

## COMPARATIVE ONTOGENY OF THE INFLORESCENCE AND FLOWER OF *HAMAMELIS VIRGINIANA* AND *LOROPETALUM CHINENSE* (HAMAMELIDACEAE)<sup>1</sup>

THOMAS MIONE<sup>2</sup> AND A. LINN BOGLE

Department of Plant Biology, University of New Hampshire, Durham, New Hampshire 03824

### ABSTRACT

A comparative developmental study of the inflorescence and flower of *Hamamelis* L. (4-merous) and *Loropetalum* (R. Br.) Oliv. (4-5 merous) was conducted to determine how development differs in these genera and between these genera and others of the family. Emphasis was placed on determining the types of floral appendages from which the similarly positioned nectaries of *Hamamelis* and sterile phyllomes of *Loropetalum* have evolved. In *Hamamelis virginiana* L. and *H. mollis* Oliv. initiation of whorls of floral appendages occurred centripetally. Nectary primordia arose adaxial to the petals soon after the initiation of stamen primordia and before initiation of carpel primordia. In *Loropetalum chinense* (R. Br.) Oliv. floral appendages did not arise centripetally. Petals and stamens first arose on the adaxial portion, and then on the abaxial portion of the floral apex. The sterile floral appendages (sterile phyllomes of uncertain homology) were initiated adaxial to the petals after all other whorls of floral appendages had become well developed. In all three species, two crescent shaped carpel primordia arose opposite each other and became closely appressed at their margins. Postgenital fusion followed and a falsely bilocular, bicarpellate ovary was formed. Ovule position and development are described. The nectaries of *Hamamelis* and sterile phyllomes of *Loropetalum* rarely develop as staminodia, suggesting a staminodial origin. However, these whorls arise at markedly different times and are therefore probably not derived from the same whorl of organs in a common progenitor. This hypothesis seems probable when one considers that the seemingly least specialized genus of the tribe, *Maingaya*, bears whorls of both staminodia and sterile phyllomes inside its whorl of stamens.

THE HAMAMELIDOIDEAE is the largest of the six subfamilies of the Hamamelidaceae and consists of five tribes and 23 genera (including the intergeneric hybrid *Sycoparrotia*). The largest of these tribes is the Hamamelideae with ten genera, including *Hamamelis* L. and *Loropetalum* (R. Br.) Oliv. Genera of this tribe are concentrated in eastern Asia (5 genera) and Queensland, Australia (3 genera), but also occur in eastern North America, eastern and southeastern Africa, and Madagascar.

*Hamamelis* is represented by six or seven species. Three or four species occur in North America (Ernst, 1963; Standley, 1937), depending on whether one recognizes *H. macro-*

*phylla* Pursh of the Gulf States as a distinct species or as a variety of *H. virginiana* (*H. var. macrophylla* (Pursh) Nutt. (Sargent, 1920). *Hamamelis virginiana*, the Common Witch-Hazel of eastern North America, is the most widely distributed species (see, e.g., Little, 1977). *Hamamelis vernalis*, with its relatively small flowers and stature is "confined to gravelly beds and rocky banks of streams in the Interior Highlands of Missouri, Arkansas, and eastern Oklahoma" (Bradford and Marsh, 1977). Interestingly, *H. virginiana* and *H. vernalis* are sympatric in a few areas and have even been observed to flower simultaneously (Bradford and Marsh, 1977). The least known American species of *Hamamelis* is *H. mexicana* of the state of Nuevo León, Mexico (Standley, 1937).

There are three *Hamamelis* species in eastern Asia (Sargent, 1890; Chang, 1979). Like *H. virginiana* in North America, *H. mollis* is widely distributed in eastern Asia, occurring at midaltitudes in seven provinces of south-central through southeastern China (Chang, 1979). Other *Hamamelis* species of eastern Asia are *H. japonica* of mountain forests in Japan (Sargent, 1890) and *H. subequalis* of two small areas of eastern China (Chang, 1979).

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<sup>2</sup> Current address: University of Connecticut, Department of Ecology and Evolutionary Biology, Storrs, CT 06269-3043.

The related genus *Loropetalum* is native to eastern Asia, where 3–4 species and one variety have been recognized. *Loropetalum* is distributed from Japan and eastern China to the Khasia Hills of northeastern India (Chang, 1979; Krüssman, 1977). The best known of these is *L. chinense*, which occurs in Japan and in 12 contiguous provinces of southeastern China (Creech, 1960; Chang, 1979; Chun, 1934). Mione (1987) reviewed the species of *Hamamelis* and *Loropetalum*.

*Loropetalum* and *Hamamelis* were treated as congeners from the time of *Loropetalum*'s first description by Robert Brown (1818). Although Brown first described *Loropetalum* as *H. chinensis*, he made note of some differences which might justify its separation as a separate genus and suggested the name *Loropetalum*. Later, Oliver (1862) raised the taxon to generic rank under this name.

Flowers of many genera of the Hamamelidaceae bear sterile appendages around the ovary. Determination of the type of floral appendage from which these structures have evolved has been problematic. For convenience, the term staminodia will be used here to designate sterile floral appendages which are most certainly derived from stamens, i.e., appendages which are morphologically similar to stamens but are sterile. The generalized term phyllome (sensu Esau, 1965) will be used to refer to sterile floral appendages which (except for putative atavisms) do not appear to be staminodial.

Previous studies of floral organogenesis in genera of the Hamamelidaceae have been made by Baillon (1871–1873, *Fothergilla*, *Hamamelis*), Shoemaker (1905, *Hamamelis*), Endress (1967, *Corylopsis*; 1976, *Fothergilla*, *Matudaea*), Wisniewski and Bogle (1982, *Liquidambar*), and Bogle (1987, *Rhodoleia*).

In this study inflorescence and flower morphology and ontogeny of *Hamamelis virginiana* and *H. mollis* are compared with that of *Loropetalum chinense*. An objective of this comparison is to provide basic information on floral organogenesis of these genera that may be used to construct phylogenetic hypotheses for the species and genera of the tribe and family. In addition, we attempt to answer the question of whether or not the sterile floral appendages which occur opposite the petals in both genera (nectaries in *Hamamelis*; sterile phyllomes in *Loropetalum*) are attributable to the same cycle of floral appendages in the common ancestor.

**MATERIALS AND METHODS**—Inflorescence and flower buds in all stages of development

were collected for all three species. For *Hamamelis virginiana*, collections were primarily made from natural populations in Durham and Lee, NH. Material of *H. mollis* (and some material of *H. virginiana*) was collected from cultivated plants on the University of New Hampshire campus. Material of *Loropetalum chinense* was collected from a shrub purchased from Kingsville Nursery, Kingsville, Maryland, and cultivated in the University of New Hampshire greenhouses. Material was collected every other week from the fall of 1985 to the fall of 1986 and immediately fixed and stored in a solution of 5% formalin-5% glacial acetic acid-90% ethyl alcohol (70%). Additional collections were made sporadically until late October of 1988.

For light microscopy most buds were dissected in 70% ethanol and observed with a dissecting stereomicroscope. Other buds were dissected, dehydrated in two or three changes of 100% ethanol and critical-point dried. This technique allowed observation of material which was too small for clear observation in alcohol, where refraction of light by the medium reduced resolution.

Specimens prepared for scanning electron microscopy (SEM) were dehydrated in two or three changes of 100% ethanol, critical-point dried for 8–10 min in a Samdri-790 using liquid carbon dioxide, mounted on stubs with conductive carbon paint, coated with about 200 Å of 60/40 gold-palladium on a Technics Hummer V Sputter Coater and examined on an AMR Model 1000 Scanning Electron Microscope at 20 kV.

Voucher specimens were deposited in the Hodgdon Herbarium (NHA) of the University of New Hampshire. Preserved material is stored in the Morphology Laboratory at the University of New Hampshire.

**RESULTS**—*Organography*—In *Hamamelis virginiana* short, occasionally branched, axillary peduncles bear clusters or heads of three (1–5) flowers and a terminal, apical residuum (Fig. 1). In its diagrammatically expanded form the inflorescence is racemose and consists of two orders of axes (Fig. 3).

Flowers of *Hamamelis virginiana* are complete, 4-merous, perigynous, and functionally bisexual (Fig. 5, 25). At maturity a subtending bract (Fig. 1, estipulate B<sub>2</sub>) and two bracteoles (Fig. 1, b<sub>3</sub>) surround each flower. The subtending bract of each flower (Fig. 1, estipulate B<sub>2</sub>; Fig. 15, rB) is directed away from the inflorescence axis and encloses the two smaller bracteoles (Fig. 1, b<sub>3</sub>; Fig. 15, rb). Sepals, petals, stamens, and nectaries occur in alternating

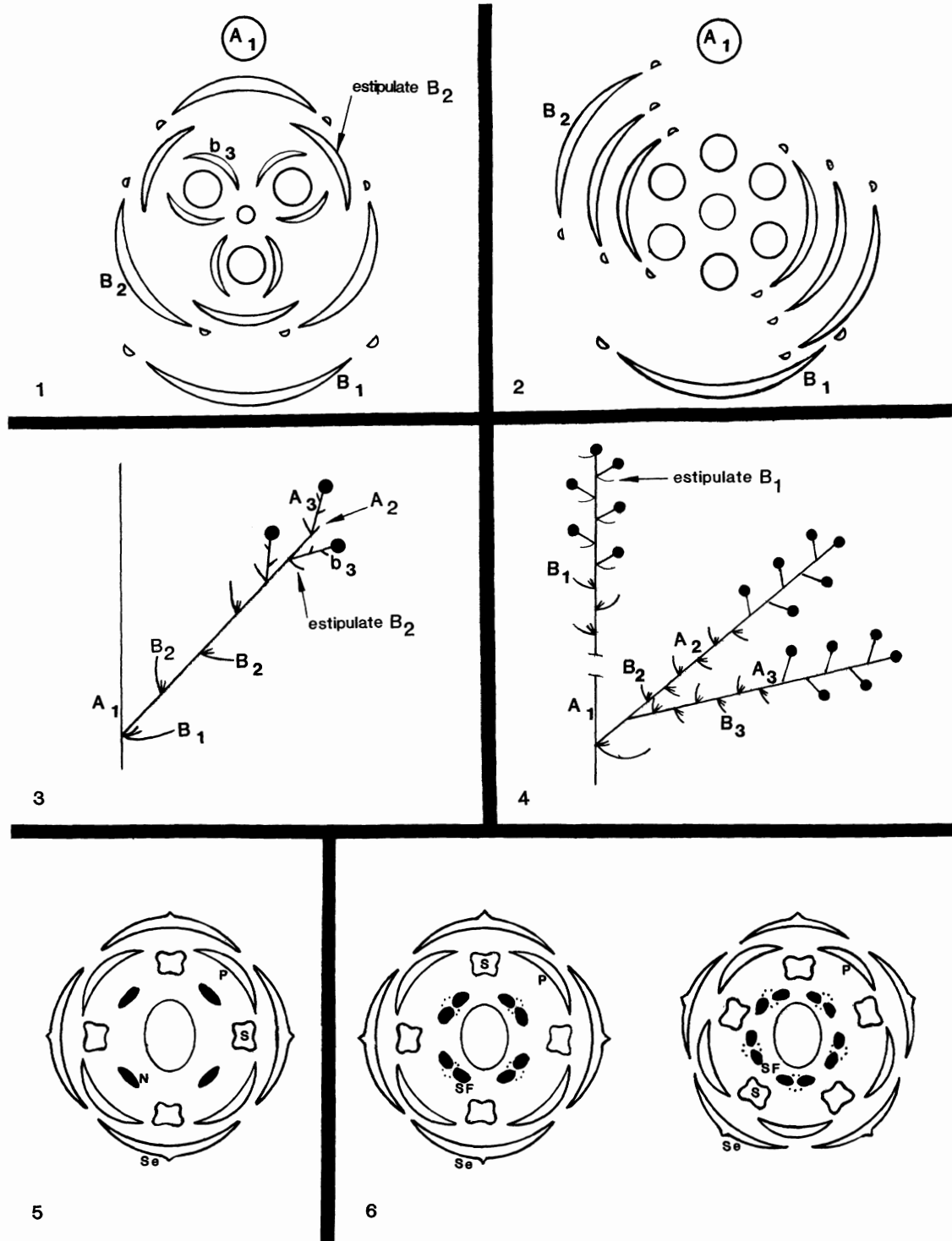


Fig. 1-6. Diagrammatic representation of inflorescence and floral organization of *Hamamelis virginiana* and *Lopetalum chinense*. 1. Inflorescence of *H. virginiana* to indicate the relationship of bracts ( $B_1$ ,  $B_2$ ), bracteoles ( $b_3$ ), flowers (large circles), apical protrusion (small circle) and the primary axis ( $A_1$ ). 2. Inflorescence of *L. chinense*, equivalent to  $A_2$  or  $A_3$  in Fig. 4, to indicate the relationship of bracts ( $B_1$ ,  $B_2$ ), flowers (circles) and primary axis ( $A_1$ ). Note absence of bracts subtending flowers. 3. An expanded inflorescence (modified raceme) of *H. virginiana* to indicate the relationship of the primary, secondary, and tertiary axes ( $A_1$ - $A_3$ ), bracts ( $B_1$ ,  $B_2$ ) and bracteoles ( $b_3$ ). 4. An expanded inflorescence (panicle) of *L. chinense* to indicate the relationship of the primary, secondary and tertiary axes ( $A_1$ - $A_3$ ) and bracts ( $B_1$ - $B_3$ ). Bracts subtending flowers present on  $A_1$ , absent on  $A_2$  and  $A_3$ . 5, 6. Floral diagrams of *H. virginiana* and *L. chinense*, respectively. Se, sepal; P, petal; S, stamen; N, nectary; SF, sterile phyllome—dots indicate possible fusion of sterile phyllome bodies.

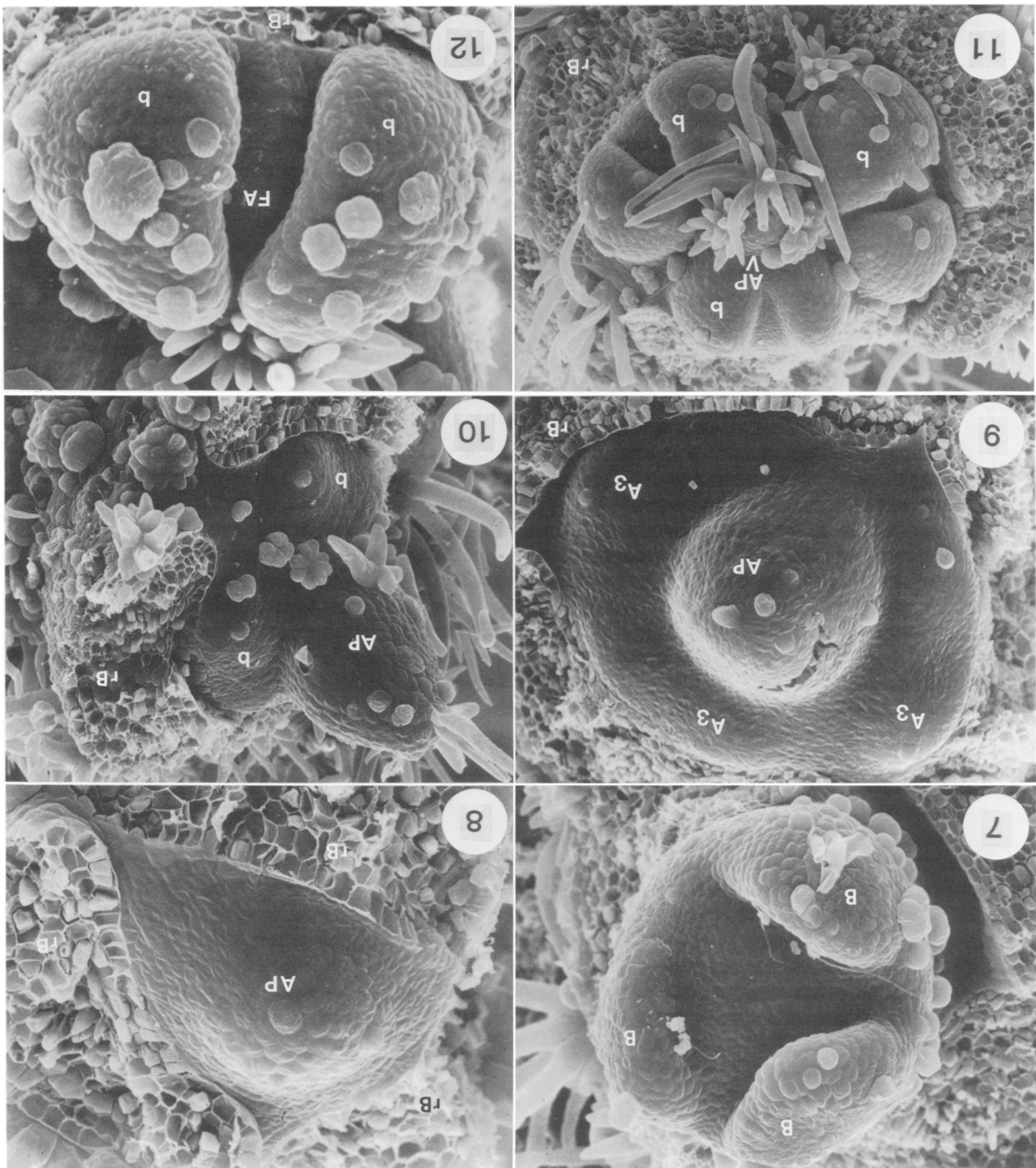


Fig. 7-12. *Hamamelis virginiana*. 7. Three sequentially initiated, stipulate, secondary bracts (B) characterize the transition to the reproductive state.  $\times 160$ . 8. An apical protrusion (AP) arises at the center of the inflorescence apex. Tertiary axes (A<sub>3</sub>) arise axillary to the stipulate, secondary bracts (removed bract, rB), removed bract.  $\times 340$ . 9. (*H. mollis*) Tertiary axes (A<sub>3</sub>) arise axillary to the stipulate, secondary bracts (removed bract, rB) around the apical protrusion (AP).  $\times 177$ . 10. Each of the three tertiary axes gives rise to a pair of lateral bractole primordia (b). AP, apical protrusion; rB removed bract.  $\times 163$ . 11. Stellate trichomes begin to develop on the bract (b) and apical protrusion (AP). rB, removed bract.  $\times 129$ . 12. A floral apex (FA) arises between each pair of lateral bractole primordia (b).  $\times 117$ .

whorls (Fig. 5). Aestivation of the obtuse sepals is slightly imbricate with the median sepals enclosing the lateral sepals. Petals are generally yellow, strap-shaped, circinate within the bud, and reflexed at anthesis. The short antesealous stamens are bisporangiate (Shoemaker, 1905); each sporangium dehisces laterally by means of an adaxially hinged valve (Fig. 25, V). The antepetalous, scalelike nectaries are short, recurved (Fig. 25) and appressed against the petals or nearly so. At maturity, small amounts of nectar are exuded from the adaxial surface of each nectary. The partly inferior, sealed ovary is falsely bilocular (Fig. 26, 27) with one anatropous, parietal, pendulous ovule inserted at the top of each locule (Fig. 28). A second ovule may abort early in development (Baillon, 1871–1873). Two adjacent, erect styles rise from the bicarpellate ovary (Fig. 24, 25, St). A year after flowering the woody, loculicidal capsule dehisces and forcibly ejects the seeds.

In a single mature flower collected in Mansfield, Connecticut, a putative atavism (reversion to a previous evolutionary state) was found: a staminodium with one completely formed, laterally borne, microsporangium within an adaxially hinged valve occurred in a position normally occupied by a nectary. Pollen of this staminodium was found to be completely formed but only 7% stainable ( $N = 320$ ) with aniline blue in lactophenol (Hauser and Morrison, 1964). Aside from the presence of this microsporangium/lateral valve, the putative atavism was nectarylike in appearance.

In *Loropetalum chinense* three to eight tightly clustered flowers terminate a slender, axillary peduncle or vegetative branch (Fig. 2). Most often the inflorescence is a panicle consisting of two sequentially maturing racemes (Fig. 4). When a vegetative branch and an inflorescence depart from a common node, the inflorescence is not branched and can be characterized as a raceme.

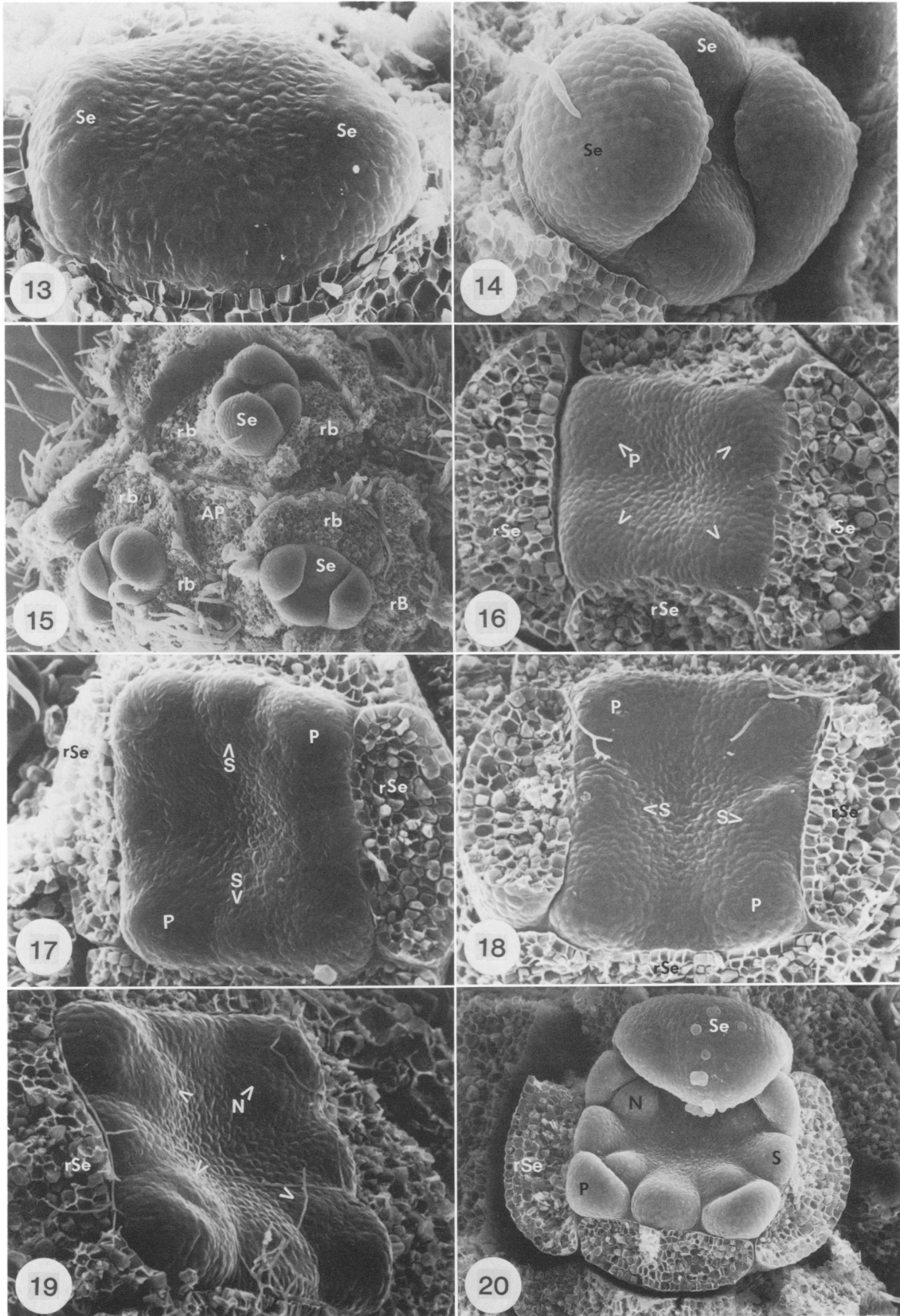
Five to six (–7) alternate, subdistichous bracts occur on each peduncle of an axillary inflorescence (Fig. 2, 4, B<sub>2</sub>). From proximal to distal portions of the peduncle, the internodes get progressively shorter and a transition occurs from obliquely based, apiculate bracts flanked by similarly shaped smaller stipules, to minute, linear bracts flanked by longer, linear stipules. The lowest bract is about 7 mm wide × 11 mm long while the highest is linear and about one mm long.

Below a terminal inflorescence, two or three (1–4) alternately arranged, stipulate bracts are transitional between stipulate leaves and the

flowers (Fig. 4). In a terminal inflorescence, one or rarely two minute, linear bracts may subtend a flower (Fig. 4, 48). When two bracts are present they may be opposite each other or one may be directly above the other. The presence of these minute bracts does not seem to have an effect on the arrangement of flowers in the inflorescence.

Flowers of *Loropetalum chinense* are complete, 4- (70%) or 5- (30%) merous ( $N = 345$ ) and functionally bisexual (Fig. 6) with a nearly inferior ovary. Sepals, petals, stamens, and sterile phyllomes occur in alternating whorls (Fig. 6). Aestivation of sepals is valvate. Flowers may have two or three adjacent sepals which are partially to entirely connate. Petals are white to cream-colored, strap-shaped, and circinate within the bud; at anthesis they remain in close proximity to each other. The antesealous stamens each bear a 0.5–0.75 mm long, produced connective at their apex. These hornlike projections are connivent toward the center of the flower and over the short styles. The anthers are tetrasporangiate. The two laterally facing valves of each pair of microsporangia are hinged at the outer margins with dehiscence occurring along a median, vertical suture. The sterile phyllomes are antepetalous, white, short, stout, fleshy bodies which are relatively minute compared to the other floral appendages (Fig. 6, 40, 41, 46, 47). We found sterile phyllomes to be either singly constructed, bilobed (rarely trilobed, Fig. 41) or to be composed of two distinctly separate units. Most often one, two, or even three sterile phyllomes of a flower were bilobed, or composed of two separate adjacent structures, while the remainder were single structures. We saw no visible evidence of nectar secretion by these structures. The bicarpellate, falsely bilocular ovary (Fig. 44) bears one parietal, pendent, anatropous ovule in each locule (Fig. 45, 46). A second ovule may abort during development (Bogle, 1968).

A putative atavism occurred in a few flowers of a single inflorescence of *Loropetalum chinense*: a staminodium occurred opposite one or more of the petals, in the position normally occupied by a sterile phyllome (Fig. 47). Both the number and morphology of the anomalous staminodia varied from flower to flower within the inflorescence. For example, in one flower a complete whorl of staminodia was present and in another flower only two staminodia were present. In flowers not having a complete whorl of staminodia, normal sterile phyllomes occurred where staminodia were not present (Fig. 47).





Rarely, a petaloid staminodium occurred in the position normally occupied by a petal. Petaloid staminodia had only one laterally facing pair of microsporangia as opposed to the two laterally facing pairs of microsporangia of a normal stamen (Fig. 49). The presence of pollen was not assessed in either of the types of staminodial-atavisms that occurred in *Loropetalum chinense*.

*Organogenesis*—In *H. virginiana*, during early spring, vegetative shoot apices arise in the axils of some of the peduncle bracts of the previous year and in the leaf axils of the growth of the current year. Each vegetative apex which is axillary to a peduncle bract and some of the apices which are axillary to leaves of the year make a transition to the reproductive state. Each apex sequentially produces three spirally arranged stipulate bracts (Fig. 3, stipulate B<sub>2</sub>). When the peduncle (secondary axis) is very small these bracts, with their corresponding pairs of stipules, remain closely appressed to the secondary axis and may form three-parted sheathlike structures. These sheaths may protect the apical meristem which, at this point, is making the transition to the reproductive state. The three stipulate bracts remain spirally arranged during elongation of the peduncle.

The transition from the vegetative to the reproductive state occurs in mid-May in Durham and Lee, New Hampshire, and is characterized by the sequential production of three spirally arranged, estipulate bracts (Fig. 1, 3, estipulate B<sub>2</sub>; Fig. 7). Each inflorescence apex then produces a somewhat conical, central apical protrusion (Fig. 8). Three tertiary axes arise sequentially around the base of the apical protrusion (Fig. 9), each in the axil of one of the estipulate bracts. The plastochron between the initiation of the tertiary axes is quite short, occasionally approaching simultaneity. At this time the apical protrusion has become determinate (Fig. 9–11, 15).

Development of the flanks of each transversely oblong apex (tertiary axis) gives rise to

a pair of dome-shaped, lateral bracteole primordia (Fig. 9, left; Fig. 10–12 and 15) that enlarge and cover the floral apex (Fig. 12). Beneath the bracteoles, an oblong floral apex forms in line with the secondary axis (Fig. 12). Trichomes then develop on the apical residuum and the newly formed bracteoles (Fig. 10–12).

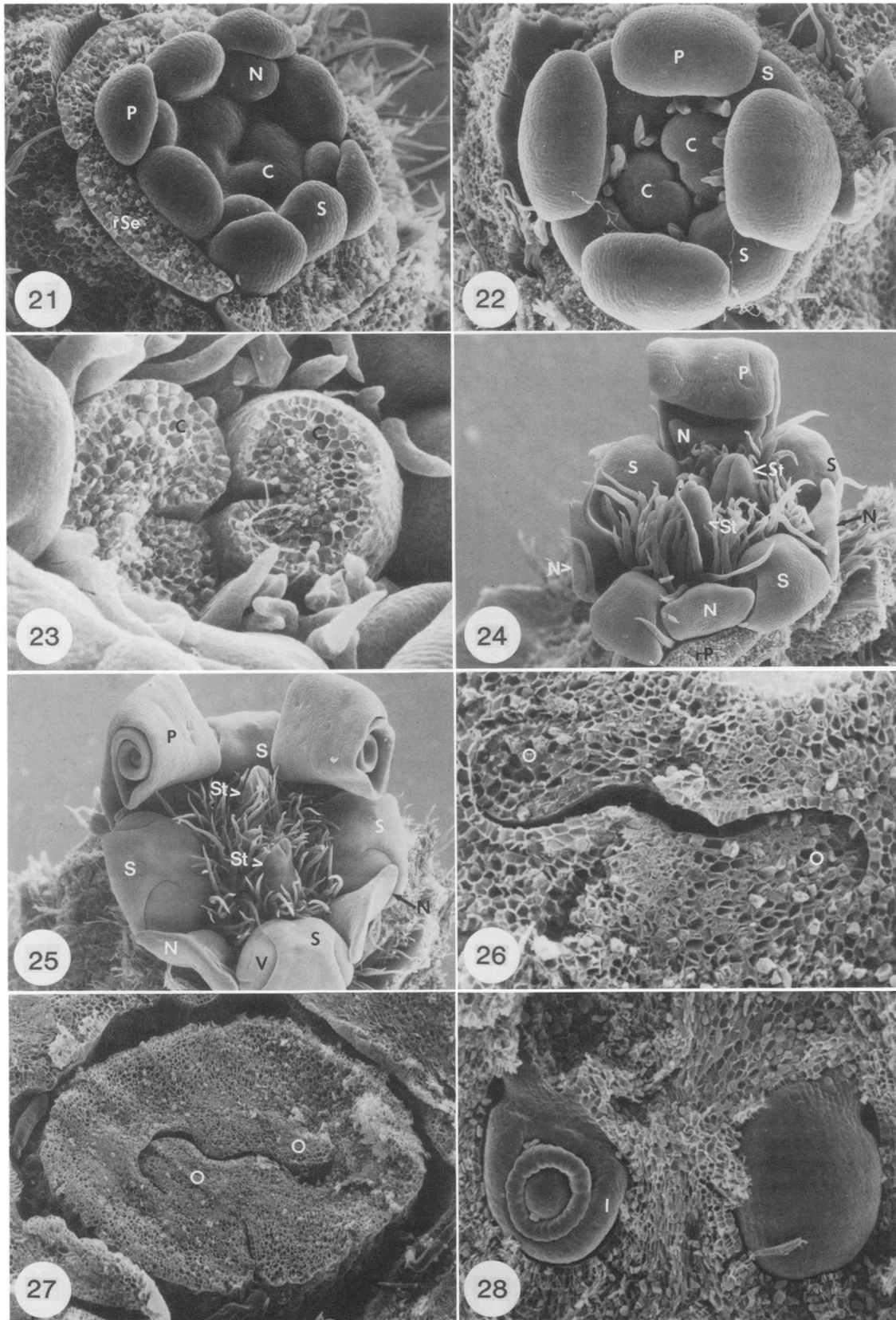
On the newly formed floral apex median sepals are initiated first with the lower median sepal arising prior to the upper median sepal (Fig. 13, lower median Se on left). Lateral sepals arise simultaneously after the median sepals have become well developed (Fig. 14, 15). The first indication that sepal aestivation will become imbricate occurs when the median sepals grow to be as wide as the floral apex plus the lateral sepals, while the lateral sepals grow only as wide as the floral apex (Fig. 16–18). At this stage the floral apex is flat, and somewhat square in outline.

Beneath the overtopping sepals, petal primordia arise simultaneously in the corners of the floral apex (Fig. 16). When petal and stamen primordia are initiated the lower median sepal is still slightly larger than the upper median sepal. After all of the petal primordia have arisen, the stamen primordia arise alternate to them. Most often, simultaneous initiation of median stamens is followed by simultaneous initiation of lateral stamens (Fig. 17). Occasionally, lateral stamens arise before median stamens (Fig. 18). The nectary primordia are then initiated simultaneously, alternate to the stamens and opposite (adaxial to) the petals (Fig. 19–21).

The center of the floral apex becomes deeply concave after initiation of the nectaries and prior to the inception of carpel primordia (Fig. 19, 20). Two crescent-shaped carpel primordia arise as mirror images of each other at the center of the floral apex (Fig. 21). The orientation of the carpel primordia is such that one is anterior and one is posterior. In other words, the carpel primordia are somewhat parallel to the median sepals. As the carpels grow upward, a centrally facing vertical cleft is retained on

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Fig. 13–20. *Hamamelis virginiana*. 13. Oblong floral apex develops in line with the secondary axis. Lower median sepal (left, Se) arises prior to the upper median sepal (right, Se). Floral apex turned 90° relative to Fig. 12. ×328. 14. Lateral sepals (Se) arise simultaneously (top and bottom) after median sepals (left and right) have enlarged. Lower median sepal (right) has remained larger than the upper median sepal (left). ×199. 15. Three floral buds are evenly distributed about the apical protrusion (AP). Se, sepal; rb, removed bracteole; rB, removed bract. ×82. 16. Petal (P, arrows) initiation occurs simultaneously at the corners of the floral apex, which is square in outline. Note that median sepals (left and right, rSe) are larger than lateral sepals (top and bottom). ×239. 17. Median stamens (S) usually arise prior to lateral stamens. P, petal; rSe, removed sepal. ×244. 18. Occasionally, lateral stamens (S) initiate prior to median stamens. P, petal. ×242. 19. Nectary primordia (N, arrows) arise simultaneously, adaxial to petal primordia. rSe, removed sepal. ×240. 20. The floral apex becomes deeply concave after nectaries (N) have become somewhat developed and prior to carpel initiation. S, stamen; P, petal; Se, sepal. ×226.





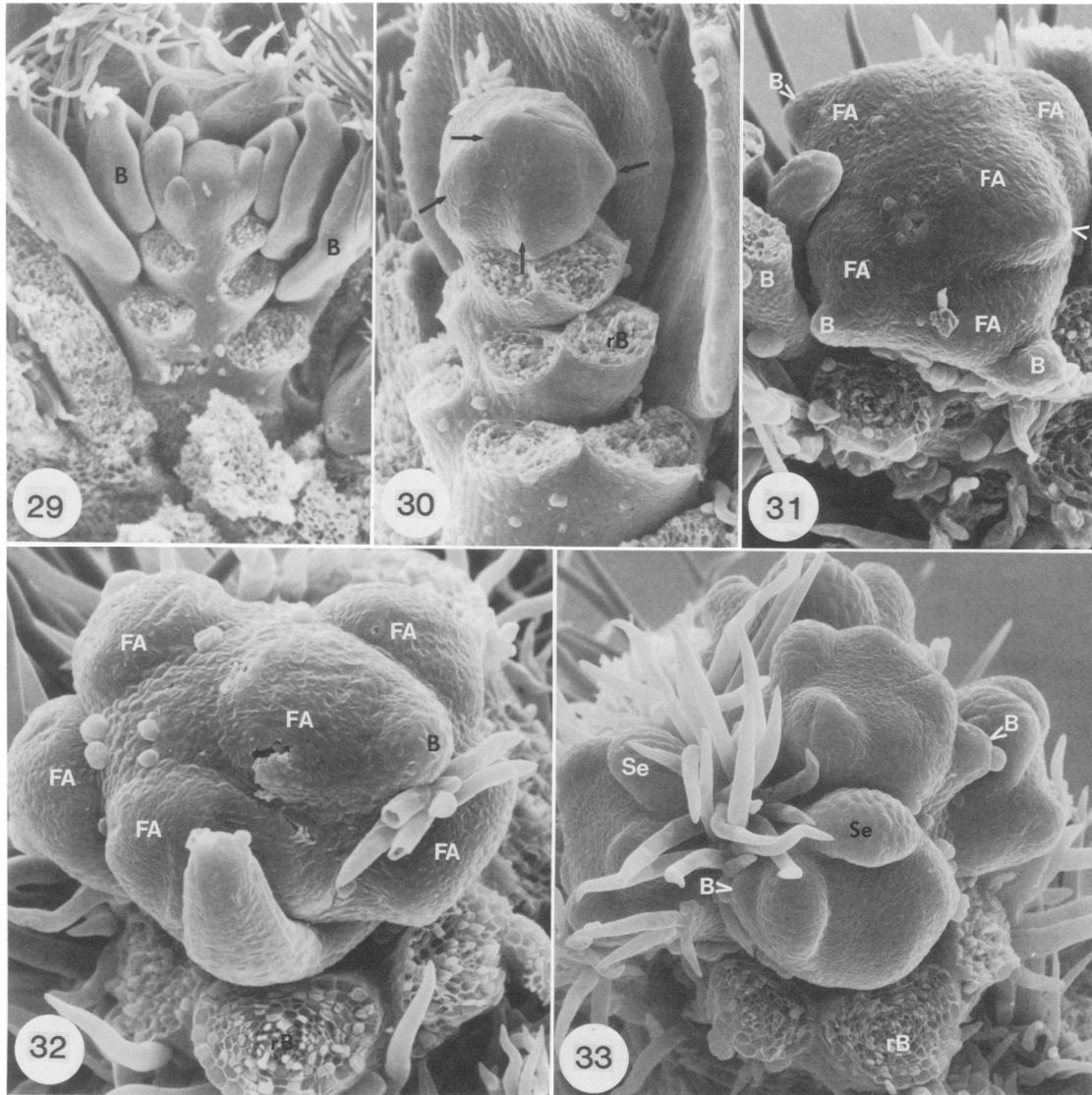
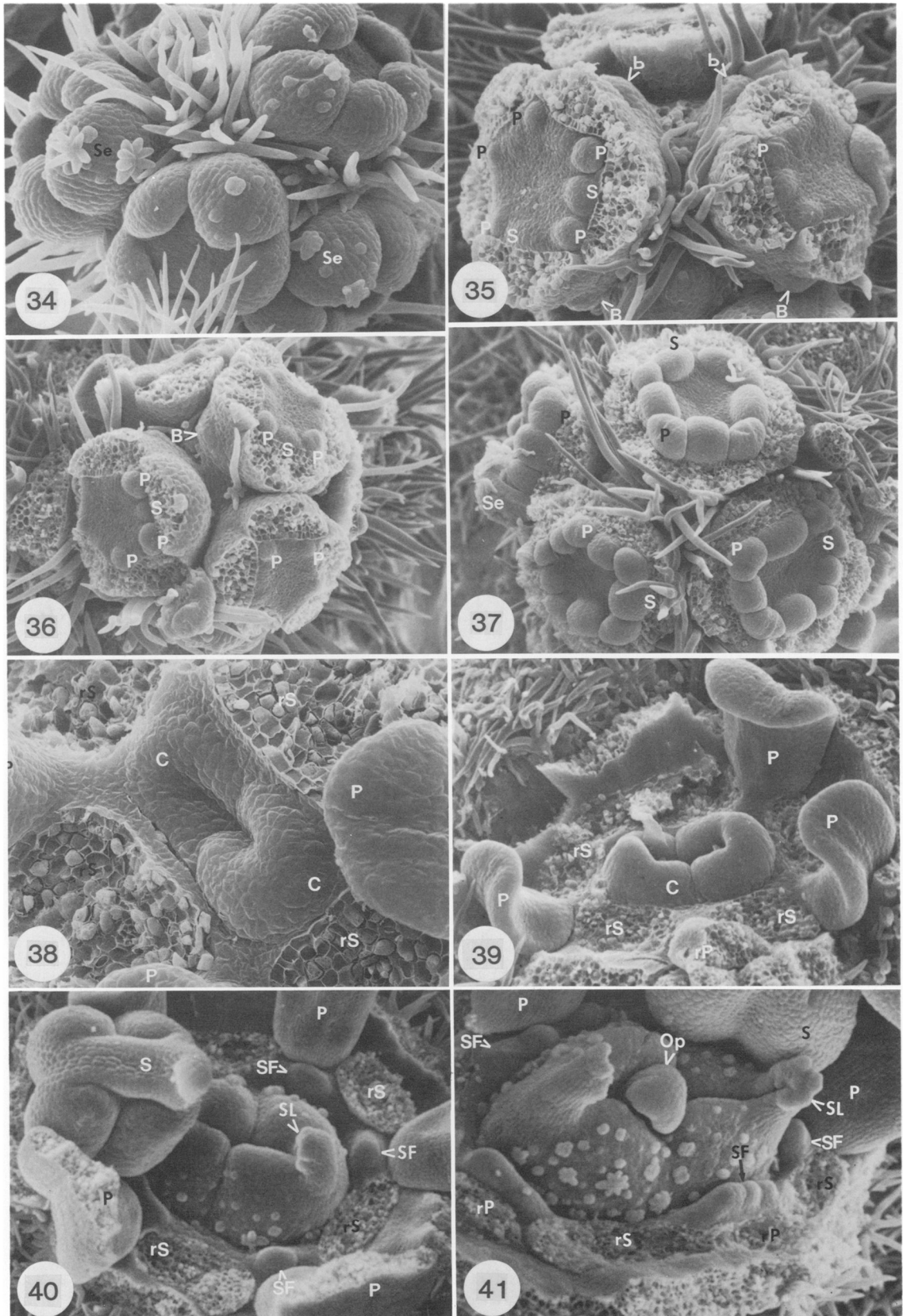


Fig. 29–33. *Loropetalum chinense*. 29. Apical meristem is small and low prior to the transition to the reproductive state. Pairs of stipules which flank the subdistichous bracts (B) have been removed.  $\times 58$ . 30. Bracts (rB) and their flanking pairs of stipules have been removed to show that initially, the inflorescence apex expands where bracts and stipules are not closely appressed (arrows).  $\times 105$ . 31, 32. Three to eight domelike floral apices (FA) arise simultaneously on the inflorescence apex. At the same time a subtending bract (B) arises abaxial to each flower.  $\times 111$ ,  $\times 133$ . 33. Sepals (Se) arise in a seemingly random manner. A bract (rB) and its flanking pair of stipules have been removed. B, bract.  $\times 102$ .

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Fig. 21–28. *Hamamelis virginiana*. 21. Two crescent-shaped carpel primordia (C) are initiated parallel to the median sepals. N, nectary; S, stamen; P, petal; rSe, removed sepal.  $\times 117$ . 22. Petals (P) broaden and elongate, stamens (S) and nectaries enlarge, carpels (C) grow upward and trichomes develop around the ovary.  $\times 65$ . 23. Transverse, hand section. Carpel (C) margins become closely appressed and postgenitally fuse.  $\times 284$ . 24. Petal (P) elongation continues, stamen (S) valves begin to differentiate, nectaries (N) become broader distally and carpels elongate into styles (St). rP, removed petal.  $\times 44$ . 25. Petals (P) become circinnately coiled while all other organs continue to differentiate. N, nectary; V, anther valve; St, style; S, stamen.  $\times 31$ . 26. Transverse, hand section. A single ovule (O) arises in each carpel. Note the falsely bilocular ovary.  $\times 257$ . 27. Transverse, hand section. Ovules (O) usually arise on opposite sides of the ovarian cavity.  $\times 59$ . 28. Longitudinal, dissection. Integuments arise as girdling primordia with the inner integument arising prior to the outer integument (I). The outer integument ceases enlarging near the funiculus, and as a result becomes crescent shaped.  $\times 135$ .



each carpel from the original crescent shape of the primordium (Fig. 22–25). At the base of the carpels the margins become closely appressed and postgenital fusion takes place resulting in the formation of the ovary. Here, the centrally facing vertical clefts give rise to the falsely bilocular ovary (Fig. 26, 27). Above the ovary each carpel elongates into a style (Fig. 24). The style retains some evidence of its original crescent shape into late flower development (Fig. 24, 25).

Most often the two ovules arise on opposite sides of the ovarian cavity (one per carpel, diagonally across from each other as seen in transverse section, Fig. 26, 27). Less commonly the two ovules arise on the same side of the ovarian cavity, one per carpel. During ovule development, integuments are initiated centrifugally (Fig. 28). Both integuments are initiated as girdling (completely circular) primordia but, near the funiculus, the outer integument ceases developing and becomes crescent shaped (Fig. 28, I). Both integuments eventually overtop the nucellus.

Late flower development is characterized by elongation of petals, differentiation of stamens and nectaries and profuse development of trichomes around the ovary (Fig. 25).

In *Loropetalum chinense*, development of inflorescences which terminate vegetative branches starts in June, but the majority of the axillary, vegetative apices make the transition to the reproductive state in late August or early September. Most often, an inflorescence which terminates a vegetative branch develops earlier than the axillary inflorescences on that branch.

Inflorescences that terminate vegetative branches are racemose in form (Fig. 4, A<sub>1</sub>). Inflorescences of lower axillary buds are usually paniculate, consisting of two sequentially maturing racemes (Fig. 4, A<sub>2</sub>, A<sub>3</sub>). If a vegetative branch departs from the node, however, the inflorescence is racemose in form. The peduncles of the axillary inflorescences elongate as the terminally borne flowers are nearing anthesis. When two floral axes depart from a node (Fig. 4, A<sub>2</sub>, A<sub>3</sub>) both develop within the same

bud scales until the expansion of the first maturing axis causes the bud scales to open. A secondary bract may be lacking in the base of the tertiary axis (Fig. 4).

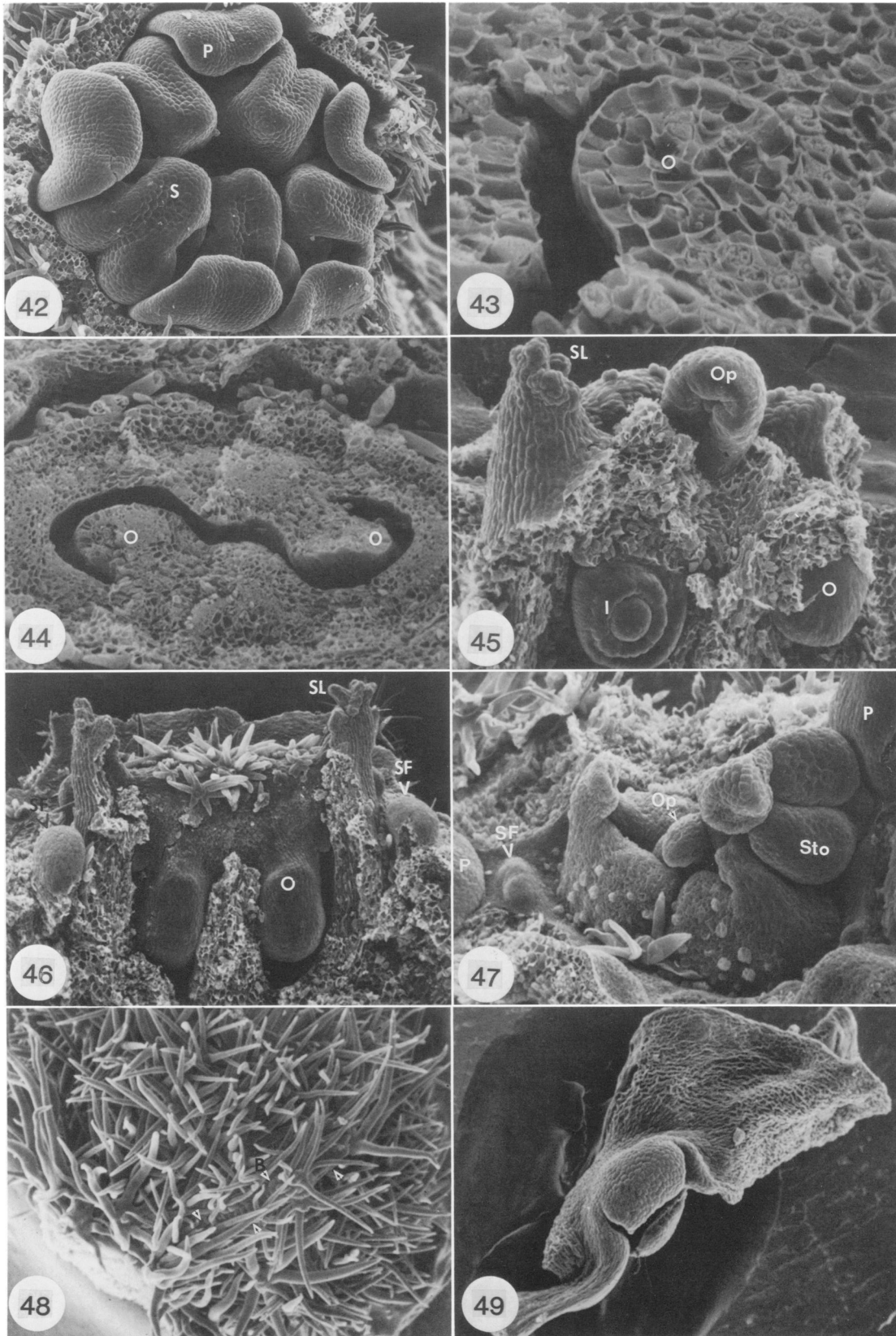
The transition of an apical meristem from the vegetative state (Fig. 29) to the reproductive state initially involves expansion of the inflorescence apex where bracts and stipules have not been closely appressed (Fig. 30, arrows). The inflorescence apex then develops three to eight floral apices; at the same time bract primordia arise to subtend each floral apex (Fig. 31, 32). Occasionally, two bracts develop opposite each other on the periphery of the floral apex (Fig. 35). When this occurs, perhaps these bracts are best interpreted as the lower being the bract to which the flower is axillary and the upper a bracteole of the floral pedicel. On axillary inflorescences these bracts cease developing after their initiation (Fig. 4, lacking on A<sub>2</sub> and A<sub>3</sub>; Fig. 33, 35; 36). On some flowers of inflorescences that terminate vegetative branches, however, these bract primordia develop into minute, linear bracts which remain closely appressed to the flower (Fig. 4, A<sub>1</sub>; Fig. 48).

Sepal primordia (four or five) arise on each floral apex in a seemingly random manner (Fig. 33). By the time the sepals are well developed, stellate trichomes have grown on their surfaces and from between the flowers (Fig. 34–37). The floral apex is generally flat during sepal development (Fig. 33–36).

Prior to the initiation of petals and stamens the sepals grow to partially cover the slightly concave apex (Fig. 34). Petal and stamen initiation is unidirectional (sensu Tucker, 1984). Petals and then stamen primordia are initiated first on the adaxial side of each floral apex (Fig. 35, 36). When petal and stamen primordia on the adaxial side of the floral apex have become domelike, petal and then stamen primordia are initiated on the abaxial side (Fig. 35, 36). Adaxial stamen primordia may be initiated at the same time as abaxial petal primordia. All petal and stamen primordia become roughly equal in size. At this stage the floral apex is somewhat

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Fig. 34–41. *Loropetalum chinense*. 34. Sepals (Se) grow to partially cover the floral apex. Stellate trichomes develop between flower buds and on sepals. ×67. 35, 36. Petal (P) and then stamen primordia (S) first arise on the adaxial portion of the floral apex and then on the abaxial portion of the floral apex. B, bract; b, bracteole. ×134, ×111. 37. All petal (P) and stamen (S) primordia become approximately the same size. Floral apex is now slightly concave. Se, sepal. ×79. 38. Two crescent shaped carpel primordia (C) arise as mirror images of each other on the floral apex. P, petal; rS, removed stamen. ×235. 39. Carpel (C) margins become closely appressed and postgenitally fuse. P, petal; rS, removed stamen. ×71. 40, 41. At the time when the stigmatic lobes (SL) are developing on the styles, sterile phyllomes (SF) arise adaxial to the petals (P). Note the presence of an anomalous protruding ovule (Op) in Fig. 41. rS, removed stamen; rP, removed petal; S, stamen; P, petal. ×52, ×58.



concave (Fig. 37). Later, as carpels are being initiated, stamen connectives elongate and become connivent (Fig. 42).

Two crescent-shaped carpel primordia arise as mirror images of each other at the center of each floral apex (Fig. 38). When carpel initiation occurs, the petals and stamens are quite differentiated. The carpel margins become closely appressed; postgenital fusion follows (Fig. 39). More rapid upward growth occurs at the fold in each carpel giving rise to the styles (Fig. 40). The styles, in turn, give rise to the stigmatic lobes (Fig. 41, 45, 46).

Sterile phyllomes are the last whorl of appendages to arise in the flowers of *Loropetalum chinense*. Sterile phyllomes arise centrifugal to the gynoecium, meaning that sterile phyllome primordia are initiated after and outside the carpel primordia (sensu Sattler, 1972). When the sterile phyllomes arise, the stamens are fully differentiated and the petals are longer than the stamens. Sterile phyllomes are initiated at about the time that the stigmatic lobes are beginning to develop on the styles (Fig. 40, 41, 47). Each sterile phyllome may arise as a single or bilobed (rarely trilobed, Fig. 41) primordium.

During ovule development (Fig. 43–46), integument development occurs as in *Hamamelis virginiana* except that outer integuments do not become crescent-shaped.

**DISCUSSION**—Our observations on the floral organogenesis of *Hamamelis virginiana* are in general agreement with those of Baillon (1871–1873) and Shoemaker (1905). Baillon indicated that median sepals are initiated sequentially; we add that the lower median sepal arises prior to the upper median sepal. Baillon found lateral sepals to be initiated sequentially. We have found lateral sepals to be initiated simultaneously. Baillon described the stamens as being initiated simultaneously. In contrast, we have found that most often simultaneous

initiation of median stamens is followed by the simultaneous initiation of lateral stamens.

Sattler (1973) found six species, each in different orders of flowering plants, to have discs initiated centrifugal to the gynoecium. On the assumption that the term disc does not imply affinity to any particular type of floral appendage (Schleiden, 1849), we are able to include the hamamelids with this condition (*Corylopsis*, *Liquidambar*, *Rhodoleia*, and *Loropetalum*; see introduction for references) and report that at least 10 genera in families representing seven different orders exhibit centrifugal initiation of discs (= sterile phyllomes in these genera).

Adjacent sepals of *Loropetalum chinense* were found to be partially to entirely connate in some flowers; this condition has not been reported previously. While our *Hamamelis* material was strictly 4-merous, Harms (1930) observed occasional apical flowers which were 5-merous and Bogle (1968) observed a few trimerous flowers of *H. virginiana*. *Loropetalum* has been reported as 4-merous by all previous workers (e.g., Hemsley, 1904; Chun, 1934; Chang, 1979). In contrast, the material we studied was 4- or 5- (rarely 6-) merous (Fig. 6).

In *Loropetalum*, petaloid staminodia were occasionally observed in the position that petals normally occupy. Similar observations have been made in several other genera of the family by Horne (1914, *Corylopsis*), Bogle (1968, *Disanthus*, *Exbucklandia*, *Rhodoleia*), and Endress (1967, *Corylopsis*). These findings suggest that in the family Hamamelidaceae, petals and stamens are homologous.

The initiation of the nectaries of *Hamamelis* immediately after the stamens, the similar morphology of these appendages during early developmental stages, and the occurrence of a staminodial-nectary (a putative atavism) suggests that nectaries of *Hamamelis* are staminodial in origin. Baillon (1871–1873) also de-

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Fig. 42–49. *Loropetalum chinense*. 42. While petals (P) elongate, stamen (S) connectives elongate and become connivent over the gynoecium. ×58. 43. Transverse, hand section. A single ovule (O) arises in each carpel. ×388. 44. Transverse, hand section. Ovules (O) most often arise on opposite sides of the ovarian cavity, ×102. 45. Longitudinal dissection. Integuments arise as girdling primordia with the inner integument (I) arising prior to the outer integument. When present, an anomalous protruding ovule (Op) arises from the opposite carpel margin from that bearing a normal, pendent ovule. Here, the protruding ovule (Op) arises from the far wall of the left carpel while the normal pendent ovule of that carpel (integuments facing viewer) is borne on the closer wall which has almost entirely been removed. The right carpel has almost entirely been removed. SL, stigmatic lobe; O, ovule. ×119. 46. Longitudinal dissection. As in *H. virginiana*, the two ovules (O) are sometimes borne on the same side of the ovarian cavity. The integuments are then oriented in the same direction, in this case away from the viewer. SF, sterile phyllomes; SL, stigmatic lobes. ×56. 47. Extremely rare occurrence of a staminodium (Sto) adaxial to a petal (P). A sterile phyllome (SF) normally occurs in this position. ×64. 48. Bristlelike bracts (B, arrows) subtend some of the flowers of terminal inflorescences. ×64. 49. Rarely, a petaloid staminodium occurs in the position a petal normally occupies. ×26.



scribed the stamens and nectaries as appearing similar during early development and went so far as to call the nectaries stamens ("étamines") during early developmental stages and "staminodes" during later developmental stages. The nearly identical vasculature of the stamens and nectaries in *Hamamelis* (Bogle, 1968; Mione, 1987) supports this conclusion.

In *Loropetalum*, the extremely rare occurrence of staminodia in the position normally occupied by sterile phyllomes (Fig. 47) may be an atavism. In several other genera of the family appendages transitional between "staminodia" and stamens have been reported (Tong, 1930). These putative atavisms could be taken as evidence that in the Hamamelidaceae sterile phyllomes are derived from stamens.

The study of floral organogenesis in these two genera has revealed that in *Hamamelis virginiana* and *H. mollis* the nectaries arise immediately after the stamens while the sterile phyllomes of *Loropetalum chinense* arise after all other floral appendages have differentiated. This difference in time of appearance may be interpreted as evidence that although these whorls of appendages are similarly positioned, they have not evolved from the same whorl of stamens in the common progenitor.

In light of this conjecture, it is interesting to note that nectaries of *Hamamelis* and sterile phyllomes of *Loropetalum* have very different vasculatures (Bogle, 1968). In *Hamamelis*, each nectary is supplied by an adaxial branch of the petal bundle (petals and sterile appendages occur on the same radii in both genera). In *Loropetalum*, however, the bundle to the base of the sterile phyllome is derived from a hypanthial vascular ring rather than directly from the petal bundle. The presence of such different vasculatures in *Hamamelis* and *Loropetalum* is incongruent with the idea that the sterile phyllomes of *Loropetalum* are derived from the same cycle of floral organs as the nectaries of *Hamamelis*, if one considers vasculature to be conservative. Furthermore, in the flowers of *Maingaya* and *Dicoryphe* (Bogle, 1984, 1988), which contain both staminodia and sterile phyllomes, the staminodia are supplied by branches of the petal trunk bundles, while the sterile phyllomes are supplied from a hypanthial vascular ring, as in *Loropetalum*.

The sterile phyllomes of *Loropetalum*, like those of other Hamamelidaceae [*Corylopsis* ("Nektarschuppen," Endress, 1967), *Liquidambar* (Wisniewski and Bogle, 1982) and *Rhodoleia* (Bogle, 1987, 1989)] arise centrifugal to the gynoecium. This common time of initiation suggests that sterile phyllomes of these genera have evolved from a common whorl of

floral appendages in a progenitor. The rare reversion of sterile phyllomes to staminodia is perhaps the only evidence of a staminodial origin for the sterile phyllomes of *Loropetalum*. If the sterile phyllomes are of staminodial origin, then if one considers the probable homology of the sterile phyllomes of *Loropetalum* with those of *Corylopsis*, *Liquidambar*, and *Rhodoleia*, a staminodial origin for the sterile phyllomes of all four of these genera must be considered.

The various arrangements of sterile phyllomes and staminodia in genera of the tribe Hamamelideae may be the result of loss and/or retention of different whorls of appendages that have been retained in *Maingaya* (Bogle, 1984), the seemingly least specialized genus of the tribe Hamamelideae. Morphological evidence for this stems from the fact that flowers of *Maingaya* possess alternating whorls of five sepals, petals, stamens and staminodia and an innermost whorl of 10 sterile phyllomes. In species of *Corylopsis*, *Tetrathyrium*, *Embolanthera*, and *Loropetalum* possessing sterile phyllomes, these structures are two-parted or bilobed, indicating probable homology with the innermost whorl of 10 sterile phyllomes present in *Maingaya*. Regarding a different line of floral specialization (leading to loss of an innermost whorl of sterile phyllomes), some species of *Dicoryphe* possess a floral plan similar to that of *Maingaya* while other species of *Dicoryphe* lack sterile phyllomes but have vestigial vasculature which suggests the former presence of an innermost whorl of phyllomes (Bogle, 1984, and in preparation). *Hamamelis* possesses four individual staminodia and no evidence of an additional, inner whorl of phyllomes.

It is likely that progenitors of the subfamily Hamamelidoideae possessed several whorls (or a spiral with several cycles) of stamens which are represented as modern whorls of petals, stamens, staminodia and sterile phyllomes. This conjecture is supported by the aforementioned evidence for a staminodial origin of nectaries and sterile phyllomes, homology of stamens and petals, and by the presence of more than one whorl of stamens in some genera of the subfamily Hamamelidoideae (e.g., *Matudaea*, Bogle, 1968, 1970; Endress, 1976).

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