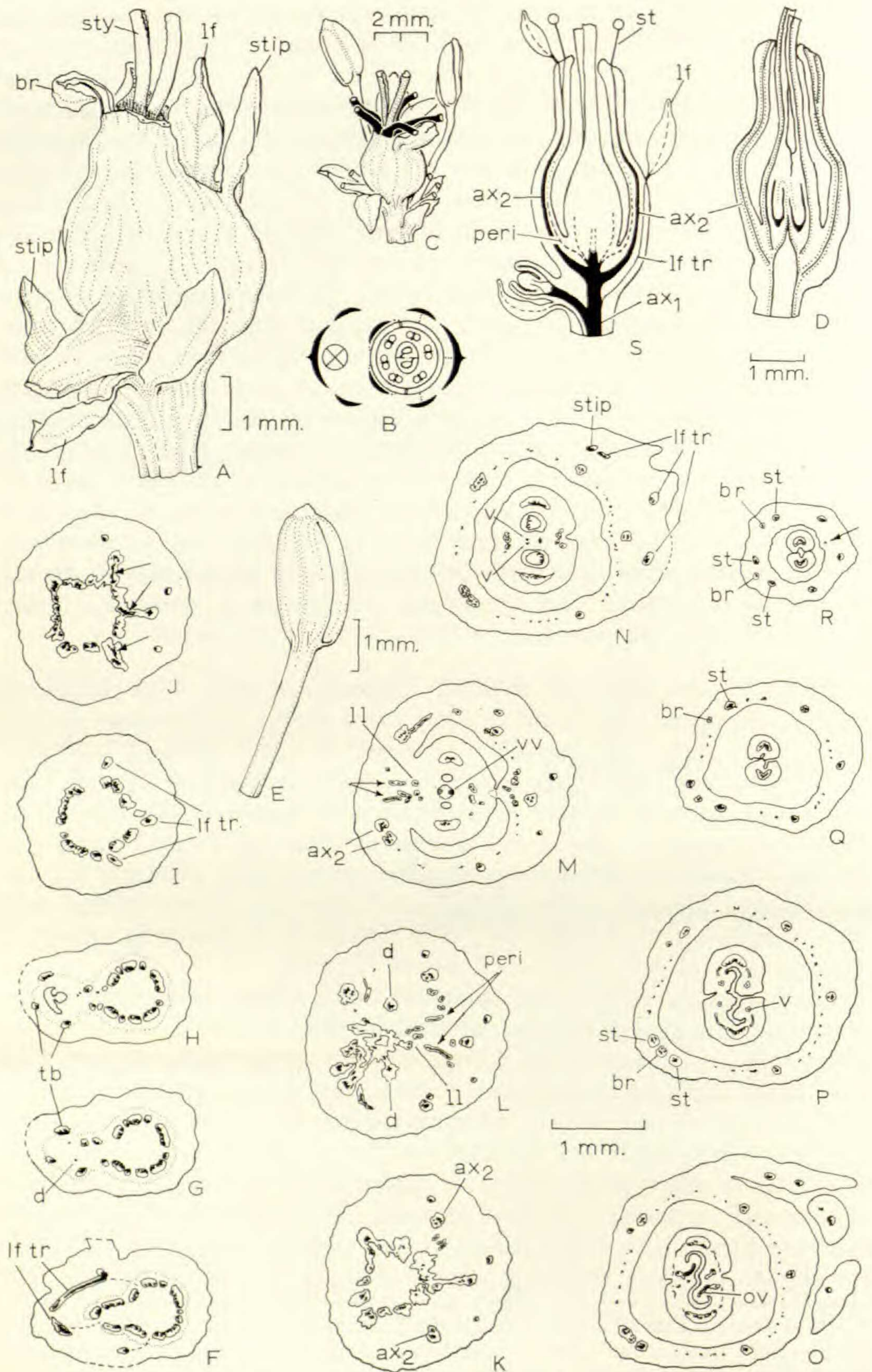


FIGURE 5. *Sycopsis dunnii*: A, view of a terminal bisexual flower and subterminal abortive sterile flower (post-anthesis); B, floral diagram; C, view of an inflorescence tip at anthesis, with two subterminal staminate flowers beneath the



traces supplying bract groups inserted on the side of the hypanthium originate from the peduncular stele well below the departure of the main vascular supply to the hypanthium, and ascend in the parenchymatous tissue near the outer surface of the hypanthium, entirely apart from the remaining vasculature (FIGURE 5I-O). In one instance the trace to a solitary distal bract was discontinuous for a considerable distance in the upper portion of the hypanthium, possibly having been disrupted by elongation of the latter (a phenomenon noted also in *Fortunearia*).

The vascular supply of a single trace to each of the bracts inserted on the rim of the hypanthium is derived within the hypanthium from narrow secondary vascular cylinders or trunk bundles which also supply the stamens and constitute the main vascular supply to the hypanthium. The major supply to the hypanthium develops from the peduncular stele well below the base of the ovary (about 600 to 700 micra below the base of the locules in the sectioned flower of FIGURE 5), where as many as seven large collateral bundles diverge on as many radii into the cortex (FIGURE 5J-L). Immediately behind each of these, and from a slightly higher level as seen in transverse sections, one to three small branches from adjacent bundles bend outward (FIGURE 5J, arrows) and take up positions on the adaxial side of the larger bundle, where they remain distinct through almost the entire length of the hypanthium, uniting with the larger abaxial portion only as the rim is approached and the strands consolidate to form a stamen trace. In transverse sections it appears that the phloem accompanying the small adaxial xylem strands is oriented laterally to adaxially, so that the aggregate of vascular strands in each group then varies in appearance from a narrow, more or less continuous to discontinuous ring of xylem strands with associated external phloem, as in a narrow stele, to two opposing tangential narrow bands of xylem with phloem on the abaxial face of the outer band, and on the adaxial face of the inner band. In some flowers a relatively substantial vascular cylinder occurs in the hypanthium, originating from the peduncular stele approximately in the transverse plane of the ovary (and in the plane of the two-ranked bracts), and ascending to supply traces to bracts and stamens on the rim (FIGURE 5M-R).

From the bases of these trunk bundles and secondary steles lateral

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terminal bisexual flower; D, longitudinal median section (semidiagrammatic) of a maturing terminal flower (bracts are out of the plane of section); E, stamen; F-H, sections through the abortive subterminal flower; F, leaf traces and developing secondary stele; G, bundles of abortive hypanthium and carpel dorsal bundles; H, fragment of abortive ovary apparent; I-R, transverse sections through receptacle and terminal flower; I, three leaf traces departing the peduncular stele; J, K, minor secondary axes to the hypanthium leaving the stele; L, peripheral bundles forming on right side; M, base of locules — note larger secondary stele and peripheral bundles on left side; N, about middle of ovary — note stipule trace, distinct ventral bundles on left; O, ovule insertion — note bracts separating from the hypanthium; P, larger secondary axis in the hypanthium has divided into three smaller units; Q, R, upper levels of hypanthium and styles; S, diagrammatic representation of a terminal bisexual "flower" interpreted as a pseud-anthium.



branches are given off to either side near the base of the hypanthium. The branches move laterally and upward in the hypanthium, often branching and anastomosing with strands from adjacent bundles. In transverse sections these branches are situated randomly between the major bundles (FIGURE 5M-O). Much of this system dies away as it ascends (at least in the post-anthesis flowers examined), but in some cases a single bundle may persist to the rim of the hypanthium between and slightly adaxial to each pair of major bundles (arrow in FIGURE 5R), suggesting a vestigial supply to abortive stamens. I could find no anatomical evidence in the hypanthium suggesting the former presence of sepals abaxial to the stamens on the rim.

Above the departure of the major bundles to the hypanthium the remaining bundles of the peduncular stele shortly consolidate to form two dorsal carpellary bundles (d), a narrow receptacular stele which enters the base of the septum to form the compound ventral bundles (vv), and two diffuse groups of traces on either side of the receptacle in the transverse plane from which are derived the compound lateral carpellary bundles (ll) centripetally, and centrifugally a series of weak traces (peri) which diverge almost horizontally into the base of the hypanthium just beneath its separation from the ovary, and about 100 to 200 micra higher than the divergence of the major hypanthial bundles (FIGURE 5L, M, S). Within the base of the hypanthium these traces, in association with some minor strands derived from branches of the main hypanthial system, form an irregular ascending, branching, and anastomosing system of bundles in the parenchyma just within the adaxial face of the hypanthium, to either side of the ovary in the transverse plane (FIGURE 5M-P, S). This system also gradually dies away as it ascends. The vascular supply to the hypanthium, therefore, consists of two independent sets of traces derived from different levels in the receptacular stele.

The ovary often appears to be fused with the hypanthium to a slightly higher level on the transverse side which bears the distal bracts (cf. FIGURE 5M). Within the pistil the compound lateral and compound ventral bundles divide in the upper half of the ovary to form distinct laterals and ventrals which fuse at the level of ovule insertion. A single ovular trace departs from the ventral of each fertile margin just prior to its fusion with the lateral (FIGURE 5O).

#### ANATOMY OF SYCOPSIS SINENSIS:

*Bisexual flowers.* Post-anthesis flowers from which the stamens had fallen were taken for sectioning from the lower half of inflorescences where there is less crowding of the flowers (cf. FIGURE 6N) and less likelihood of deformation of the receptacular vasculature.

A cylindrical pedicellar stele subtends the flower. In the receptacle 8 to 13 large bundles diverge sharply from the stele to enter the base of the hypanthium, in which they ascend more or less directly to the rim. Some of the bundles function only as traces to the shallow perigon tube and its irregular lobes, while others are trunk bundles supplying traces



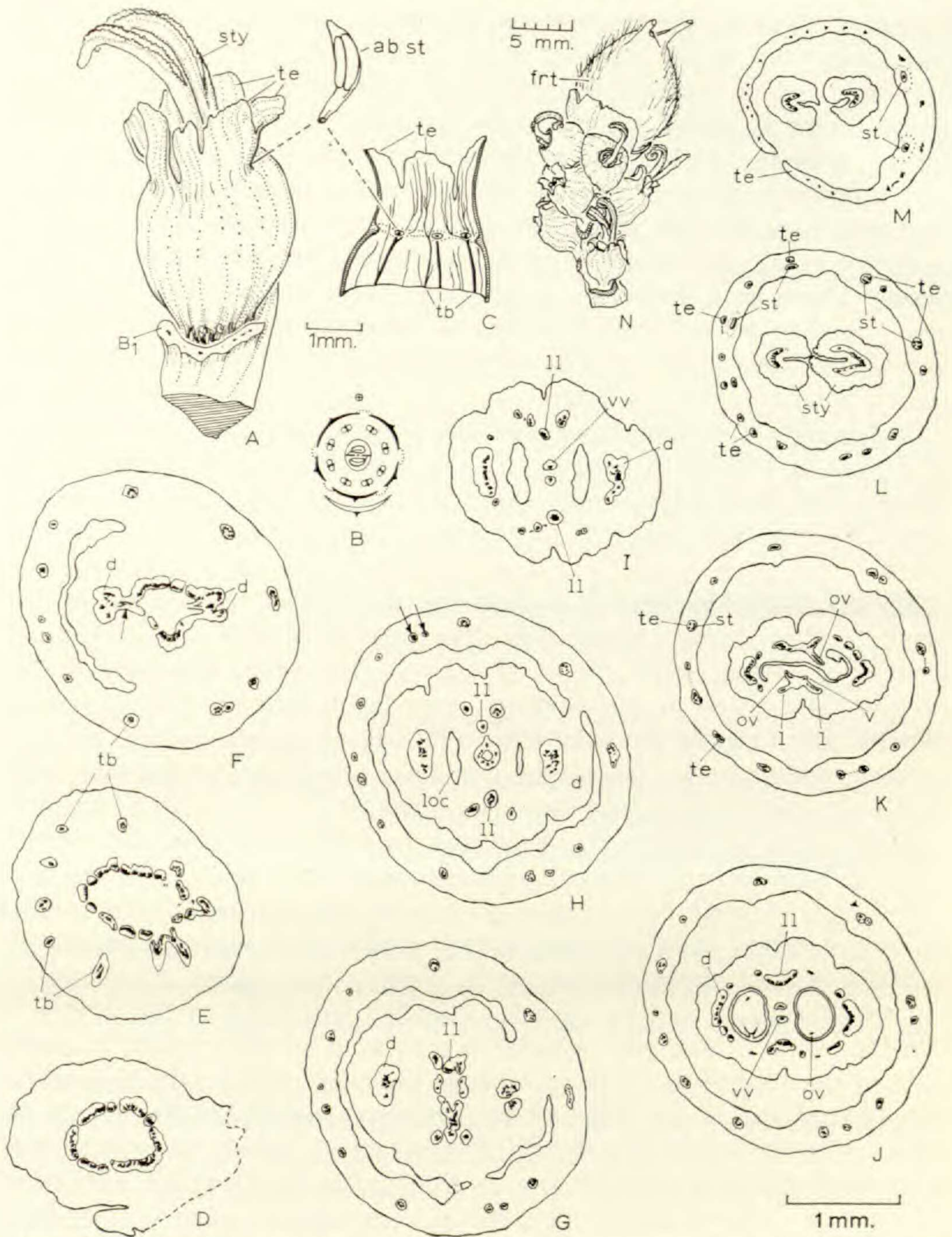


FIGURE 6. *Sycopsis sinensis* (bisexual flower): A, post anthesis flower — note irregular lobing of the perianth tube, one sterile stamen shown; B, floral diagram; C, drawing from cleared portion of the mature hypanthium showing perianth lobes, stamen scars, trunk bundles, irregular vasculature of the lobes; D-M, transverse sections of post-anthesis flower; D, pedicellar stele and base of primary bract; E, receptacle — note departing hypanthial trunk bundles and part of receptacular stele; F, base of ovary, carpel dorsal bundles forming; G, base of ovary, compound lateral bundles forming; H, base of locules — note residual receptacular stele in base of septum; I, slightly above locule bases — note compound ventral bundles; J, mid-height in ovary; K, insertion of the ovules; L, formation of tepal and stamen traces in hypanthium; M, insertion of stamens on the hypanthium rim; N, fruiting inflorescence, only terminal flower in fruiting condition — note splitting hypanthium.



to both stamens on the rim and to the tepals. At various levels in the hypanthium the trunk bundles may produce single lateral branches which function as dichotomizing traces to the perigon (cf. FIGURE 6C), but branching is sparse within the hypanthium. I could find no regular patterns in either the lobation of the perigon, or in its vascularization.

In transverse sections some of the hypanthial bundles are collateral, while others, particularly the trunk bundles, are somewhat variable, often appearing as narrow vascular cylinders as in the hypanthium of *Sycopsis dunnii*. There is no evidence, however, of the two systems of numerous minor bundles derived from branches of the trunk bundles and from the receptacular stele in the vicinity of the developing compound lateral carpellary bundles, as in *S. dunnii*.

Occasionally a discontinuous vascular bundle, such as those indicated by arrows in FIGURE 6H, appears in the hypanthium. In this particular instance the larger bundle was about 500 micra long, while its smaller companion was only about 80 micra long. Both ended blindly above and below.

Slightly below the level of stamen insertion many, but not all, of the trunk bundles divide tangentially. The adaxial branch (st) enters the base of a stamen, while the outer branch (te) enters the base of the perigon tube, where it dichotomizes irregularly, forming 2 to 3 smaller bundles which supply the tepal lobes (FIGURE 6C, K-M).

Above the departing hypanthial bundles a prominent receptacular stele continues upward for a short distance (about 200 to 350 micra in the post-anthesis material examined), becoming broadly elliptic in the median plane in transverse sections as the dorsal carpellary bundles (d) organize and depart. As each dorsal moves away from the stele one or two median or lateral traces from it bend sharply inward and return almost horizontally toward the stele (arrow in FIGURE 6F), where they are incorporated into a smaller vascular cylinder remaining at the center of the receptacle. From this cylinder two to four bundles depart on either side in the transverse plane to take up positions in the bulging walls of the exocarp and on the edges of the septum as lateral bundles (l) or diffuse compound lateral bundles (ll, FIGURE 6G-I). Their departure leaves two small opposing vascular arcs in the median plane which consolidate to form a narrow, largely procambial receptacular cylinder containing several strands of protoxylem in the base of the septum (FIGURE 6G-H). At the base of the locules the hypanthium is essentially free from the superior ovary, and the major bundles of both are apparent in transverse sections.

Within the ovary the dorsal bundles are relatively massive and occupy prominent dorsal bulges in the carpel walls. In the bundle groups at either edge of the septum the central bundles function as the compound laterals, while the lateral bundles move outward into lateral bulges and eventually ramify and anastomose into the vascular networks of the carpel walls. The narrow receptacular cylinder in the base of the septum shortly divides to form two compound ventral bundles which ascend unbranched



to the base of ovule insertion where each dichotomizes. The distinct ventrals thus formed then fuse with adjacent distinct lateral bundles. The ovule traces are supplied from the ventrals just prior to fusion (FIGURE 6J, K). In some ovaries it appears that the ventral bundle of the fertile margin goes entirely to the ovular funiculus, free of any connection to the adjacent lateral bundle, but such connections may form later in the ontogeny of the ovary. The marginal ventral bundles in each style soon become associated with the dorsal bundle to form a vascular arc, rather than three distinct bundles (FIGURE 6L, M).

*Staminate flowers.* The hypanthium is strongly reduced, and the gynoecium rudimentary in the sessile staminate flowers (FIGURE 7A). The shallow, membranaceous perigon tube which projects above the rim of the hypanthium is irregular in its lobing and vascularization. The lobes bear long dark-brown stellate hairs on their distal margins. The tepals indicated in the floral diagram (FIGURE 7B) correspond to the lobes of the perigon tube as they appeared in the sectioned flower illustrated.

A well organized pedicellar stele was present in some, but not all of the specimens examined. A reduced pedicellar stele may be present only as a lobe of the peduncular stele on the lower side of the flower, while on the upper side the bundles to the receptacle originate from the margins of a gap in the peduncular stele.

In the receptacle of the flower the entire stele is incorporated into 9 to 12 large bundles, most of which enter the hypanthium (FIGURE 7C-E). In the median plane two dorsal carpel bundles (d) are derived either from a single bundle of the stele, or by the fusion of 2 to 3 traces from adjacent hypanthial bundles (FIGURE 7E, F). No compound ventral or lateral carpel bundles are formed, but there is frequently the appearance of vestigial traces to such bundles in the form of protoxylem strands which bend inward from the bundles in the receptacle at the level of dorsal bundle formation.

The ascending bundles in the shallow hypanthium may remain entire, or give rise to one or two lateral branches which eventually supply the perigon tube (FIGURE 7H). The trunk bundles, situated on the radii of the 7 to 10 stamens, branch just below the insertion of the stamens to produce a large adaxial stamen trace (st), and a smaller abaxial trace (te) which enters the perigon tube, where it may divide irregularly and supply branches to a tepal. A few (1 to 3) bundles in the hypanthium divide at about the level of stamen insertion to provide traces to the perigon only. There was no correlation between the number of bundles in the hypanthium and the number of stamens on its rim in the flowers examined.

In *Sycopsis*, as in *Distylium*, it becomes difficult to distinguish between flower and inflorescence. The flowers, especially, present problems of interpretation and nomenclature, particularly the tubular structure surrounding the ovary and bearing the stamens. This has been termed an urceolate receptacle (Harms 1930; Tong 1930; Walker 1944; Vink 1957), a hy-



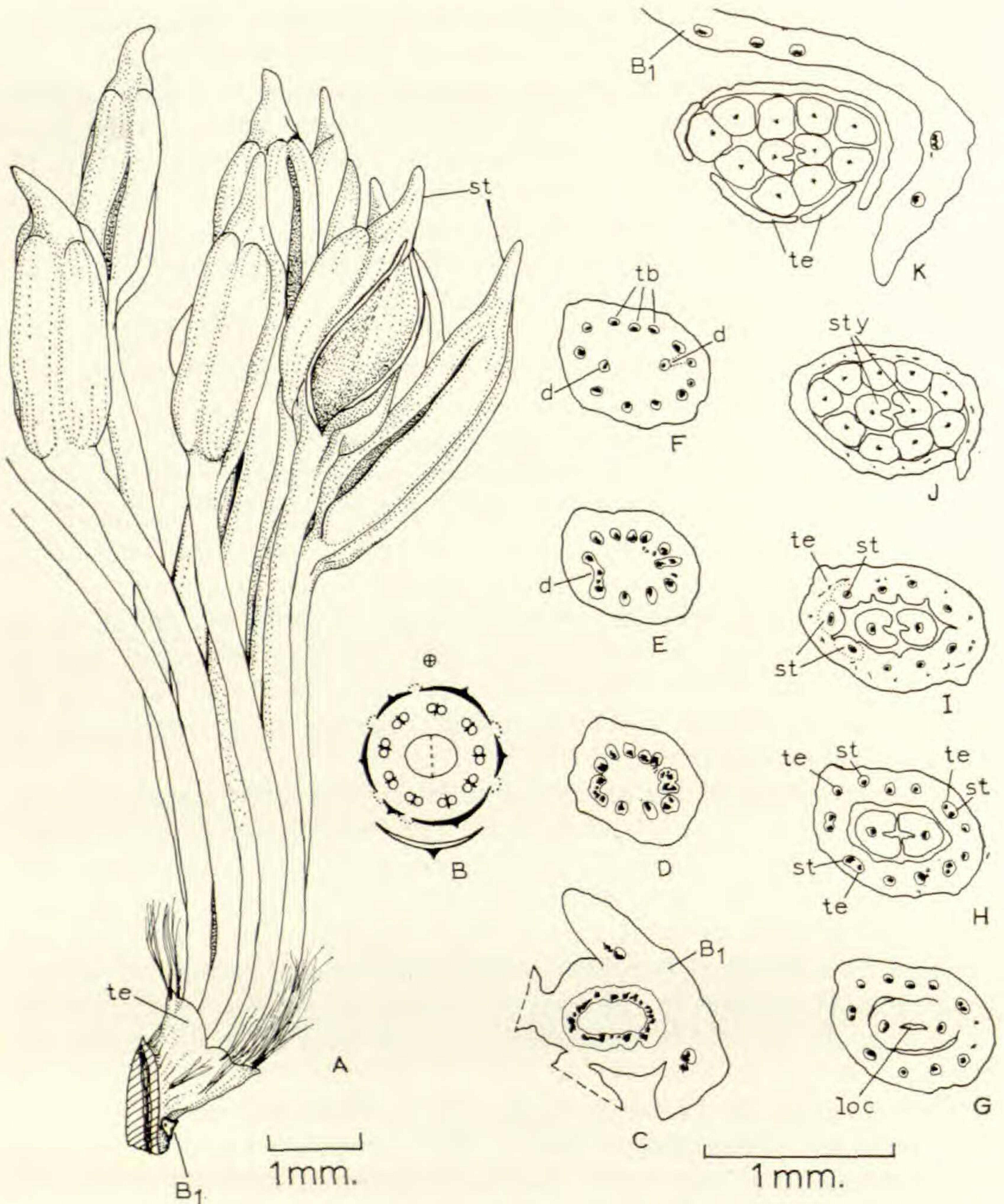


FIGURE 7. *Sycopsis sinensis* (staminate flower): A, flower at anthesis — note irregularly lobed syntepalous perianth; B, floral diagram; C-K, transverse sections of a flower at anthesis; C, pedicellar stele and primary bract (bract omitted in figures D-J); D, expanding pedicellar stele; E, receptacle — note developing carpel dorsal bundles; F, receptacle — note hypanthial trunk bundles and carpel dorsals; G, rudimentary, unilocular ovary and separating hypanthium; H, hypanthial trunk bundles dividing to form perianth and stamen traces; I, insertion of stamens on hypanthium; J, through the perianth tube, filaments, and styles; K, separation of some tepals and upper portion of the primary bract.

panthium bearing calyx lobes (Endress & Anliker 1968, ref. *S. sinensis*), or a calyx tube with short lobes (Oliver 1860; Niedenzu 1891).

The nature of the perianth has also proved problematical. Hemsley (1907), in his original descriptions and illustrations of *Sycopsis dunnii*,



*S. tutcheri*, and *S. philippinensis* (= *S. dunnii*), clearly indicates the unilateral insertion, variability in number, and morphological similarity of the "bracteoles" of the inflorescence and the "sepals," counting as the latter the 1 to 3 bracts occurring on the hypanthium rim. The variability in the numbers of sepals is also evident in the species descriptions in Walker's (1944) revision of the genus. Vink (1957), in his comparative notes on the flowers and bracts of *Distylium stellare* and *Sycopsis dunnii*, concluded that the flowers of *Sycopsis* are also asepalous, and that the usually trimerous bract groups at the base, sides, and rim of the urceolate hypanthium are actually reduced stipulate leaves. The vascular supply to the bract groups, described above, clearly indicates that his interpretation is correct, at least for *S. dunnii* and *S. laurifolia*. The foliar nature of the tepals of *Sycopsis sinensis* and *S. griffithiana* is not so clear cut, however. In these species the 5 to 7 tepals are inserted in a single cycle on the rim of the hypanthium, projecting beyond the rim as an irregularly lobed and fused perigon tube. Oliver (1861), in his original description of the genus, based on *S. griffithiana*, states of the perianth "it is doubtful how far the lobation and degree of obliquity of the calyx limb is constant." He later (1890) described the perianth of *S. sinensis* as "calycis tubo irregulariter fisso." Vink's interpretation of the bracts of *S. dunnii* does not appear directly applicable to the markedly different perianths of these two species.

Interpretations of the sexual condition of the flowers have varied. Oliver described the flowers of *S. griffithiana* as unisexual through abortion, and questioned whether they were ever hermaphrodite. Walker found the flowers of the genus to be "unisexual and monoecious or andromonoecious," while Vink considered them "polygamous monoecious." In cultivated specimens of *Sycopsis sinensis* Endress (Endress & Anliker 1968) found only bisexual and staminate flowers (i.e., andromonoecious). He observed that the buds of all flowers are bisexual, and that the stamens develop in all flowers, but that the ovary is abortive in many. The pistillate flowers reported in the literature actually represent bisexual ones from which the stamens have fallen. He also found that inflorescences terminal on short or long shoots contained mostly bisexual flowers, with only one or two basal staminate flowers, while inflorescences from lateral buds were in many cases entirely staminate and soon deciduous.

Stamen development is often irregular in bisexual flowers of *Sycopsis sinensis* with several stamens abortive. This condition has also been noted in *S. griffithiana* by Oliver (1860), and in the generic description by Vink (1957, presumably for *S. dunnii*). Walker noted that the hypanthium does not develop and enlarge with the fruiting ovary, as do the hypanthia of other genera of the family, but splits irregularly almost or quite to the base, forming a shallow 2- to 3-valved cup around the base of the mature fruit (FIGURE 6N, terminal fruiting flower). In *S. laurifolia*, however, as in *Sinowilsonia*, the hypanthium does appear to develop with the fruit, forming a thin papery urceolate covering which ruptures only as the woody capsule within springs open.



The morphology and anatomy of *Sycopsis dunnii* and *S. laurifolia* indicate that their floral apparatus is rather specialized. Such morphological features as the open spicate to paniculate inflorescences; the terminal position of the functional ovaries; the reduction of lateral flowers to a staminate condition; the form and dehiscence of the anthers; the absence of tepals; the presence of reduced or modified stipulate leaves as the bracts of the inflorescence; and the crowding out of subterminal lateral flowers through the failure of internode elongation, all suggest a relatively close relationship to the genus *Distylium*.

The complex structure of the hypanthium in *Sycopsis dunnii* and *S. laurifolia* is indicated by such anatomical features as the presence of leaf traces, independently derived from the peduncular stele, supplying the bracts on the side of the hypanthium; the presence in some flowers of secondary vascular cylinders supplying bracts and stamens on its rim; and the two complex systems of minor peripheral bundles or trunk bundle branches in its base.

The accumulated evidence suggests that the hypanthium in *S. dunnii* and *S. laurifolia* may consist of foliar, axial, and floral tissues attributable to bracts and staminate flowers of subterminal nodes, which, through condensation of the inflorescence axis, have developed upwards and fused into a tube around the naked ovary of a terminal pistillate flower. If this interpretation is correct it would appear that, as in *Distylium*, only naked unisexual flowers are present in the inflorescence, with the staminate flowers incorporated into the hypanthium around the pistillate flower, forming a bisexual pseudanthium. The hypanthium is thus neither "appendicular" nor "receptacular" (cf. discussion of these terms in Eames, 1961, p. 249, 250). It is suggestive of the syconium of *Ficus*, but differs both morphologically and anatomically (cf. Condit 1932). The term hypanthodium may be appropriate for it (see footnote 1). The ultimate fate of the hypanthium as an outgrown, ruptured structure at the base of the fruit further suggests that it is not an intrinsic part of a bisexual, perigynous flower. The exceptional behavior of *S. laurifolia* in this respect should be investigated. The vestigial peripheral bundles in the receptacles and ovaries of *S. dunnii* and *S. laurifolia*, although suggestive of the peripheral bundles in the ovary of *Distylium*, are less numerous and more localized in their origin from the receptacular stele and do not persist in the base of the ovary. Their direct contribution to the hypanthium suggests that they may represent the vestigial supply to subterminal lateral organs squeezed out in the condensation of the axis and no longer apparent morphologically, but possibly incorporated into the hypanthium. I have attempted to express this interpretation of the pseudanthium of *Sycopsis dunnii* diagrammatically in FIGURE 5s.

*Sycopsis sinensis* and *S. griffithiana* differ strongly from the other species of the genus in the morphology of their inflorescences and flowers, particularly in the absence of obvious reduced stipulate leaves or bract groups associated with the flowers, and the disposition of the tepals in a single cycle on the hypanthium rim. However, the two groups of species show



some similarity in their leaf form, and in the possession of urceolate hypanthia which are ruptured by the developing fruit. Anatomically, *S. sinensis* differs from *S. dunnii* in the absence of prominent secondary vascular cylinders and of the two minor bundle systems in the hypanthium. Vink's interpretation of the inflorescence bracts of *S. dunnii* would apply to *S. sinensis* only if one hypothesizes that, through a process of continued inflorescence reduction and further modification of the floral apparatus, terminal bisexual flowers such as those seen in *S. dunnii* become the axillary, sessile, apparently bisexual flowers of *S. sinensis*, with the inflorescence bracts localized in a cycle on the hypanthium rim in each flower. The irregular number and form of the tepals, the irregular number, insertion, and development of the stamens, and the irregular vascular supply to the hypanthium, perianth, and androecium might tend to support such an interpretation. But a better alternative lies in the fact that *Sycopsis sinensis* is closer morphologically to *Parrotia persica*, even though the two species differ strikingly in their leaf form, and in the degree of development of their hypanthia. The existence of morphologically intermediate first generation hybrids between them, in conjunction with the morphological and anatomical differences separating *S. sinensis* and *S. dunnii*, strongly suggests that the two groups of species in *Sycopsis* are not congeneric.

3. **Parrotia** C. A. Meyer, Verz. Pfl. Caucasus 46. 1831      FIGURES 8, 9.

A monotypic genus, containing only *Parrotia persica* (DC.) C. A. Mey., a species of small (ca. 5 m.) shrubby trees forming the characteristic arborescent component of the moist deciduous forest on the south shore of the Caspian Sea in northern Iran, where it is endemic. Its leaves are rather similar in appearance to those of *Parrotiopsis*, *Fothergilla*, and *Hamamelis*, often becoming brightly colored in the fall.

**MORPHOLOGY:** The inflorescence of *Parrotia* ( $n = 12$ , Pizzolongo 1958) consists of 2 to 8 small, inconspicuous, perfect or staminate flowers clustered in a terminal or axillary, involucrate, bracteate head. Staminate flowers, when present, are usually basal in the head, and result from reduction of the ovary. The flowers are sessile in the axils of large, broad, primary bracts ( $B_1$  in FIGURE 8A) which are similar to the primary bracts of *Sycopsis sinensis* in their dark-brown, stellately pubescent abaxial surfaces and glabrous adaxial surfaces. The primary bracts become sharply reduced upward in the inflorescence, and secondary bracts are generally absent.

The perianth consists of a perigon of 5 to 9 (to 10, according to Endress, 1968) green tepals which are irregular in width and length, and bear long, dark-brown, silky tufted hairs at their tips. The tepals are inserted with the stamens on the rim of a shallow hypanthium. Above the hypanthium rim the tepals may be free or irregularly connate and lobed. Ten to fourteen (8 to 15) stamens are inserted irregularly on the hypanthium rim in no particular order with regard to the tepals. The stamens are similar



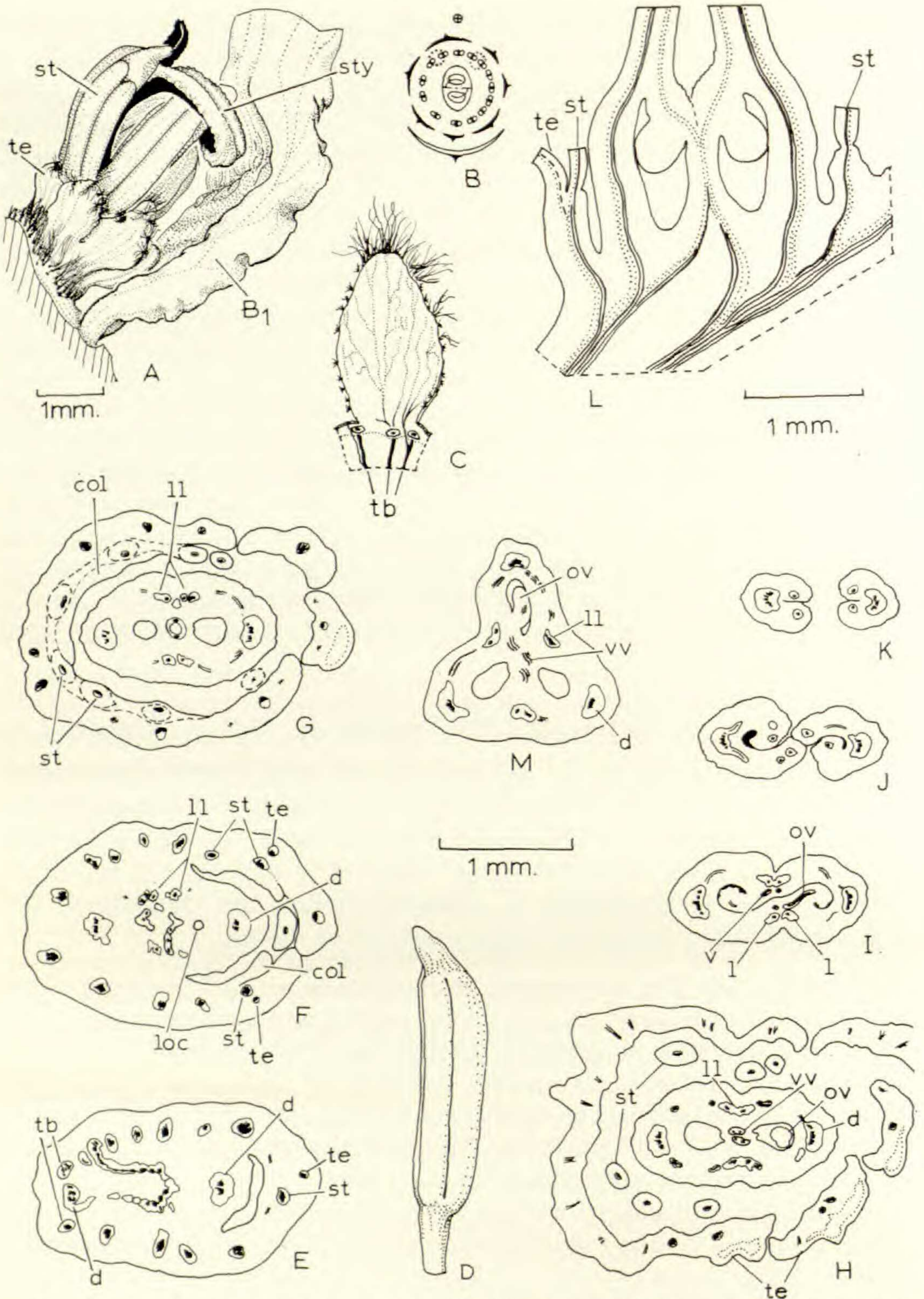


FIGURE 8. *Parrotia persica*: A, view of a flower at anthesis; B, floral diagram; C, drawing from a cleared segment of a hypanthium — note stamen scars, trunk bundles, irregular vascular supply to the tepal; D, stamen; E-K, transverse sections (slightly oblique) of a post-anthesis flower; E, through receptacle — note partially formed receptacular stele, and partial separation of the hypanthium; F, receptacle — note departing compound lateral bundles from the abbreviated receptacular stele; G, ovary near locule bases — note insertion of stamens and parenchymatous collar on hypanthium; H, mid-ovary — note perigon tube and



to those of *Sycopsis sinensis* in their strongly exerted, dark-red, linear-oblong anthers, each of which contains four pollen sacs and dehisces laterally by means of simple longitudinal slits. The anther connective is produced as a short apiculus (FIGURE 8D). On the inner edge of the hypanthium rim a number of small, vascularized, parenchymatous lobes, or a partial shallow collar, may alternate with or enclose the bases of the stamen filaments (col, FIGURE 8F, G). In the mature, non-fruiting flower the collar appears as a thickened and irregularly lobed ring of tissue on the rim, the protuberances of which suggest the abortive development of floral organs. (FIGURE 9A).

The hypanthium closely surrounds the base of a superior or nearly superior 2(-3)-carpellary ovary which is rudimentary at anthesis. The styles are long and recurved, with extensive papillate stigmatic surfaces along the length of their ventral faces.

In isolated instances tepals of *Parrotia* become quite leaf-like in appearance, with a petiole and short narrow blade (FIGURE 9A), and are similar in this respect to reduced stipulate leaves in the inflorescences of *Distylium racemosum* or *Sycopsis dunnii*. Furthermore, in a considerable number of flowers examined, particularly from the large tree in the Arnold Arboretum, but in other collections as well, aberrant carpels or bicarpellary ovaries have been observed in different positions around the functional ovary. These are inserted not on the receptacle, but on the inner face or rim of the hypanthium (FIGURE 9B, C). From 1 to 3 small ovaries of this type have been found on the hypanthium in single flowers, and in two or three flowers of the same inflorescence, occasionally developed to the point of containing rudimentary ovules. Sections of a flower containing two such ovaries are illustrated in FIGURE 9D-F, and their anatomy is briefly described below.

**ANATOMY:** A pedicellar stele may subtend some flowers, but is scarcely discernible beneath others in the material examined. In the latter case many of the bundles which function in supplying the hypanthium and gynoecium appear to develop almost directly from the margins of a large gap in the peduncular stele, or from a very short and longitudinally distorted cylinder of loosely arranged bundles which diverge from the gap.

In the receptacle, well below the base of the locules, 10 to 13 prominent bundles diverge from the pedicellar stele to enter the base of the hypanthium. Within the hypanthium the trunk bundles vary somewhat in the kind and numbers of organs they supply. In general, each trunk bundle divides just below the rim to supply one abaxial trace (te) to a tepal and another larger trace (st) to the base of a stamen (FIGURE 8E-G). Variations from this pattern include bundles which supply only a stamen, only a perianth lobe, or two closely set stamens and a perianth lobe. In some young flowers stamens have been found on the rim with no apparent vas-

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free tepals; I, ovary, through level of ovule insertion; J, through the style bases; K, through styles; L, median longitudinal section (semidiagrammatic) through a flower; M, transverse section through a tricarpellary ovary.



cular connection through the hypanthium between the base of the filament bundle at the level of insertion and the receptacular stele. The number of traces to the base of a particular perianth lobe varies with its breadth and with the number of stamens included within the width of its base. The trunk bundles may appear collateral in transverse sections, or occasionally as narrow vascular cylinders.

In addition to the bundles described above, lateral branches from the trunk bundles, largely procambial at anthesis, were observed to move adaxially within the hypanthium to end blindly at the base of the lobes of the shallow parenchymatous collar (col) on the inner edge of the rim. The significance of these traces is uncertain, but they could indicate the abortive development of stamens in these positions.

In the ovary at anthesis only the dorsal carpel bundles are apparent, usually as protoxylem strands. The septum and ovules are scarcely, if at all, developed. In the post-anthesis ovary the dorsal bundles are prominent, and develop in close association with the hypanthial bundles (FIGURE 8E, left side). The long internode apparent between the separation of the hypanthial bundles and the carpel dorsal bundles from the receptacular stele in *Sycopsis sinensis* is absent in the receptacle of *Parrotia persica*.

The compound lateral bundles (ll) originate from the receptacular stele in the transverse plane well above the departing dorsal bundles, and ascend as multi-stranded vascular bands at each edge of the septum. The central bundles in each band consolidate into a broad vascular arc in the upper half of the ovary. In polarized light two distinct protoxylem strands are apparent in each arc, indicating two adjacent lateral bundles. The individual lateral bundles separate at about the level of ovule insertion (FIGURE 8F-I).

Above the departure of the compound laterals the remaining portions of the receptacular stele consolidate to form a narrow and largely procambial cylinder. At about mid-height in the septum the cylinder divides in the median plane to form two largely procambial compound ventral bundles (vv, FIGURE 8H, M). The latter divide transversely just below the level of ovule insertion, and the individual ventral bundles shortly supply traces to the ovules, then fuse with the adjacent lateral bundles and pass upward as the marginal bundles of the styles (FIGURE 8H-K).

In the base of some ovaries examined a few small procambial bundles occur which are similar to the peripheral bundles in the base of the ovary of *Distylium*. They originate from the receptacular stele well above the departure of the hypanthial bundles and mainly in the vicinity or even from the base of the departing compound laterals. They are deflexed, and appear to end blindly near the periphery of the ovary base, near or just below the level of separation of the hypanthium from the ovary. Occasionally branches from such a bundle can be traced into and upward in the hypanthium, where they end blindly in or near the parenchymatous collar, and upward in the ovary wall above the level of their separation from the stele.



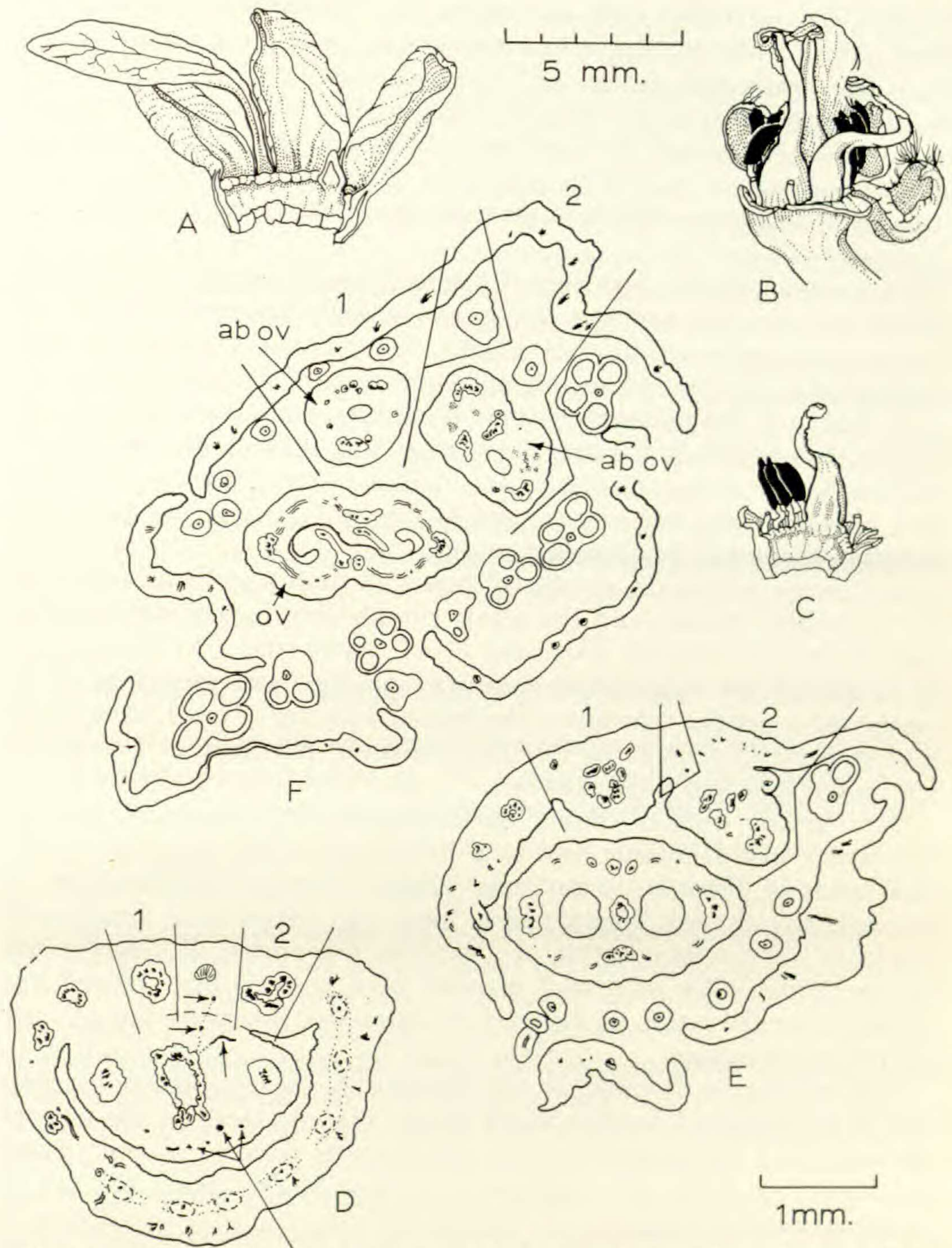


FIGURE 9. *Parrotia persica*: A, leaf-like tepal on hypanthium rim; B, whole flower, near tepals excised — note the single carpel (right) on the hypanthium, with suture directed outward; C, section of hypanthium from B, bearing the carpel; D-F, transverse sections through a flower bearing two anomalous ovaries on the hypanthium (slightly oblique); D, through base of functional ovary and hypanthium (above) — note the two steles in the hypanthium; E, ovaries and abaxial stamens and tepals forming on the hypanthium; F, areas of perianth and androecium supplied by each stele indicated as zones 1 & 2.

In those flowers containing anomalous ovaries on the hypanthium rim, anatomical study shows that a substantial vascular cylinder is pinched



off from the pedicellar stele and enters the hypanthium beneath each ovary. Most of the bundles in each cylinder are used up in supplying the ovary, but tepals and stamens adjacent and abaxial to the ovary on the rim also receive their traces from the cylinder. In FIGURE 9D-F the sectors (1 and 2) of the perigon and androecium supplied by two such steles are indicated. However, no regular pattern of insertion and vascular supply of tepals and stamens relative to the anomalous ovaries was apparent.

The morphological resemblances between *Parrotia persica* and *Sycopsis sinensis* are striking, and the description of the intergeneric hybrid  $\times$  *Sycoparrotia* confirms their close affinity. They are very similar in their capitate inflorescences; in the form and pubescence of the primary inflorescence bracts; in the pubescence, variable number, and extremely irregular form of their tepals; in the irregular number and insertion of the stamens, and the similar form, dehiscence, and reddish color of their anthers; in their essentially superior ovaries; and in the irregular vascular supply to the hypanthium and its attendant organs.

In *Parrotia persica* the number of tepals (5 to 10) and stamens (8 to 15) is usually greater, and the tepals considerably longer and broader, than in *Sycopsis sinensis*, which has 4 to 7 tepals and 5 to 10 stamens. In *S. sinensis* the hypanthium is longer, and the basal connation of its tepals into a perigon tube above the hypanthium rim is more pronounced than in *Parrotia persica*. In fruit the shallow hypanthium of *Parrotia* is not ruptured, as in *Sycopsis sinensis*.

But *Parrotia* exhibits certain morphological and anatomical features in common with *Distylium*, and to a limited extent with *Sycopsis dunnii*. The tepals of *Parrotia*, in particular, suggest varying manifestations of the reduced stipulate leaves which form the inflorescence bracts and "perianth" in the pseudanthia of *Distylium racemosum*, *D. gracile*, and *D. buxifolium*. The occasional presence of a reduced but obvious leaf blade among the tepals of *Parrotia* enhances this interpretation of their morphological nature.

Also striking in *Parrotia* is the presence in the receptacles of some flowers of peripheral bundles which supply branches both to the base of the ovary and the base of the hypanthium, as in *Sycopsis dunnii*. These are similar in origin and appearance to those of *Distylium*, but not as numerous or as strong.

On the basis of the available evidence it appears possible that the flower of *Parrotia persica* may represent a pseudanthium of a more advanced type than that seen in *Distylium*, developed through the complete reduction of an inflorescence axis, and resulting in the aggregation of reduced stipulate leaves (bracts) of subterminal nodes, and modified naked staminate flowers of suppressed lateral axes, around the functional ovary of the naked terminal pistillate flower. I have observed terminal and lateral pseudanthia approaching this level of reduction in some relatively reduced inflorescences of *D. gracile* and *D. buxifolium*. The union and elevation of the bracts and modified staminate flowers on the shallow



hypanthium may explain the variability in the number of bundles supplying the base of the hypanthium, and the variability in their form. The peripheral bundles of the receptacle may be attributable to suppressed lateral organs of the condensed inflorescence axis, and the appearance of abortive carpels or ovaries on the hypanthium in otherwise normal flowers may be due to the aberrant development of pistils attributable to the terminal ovaries of lateral axes which are usually suppressed in the pseudanthium. The occurrence of these anomalous ovaries, and leaf-like bracts, on the hypanthium is certainly teratological, and of only secondary importance as evidence. But such organs have not been observed on hypanthia in any other genus of the family, and should not be ignored.

The interfertility of *Parrotia persica* and *Sycopsis sinensis* indicates that they are relatively recent derivatives of a common ancestral stock. If the above interpretation of the *Parrotia* flower is correct, then the longer hypanthium of *Sycopsis sinensis* may represent only an elaboration in length of a shorter ancestral hypanthium, perhaps as in *Parrotia*, with concomitant reduction in the number of bracts and stamens inserted on the rim of its narrower throat, and in increased basal connation of the tepals above the rim.

4. *Fothergilla* J. A. Murray, Syst. Veg. ed. 13. 418. 1774. FIGURE 10.

The genus *Fothergilla* consists of two species of low deciduous shrubs which usually reach a height of 1 to 3 meters and frequently form dense clumps through rhizomatous proliferation (Ernst 1963; Weaver 1969). The species are limited in distribution to the coastal plains and uplands of the southeastern United States.

**MORPHOLOGY:** The inflorescence of *Fothergilla* contains numerous sessile flowers solitary in the axils of broad primary bracts spirally arranged in a terminal spike (FIGURE 10A). The flowers are incomplete, perigynous, and generally bisexual, although a few basal flowers in the inflorescence may be functionally staminate, containing only a rudimentary ovary. The perigon and androecium are inserted on a shallow, campanulate hypanthium which surrounds the ovary and is fused with it for its lower third. The perianth consists of 5 to 7 (-8) small, irregular tepal lobes (te) of variable size and position (FIGURE 10A, I-K). I found 18 to 24 stamens in flowers of *Fothergilla gardenii* ( $n = 24$ , Weaver 1969), and up to 31 stamens in those of *F. major* ( $n = 36$ , Weaver 1969; Weaver found 12 to 24 stamens in *F. gardenii*, and 22 to 32 in *F. major*), inserted in a single cycle on the rim of the hypanthium with their bases enclosed externally by the lobes of the perigon and internally by a shallow, much lobed inner parenchymatous lip (col) of the hypanthium (FIGURE 10I-K). The distally clavate, unequal filaments are several times longer than the hypanthium, and bear small, basifixed anthers which contain four pollen sacs. Anther dehiscence is subvalvate and lateral by means of longitudinal I-shaped slits (FIGURE 10c). There are no staminodia. The ovary is up to one-fourth semi-inferior. The two carpels terminate in filiform styles with inconspicuous



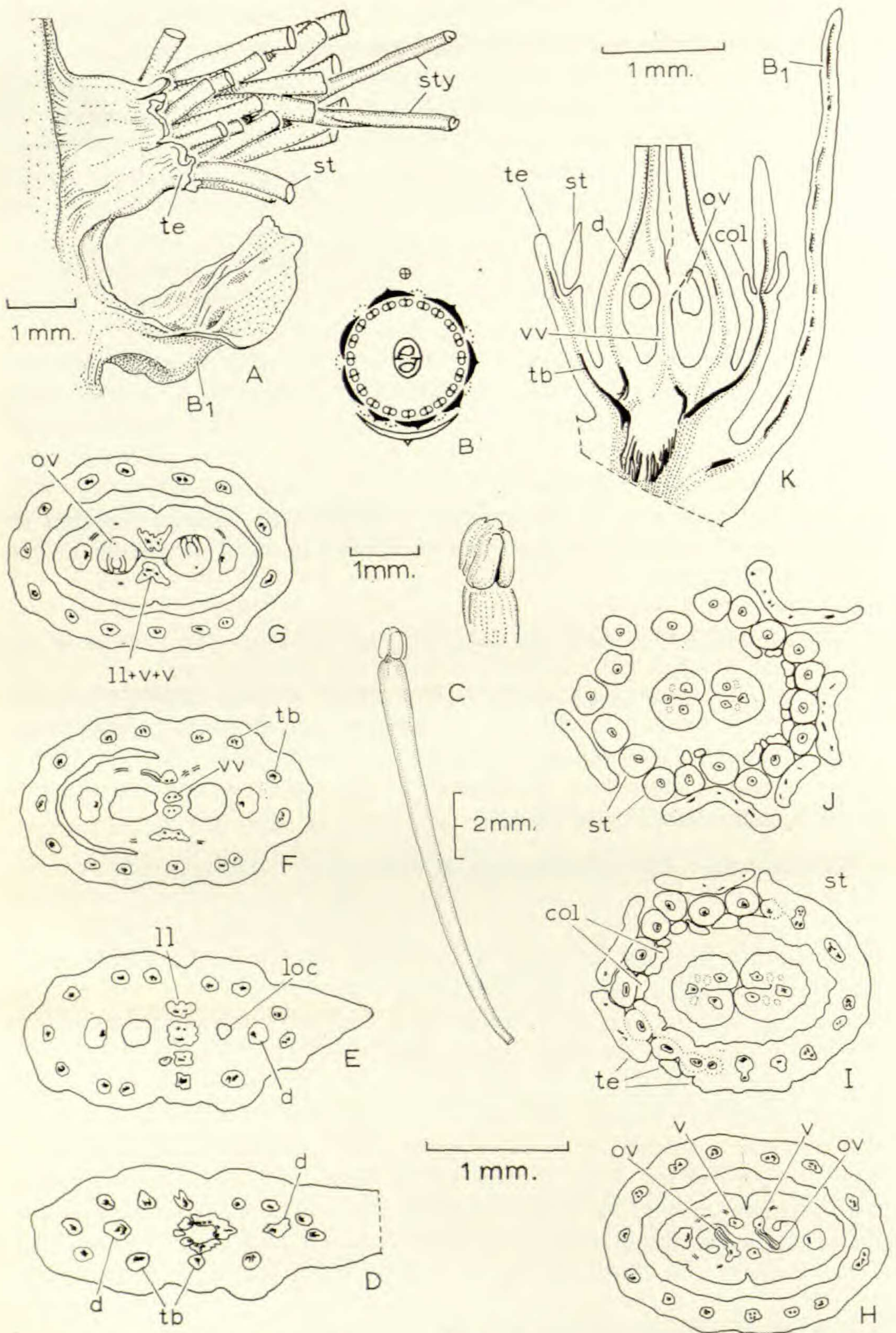


FIGURE 10. *Fothergilla gardenii*: A, a flower at anthesis, stamens and styles cut away; B, floral diagram; C, stamen; D-J, transverse sections through a flower at anthesis; D, through receptacle — note dorsal bundles and receptacular stele; E, bases of the locules — note compound lateral bundles and residual receptacular stele; F, partial separation of the hypanthium, compound ventral bundles formed;



papillate stigmas within the folded margins of the distal half. Each locule contains one or occasionally two ovules, the lower of which is fertile.

**ANATOMY:** The vascular supply to the base of each flower varies from a short but cylindrical pedicellar stele to a reduced condition in which a variable number of large bundles enter the receptacle directly from the margins of an elongate gap in the peduncular stele.

In the receptacle, well below the base of the locules, several large trunk bundles (tb) diverge from the pedicellar stele to enter the base of the hypanthium, eventually to supply the perianth and androecium. An internode is not present in the receptacular stele between the trunk bundles and the carpel dorsal bundles, and the latter are formed at either side of the receptacle in the median plane by the fusion of 2 to 3 lateral branches from single or adjacent trunk bundles (d in FIGURE 10D, E). Above the departure of the associated trunk and dorsal bundles the remaining bundles of the receptacular stele converge on the center of the receptacle to form a narrower receptacular cylinder (FIGURE 10D) which then shortly gives rise to two compound lateral bundles (ll) to either side in the transverse plane. The remaining traces in the stele consolidate to form a still narrower and largely procambial cylinder which enters the base of the septum. In polarized light at least two strands of protoxylem appear in this cylinder, situated on opposite sides in the transverse plane (FIGURE 10E).

The number of bundles entering the base of the hypanthium approximates half the number of stamens eventually supplied, but there is no exact correlation in this respect. Within the hypanthium the number of trunk bundles is increased by branching. Rarely, lateral branches from adjacent bundles fuse to form a single trunk bundle. More often, minor lateral branches of the trunk bundles end blindly in the hypanthium slightly below the level of stamen insertion.

Each stamen receives a single trace. A single trunk bundle may supply only one stamen, but many of the trunk bundles branch immediately below the insertion of the stamens to form 2 to 3 stamen traces. In addition, almost every trunk bundle produces a single, relatively minor trace (te) at this level, which enters the base of a tepal. Occasionally a relatively weak hypanthial bundle will supply only a tepal. There was no apparent regularity in the vascular supply to the tepals. Within the tepal the traces may branch, and anastomoses may form between adjacent branches.

In the ovary the division of the compound ventral (vv) and compound lateral (ll) bundles to form distinct ventrals and laterals usually occurs slightly below the level of ovule insertion, as figured by Horne (1914), but occasionally the compound laterals were observed to divide in the lower half of the ovary, or to remain entire to a level slightly above ovule insertion. The free ventral and lateral bundles of each margin then fuse,

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g, ovary — note fusion of compound lateral and compound ventral bundles; h, ovule insertion; i, insertion of the stamens on the hypanthium; j, through the various organs of the flower; k, nearly median longitudinal hand section (semi-diagrammatic) of a flower at anthesis.



and immediately above the point of fusion an ovular trace separates from the ventral bundle of each fertile margin and enters the funiculus of the ovule (FIGURE 10H).

At anthesis the upper portions of the ventral bundles are frequently in only a procambial condition, and in some carpels the ventral bundle to the sterile margin appears to die out soon after separating from the adjacent ventral which supplies the fertile margin.

*Fothergilla*, one of the better known genera of Hamamelidoideae, is widespread in cultivation and easily accessible for study. Baillon (1871) described the organogeny of *Fothergilla alnifolia* L. (= *F. gardenii* Murr.). According to his observations 5 to 7 short sepal primordia develop successively on the rim of a shallow, cupulate receptacle. The first and second primordia appear on either side, then the others develop in the intervals between the first two. Later, one stamen primordium develops before each small sepal, then 2, 3, or 4 stamen primordia appear secondarily on the sides of each initial stamen. Baillon considered the smaller, secondary stamen primordia opposite each calyx lobe to be exterior to the primary stamen initial, and interpreted the groups of stamens as having arisen through the divisions of a primitive stamen opposite each sepal. He did not interpret his observations in terms of cycles of stamens.

Tong (1930), however, states that the normal number of stamens is 14 in *Fothergilla major*, arranged in two whorls, the outer of which alternates with the calyx lobes. He considered the outer whorl of stamens derived through the transformation of petals to stamens, a view which he attributes justifiably also to DeCandolle (1830), and Griffith (1838). Excess stamens were interpreted as being derived through splitting of stamen primordia. Tong's floral diagram accordingly shows the stamens arranged in two cycles.

Shoemaker (1905) observed some stages of the organogeny and embryology of *Fothergilla gardenii*. His observations on the development of the stamens agree with those of Baillon. Flint (1957) has provided a detailed description of megasporogenesis and megagametogenesis in both *Fothergilla gardenii* and *F. major*.

Horne (1914) illustrated his brief description of the floral vasculature of *Fothergilla major* with three drawings of transverse sections at critical levels. My observations on *Fothergilla* are in general agreement with those of Horne.

There is a slight difference in the relative positioning of the stamens on the rim of the hypanthium, so that the stamen opposite the mid-line of each tepal appears slightly adaxial to its neighbors. This is especially apparent in those flowers having more numerous stamens (*Fothergilla major*), but it is not sufficiently pronounced either morphologically or anatomically to provide a basis for recognizing more than one cycle of stamens on the hypanthium.

The lobed collar on the inner edge of the hypanthium rim of *Fothergilla* is similar to that seen in *Parrotia persica*, but there is no vascular supply



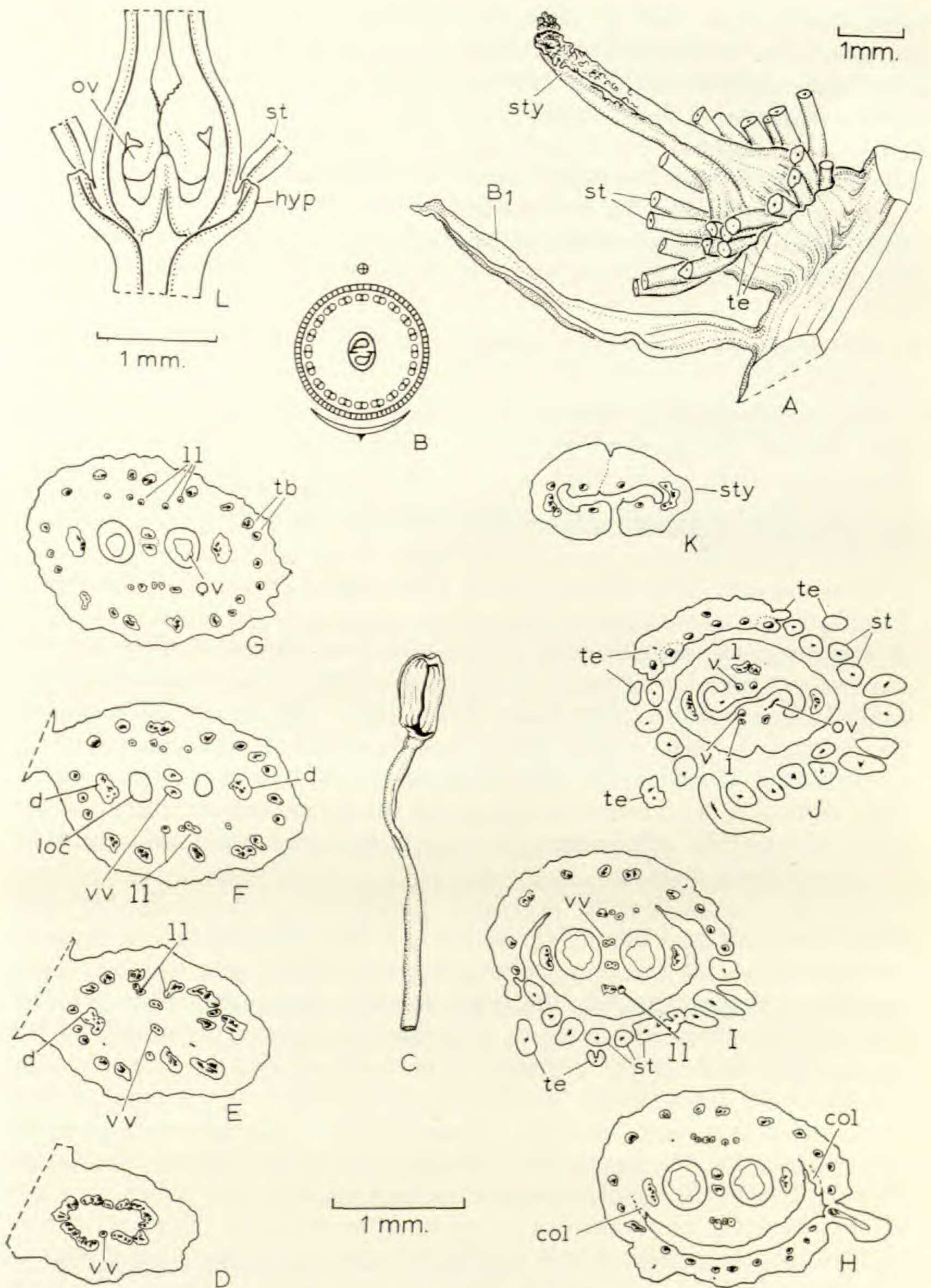


FIGURE 11. *Parrotiopsis jacquemontiana*: A, flower at anthesis, stamens cut away; B, floral diagram; C, stamen; D-K, transverse sections through a flower at anthesis; D, pedicellar stele; E, through the receptacle — note gynoecial bundles differentiating; F, bases of the locules; G, ovary — note diffuse compound lateral bundle traces; H, partial separation of the hypanthium, compound lateral bundle traces consolidating; I, ovary — note individual ventral bundles forming; J, ovule insertion; K, through the style bases; L, median longitudinal hand-section (semidiagrammatic) of a flower at anthesis.



evident to its base. Nor is there any evidence in the receptacle of peripheral bundles or vestigial vasculature of any kind. The loss of an internode in the receptacular stele, resulting in the close association or partial fusion of the carpel dorsal bundles with the hypanthial trunk bundles, is also seen in *Parrotia*, but in both genera a segment of the receptacular stele intervenes below the departure of the compound lateral bundles, and continues upward into the base of the septum. The origin of the ovular traces above the fusion of the lateral and ventral bundles is a deviation from their departure prior to fusion in *Distylium*, *Sycopsis*, and *Parrotia*.

5. *Parrotiopsis* (Niedenzu) Schneider, Handb. Laubholz. 1: 429. 1905.  
FIGURE 11.

This monotypic Asian genus of deciduous shrubs or small trees is known only through the species *Parrotiopsis jacquemontiana* (Decne.) Rehd., which has a restricted distribution in the Himalayan mountains of northern Kashmir, West Pakistan, and Afghanistan (see Kammeyer 1957, p. 73, for distribution map).

**MORPHOLOGY:** The inflorescence of *Parrotiopsis* ( $n = 12$ , Anderson & Sax 1935) contains about a dozen small, inconspicuous flowers arranged in a terminal subcapitate spike. The blades and stipules of the leaves at the two or three lowest nodes of the inflorescence are conspicuously expanded into spreading white bracts which form a showy involucre around the flowers. A single sessile flower, usually staminate through reduction of the ovary, is axillary to each set of involucre bracts. Primary bracts may subtend a few flowers just above the involucre, but are absent at the distal nodes of the inflorescence, and secondary bracts were not present in the material examined.

The flowers are regular, apetalous, perigynous, and usually bisexual, with a semi-inferior ovary (FIGURE 11H, L). The perianth and androecium are inserted on the rim of a shallow, cupulate hypanthium which is fused basally with approximately the lower third of the ovary, while the free portion of the hypanthium forms a shallow cup around the middle of the ovary. The limb of the perianth is reduced to irregular lobes on the margin of the hypanthium. Occasionally one or two tiny, pubescent tepals, less than 1 mm. long, develop. About 21 to 25 stamens with unequal, terete filaments, are inserted in a single cycle on the rim of the hypanthium. The small, oblong, truncate anthers contain four pollen sacs and dehisce laterally by means of four valves (FIGURE 11C). The anther connective may be produced as a very short apiculus on the adaxial edge of the truncate tip. A very shallow, thin, parenchymatous collar on the inner edge of the hypanthium encloses the stamen filament bases. In the ovary one or occasionally two ovules are found in each locule. The styles are linear, with papillate stigmas running nearly the entire length of the ventral margins.

**ANATOMY:** A cylindrical pedicellar stele is present beneath each flower. In the receptacle the stele expands as 13 to 19 trunk bundles differentiate



and diverge toward the periphery to enter the base of the hypanthium (FIGURE 11D-H). Adnation between the bundles of the hypanthium and gynoecium in *Parrotiopsis* is relatively advanced over that in *Parrotia* and *Fothergilla*, as evidenced by the fact that there is no indication of a vascular cylinder in the receptacle.

The 13 to 19 trunk bundles (tb) which enter the base of the hypanthium eventually supply 21 to 25 stamens, as well as the tepals. As in *Fothergilla*, each stamen receives a single trace (st) from a trunk bundle, and some trunk bundles divide within the hypanthium to form additional bundles, or divide just below the insertion of the stamens to form two or three stamen traces (FIGURE 11F-I).

The limb of the perianth is so reduced that few of the lobes were vascularized in the material which I examined. The few traces (te) produced by the trunk bundles to the tepal lobes are very inconspicuous at anthesis. This is in contrast with *Fothergilla*, in which almost every one of the numerous trunk bundles produces a single abaxial branch to the perianth. Because of this reduced condition I am unable to confirm Saunder's observation (1939) that the stamens are supplied from both the midveins and lateral veins of the calyx lobes.

In the receptacle the gynoecial bundles appear to have independent origins in the fusions of branches from the bundles of the expanding pedicellar stele, rather than arising from a cylindrical receptacular stele. At either side of the receptacle in the median plane 3 to 4 small branches from diverging trunk bundles converge and fuse to form a carpel dorsal bundle (d, FIGURE 11E, F). In the transverse plane 4 to 6 traces converge centripetally to function in the formation of the compound ventral (vv) and compound lateral bundles (ll). The compound ventrals are often the first to differentiate, in some flowers appearing as a single bundle on each side of the receptacle (FIGURE 11C, E), while the compound laterals form at a slightly higher level as an aggregation of 4 to 5 weak bundles arranged in a loose band at each edge of the septum (FIGURE 11F, G).

In the ovary the several bundles of each compound lateral consolidate distally to form a narrower band, or a single broad bundle which dichotomizes at about the level of ovule insertion to form the independent lateral bundles (l). The compound ventrals divide above the middle of the ovary, forming four ventral bundles (v) which fuse with the adjacent laterals at the level of ovule insertion. Ovular traces (ov) depart from the ventrals of the fertile margins just prior to this fusion (FIGURE 11H-J).

The genus *Parrotiopsis*, like *Fothergilla*, is also widespread in cultivation, and has been studied by several workers. Horne (1914) included two figures of transverse sections illustrating the basic vascular pattern of the ovary (as *Parrotia Jacquemontiana*), and in one of these two ovules are conspicuous in each locule. Tong (1930) interpreted the stamens of *Parrotiopsis* as forming three alternating septenate cycles within a cycle of seven calyx lobes. Saunders (1939) described the origin of the stamen traces as being "detached from the sepal lateral veins as well as from



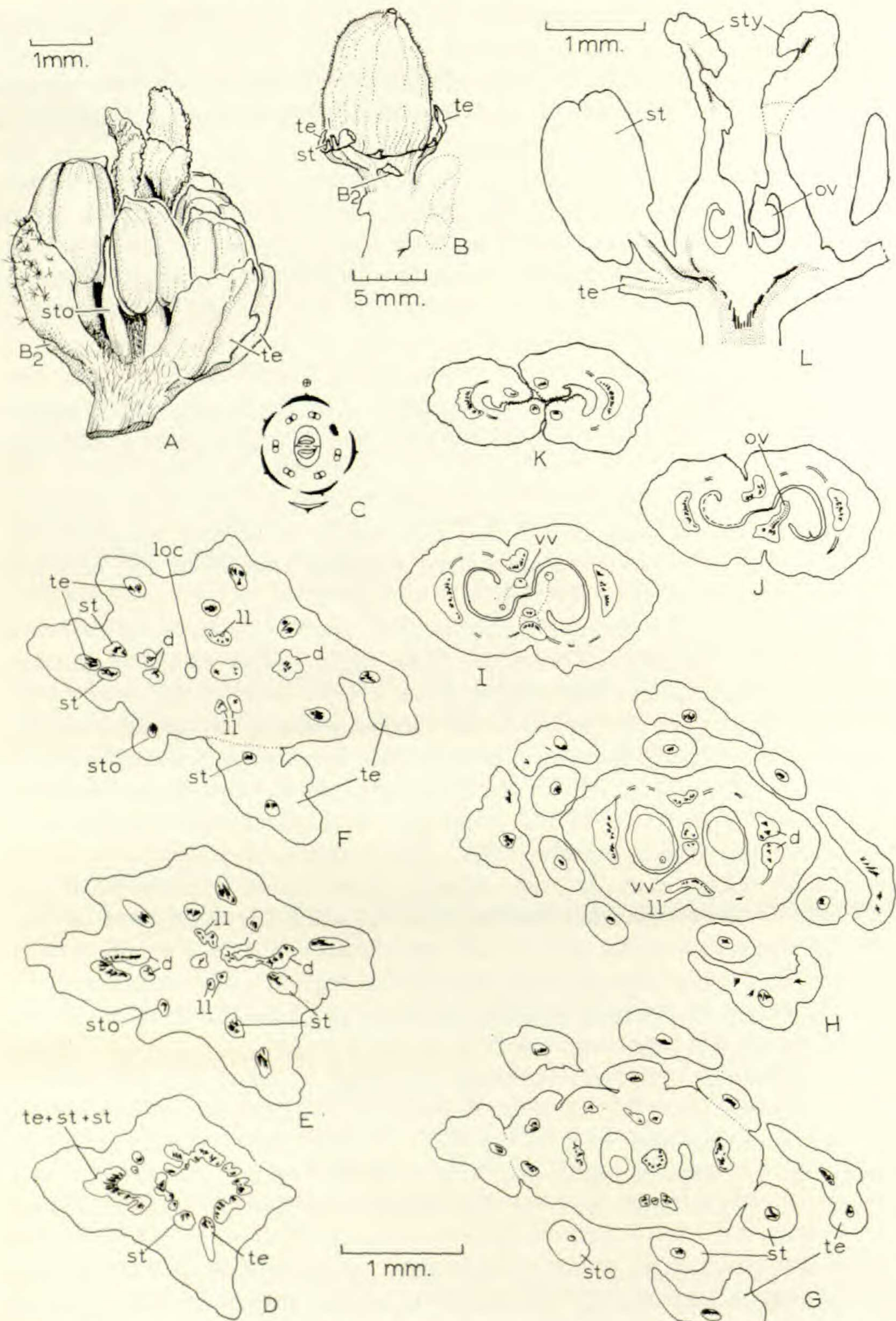


FIGURE 12. *Molinadendron sinaloense*: A, view of a flower at anthesis; B, nearly mature fruit — note shallow hypanthium; C, floral diagram; D-K, transverse sections of a flower at anthesis (slightly oblique); D, through the receptacle, some tepal and stamen traces forming; E, receptacle, gynoecial bundles forming (d, ll); F, bases of the locules, insertion of some tepals and stamens; G, stamens separating from base of the ovary; H, about mid-height in the ovary; I, base of ovule insertion; J, top of ovule insertion; K, through the style bases; L,



the midrib bundles and [standing] in a single ring." Kaul (1969) found that the endosperm is *ab initio* cellular in *Parrotiopsis*.

The systematic affinities of the genus are indicated by the fact that at one time or another, *Parrotiopsis jacquemontiana* has been included in both *Fothergilla* (Niedenzu 1891) and *Parrotia* (Decaisne 1844), as well as by Rehder's statement (1920) that *Parrotiopsis* differs from *Fothergilla* "only in the capitate inflorescence supported at the base by large bracts, [and] in the less numerous stamens with linear not club-shaped filaments . . .", a view expressed earlier by Hooker (1896). However, *Parrotiopsis* is more advanced than *Fothergilla* in its fewer-flowered, more congested inflorescences, in the extreme reduction of its perianth, and in the slightly more pronounced adnation between hypanthium and ovary. It is also more advanced anatomically in the absence of a residual receptacular cylinder, resulting in basal adnation between the hypanthial and gynoecial vascular systems. The diffuse origin of the compound lateral bundles, and the individuality of the compound ventrals in the receptacle, are apparently artifacts of the reduction of the receptacular stele and the greater adnation between hypanthium and ovary. I could find no morphological or anatomical basis for assigning stamens to more than one cycle on the hypanthium.

6. *Molinadendron* Endress, Bot. Jahrb. 89: 353. 1969. FIGURE 12.

The genus *Molinadendron* is a small Central American group recently segregated from *Distylium* Sieb. & Zucc. (cf. Harms 1933; Walker 1944; Gentry 1948; Balgooy 1966). The genus contains three as yet little known species of large evergreen trees. *Molinadendron guatemalense* (Radlk. ex Harms) Endress is apparently restricted to the vicinity of Coban, Guatemala. *Molinadendron hondurensis* (Standl. in Walker) Endress occurs widely in Honduras, while *M. sinaloense* (Standl. & Gentry) Endress is restricted to the mountains of the State of Sinaloa, Mexico. The following descriptions are based primarily on material of *M. sinaloense* which I collected in 1964. In addition, flowers from herbarium sheets of the other two species were also examined anatomically, and showed no significant difference from those of *M. sinaloense*.

**MORPHOLOGY:** The inflorescences of *Molinadendron sinaloense* are axillary or terminal on short lateral leaf-bearing shoots of the current season's growth. Each consists of about a dozen small inconspicuous flowers spirally arranged in a short, congested spike. The proximal flower may be axillary to a much reduced stipulate leaf, the blade of which may be little more than a narrowly triangular bract. Intermediate flowers in the inflorescence are subtended by obvious primary bracts which are more or less hooded and cover the flower in bud; but at distal nodes the primary bracts are reduced and adnate to the base of the flower, often intergrading with the tepals of the perigon. Similarly, a pair of subopposite secondary

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longitudinal section through a post-anthesis ovary, rather oblique — note slightly perigynous insertion of stamens.



bracts may subtend the lowest flower or two, but at higher nodes these either fail to develop, or are adnate to the floral receptacle and indistinguishable from the tepals. It is often easier to fix the presence and position of these bracts in the elongated, more open fruiting inflorescence than at anthesis.

The flowers at anthesis are sessile or nearly so, incomplete, subperigynous, and bisexual. The perianth consists of 2 to 8 linear to broadly cuneate-dentate and sometimes cucullate tepals (or fewer if some of these are secondary bracts). Petals are absent. Two to eight (usually 5 to 7) bright-red stamens are arranged in a single cycle around the base of the sessile, broad-based ovary. The anthers, which are short-oblong with a truncate apex and a short adaxial apiculus, are borne on short terete filaments which elongate after anthesis. Each anther contains four pollen sacs, and dehisces laterally by means of four narrow, longitudinal valves. The two- (occasionally three-) carpellary ovary appears superior but is slightly sunken in the broad receptacle, and hence slightly inferior. It is incompletely bilocular, and contains one or sometimes two (then one on each margin) ovules in each locule. The placentation is parietal in my material, rather than axial as described by Endress (1969) (cf. FIGURE 12I). The styles are exerted, recurved, and somewhat expanded distally, with extensive papillate stigmatic surfaces.

The basal flower(s) and sometimes the terminal flower in an inflorescence may be staminate through reduction of the ovary. Abortive stamens, reduced in varying degrees to subulate sterile filaments (sto in FIGURE 12A), and abortive linear, bristle- or scale-like, pubescent perianth bracts frequently appear in any part of the inflorescence. A striking feature of the flowers is the irregularity in number and insertion of the tepals and stamens. There appears to be a rough correlation between the number of stamens and the number of tepals in the perianth. They are often equal, with a stamen opposite each tepal, but frequently the number of stamens is larger, and their insertion irregular. And in some flowers the stamens alternate with the tepals. In fruit the marcescent tepals and stamens, or their basal portions, are prominent on the rim of the very shallow hypanthium around the base of the nearly superior bony capsule (FIGURE 12B).

**ANATOMY:** In the pedicel a short cylindrical stele assumes an elliptic configuration as its vascular strands become organized into traces to the floral organs. Each tepal (te) receives a single trace, as does each stamen (st). Opposing tepals and stamens frequently receive their traces from a common trunk bundle in the receptacle, but this is not a constant feature, since, in some cases, each may be supplied by a trace derived independently from the stele. Alternating tepals and stamens each receive independent traces from the stele. When two stamens oppose a single tepal each stamen is supplied by an independent stamen trace, rather than by branches of a single stamen or tepal trunk bundle. In transverse sections the adnation of the perianth and androecium to the base of the ovary is evident (FIGURE 12F, G).



In the receptacle, the carpel dorsal bundles may be fused basally for a short distance with some of the traces supplying the perianth and androecium as a result of the loss of an intervening internode in the receptacular stele. However, a short segment of the stele persists above the departure of these traces, giving rise to the compound lateral and compound ventral bundles.

At the median sides of the expanding receptacular stele, 2 to 3 small vascular strands from diverging tepal or stamen bundles move centripetally to associate or fuse into a dorsal bundle (d in FIGURE 12E, F). In the base of the ovary a dorsal bundle may be entire (FIGURE 12E, right side) or consist of two large collateral bundles which then fuse at a higher level into a single broad bundle (FIGURE 12E-G, left side).

Above the departure of the sepal, stamen, and dorsal bundle traces the residual bundles of the receptacular stele move toward the center of the receptacle. In the plane of the septum 1 to 3 of these on each side cease their centripetal movement and assume a position about midway between the periphery and the center. These form the compound lateral bundles (ll) at each edge of the septum. The remaining residual bundles converge and form a narrow cylinder in the base of the septum (FIGURE 12E, F).

A compound lateral may appear as a single broad bundle in the base of the ovary, or as a group of 2 to 3 vascular strands which fuse above into a common compound bundle (FIGURE 12E-H). The compound laterals usually dichotomize transversely at the level of ovule insertion or slightly above.

The narrow residual receptacular cylinder divides about midway up the septum to form two compound ventral bundles (vv), each containing 1 to 3 strands of protoxylem, which diverge toward the edges of the septum.

At anthesis the compound ventrals and laterals may vary in form in the upper part of the septum and parietal placentae. Usually each dichotomizes in the transverse plane at about the level of ovule insertion to form individual ventral and lateral bundles which then fuse in pairs and pass into the styles as marginal bundles. In this case the ovular trace originates from an individual ventral bundle prior to its fusion with the adjacent lateral. Sometimes, however, the compound ventral and lateral bundles fail to divide, but fuse in the placenta, and the bundle thus formed then dichotomizes at a slightly higher level to form the marginal bundles of the styles. In this case the ovular trace may originate from the compound ventral either below or above its fusion with the compound lateral. Exceptionally a compound ventral bundle will pass into the funiculus of the ovule without dividing, with no discernible connection to the adjacent compound lateral bundle. The latter condition may be due to the immature state of the ovary and its vasculature at anthesis, or it may represent a form of reduction in the vascular pattern of the ovary concomitant with reduced size. It has been noted in other genera of the family as well.

The flowers of *Molinadendron* differ from those of *Distylium* in their spicate arrangement; in the presence of a perianth; in their bisexual condition (or occasionally staminate through reduction of the ovary);



in the valvate dehiscence of the anthers; in the slightly inferior condition of the ovary, and in the persistence of the sepals and stamens on the rim of a very shallow hypanthium around the base of the fruit (FIGURE 12B. See also Gentry 1948, *figure 1*). Anatomically, the vestigial peripheral bundles of the *Distylium* ovary are absent, the carpel dorsal bundles are fused basally with the tepal and stamen traces, and fusion of adjacent lateral and ventral bundles in the septum and placentae tends to be more advanced.

Perhaps the most striking feature of the flowers is the irregularity in the numbers and insertion of the tepals and stamens, and the intergradation of the primary and secondary bracts with the tepals. One is frequently at a loss to know which is which. Endress (1969) concluded that "*Molinadendron* does not even belong to the tribe Distylieae (*Distylium*, *Sycopsis*, *Matudaea*), but shows more relationship to *Fothergilla*/*Parrotiopsis* and *Fortunearia*/*Sinowilsonia*." However, the pollen morphology of *Molinadendron* differs markedly in the form of its exine reticulum, and in the shape and sculpturing of its apertures (Chang 1960, Bogle, unpublished scanning electron micrographs), from that of *Fothergilla* and *Parrotiopsis*, and is closer to that of *Sinowilsonia* and *Distylium*. The distinct one-trace tepals of *Molinadendron* also differ from the irregularly vascularized tepals of *Fothergilla*.

The genus *Fortunearia* differs from *Molinadendron* most strikingly in its regular, complete, usually pentamerous flowers, as well as in its numerous-flowered racemose inflorescences, subvalvate anther dehiscence, and half-inferior ovaries. Each sepal in *Fortunearia* receives one median and two lateral traces. In *Sinowilsonia*, unisexual flowers and inflorescences are well developed, and the flowers are racemosely arranged, regular, more or less complete, and usually pentamerous, with an urceolate hypanthium surrounding the superior ovary in the pistillate flowers. Stamen dehiscence in the staminate flowers is subvalvate, by means of I-shaped slits, as in *Fortunearia*.

These morphological differences, in conjunction with its New World distribution, suggest that *Molinadendron* occupies a relatively isolated position among the apetalous Hamamelidoideae.

#### 7. *Matudaea* Lundell, *Lloydia* 3: 209. 1940

FIGURE 13.

The genus *Matudaea* consists of only two poorly defined species of large, possibly evergreen trees distributed in Mexico and Central America. *Matudaea trinervia* is known from a few scattered locations in Honduras, Guatemala (Standley & Steyermark 1946), and the State of Chiapas, Mexico. *Matudaea hirsuta* Lundell (1961) is known only from a small area in the southern part of the State of Mexico, and differs from *M. trinervia* principally in its densely hirsute twigs. Specimens more or less intermediate between these two species have been collected in the State of Jalisco, Mexico, by McVaugh *et al.* (personal communication).

The following descriptions are based primarily on flowers of *Matudaea*



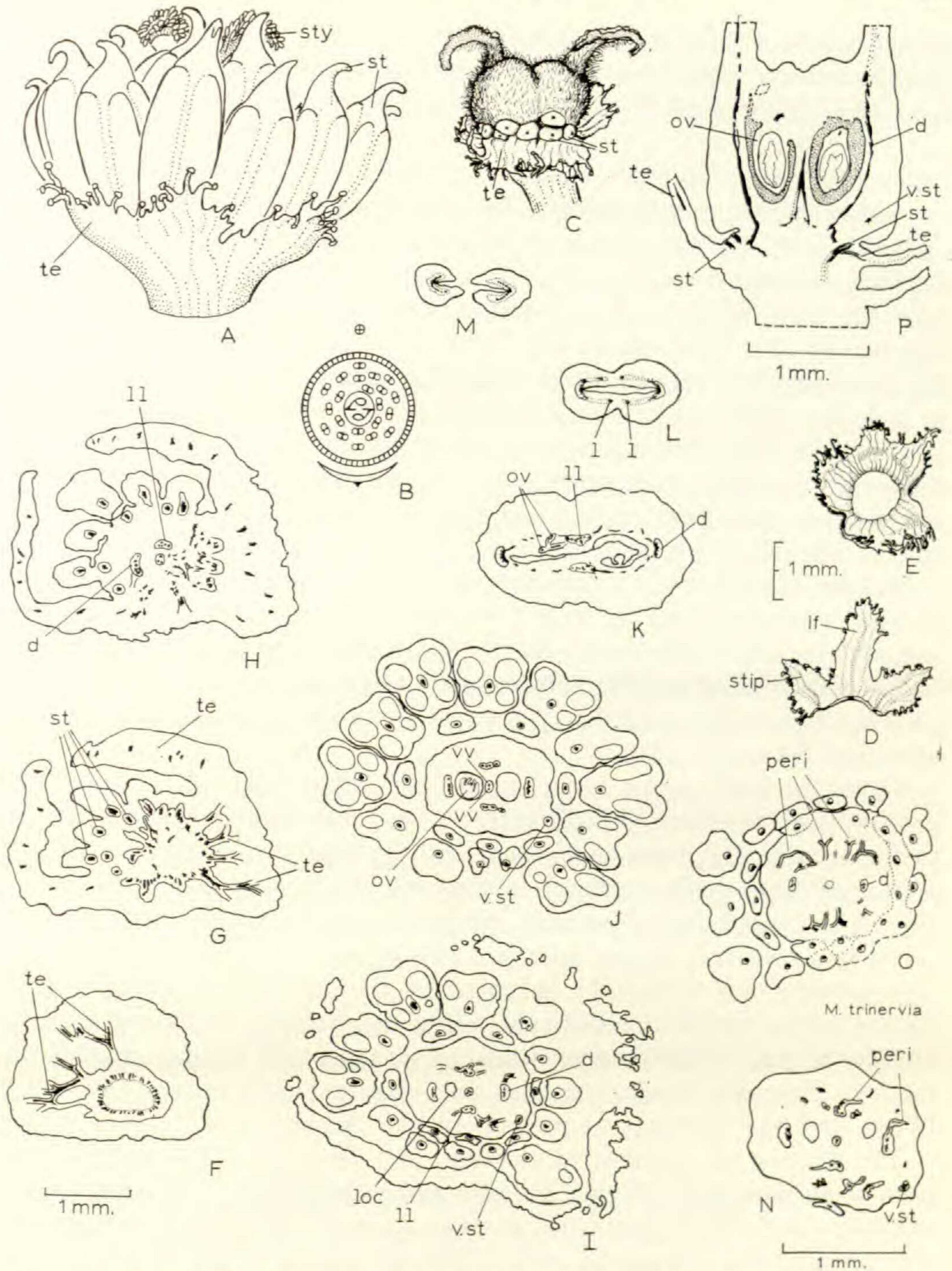


FIGURE 13. *Matudaea hirsuta*: A, flower at anthesis; B, floral diagram; C, post-anthesis flower — note stamen scars crowded beneath the enlarging ovary; D, stipulate primary bract; E, deciduous syntepalous perigon; F-M, transverse sections through a flower at anthesis (slightly oblique); F, pedicellar stele and departing perianth bundles; G, through receptacle, sepal traces departing to right, stamen traces to the left; H, receptacle, part of gynoecial vasculature formed; I, base of one locule — note vestigial stamen trace and some peripheral bundles in the ovary wall; J, about mid-height in the ovary; K, ovule insertion; L, through fused carpels above the ovules; M, through style bases; N, section through ovary just above the level of I, enlarged slightly to show vestigial vasculature; O, section through base of ovary of *M. trinervia* — note vestigial vasculature; P, near-median longitudinal section through an ovary.



*hirsuta* which I collected in Mexico in 1964. Flowers of *M. trinervia* from herbarium specimens were also examined anatomically, and appear to agree with those of *M. hirsuta*.

**MORPHOLOGY:** The inflorescences of *Matudaea* are small, congested, and either spicate or paniculate. They are borne in the axils of the two-ranked leaves. Both the leaves and their associated inflorescences become abruptly reduced toward the tip of the shoot axis. The distal leaves may take the form of a much reduced lamina, no larger than its flanking stipules, or of a bract either free from, or variously fused with the two bracteate stipules. At the distal nodes the inflorescences become reduced to a single, short pedicellate, or sessile flower, and the tip of the shoot axis may become similar in appearance to the lateral inflorescences along its length. Larger inflorescences in my collections attain a length of about 2 cm., and bear one or two short secondary axes at the proximal nodes. The secondary axes may bear one or more flowers.

Flowers are situated in the axils of bract-groups which are arranged along the primary and secondary axes in the same one-half phyllotactic sequence as that of the leaves on the shoot axis. The bract-groups represent a reduced leaf and its stipules, an interpretation which is supported both by the obvious reduction of the leaf along the shoot and inflorescence axes, and by nodal anatomy.

There has been much reduction in the inflorescence. Failure of the primary axis to elongate sufficiently at its base results in congestion of proximal secondary axes in the leaf axil, so that two or more axes may appear to have distinct origins in the axil. Failure of internode elongation at the distal end of an axis results in congestion and eventual abortion of subterminal flowers or axes. The compound nature of some few-flowered spikes is frequently indicated by the presence of reduced bracts of the second or third order subtending the flowers of the spike. Congestion in the inflorescences leads to ontogenetic fusions among the various bracteate organs of the axes, particularly between secondary bracts and the syntepalous perigon of the flower.

The flowers are regular, incomplete, and bisexual. The perianth consists of an irregular, syntepalous, circumscissile perigon. The androecium contains 18 to 30 hypogynous stamens, inserted in a congested, shallow ring around the base of the ovary (FIGURE 13C, P). The oblong anthers are subsessile in bud, but strongly exerted at maturity. Each contains four pollen sacs, and dehisces laterally by means of four longitudinal valves. The anther connective is produced as a short apiculus. The two-carpelled superior ovary contains one or occasionally two ovules in each locule. Each carpel terminates in a free, elongate, recurved style, with expanded papillate stigmatic margins.

In bud the perigon forms a cap which tightly encloses the stamens and ovary. At anthesis the cap splits irregularly and longitudinally from an apical pore, expanding to form an irregularly lobed cupulate or reflexed perianth tube (FIGURE 13A, C, E). The margins of the lobes are incised



with many often capitate fimbriae. The tube is shed by means of a circumscissile abscission layer which forms at its base around the rim of the slightly expanded receptacle. There is no morphological indication of the number of tepals incorporated into the tube. In some flowers the stamens appear to be inserted in a more or less spiral fashion, but in others, particularly those with fewer stamens, there is a faint tendency toward an irregularly whorled arrangement approaching three alternating cycles (cf. floral diagram, FIGURE 13B). There is no external evidence of staminodia between the stamens and the ovary.

**ANATOMY:** The cylindrical pedicellar stele subtending each flower expands rapidly as it enters the receptacle, with some dichotomizing of its bundles. There is little or no regularity or pattern in the vascular supply to the various floral organs. A particular bundle in the receptacle may supply a single organ, or through divisions and anastomoses contribute to more than one

A number of traces (9 to 12) diverge from the pedicellar stele to supply the base of the perianth (te in FIGURE 13F, G). Some of these undergo branching, and the branches of adjacent bundles frequently anastomose, while still within the receptacle. Although usually irregular and complex, the patterns of origin, branching, and anastomosis of the perianth traces in some flowers approach the pattern seen in the nodal anatomy of the foliage leaf (as described in *Distylium*), and suggest the connation of modified stipulate bract groups to form an irregular perigon. In this respect it should be noted that the primary and secondary bracts subtending the flowers have incised margins with capitate fimbriae like those of the perianth lobes (FIGURE 13D, E).

Above the departing perianth traces the supply to the androecium forms. In many cases the stamen trace is formed by the fusion of two bundles in the receptacle, and sometimes of three. Occasionally a single bundle will branch into three, the central trace of which will supply the outer (or lower) of two stamens lying on a given radius, while the two lateral bundles fuse to form the trace to the inner, and morphologically higher, stamen.

As the numerous traces to the androecium diverge, the remaining bundles of the receptacular stele converge centripetally to form the vascular supply to the gynoecium. In transverse section at this level this short internode of the receptacular stele appears as a complex vascular plexus, as seen toward the right side of FIGURE 13H, with part of the gynoecial system evident (dorsal bundle, compound lateral bundle) toward the left side.

In the base of the ovary two dorsal bundles (d), two compound lateral bundles (ll), and a narrow residual receptacular cylinder are apparent. Each of these has a complex and independent origin in the anastomosis of several vascular strands. Also at the base of the ovary one encounters a series of vestigial bundles, suggestive of the peripheral bundles in the ovary of *Distylium*, of which the morphological origins are not known



(peri in FIGURE 13O, of *Matudaea trinervia*, Standley 25570). These may be entirely procambial at anthesis, or contain small strands of protoxylem, and appear to branch and anastomose to a certain extent. In flowers of *Matudaea hirsuta* in my collections, similar vestigial bundles were found originating from the bases of the dorsal and compound lateral bundles (FIGURE 13N). These are similar in this respect to certain hypanthial bundles in several genera of petaliferous Hamamelidoideae (Hamamelideae) which are adnate basally to the gynoecial system, but eventually separate to supply organs on the hypanthium.

In the ovary, the residual receptacular stele dichotomizes in the septum just above the base of the locules. The two compound ventral bundles formed ascend to the placentae where each fuses with the adjacent compound lateral bundle. Just prior to this fusion each compound ventral usually provides a single ovule trace to one of the solitary ovules. But ovular traces have also been observed to depart above the point of fusion (FIGURE 13K). Slightly above the level of fusion the compound bundle formed dichotomizes to provide marginal bundles to the style bases.

The inflorescences of *Matudaea* are similar to those of *Distylium racemosum* in their progressive reduction upwards along the shoot, resulting in the merger of inflorescence and shoot distally, and in the abortion of subterminal flowers beneath the terminal flower, due to congestion caused by the failure of the distal internode to elongate. It often appears that in the last stages of its reduction, the subterminal flower develops as a small knot of capitate fimbriae at the base of the terminal flower. But the flowers of *Matudaea* are apparently bisexual, with a definite perianth, rather than unisexual or obviously pseudanthial and atepalous, as in *Distylium*, and there is no direct morphological evidence that the stamens of *Matudaea* are attributable to subterminal naked staminate flowers aggregated about the base of a terminal naked pistillate flower, as in *Distylium*. *Matudaea* thus stands apart from the other apetalous Hamamelidoideae by virtue of its calyptrate perianth and numerous hypogynous stamens, the latter being approached only by the fewer and subperigynous stamens of *Molinadendron*. Its pollen is also distinct, and has apparently not been described in the literature.

Anatomically there is no parallel among the other apetalous genera to the complex vasculature of the perianth. The vasculature of the ovary, like that of *Molinadendron*, is relatively advanced in the fusion of compound ventral and lateral bundles in the placentae, rather than of individual bundles, and in the origin of the ovule trace from the compound ventral, either above or below the level of fusion. The nature of the vestigial vasculature in the base of the ovary is problematical. The presence of a perianth and numerous hypogynous stamens would suggest that these bundles may represent traces to a number of abortive stamens. A specific example of an apparently vestigial stamen, adnate to the base of the ovary and receiving such a trace, is illustrated (v st, in FIGURE 13I, J, N). If this interpretation should prove to be correct, the flower



of *Matudaea* with undifferentiated perianth, numerous hypogynous stamens, and superior ovary, could represent a relatively primitive type, morphologically, among the apetalous Hamamelidoideae. However, the vestigial vasculature is similar to that of *Distylium*, and considered in conjunction with the irregular vascular supply to the perianth, and the similarities of inflorescence morphology, suggests the need for further study and for more information from other areas of investigation before the idea of a pseudanthial origin of the flowers can be discarded entirely.

## DISCUSSION

The morphological and anatomical observations recorded above reveal a striking diversity of floral forms and structures which share no common basic pattern. Several parallel lines of specialization appear to be represented, some of which transgress currently recognized generic and tribal limits.

A perianth is absent in *Distylium*, and in those species of *Sycopsis* related to *S. dunnii*. The morphology and vascular supply of the inflorescence and "floral" bracts in these two groups clearly indicate that they represent reduced stipulate leaves. In *Sycopsis sinensis*, *S. griffithiana*, and *Parrotia persica* an irregular perigon of 4 to 10 tepals is inserted on the rim of a shallow to deep hypanthium.<sup>3</sup> The tepals of *Parrotia* are typically more numerous (6 to 10), and more variable in width and length, than those of *Sycopsis sinensis* (4 to 7; cf. Endress & Anliker 1968, *figs.* 3, 4), usually appearing as distinct bracts rather than as irregular lobes of a syntepalous perigon tube as in *Sycopsis sinensis* and *S. griffithiana*. The perianth in the latter species appears to represent only a modified form of that seen in *Parrotia*, with increased fusion among the tepals to form the perigon tube beyond the rim of its longer hypanthium. The 5 to 8 tepals of *Fothergilla*, although smaller in size, are similar to those of *Parrotia* and *Sycopsis sinensis* in their variable width and irregular vascular supply, and may represent a modification from a perigon similar to that of *Parrotia*. Such reduction may be observed also in the minute, irregular tepals of *Parrotiopsis*, which are so poorly developed that little can be said about their vascular supply.

In the androecia of all seven genera the stamens are variable in number and insertion relative to the members of the perianth, and are strongly exerted. The 18 to 30 hypogynous stamens of *Matudaea* would appear to mark this genus as rather unspecialized among the apetalous taxa. It is not clear whether the large numbers of perigynous stamens on the hypanthia of *Fothergilla* (12 to 32) and *Parrotiopsis* (21 to 25) are derived from a many-stamened, hypogynous ancestor similar to *Matudaea*, or whether they have developed secondarily from an ancestral type, per-

<sup>3</sup>The reader is reminded that the term hypanthium is used here only in a descriptive sense, and he is referred to the section on General Considerations, above, for a brief discussion of the morphological nature of the hypanthium in the Hamamelidoideae.



haps similar to *Parrotia* (8 to 15). The seven to ten stamens inserted around the narrower mouth of the hypanthium in *Sycopsis sinensis* probably represent a slight reduction from a larger ancestral number on a more extensive hypanthium rim, such as that seen in the closely related *Parrotia persica*. Three to seven perigynous stamens have been counted in *Sycopsis dunnii*, while two to six stamens occur in the subperigynous flowers of *Molinadendron*, and in the staminate flowers of *Distylium*.

Anthers vary in size and shape among the genera from small and slightly oblong (*Fothergilla*, *Parrotiopsis*) to large and linear-oblong (*Parrotia*, *Sycopsis sinensis*). The anther connective is barely, if at all, produced as an apiculus in *Fothergilla* and *Parrotiopsis*, and slightly to moderately produced in the other genera, becoming longest in *Matudaea*, *Parrotia*, and in the male flowers of *Sycopsis sinensis*. Dehiscence is by means of four more or less distinct valves in *Fothergilla*, *Parrotiopsis*, *Matudaea*, and *Molinadendron*, by slits which tend toward a subvalvate condition in *Distylium* and several species of *Sycopsis*, and by simple slits in *Sycopsis sinensis* and *Parrotia*. Although the flowers and stamens of these apetalous genera are presumably modified for wind pollination, the conspicuous white involucre bracts surrounding the inflorescence of *Parrotiopsis*, and the dense clusters of long, white, clavate stamen filaments in *Fothergilla*, suggest adaptations toward visual attraction of insect pollinators. Unfortunately, observations regarding such characteristics as floral fragrance and pollinators are lacking in the literature.

A hypanthium is absent in *Matudaea* and *Distylium*, and only weakly developed in *Molinadendron*, where it is more obvious around the base of the mature fruit. The shallow hypanthium of *Parrotia* is free of any fusion to the ovary wall, but the hypanthia of *Fothergilla* and *Parrotiopsis* are partially adnate to the base of the ovary. The tubular hypanthium of *Sycopsis sinensis* probably represents an elaboration of a shallower ancestral type, such as that of *Parrotia*, but the morphological nature of the more or less urceolate hypanthium in *Sycopsis dunnii* and its related species is not entirely clear. It may represent the fused tissues of reduced stipulate leaves, and associated axillary axial and floral tissues into a tube around an ovary, and may not be homologous at all with the hypanthium of *Sycopsis sinensis*.

The general characteristics of the gynoecium in the subfamily Hamamelidoideae have been described above (see General Considerations). Among the apetalous genera the position of the ovary ranges from superior to partially inferior. The pistil of *Distylium* is apparently superior morphologically, but the presence of a vestigial peripheral bundle system in its base, in conjunction with the absence of a perianth and androecium, suggests the possibility that it may be only secondarily superior. A vestigial system of peripheral bundles is also present in the base of the superior ovary of *Matudaea*, but in the presence of a perianth and androecium this vasculature may represent vestigial traces to abortive stamens. The superior ovaries of *Sycopsis sinensis* and *Parrotia*, although lacking well developed vestigial bundle systems, are associated with other morph-



ological and anatomical peculiarities which suggest a relationship to *Distylium*, and the possibility that their ovaries may also be secondarily superior. The ovary of *Fothergilla* varies from more or less hypogynous to one third inferior (cf. Weaver 1969), while in the closely related *Parrotiopsis* the lower fourth or third of the ovary is adnate with the proximal portion of the hypanthium. The pistil of *Molinadendron* is sessile and slightly inferior in an expanded receptacle.

Considering only the evidence of floral morphology a general trend of floral development among the apetalous Hamamelidoideae could be hypothesized to have progressed from a relatively primitive, bisexual flower, containing a perianth consisting of a variable number of undifferentiated tepals, numerous hypogynous stamens, and a superior bi- or tricarpellary ovary, essentially as in *Matudaea* (which differs in having the tepals fused in a tubular perigon). From this basic plan could be derived forms in which the tepals and stamens have become fused basally into a shallow, hypogynous hypanthium (*Parrotia*, *Fothergilla*), possibly accompanied by reduction in stamen number (*Molinadendron*, *Parrotia*, *Sycopsis sinensis*), and partial adnation of the hypanthium to the ovary (*Fothergilla*, *Parrotiopsis*). Elaboration of the hypogynous hypanthium into an urceolate tube, possibly accompanied by reduction and loss of the tepal lobes morphologically (*Sycopsis dunnii* and related species), and suppression of the development of the gynoecium in lateral flowers of the inflorescence axes (*Sycopsis dunnii*), or in some whole inflorescences (*Sycopsis sinensis*), would lead to more advanced andromonoecious floral types (*Sycopsis*). Finally, suppression of the hypanthium and its associated perianth lobes (if present) would lead to terminal naked pistillate flowers and lateral naked staminate flowers (*Distylium*). The vestigial vasculature in the base of the pistil of *Distylium* would then be attributable to the lost hypanthium, rather than to lost stamens as hypothesized for *Matudaea*. This sequence appears reasonable with regard to the progressive steps of modification necessary to derive the various floral forms involved. It differs from that proposed by Tong (1930) and Harms (1930) in that they derived the polygamous, apetalous genera of the tribes Fothergilleae and Distylieae from a petaliferous ancestral type through the transformation of petals into stamens, rather than from an apetalous ancestral type such as *Matudaea*, which was unknown at that time.

In such a series the flowers would represent euanthia, and the morphological nature of the perigon, lacking only in *Distylium* and those species of *Sycopsis* related to *S. dunnii*, and of the hypanthium, would be homologous. If correct, the apetalous genera of Hamamelidoideae may represent the remnants of a line of floral specialization quite apart from that which gave rise to the petaliferous genera, for *Matudaea* has no close morphological counterpart among the petal bearing members of the subfamily. Among the latter group, on the basis of accumulated evidence of wood anatomy, pollen morphology, floral morphology, and floral vascular anatomy (personal observations, in manuscript), the most



primitive genera appear to be *Maingaya* Oliv. and *Dicoryphe* Thou. Their pentamerous (or tetramerous in some species of *Dicoryphe*) flowers contain alternating cycles of sepals, petals, 5(-4) stamens, 5(-4) large staminodia which approach the stamens in shape, and an inner cycle of 10(-8) scales or lobes, all inserted perigynously on the rim of a tubular hypanthium above a half-inferior or essentially inferior ovary.

However, in view of the unusual features of floral morphology and vascular anatomy in *Distylium*, *Sycopsis*, and *Parrotia*, it may be worth considering another, more speculative, interpretation of the course of floral development among at least some of the apetalous genera, leading from a hypothetical unisexual, monoecious, ancestral type, to bisexual pseudanthia through the condensation of inflorescences and the aggregation of staminate and pistillate flowers within a cycle of bracts. Among extant genera the species of *Distylium* could represent an early stage in the development of such pseudanthia. Its naked unisexual flowers have probably been derived from those of a bisexual ancestor through the suppression of the perianth and gynoecium in the case of the lateral staminate flowers, or of the perianth and androecium in the terminal pistillate flowers on each inflorescence axis. Such reduction must be assumed regardless of the phylogenetic sequence in which the genus is placed. The vestigial vasculature in the base of the terminal functional ovaries is evidence of the former presence of such organs. In this genus the condensation of inflorescence axes and the aggregation of bracts and staminate flowers around a terminal pistillate flower have already produced a condition in which the external identity, and even the anatomical identity, of the individual flower is lost, and the inflorescence merges into a false flower.

From a common ancestor with unisexual flowers more or less similar to those of the present day distyliums, the apparently bisexual flowers of *Sycopsis dunnii* and its related species may have developed through a more pronounced reduction of inflorescence axes, resulting in the aggregation and fusion of lateral trimerous primary bract groups with their associated axillary axial tissues and staminate flowers into a tubular false hypanthium around a naked terminal pistil.

From a similar hypothetical ancestor, the capitate inflorescences and bisexual flowers of *Parrotia* could have evolved through the condensation of entire lateral inflorescence axes, resulting in the aggregation and fusion of a variable number of primary bract groups and highly modified lateral staminate flowers in a shallow hypanthium around the persistent naked terminal pistil.

From a condition such as that seen in *Parrotia* it is only a short step, in one direction, to *Sycopsis sinensis* through a lengthening of the hypanthium, with concomitant reduction in the number and size of "tepals," and in the number of stamens developed on its narrowed rim. The morphological origins of the hypanthium of *S. sinensis* would then appear to differ somewhat from those of the similar structure in *S. dunnii*, and the two species would represent an interesting case of phylogenetic



convergence, resulting in urceolate hypanthia that are ruptured by the developing fruit. In another direction could be derived *Fothergilla* and *Parrotiopsis*. In these genera the increased number of stamens may represent either the retention of an ancestral condition or a secondary development.

In the context of a pseudanthial interpretation, the flowers of *Matudaea* might represent a less advanced New World counterpart of *Parrotia*, its aggregated connate bracts not yet having become fused in a hypanthium with the stamens. The vestigial vasculature in the base of the ovary, like that in *Distylium*, might then be attributable to a phylogenetically lost floral envelope which once surrounded the ovary. In *Molinadendron*, on the other hand, the irregular relationships and variable numbers of the stamens and one-trace tepals are suggestive of an aggregation of bracts and stamens similar to those seen in some highly reduced inflorescences of *Distylium buxifolium*.

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