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.

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

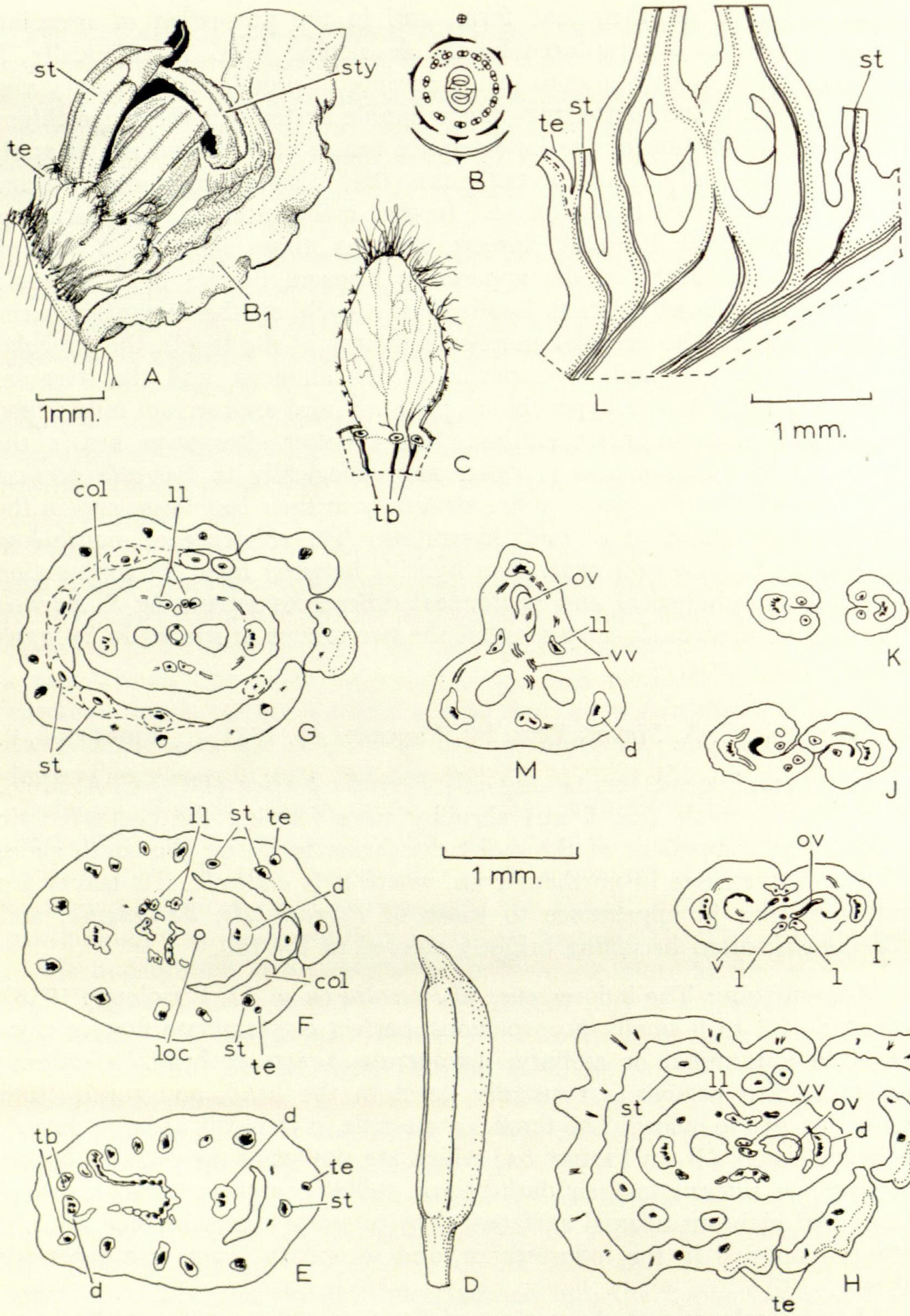

FIGURE 8. **Parrotia persica:** A, view of a flower at anthesis; B, floral diagram; C, drawing from a cleared segment of a hypanthium — note stamen scars, trunk bundles, irregular vascular supply to the tepal; D, stamen; E-K, transverse sections (slightly oblique) of a post-anthesis flower; E, through 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 exserted, 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.

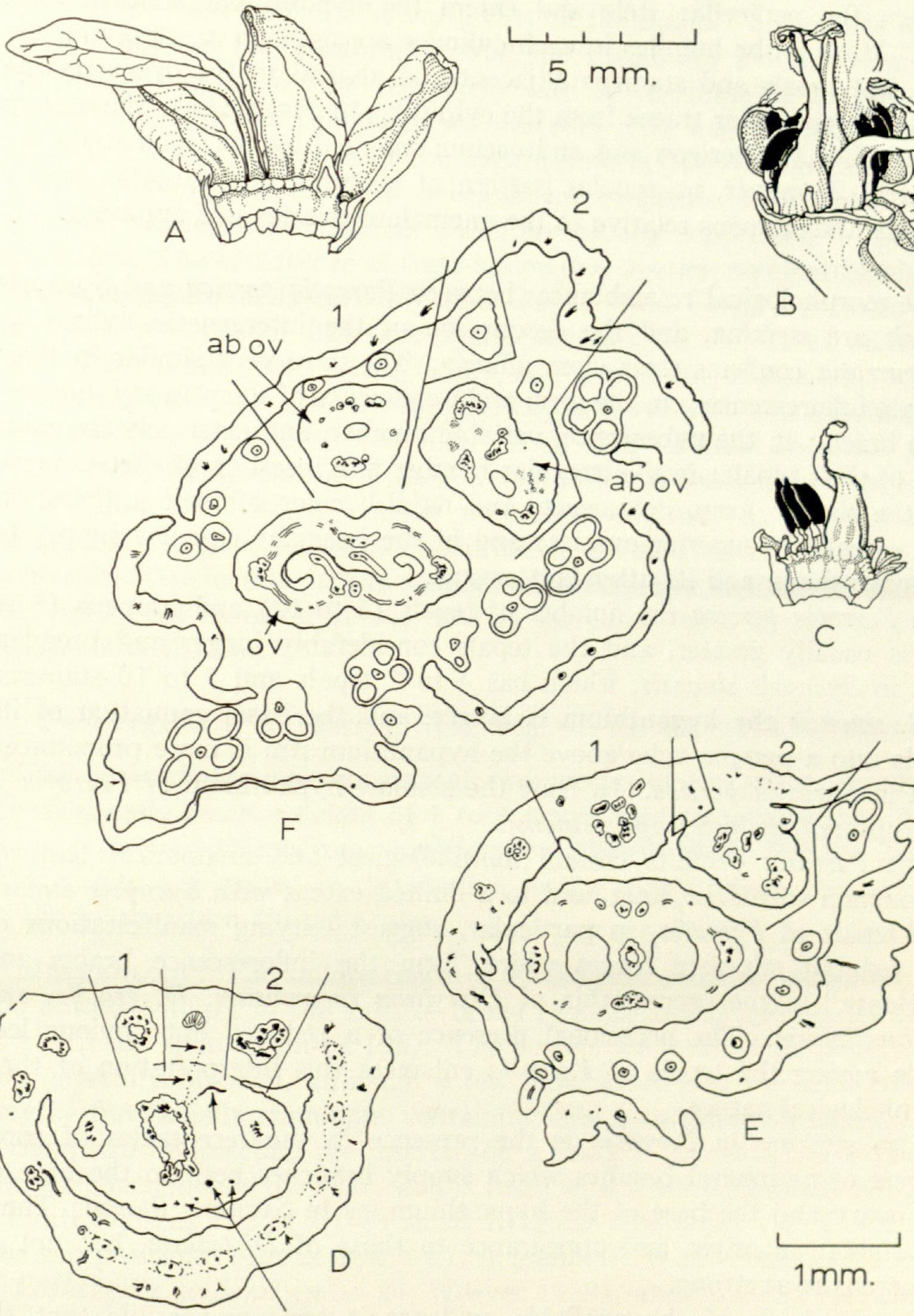

FIGURE 9. **Parrotia persica:** A, leaf-like tepal on hypanthium rim; B, whole flower, near tepals excised — note the single carpel (right) on the hypanthium, with suture directed outward; C, section of hypanthium from B, bearing the carpel; D-F, transverse sections through a flower bearing two anomalous 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 × *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