

Taxonomic Study of the Caprifoliaceae

By

Nobuyuki FUKUOKA

Shoei Junior College, Kobe

(Received September 5, 1972)

ABSTRACT Definitions are revised for various taxonomic characters of the Caprifoliaceae with special reference to the rank of tribe, and an attempt is made to elucidate the systematic relationship among the tribes of this family. Special observation and discussion are given from the standpoint of comparative morphology, especially of the floral anatomical investigation. As the result of this study, an artificial key to six tribes and fourteen genera is given.

Introduction

The family Caprifoliaceae includes some 15 genera and 300 species mainly in the temperate region of Northern Hemisphere. Several species are known in the mountains in the tropics and in South America, Australia, and New Zealand. A variety of the morphological features as well as the classification of this family are not sufficiently established.

According to the current definition, the Caprifoliaceae have opposite leaves without true stipule, inferior ovary with more than two loculi, sympetalous corolla, and seed with endosperm. The presence of the stipular appendages makes obscure the distinction between the Caprifoliaceae and the Rubiaceae. From the floral anatomical investigation, *Sambucus* is suggested to have a relation to the Cornaceae, and the tribe Linnaeae resembles the Valerianaceae. The serological study shows the similarity of the Caprifoliaceae, especially of *Sambucus*, to the Cornaceae. In the morphology of inflorescence, *Sambucus* and *Viburnum* seem to have relationship to the Saxifragaceae (especially *Hydrangea* and *Schizophragma*) as well as the Cornaceae and the Araliaceae.

The systematic study of this family has been made by many taxonomists, and this family has been variously classified. The tribal position of some genera is still doubtful, and the recognition of some genera is not yet discussed minutely. The definition of the infrageneric taxa in some genera still remains obscure. Morphologists studied the Caprifoliaceae in detail, and have suggested the emendation for taxonomical conception on the basis of their comparative studies of morphology.

The informations from the morphological field are useful for the taxonomy of this family. For regarding the floral anatomical study, for instance, the ovary of this family shows the various degrees of the abortion and the reduction in the number of carpels and ovules as well as the fusion and the reduction of vascular supply. The evolution of these features in the Caprifoliaceae may correspond with the evolution in the rank of the tribes and the genera. It is rather pity that the taxonomists can hardly have succeeded to make the system of the Caprifoliaceae sufficiently based on such useful informations proposed by the morphologists.

The present paper is intended to elucidate the natural relationship of the Caprifoliaceae. For this purpose, I have studied the taxonomic characters from the standpoint of comparative morphology, and the evolutionary trend for each character has been discussed. As in the case of every evolutionary morphology, parallelism is often met with in various features of this family. Parallelism leads the classification to the erroneous taxonomic groups, so we should carefully examine whether the resemblance of features is resulted from the parallelism or not. It is highly necessary to recognize the variation of every taxonomic character for the definition of the taxa. The observation on the floral morphology has not yet been made evenly throughout the Caprifoliaceae, and I have devoted much of my time for the floral morphology, especially on the little known species and/or features.

In this work, I could have treated the materials mainly from Japan and its neighbouring area, though the materials gathered recently from Himalayas and Southeast Asia are also used for my study. Some of the European and North American species cultivated in our country are observed in the sake of the floral anatomical investigation.

Historical Account

De Candolle (1) divided the Caprifoliaceae into two tribes, Sambuceae and Lonicereae, by the difference in corolla and style. The former consists of *Sambucus* and *Viburnum*, and the latter *Triosteum*, *Diervilla*, *Lonicera*, *Leycesteria*, *Symphoricarpos*, *Abelia*, *Linnaea*, *Aidia*, *Valentiana*, and *Karpeton*.

Concerning the division of the tribes, Hooker (2) followed in the main to de Candolle's opinion. He belonged *Adoxa* (now to Adoxaceae) to the tribe Sambuceae, *Microsplenium* (now to *Machaonia* of Rubiaceae), *Pentaptyxis* (now to *Leycesteria*), and *Alseuosmia* to the tribe Lonicereae, and excluded *Aidia*, *Valentiana*, and *Karpeton* from the Caprifoliaceae.

In 1891 and 1892 Fritsch (3, 4) proposed his own system of this family as follows:

Sambuceae: *Sambucus* ——— leaf pinnate; anthers extrorse; corolla actinomorphic; ovary 3- to 5-celled, and each loculus with one ovule; and drupe.

Viburneae: *Viburnum* and *Triosteum* ——— leaf simple or rarely pinnate; anthers introrse; corolla actinomorphic or zygomorphic; ovary 1- to 5-celled; and drupe with 1- to 5-seeds.

Linnaeae: *Symphoricarpos*, *Dipelta*, and *Linnaea* (including *Abelia*) ——— leaf

simple; anthers introrse; corolla actinomorphic or zygomorphic; ovary 3- to 4-celled, two abortive carpels with several small ovules and the others being fertile ones with one ovule; and fruit fleshy or dry.

Lonicereae: *Alseuosmia*, *Lonicera*, *Diervilla*, and *Leycesteria* ——— leaf simple; anthers introrse; corolla actinomorphic or zygomorphic; all the loculi with many ovules; and fruit berry or capsule.

To define the tribes, thus, he took up mainly the differences in the anatomy of the ovary, especially of the number of loculi and of ovules for each loculus. In addition to these features, the differences in leaf, anthers, corolla, and fruit were considered. The tribe Sambuceae were divided into two tribes, Sambuceae and Viburneae, and the tribe Lonicereae into two tribes, Linnaeae and Lonicereae. Fritsch (3, 4) placed *Triosteum* in the tribe Viburneae, because he took up much importance to the loculi, each of which has a single ovule. In spite of this classification of him, he seemed to be doubtful for the affinity between *Triosteum* and *Viburnum*, and noted (2) that *Triosteum* might belong to the status between the tribes Viburneae and Lonicereae, since this genus had elongated style and zygomorphic corolla like as *Lonicera*.

Subsequent to Fritsch, Nakai (5) separated *Diervilla* (including *Weigela*) from the tribe Lonicereae as a distinct tribe Diervilleae which had been previously recognized by Meyer (6). The former is characteristic of berry and the latter of two-valvate capsule. On the other hand, Diels (7) supported Fritsch's opinion on the recognition of the tribes, and placed *Dipelta* in the tribe Lonicereae as well as *Lonicera*, *Diervilla*, and *Leycesteria*.

Recently, Wagenitz (8) revised comprehensively the classification of the Caprifoliaceae in which five tribes were recognized. However, *Alseuosmia*, *Memecylanthus*, and *Pachydiscus* are excluded from this family. The affinity between these genera and some other families is suggested by many taxonomists, though Airy Shaw (9, 10) segregates them as a distinct family, Alseuosmiaceae. This family is characteristic in alternate leaf, actinomorphic corolla, and two-celled ovary. Concerning the taxonomic position of *Triosteum*, Wagenitz (8) suggested to segregate this genus as a distinct tribe from the tribe Viburneae. To the tribe Diervilleae are newly added by him *Carlemannia* and *Silvianthus* which are included in the Caprifoliaceae by Kern & van Steenis (11), though these two are also segregated as the Carlemanniaceae by Airy Shaw (10, 12).

In 1969, Hutchinson (13) published the second volume of his comprehensive "The Genera of Flowering Plants", in which he revised the Caprifoliaceae including the rare and little known genera. The Alseuosmiaceae are reduced to a tribe of this family. *Carlemannia* and *Silvianthus* are belonged to the tribe Viburneae, since they have actinomorphic corolla whose base is never saccate. *Triosteum* is excluded from this tribe and is treated as a distinct tribe. From the zygomorphic corolla, elongated style with a capitate stigma, and woody habit, the tribes Linnaeae and Diervilleae are regarded as the synonyms of the tribe Lonicereae, in which *Heptacodium* described by Rehder (14) is included. To define the tribes, Hutchinson takes up the characteris-

tics of leaf, corolla, style, stigma, and habit, regardless of the floral anatomical features.

The Caprifoliaceae have also been studied by the morphologists independent from taxonomy. Wilkinson (15~18) published a series of the floral anatomical studies of this family. As a result of these detailed studies, she concluded that *Triosteum* should be segregated as a distinct tribe. From the floral anatomical features, *Sambucus* and *Viburnum* resemble to each other, differing distinctly from the other members of this family.

From the wood anatomical investigation, Metcalfe & Chalk (19) emphasized that *Sambucus* was widely segregated from the remains of the Caprifoliaceae. Recently, Airy Shaw (10) followed an opinion that *Sambucus* was regarded as a monotypic family.

Troll & Weberling (20) make the morphological study on the inflorescence throughout the Caprifoliaceae. According to their opinion, all of the genera included by Hutchinson (13) in this family do not seem to belong to this family. Concerning the taxonomic position of *Triosteum* and *Symphoricarpos*, they suggest that both the genera belong to the tribe Lonicereae against the current opinion.

Concerning the taxonomic position of *Heptacodium*, Rehder (14) noted that this genus resembled closely *Lonicera* Sect. *Caprifolium* in the inflorescence and *Abelia* in the structure of ovary and the fruit. From the anatomical study on leaf and wood, Metcalfe (21) supports to place *Heptacodium* in this family. Weberling (22) publishes an opinion that this genus belongs to the tribe Lonicereae from the inflorescence.

Taxonomic Character

Leaf

The leaves are opposite in the Caprifoliaceae except in *Alseuosmia*, *Memecylanthus*, and *Pachydiscus*, all of which are sometimes excluded from this family. These genera have alternate leaves.

In the Caprifoliaceae the stipulary appendage is sometimes observed at the base of leaves. The appendage of *Sambucus* is various: discoid gland, laciniate, or foliaceous in shape. In some species of *Viburnum*, i.e. *V. opulus*, *V. wrightii*, and others, there are the filiform glandular appendage or often absent in some cases. *Leycesteria*, *Lonicera*, *Symphoricarpos*, and *Triosteum* have often earlap-like appendage at the base of leaves and the appendages often fuse to each other. These appendages are sometimes described as stipule or interstipule. Influenced by the common nature of the presence of such stipulary appendage, taxonomists sometimes suggest the relationship between the Caprifoliaceae and the Rubiaceae whose leaves have always the stipule at the base. However, Weberling (23) does not regard the stipulary appendage as stipule but the rudimentary lowermost leaflet of compound leaf. He presents the reasons for his conclusion as follows: these appendages of the Caprifoliaceae are variable in shape and size even in a single individual comparatively with the real stipule in general, and the petiole is obscure at the part between leaflet or lobe and

stipulary appendage on the primordium of the leaf in *Sambucus racemosa* and *Viburnum opulus*, though three parts, blade, petiole, and stipule, are easily recognizable even in the primordium on the material with the real stipule. According to the histogenetical study on the leaf of *Viburnum opulus* by Cross (24), the stipulary appendages are slightly conduplicate like the lobes of the leaf, the cross section of the young appendage resembles histologically that of the young lobe, and provascular tissues in the appendage appear in the center like the lobes of leaf. He has concluded that the stipular appendages are the vestigial lobes of leaf.

As Fritsch (3) took up the differences in the constitution of leaf as one of the features to discriminate the tribe Sambuceae from the other tribes, there are two types of the leaf in the Caprifoliaceae: pinnately compound in *Sambucus* and simple leaf in the rest of this family. In the latter there are rarely trilobed leaf as in some species of *Viburnum*, i.e. the most of Sect. *Opulus*, some of Sect. *Tinus*, and others. In *Viburnum erosum* the leaf is sometimes pinnatifid.

Concerning the duration of the leaf two types are distinguished in the Caprifoliaceae: deciduous in most of this family and persistent in some genera, *Linnaea*, some of *Viburnum* and *Lonicera*, and a few of *Sambucus* and *Abelia*. Among the members with persistent leaves only the monotypic genus *Linnaea* is distributed to the subarctic region of Northern Hemisphere, and the others to the ranges from tropic to subtropic, only a few of them extending to warm temperate regions. In *Lonicera japonica*, the plants in Formosa have persistent leaf and bloom in winter, though the leaf of Japanese plants is semipersistent, i.e. most of matured leaf are colored in autumn and fall off in winter, but the small leaf at the upper part of shoot is persistent during cold season. Judging from these facts, the presence of the persistent leaf in the Caprifoliaceae seems to be correlated with the climate.

Habit

The plant of this family is mostly lower tree or shrub, except for *Triosteum* and *Sambucus* Sects. *Ebulus* and *Scyphidanthè* which are perennial herb with erect stem. Nakai (5) evaluated the herbaceous habit of *Ebulus* including *Scyphidanthè* to distinguish this generically from *Sambucus*. However we can sometimes observe the herbaceous to shrubby or arboreous habit in various members within a genus, as in the cases in *Hedyotis*, *Mussaenda*, *Cornus*, *Clematis*, and others. Accordingly, the sole difference in habit is not sufficiently reasonable as the feature to distinguish the genera. Arboreous and shrubby members usually have erect or suberect habit. In *Linnaea*, however, main axil creeps on the ground. In *Zabelia integrifolia* the young stem sometimes creeps on the ground and its nodes sometimes bear roots, but old one is erect or suberect. Climbing shrub is found in *Lonicera* Sect. *Ninnoa* and most of Subgen. *Caprifolium*. In *Viburnum*, also, only one species *V. beccarii* has the stem climbing up large tree, though a closest ally, *V. cylindricum*, has an arboreous habit. Therefore, climbing habit is not so important feature to define the infrageneric taxa of *Viburnum*.

Inflorescence

The inflorescence has been considered as one of the most important key characters

for the classification of the Caprifoliaceae, especially for the infrageneric taxa. Troll & Weberling (20) made the morphological study on the inflorescence of this family and proposed some emendations for the taxonomy of this family. They classified the inflorescence of this family into three types: Sambuceae and Viburneae are monotelic; Lonicereae are polytelic; and Linnaeae and Diervilleae are transitional. From the observation of inflorescence they supported the current opinion to divide the Caprifoliaceae into five tribes. For the taxonomic position of the genera *Triosteum* and *Symphoricarpos* they proposed an emendation: these genera belong to the tribe Lonicereae, because their inflorescence shows polytelic type in which no terminal flower is found in the axis of inflorescence. They mentioned also that all the genera *Alseuosmia*, *Pachydiscus*, *Memecylanthus*, *Carlemannia*, and *Silvianthus* did not seem to belong to the Caprifoliaceae. I have recently (25) published a brief note on the inflorescence of the tribe Linnaeae, and the relationship among the genera of this tribe was elucidated to some extent.

In the Caprifoliaceae there are two types of inflorescence: cyme and raceme. The former is found in *Sambucus*, *Viburnum*, the tribes Diervilleae, and most of Linnaeae, and the latter in *Triosteum*, *Symphoricarpos*, and the tribe Lonicereae. From the structures of the inflorescence *Sambucus* and *Viburnum* closely similar to each other. In both the genera the inflorescence is corymb and panicle. *Sambucus* Sect. *Scyphidanthe* has gland bodies on corymb. In some sections of *Viburnum* corymb bears sterile flowers on the periphery.

In some species of *Triosteum* of the tribe Viburneae, the inflorescence is spike whose partial florescence consists of three flowers. In this respect, as Troll & Weberling (20) mentioned, this genus is not related to *Viburnum* but *Lonicera* Subgen. *Caprifolium*. The inflorescence of *Symphoricarpos* is racemose. Therefore, this genus is distinct from the remains of the tribe Linnaeae. Troll & Weberling (20) have proposed an opinion that *Symphoricarpos* belongs to the tribe Lonicereae. However, this opinion is not supported by any of the other taxonomic characters, especially by floral anatomical features (Fukuoka, 26).

Flower

The features found in the flower have long been taken up as the most important characteristics of the classification of the family Caprifoliaceae, like in the case of most of the angiospermous families. Fritsch (3) defined the tribes of our family mainly by the difference in the floral morphology, especially in the anatomical features of the ovary. Distinguishing *Diervilla* from the other members of the tribe Lonicereae, Nakai (5) established the tribe Diervilleae based on the difference in the ovary and fruit. Wilkinson (15~18) described various features of the flowers, both morphologically and anatomically. Her contribution in this field is valuable, and the relationship among genera of the Caprifoliaceae becomes much recognizable by her data. Recently, Hutchinson (13) proposed to separate a few tribes chiefly defined by the features of the floral morphology. For elucidating the natural relationship among the tribe Linnaeae, useful are floral characters, such as the form and vascularization

of corolla, number of anthers, the anatomical features of ovary, and so on (Fukuoka, 26).

Ovary

The anatomical features of the ovary are most complex and indicate in many ways the taxonomic differences and relationships among the members of the Caprifoliaceae. Since Fritsch's appropriate proposal, the taxonomists pay their attention to the differences in anatomical features of the ovary for recognizing the tribes of this family. The most comprehensive features observed are the number of loculi and ovules, and whether the ovary has abortive carpel or not. Wilkinson (15~18) made detailed observation on the anatomy of the ovary of this family and noted various opinions to correct and added the taxonomical recognition. Recently I (26) have published a paper in Japanese discussing the phylogeny of the tribe Linnaeae, in which the anatomical features of the ovary are regarded as one of the most important characters to trace the evolutionary relationship among genera. These anatomical features should be reviewed and discussed concerning to each species.

Sambucus ——— Wilkinson (16) studied anatomically the flower of *S. canadensis* and *S. racemosa* subsp. *pubens*. I have reexamined *S. canadensis* and have added the observation on *S. javanica* subsp. *chinensis*, *S. nigra*, and *S. racemosa* subsp. *sieboldiana*. The floral anatomical features will be summarized here comparing my observation with Wilkinson's.

According to Schwerin (27), the number of loculi for each ovary of this genus, especially of Sect. *Sambucus*, is fairly variable even in a single cyme. The number of loculi is less than six in a single ovary, and the ratio of the number of the highest occurrence amounts more than three-fifth among the ovaries observed even in the variable cases. The commonest number of the loculi in an ovary is useful to distinguish the sections and sometimes even the species of this genus: three-celled ovary in Sects. *Botryosambucus*, *Ebulus*, *Scyphidanthè*, and *Tripetalus*; four-celled in *Tetrapetalus*; three- to five-celled in *Sambucus*; and five-celled ovary in *Heteranthe*. In the three-celled species *S. nigra* (pl. 3-6), I have observed the two-celled ovary in only one of five specimens (pl. 3-5).

Each of the loculi is usually occupied by a fertile and pendulous ovule. The ovary of *S. canadensis* is usually four-celled (pl. 2-4), but I have observed two specimens with five loculi (pl. 2-2). Among them, one specimen has a loculus bearing an abortive and small ovule attached at higher level and situated above the other four which grow typically (pl. 2-3). This specimen is structurally comparable with a five-celled fruit usually bearing only four seeds (see Fukuoka, 28). The loculi are elongated upwardly into the lobes of the transmitting tissues (fig. 1). At the base of the transmitting tissue in all the five taxa ever treated, there are observed a group of larger cells (pl. 1-6, 2-3 & 6, & 3-1~4). Wilkinson (16) has suggested that these cells are vestigial ovules. As confirmed in longitudinal section (pl. 3-1 & 4), however, these cells form a ball which is always situated at the apex of loculus.

The vascular bundle divides into three to six strands at the upper level of pedicel

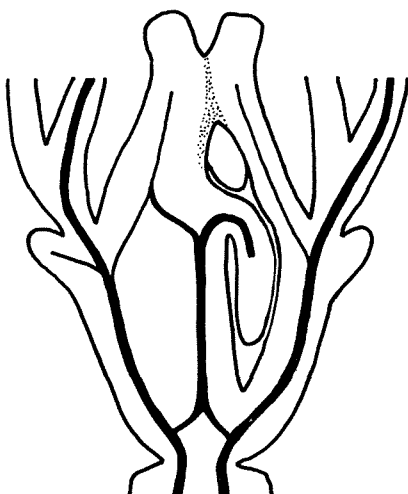


Fig. 1. Longitudinal section of flower in *Sambucus*, showing a rudimentary ovule, a fertile one, and vascular supply. Calyx-stamen bundle (left) gives off lateral ventral trace; corolla bundle (right) branches a dorsal trace; and central bundle divides into a fertile ovular bundle and ventral strands.

(pl. 1-1). At the higher level where ovary becomes larger in outline but still below the bottom of loculi, these three to six strands proceed to the periphery and are dividing into nine to ten, remaining three to five in the center of ovary in three species (pl. 1-2~3, & 2-1). In *S. nigra*, seven to eight strands proceed to the periphery and run up there (pl. 3-6). Number of peripheral bundles of this species seems to corresponds to four-merous flower.

The strands in the center join together to form a central bundle in *S. javanica* subsp. *chinensis*, *S. nigra*, and *S. racemosa* subsp. *sieboldiana* (pl. 1-4, 2-9, & 3-5~6). In *S. canadensis*, on the other hand, the ventral strands, i.e. the several strands in the center of ovary, do not fuse to each other. Wilkinson (16) describes that the ventral strand are opposite to the loculi, and not between them. In my observation, however, the position is indistinct as seen in pl. 2-4. Just below the position of the attachment of ovules the central bundle divides into six strands in the three-celled series: three supply to three ovules, and other three run up toward the wall of ovary along the septa and fuse to the strands separated from the peripheral bundles (pl. 1-5 & 2-5).

Concerning the separation of the calyx supply, three types are observed as follows. In *S. canadensis* and *S. nigra*, each of peripheral bundles gives off centrifugally a calyx supply. Each of every other four (four-merous flower in *S. nigra*) or five strands run

in the center of each of four or five calyx-lobes and arrives near the apex of lobes, and each of other four or five small traces entering into the position between lobes, becomes extinct there or divides into two traces at the base of calyx tube. Each of these two extends oppositely to the base of lobes along calyx tube, though they never enter into the lobes and do not reach the other calyx strand entering in the center of lobe. In *S. javanica* subsp. *chinensis*, every other five peripheral bundles give off calyx supplies, though other five do not supply any calyx trace. In these species, the main calyx strands do not divide (pl. 1-7). In *S. racemosa* subsp. *pubens* (as observed by Wilkinson) and *sieboldiana* the minute calyx is supplied by no strand. In two flowers of the former Wilkinson (16) observes that a single peripheral bundle gives off a calyx trace.

Four or five peripheral bundles giving off calyx strand entering in the center of calyx lobes supply to stamens, and others are the corolla supplies. Each of the latter branches into three at the base of corolla (pl. 1-5).

The carpellary supplies are variable with in a single species. As mentioned above, a central bundle divides into the various numbers of strands in accordance with

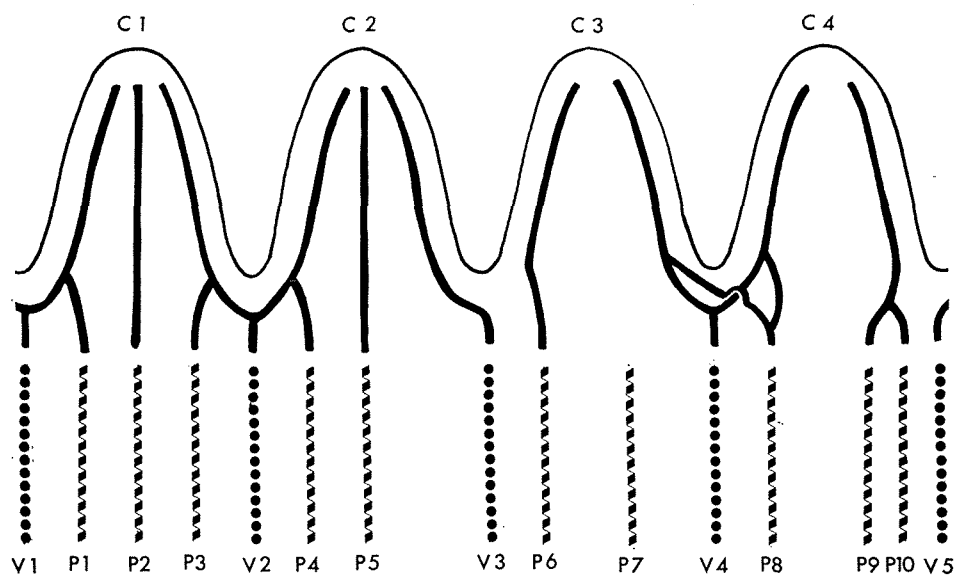


Fig. 2. Diagram showing various vascularizations of carpels in *Sambucus*. C1: carpel supplied by a dorsal trace given off from peripheral bundle (P2) and by two ventral traces, each of which is joined by a lateral trace branching from peripheral bundles (P1 & P3); C2: a ventral trace supplied by no lateral trace; C3: a ventral trace substituted by a lateral trace and absence of dorsal trace; C4: a lateral trace dividing into two traces, each of which supplies to a ventral trace of different carpels. ~~~~~ : fusing with peripheral bundles P1~10; : fusing to each other as a central bundle. Explanation in text.

the number of carpels. These strands do not branch (fig. 2-V3 & V5) or branch further into (fig. 2-V1, V2, & V4), which are regarded as the ventral strands of neighbouring carpellary margins. Each of the ventral strands is usually supplied by one lateral trace, which is given off from a peripheral bundle (fig. 2-P1, P3, & P4) just below the attachment of calyx (fig. 1 & pl. 2-2). In some cases, one trace given off from a peripheral bundle divides into two lateral traces as in *S. canadensis* (fig. 2-P8). The lateral trace joins to a ventral strand, or in the case in which the ventral strand does not divide into two, the lateral trace sometimes does not fuse to but pairs with ventral strand (fig. 2-V3 & P6). There are observed the cases that two traces given off from neighbouring peripheral bundles fuse to each other and then extend to the inner side of ovary (fig. 2-P9 & P10). This fused trace does not join to ventral strand but pairs with (fig. 2-V5, P9, & P10). On one specimen of *S. nigra*, two traces branched from two peripheral bundles extend horizontally and join together. After then, this strand gives off centrifugally a calyx trace and centripetally a lateral one. On the other hand, dorsal trace is difficult to distinguish from ventral one, because the portion of these traces is sometimes obscure and some of lateral ventral traces do not fuse to ventral strand but pairs with (pl. 1-6 & 2-6). In *S. canadensis*, the three dorsal traces are evidently separated from peripheral bundles at least (pl. 2-3 & 6). In *S. javanica* subsp. *chinensis* and *S. nigra*, one or two dorsal traces among three carpels seem to be given off (pl. 1-6), though *S. racemosa* subsp. *sieboldiana* does not seem to have the dorsal trace (pl. 3-3).

Evolutionary trend. We have as yet no enough informations to summarize the evolutionary trend of the floral anatomical features of this genus, though it becomes obvious that the evolutionary trend in calyx and carpellary supplies is recognized.

Concerning the calyx supplies, there are three evolutionary trends as follows:

1) In primitive stage, all the peripheral bundles give off a calyx supply. Among them, every other five situating to the opposite portions of calyx lobes extend near the apex of lobes, and others enter to the position between lobes. Each of the latters divides into two, each of which does not reach to the lobe but extends oppositely to the base of lobes along calyx tube. In the prototype of the calyx supply of *Sambucus*, these traces may have formed a vascular ring at the base of calyx tube as in *Lonicera*, *Symphoricarpos*, and others.

2) In probably derived one from this, each of calyx lobes is supplied by a single trace as the result of the reduction of the trace entering to the portion between lobes.

3) In the most advanced case, there are no calyx supply.

First stage is found in *S. canadensis* and *S. nigra*. The calyx supply of *S. javanica* subsp. *chinensis* shows second one. According to Wilkinson (16), that of *S. canadensis* is regarded as this stage. As mentioned already, however, this species is the representative of first stage. Third stage is found in *S. racemosa* subsp. *pubens* and *sieboldiana*, though the intermediate between second and third ones is known in the former.

The carpellary supplies separated from peripheral bundle are much variable. Judging from the various forms of the living species, the prototype of this feature may be suggested as follows. At the receptacle the strands remaining in the center fuse

to each other and form a specific number of strands in accordance with the number of carpels. These ventral strands do not join together and run up in the center of ovary as in the case of *S. canadensis*. Each of them has divided into two marginal strands just above the attachment of ovules and these two have been respectively supplied by a lateral trace given off from different peripheral bundles. This is supported by the fact that a pair of two strands are observed at each of the ventral portions of carpels in all the specimens of *Sambucus* treated. All of the carpels have had a dorsal trace separated from peripheral bundle as in the case of *S. canadensis*. The ventral strands show a trend to join together at the base of ovary. Often no peripheral bundle supplies to one of the two lateral traces for each carpel. There are the cases in which the carpel has no dorsal trace separated from peripheral bundle. The various patterns of the carpellary supplies in living species seem to have occurred as the result of the various combinations of such reduction and fusion.

Viburnum — Wilkinson (17) observed minutely the anatomical features of the ovary in fourteen species belonging to seven sections of *Viburnum* in Rehder's system. Among them, *V. carlesii*, *V. dilatatum*, *V. plicatum* (as *V. tomentosum*) and *V. sieboldii* are native to Japan. I have reconfirmed her observation on these four species and the following twelve species are newly observed here: *V. cylindricum*, *V. erosum*, *V. furcatum*, *V. japonicum*, *V. odoratissimum*, *V. opulus* var. *calvescence*, *V. phlebotrictim*, *V. suspensum*, *V. tashiroi*, *V. tinus*, *V. urceolatum*, and *V. wrightii* belonging to all the nine sections. In the five other species only the number of peripheral bundles are observed by means of boiling the mature fruit in KOH solution.

Hooker (2), Clarke (29), Fritsch (3), and others valued the difference in the number of loculi in a fruit as a key character to define the sections of this genus: one-, two-, or three-celled fruit. Wilkinson (17) observed the presence of three loculi for all the members of the genus studied. This is testified here that sixteen species in this genus including *V. cylindricum* and *V. odoratissimum* have three-celled ovary. Clarke (29) and Fritsch (3) described that the former had one-celled ovary and the ovary of the latter was two-celled. Each ovary consists of one large and fertile locusus and two small and abortive ones which are usually situated at just above or at the nearly same level as a fertile locusus (fig. 3, pl. 4-8, & 5-8). The fertile loculi containing a single fertile and well-developing ovule, and the small locusus contains a few rudimentary abortive or almost extinct ovules.

Wilkinson (17) speculated the evolutionary course of the ovary in this genus as follows. In prototype of this genus they might have the parietal placentation consisting of three carpels. Among these carpels two were reduced to the abortive loculi and one became a well-developing locusus. A fused common placenta of two abortive carpels bears a fertile ovule which is in the locusus of the carpel opposite to the abortive ones as a result of enlargement of this placenta, fusion of the placentae of the abortive carpels, and reduction of two loculi (see Wilkinson's (17) figure 15~19). There are several forms of the placenta bearing a fertile ovule. The largest placenta is found in *V. odoratissimum*, *V. sieboldii*, and *V. suspensum*, whose placenta is circular in cross section at the middle level of ovary even at the time of blooming (pl. 4-2

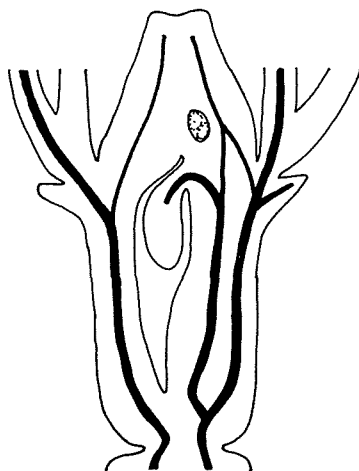


Fig. 3. Longitudinal section of flower in *Viburnum*, showing fertile loculus and abortive one, and vascular supply.

& 7-5~6 & 8). At upper level the cross section of the placenta draws convex at apex (pl. 4-3). In *V. furcatum*, *V. plicatum*, and *V. carlesii*, a placenta is raised but not so distinctly in a loculus as seen in pl. 5-2~3 in blooming. In young fruit of these species, the placenta enlarges and the outline of the loculus becomes waved in cross section according to the convex apex of the placenta. Wilkinson's (17) figure shows that the placenta of *V. dentatum* develops similar to that of the above three (see her fig. 4). In *V. tinus* the cross section of loculus is circular at the lower level of ovary, though the placenta is raised like as *V. furcatum* at the middle level (pl. 8-2). The cross section of ovary in blooming is comparable to the cross section of drupe in this species. In the other species studied, a fertile loculus is rather irregularly linear in cross section at the middle level of an ovary during blooming (pl. 7-4), and a placenta scarcely develops, though the loculus becomes usually waving in outline in cross section of the young fruit.

To classify the sections of this genus, Rehder (30) took much values on the differences in the various shapes of the seed. As correctly mentioned by Billings (31), however, the seed coat of this genus is not made from the integument of the ovule but the solid innermost layer of ovary. Therefore the shape of the seed is determined by the form of the innermost layer of a fertile loculus. Accordingly, it may be fruitful to reexamine the Rehder's system observing the development of the innermost layer of fertile loculus.

Pl. 7-5~7 shows the various stages of developing process from ovary to mature fruit in *V. odoratissimum*. The growth of the size of fruit is in accordance with the enlargement of each of the cells of ovary, especially in the parenchyma. The shape

of the stone is well corresponding to that of ovary in blooming. In *Viburnum* generally is observed such a correlation between the shape of the inner layer of fertile loculus as well as the shape of placenta and that of the seed coat, i.e. endocarp. The shape of the endocarp, therefore, seems to be important as the features to define the infrageneric taxa of this genus as has been done by Rehder's classification.

In the pedicel the vascular bundles are combine to form a loop in cross section with occasional interruption. In case the ovary has the bract at the base, the bract supply runs from the vascular ring. As clearly observed in *V. urceolatum* and *V. phlebotrichum*, a vascular ring separates into five bundles in the very narrow receptacle. I have confirmed that a central bundle is separated from a peripheral bundle situated at the ventral side of ovary below loculus in *V. sieboldii*, *V. tinus*, and *V. urceolatum* (pl. 4-1~2 & 6-3~4). In *V. phlebotrichum*, the central bundle is observed to consist of a few strands separated centripetally from peripheral bundles just below the bottom of loculus.

At the level lower than the middle portion of ovary, the central bundle of *V. sieboldii* is round in cross section (pl. 4-3), but this takes an appearance of V-shape in outline at the upper level than that (pl. 4-4). In that V-shaped central bundle Wilkinson (17) distinguished a fertile ventral strand, two small ventral ones, a pair of fertile ovular traces, and four abortive ovular ones. I could not observe these strands actually. She also observed that a trace supplied to the abortive ovule in some specimens of *V. sieboldii*, though I could not find any materials to support her observation. Separating a fertile ovular strand and two sterile ventral ones, the strand becomes round again in cross section and runs up to the pistil as a fertile ventral strand (pl. 4-5).

In *V. odoratissimum*, also, the central bundle becomes V-shape before separation of the sterile ventral strand and the fertile ovular one. In *V. suspensum*, *V. tinus*, and *V. urceolatum*, the central bundle gives off a large bundle narrowly lanceolate in cross section, and the latter divides again into three, a fertile ovular strand and two sterile ventral ones (pl. 6-5~7).

Except for the species mentioned above, this separation of two sterile ventral strands from the central bundle is found in various species such as *V. acerifolium*, *V. cassinoides*, *V. lantana*, *V. lentago*, *V. nudum*, *V. trilobum*, *V. opulus* (these seven are observed by Wilkinson), and *V. opulus* var. *calvescens*. In this species, the central bundle does not become V-shape and narrowly lanceolate in cross section but round.

According to Wilkinson (17) the sterile ventral strand is absent in *V. carlesii*. In my own observation, however, there are some specimens of this species whose central bundle gives off a large bundle narrowly lanceolate separating only a small sterile ventral trace (pl. 8-1).

In *V. rhitidophyllum*, most of *V. alnifolium* (these two by Wilkinson), *V. cylindricum*, *V. dilatatum*, *V. erosum*, *V. furcatum*, *V. japonicum*, *V. phlebotrichum*, *V. tashiroi*, and *V. wrightii*, on the other hand, the central bundle does not give off any sterile ventral strand. In *V. furcatum* and some specimens of *V. carlesii*, a fertile ovular bundle is narrowly lanceolate in cross section (pl. 5-6). In the other species whose ovary has

no sterile ventral strand, a fertile ovular strand is not so large and narrowly lanceolate but small and round in outline. In two specimens of *V. phlebotrichum* among five, the central bundle does not branch but supplies (as a whole) to a fertile ovule. When the central bundle branches into a ventral strand and a fertile ovular supply, the former is very small in size comparatively with the latter as well as with a lateral ventral strand given off from peripheral bundle.

Wilkinson (17) reports in *V. acerifolium* and some specimens of *V. cassinoides* that the sterile ventral strands become free but do not reach the placentae. I have observed such a case in *V. plicatum*, in which two sterile ventral strands are branching from the central bundle and extend to the placentae within short distance. As the result the central bundle becomes V-shape in cross section like as *V. sieboldii*, though the arms of the V-shaped bundle do not extend further and become extinct. In one specimen of *V. plicatum*, a sterile ventral strand reaches the placenta and run up there to the style.

In some specimens of *V. opulus* var. *calvescens*, the central bundle gives off double fertile ovular strands which fuse to each other just beyond the level of their separation (pl. 7-3). In the other species studied, such double ovular strands have not been observed.

As mentioned above, the peripheral bundles are separated at the level of receptacle. In *V. furcatum* and *V. cordifolium*, there are eight to ten peripheral bundles even at the level below the loculus, like in the case of *V. alnifolium* and *V. dentatum* observed by Wilkinson (17) (pl. 5-1~4). *V. cotinifolium* has seven to eight peripheral bundles, and *V. burejaeticum* has seven ones. *V. erubescence*, *V. odoratissimum*, *V. sieboldii* and *V. suspensum* have six bundles in the periphery at the middle level of ovary in addition to a bundle which is formed by the separation of a dorsal trace of fertile loculus from peripheral bundle as described in the following page (pl. 7-8). In *V. carlesii*, *V. plicatum*, and *V. tinus*, whose peripheral bundles are five in number, there are sometimes observed the separation of a dorsal strand of the fertile loculus at the lower half of ovary. In *V. dilatatum*, *V. erosum*, *V. cylindricum*, *V. japonicum*, *V. opulus*, *V. phlebotrichum*, *V. tashiroi*, *V. trilobum*, *V. urceolatum*, and *V. wrightii*, the peripheral bundles are five in number (pl. 7-4).

As for the peripheral bundles, *V. furcatum* seems to be most primitive in this genus. It seems to be appropriate, therefore, to describe here the vascularization of the peripheral bundles and the carpellary supplies of this species in detail. Each of the peripheral bundles 1, 3, 5, 7, and 9 branches to a calyx and stamen supplies just below the level of attachment of calyx (fig. 4 & pl. 5-7). Each of the peripheral bundles 2, 4, 6, 8, and 10 supplies to the corolla separately. Nearly at the same level as the separation of the calyx supply, the peripheral bundles give off centripetally the carpellary supplies. The peripheral bundle 1 supplies to a fertile ventral strand, each of 2 and 10 gives off a dorsal trace of the abortive loculus and the trace sometimes branches again two traces, each of 4 and 8 gives off a lateral ventral trace between an abortive loculus and a fertile one and the trace usually branches into two, and each of 5, 6, and 7 separates a dorsal trace. These carpellary traces arrange as in pl. 6-1 at

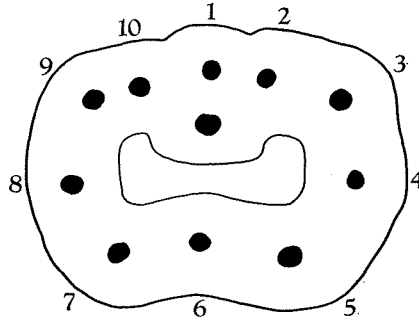


Fig. 4. Cross section at middle level of ovary in *V. furcatum*, showing a raised placenta and ten peripheral bundles (1~10). Explanation in text.

the base of the style, and then at the upper level they fuse to each other as in pl. 6-2.

In the species having five peripheral bundles, on the other hand, the peripheral bundles divide as follows: II and V divide radially into three bundles separately, IV into two, and I and III do not divide radially (fig. 5 & pl. 4-1~6). As the result, the peripheral bundles are ten in number as in the case of *V. furcatum*. Among these ten bundles every other five are the calyx-stamen supplies and the others supply to the corolla.

Nearly at the same level of radial division, five peripheral bundles I to V give off the carpellary traces centripetally, though it is much variable how divide the carpellary traces even in a single species. In most cases, the fertile ventral strand unites a trace

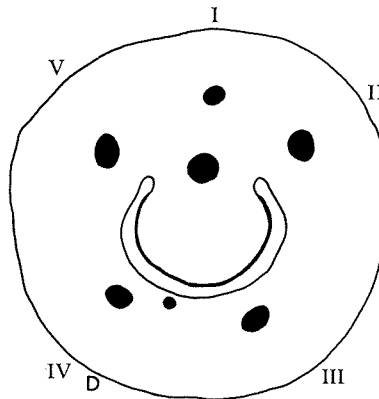


Fig. 5. Cross section at middle level of ovary in *V. odoratissimum*, showing a circular placenta, five peripheral bundles (I~V), and a dorsal trace (D) of fertile locus. Explanation in text.

separated from the peripheral bundle I, though there are a few examples in which no peripheral bundle branches any trace running into the fertile ventral strand as in *V. odoratissimum*, *V. tashiroi*, and some of *V. tinus*. Each of the traces separated from the peripheral bundles II and V is running upwards, uniting with each of the two sterile ventral strands, respectively, if any, for the latter are not usually separated from the central bundle. Those traces are sometimes branching into two. It is often observed that each of the peripheral bundles II and III, or IV and V gives off a lateral trace of the sterile ventral strand in *V. dilatatum*, *V. phlebotrichum*, *V. plicatum*, *V. tinus*, *V. wrightii*, and others. Such lateral ventral traces are sometimes given off from the peripheral bundles III and IV, instead of II and V in *V. odoratissimum*, *V. sieboldii*, *V. tashiroi*, and others. The dorsal trace for the two abortive loculi is supplied by a trace separated from the peripheral bundles II or V. The dorsal trace of the fertile loculus is in most species branched from IV, but in a few cases from III or both from III and IV, as in some of *V. dilatatum*, *V. wrightii*, and so on. The separation of this dorsal trace is usually observed at the same level as that of the separation of the other carpellary traces, but that ranges in the level between the receptacle and the middle portion of ovary in *V. odoratissimum*, *V. suspensum*, *V. sieboldii*, some of *V. carlesii*, *V. plicatum*, and *V. tinus* (pl. 7-8 & 8-1~2). In *V. cotinifolium*, also, this dorsal trace seems to separate at the lower half of ovary.

Evolutionary trend. As mentioned above, various are the vascularizations of the ovary of *Viburnum*. An evolutionary trend of the floral anatomy of this genus is suggested as follows chiefly in accordance with Wilkinson (17).

Concerning the peripheral bundles, there are eight to ten bundles at the lower half of ovary in primitive forms, as in Sect. *Pseudopulus*, some of Sect. *Lantana*, and *V. dentatum* of Sect. *Odontotinus*. In advanced ones, the peripheral bundles are five in number as in most of the other members. Judging from the mode of separation of the carpellary traces and the radial division of the calyx-stamen supplies as well as the corolla ones in the five peripheral bundles, these five bundles seem to be derived from the fusion of ten bundles as follows: the peripheral bundles 2, 3, and 4 unite to the peripheral bundles II; 5 and 6 to III; 8, 9, and 10 to V. The peripheral bundles 1 and 7 do not fuse and each of them corresponds to I and IV respectively (figs. 4 & 5). In case the fusion of ten peripheral bundles occurs only in part, the peripheral bundles result in six to nine in number.

The separation of the carpellary supplies from peripheral bundles is very complex and various even within a single species, so this feature is not yet thoroughly observed. The fertile loculus has usually a single dorsal trace given off from the peripheral bundle. In *V. furcatum*, however, the dorsal traces of this loculus are three in number. According to Wilkinson (17), the dorsal trace of fertile loculus is given off from a peripheral bundle in all the species including *V. alnifolium* of Sect. *Pseudopulus*. In most species of this genus, the separation of this dorsal trace arises at the upper level of ovary. Sect. *Thyrsosma* and some of Sect. *Viburnum* have a dorsal trace of fertile loculus usually separated from the peripheral bundle at the lower level of ovary.

On the separation of the fertile ovular strand, there are two types observed in

this genus. The primitive stage may be that in which the central bundle gives off double fertile ovular strands fusing to each other just beyond their separation as seen in some specimens of *V. opulus* var. *calvescens* (fig. 6-A & pl. 7-3). In all the other species studied, on the other hand, a single fertile ovular strand is separated.

The following evolutionary trend may be suggested here concerning the central bundle.

1. In a most primitive stage a pair of the sterile ventral strands and a fertile ovular one are given off from the central bundle (fig. 6-C).

2. In a form advanced than this, there is no sterile ventral strand but a fertile one which runs up into the pistil (fig. 6-E~F).

3. The most advanced case is known in some of *V. phlebotrichum* of Sect. *Odontotinus* in which the central bundle does not branch and supplies directly to a fertile ovule in the whole (fig. 6-G).

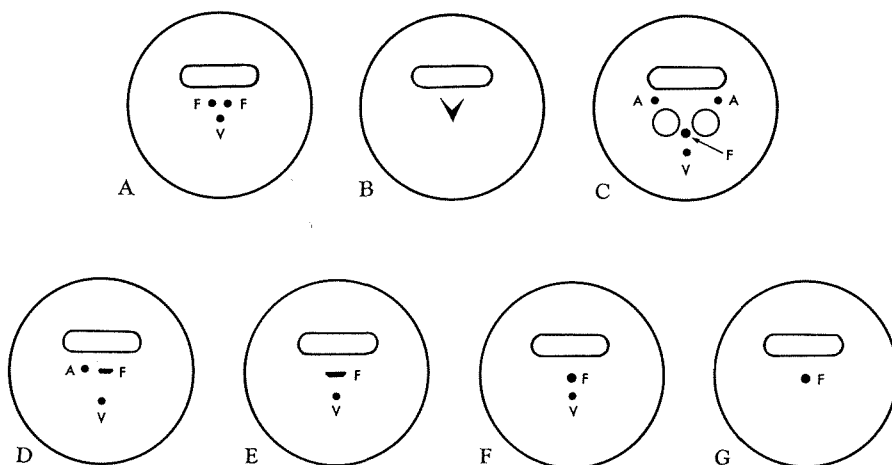


Fig. 6. Diagram showing an evolutionary trend of central bundle in *Viburnum*. V: fertile ventral strand; A: abortive ventral one; and F: fertile ovular one. Explanation in text.

The first stage is known for the species of Sects. *Lentago*, *Opulus*, *Pseudopulus*, *Thyrsosma*, some of Sect. *Viburnum*, *V. furcatum* of Sect. *Pseudotinus*, and *V. acerifolium* of Sect. *Odontotinus*. Among them two types of the central bundle are recognized as follows: in one type the central bundle becomes V-shape in cross section as seen in *V. sieboldii*, *V. odoratissimum*, *V. opulus* var. *calvescens*, and others (fig. 6-B); and in the other probably derived type, the central bundle gives off at first a large and narrowly oblong or broadly crescent shaped bundle and then the latter branches a fertile ovular strand as well as a pair of the sterile ventral ones as in the case of *V. suspensum*, *V. tinus*, and some of *V. urceolatum*, and others (fig. 6-E). The former is considered to be more primitive than the latter, because the central bundle should be in V-shape as the

result of the expansion of two sterile ventral strands.

The second stage is further divided into two types by the difference in the fertile ovular supply: one is larger and narrowly oblong in cross section (fig. 6-E), and the other is small and round (fig. 6-F). The former is seen in *V. rhytidophyllum* of Sect. *Viburnum* (as observed by Wilkinson), *V. furcatum*, and *V. alnifolium* of Sect. *Pseudotinus*, and the latter is known in Sect. *Odontotinus*. Comparing the sterile ovular and ventral strand of *V. carlesii*, *V. furcatum*, and *V. suspensum* with large fertile ovular strand of *V. carlesii*, such a large ovular strand is considered to be resulted from the absence of separation of the two sterile ventral strands. The intermediate forms are observed between the first and the second stages in some specimens of *V. carlesii* (fig. 6-D). In *V. plicatum*, a pair of the sterile ventral strands are given off from the central bundle, though these strands do not reach the position of sterile placentae.

Triosteum — The details of floral anatomy of *Triosteum* have been described by Wilkinson (18) on *T. perfoliatum*. I have observed anatomically the ovary of *T. sinuatum*, and will describe here the features of the latter with comparison to those of the former.

As described by Wagenitz (8), an ovary of this genus has always four loculi, three fertile and a single abortive one. Each of the former contains a single pendent ovule occupying most of the loculus even in flowering (pl. 8-5). In *T. sinuatum* the latter is narrowly compressed and its placenta becomes bi-lobed at the top of loculus (pl. 8-5).

In the pedicel the vascular bundles draw a ring in cross section. At the level of receptacle in cross section, there are observed eight bundles, though they are decurrenting to the neighbouring ones (pl. 8-3). The eight bundles proceed to the peripheral portion, and the inner bundles united each of neighbouring ones form an inner ring (pl. 8-4).

Concerning the peripheral bundles, three smaller ones surround an abortive carpel, and three larger ones are situated at the dorsal portion of the fertile carpels and the other two larger ones between each two of the three. Wilkinson (18) observes that in *T. perfoliatum* the bundle surrounding the abortive carpels is large and crescent-shaped below the loculus, and then it divides into three in upper level. At the long sterile neck of ovary the peripheral bundles become close to each other.

The number of the calyx lobes of *T. sinuatum* varies from three to five. When the calyx-lobes are three, each of two lobes is supplied by three bundles, and larger one by five bundles. After the separation of the calyx supplies, ten bundles are distinct. They supply to the corolla and the stamen.

In *T. sinuatum* the wall of ovary consists of two kinds of tissues, those surrounding the loculi, and the other (pl. 8-5). The former is composed of fibriform cells without crystal and grows solid after blooming. In mature fruit the seed is surrounded by this solid tissue. The latter of globular cells like the parenchyma of ovary of the other genera and contains some crystals. These cells do not grow so solid as the former tissue even at maturity.

A single bundle supplies to each of three loculi. As the result of the separation of three ovular bundles, the central bundle divides into four which remove slightly

to the periphery like as the ventral strands of *Sambucus*. These four bundles run up into the style.

Tribe Linnaeaceae — In the tribe Linnaeaceae Wilkinson (16) observed the floral anatomy of *Symphoricarpos album* var. *laevigatus*, *S. orbiculatus*, *Linnaea borealis*, *Kolkwitzia amabilis*, *Abelia chinensis*, and *A. grandiflora*. In 1968 I (26) summarized in Japanese the evolutionary trend of the floral anatomy. In this study *S. orbiculatus*, *L. borealis*, and *K. amabilis* were reexamined, and *Dipelta yunnanensis*, *A. serrata*, *A. spathulata*, *A. tetrasepala*, *Zabelia biflora*, and *Z. integrifolia* were there newly observed.

As the key character to define the tribe Linnaeaceae, Fritsch (3) took up much importance the presence of the abortive and fertile carpel. The ovary consists of two fertile and two abortive carpels in *Symphoricarpos* and *Dipelta* (pl. 8–6), and a single fertile and two abortive ones in the remains of this tribe (pl. 9–1~4 & 9). Each fertile carpel contains only one well-developing ovule which usually develops to a seed. The others bear several small and abortive ovules alternately in two rows, except for *Z. biflora*. In this species the margin of abortive carpel does not lobed. In a few cases, these are two fertile and two abortive carpels for an ovary as in *Linnaea*, *Abelia*, and *Zabelia*.

The ovary has often the long sterile neck at the top. An extremely developed sterile neck is found in *Kolkwitzia*. *Dipelta*, *Abelia*, and *Zabelia* have also rather long sterile neck. In *Symphoricarpos* and *Linnaea* the sterile neck does not develop so distinct.

In the cross section of the pedicel, the bundles are variable according to the genera of the tribe Linnaeaceae. In *Symphoricarpos*, *Dipelta*, and *Kolkwitzia*, the bundles form a loop in outline, though the bundles divide radially at the upper level of pedicel. In *Linnaea* there are six small bundles (pl. 8–7). At the upper portion of the two-flowered peduncle of *A. serrata*, *A. spathulata* and *A. tetrasepala*, a bundle branches into two running up to the level of attachment of bracts (pl. 9–7). At the lower level of the pedicel of *Zabelia* treated, there are two bundles, each of which divides into two at the upper (pl. 10–1).

In this tribe an ovary is usually subtended by bracts and bractlets whose supplies are variable according to genera. In *Dipelta*, an ovary has a pair of bracts and bractlets which adnate to the lower half of ovary and appear to fuse to each other at the base. I can not confirm the vascularization of bract and bractlet supplies of this genus. Because the bract and bractlet supplies fuse to each other at the base and then branch diversely. The ovary of *Linnaea* is subtended by a pair of bracts and bractlets. The formers fuse to the base of ovary, and the latters fuse or embrace to the lower half (pl. 9–1). Each of the subulate bracts is supplied by a single bundle, and each of larger bractlets by three (pl. 8–8 & 9–1). In *Symphoricarpos*, *Kolkwitzia*, *Abelia*, and *Zabelia*, a single bundle enters to each of bracts and bractlets (pl. 9–7).

After the separation of bract and bractlet supplies, several bundles proceed to the periphery of ovary in this tribe, except in *Zabelia*: eight in *Symphoricarpos* and *Dipelta* seven to eight in *A. spathulata* and *A. tetrasepala*, seven in *Linnaea*, and five to six in *A. serrata* (pl. 9–8). In *Zabelia*, four bundles divide radially and join together at

receptacle, and then the peripheral bundles result in six in number below a fertile loculus. Some of these peripheral bundles often fork at the level further up, so the number of peripheral bundles are more in number at the upper portion, eight to ten in *Symphoricarpos* and *Kolkwitzia* (pl. 8-6), nine to ten in *Dipelta*, ten in *Linnaea* (pl. 9-2~5), and seven to ten in *Zabelia*. In *Abelia* the bundles proceeding to the periphery at receptacle usually do not divide but run up to the upper portion of fertile part or to sterile neck. In *Zabelia*, each of peripheral bundles elongates along the wall of ovary and join together at the upper level, i.e. peripheral bundles become a ring surrounding loculi (pl. 10-2). In rare case, the peripheral bundles of this genus are distinct even at the sterile neck like as the other members (pl. 10-3). Wilkinson (16) observed the four-celled ovary of *Linnaea* whose peripheral bundles are twelve in number at the middle portion of ovary.

In case number of the peripheral bundles are less than nine in *Symphoricarpos*, *Linnaea*, *Dipelta*, and *A. spathulata* having five calyx-lobes, the peripheral bundles become ten as result of the radial division of the bundles situating at the radii of septa at the upper portion of fertile part of ovary. In the other members, on the other hand, the number of the peripheral bundles running up to the top of the sterile neck are less than nine: eight to nine in *A. tetrasepala*, eight in *Kolkwitzia*, and six in *A. serrata*.

After the separation of peripheral bundles from receptacular stele, the bundles remaining in the inner side approach the center in *Symphoricarpos*, *Linnaea*, *Kolkwitzia*, *Abelia*, and *Zabelia*. In *Symphoricarpos* these strands fuse to form a rectangular cylinder at the base of loculi. The cylinder sometimes bends inward at the upper level resulting in two V-shaped bundles. The central bundle divides into two broad linear bundles facing to the fertile loculi at the lower level. Each of these linear bundles separates two fertile ovular supplies which are at first V-shaped but often separate from each other. The linear bundles are divided at the point separating the fertile ovular supplies, and sometimes fuse to the segment in opposite bundles forming V-shaped bundles. As the result of them, the central bundle becomes four V-shaped bundles, two V-shaped and four oblong bundles, or eight oblong bundles. Each of the fertile ovules is supplied by two inner bundles in *Symphoricarpos*. In *Dipelta yunnanensis* two opposite groups of three strands approach the center. They fuse to form an oblong bundle and convex at the center in cross section at the base of ovary. At further upper level an oblong bundle divides into two oblong ones becoming gradually round in cross section. At the upper half each of the two central bundles gives off abortive ovular supplies in two rows. Slightly below the level of the attachment of abortive ovules, central bundle divides into six strands. Among them smaller four are ventral to carpels, and larger two supply to the fertile ovules. Ventral and ovular strands of *Linnaea* fuse to form one larger and one smaller strands below loculi (pl. 9-1). The former supplies to a fertile ovule, and the latter supplies to abortive ovules and then divides into three, each becoming a ventral strand of carpel at the upper level of ovary (pl. 9-2~5). In *Kolkwitzia*, *Abelia*, and *Zabelia*, the strands approaching the center fuse to a central bundle. In these genera the central bundle

divides into a larger bundle and a smaller ventral strands after separating the supplies to abortive ovules. A larger bundle separates a fertile ovular supplies, and then forks into two ventral strands. In one specimen of *A. serrata*, a central bundle divides into three after the separation of abortive ovular supplies, and a fertile ovular one is branched from one of the three. In four-celled ovary of *Z. biflora*, a central bundle divides into four smaller and two larger strands as in *Dipelta*. The smaller strands are ventral running up to the style, and the larger ones supplies to the fertile ovules. In one specimen of three-celled ovary of this species, a central bundles divides into two ventral strands, and then a ventral one is given off centripetally from peripheral bundles fusing to form a ring at the sterile neck.

All the peripheral bundles give off two or three calyx supplies in the tribe Linnaeae, except *Zabelia* (pl. 8-9). In case a peripheral bundle separates a calyx supply, the latter soon divides into two to three. In *Zabelia* a ring of peripheral bundle gives off four calyx supplies which divide into several strands at the base of calyx. When there are eight distinct bundles, each of every other four gives off a calyx supply (pl. 10-3).

In *Symphoricarpos*, according to Wilkinson (16), most of the peripheral bundles give off obliquely a minute trace from each of inner face of the bundles at nearly the same level as separating calyx supplies, and then peripheral bundles combine together to form a ring. After that the bundles become ten in number. Among these ten every other five are corolla supplies and the others are stamen ones. After the separation of calyx supplies, peripheral bundles count nine in *Linnaea*, *Kolkwitzia*, and *Abelia*, and a vascular ring divides into eight in *Zabelia*. Among them four bundles supply to four stamens, and others enter into corolla (pl. 9-6).

Evolutionary trend. The number of the carpels shows a trend to decrease from four to three. Four-carpellate ovary is found usually in *Symphoricarpos*, *Dipelta* (pl. 8-6), and rarely in all the other general of the tribe Linnaeae. Three-carpellate one is derived from the reduction of a fertile carpel among four carpels (pl. 9-2 & 9).

There are two types in the shape of ovary in accordance with that of loculi: the one is globose, and the other elongated and compressed with long sterile neck. The former seems to be more primitive than the latter, for in globose ovary the abortive loculus is almost the same as the fertile one in length but in shape, contrary to the case of compressed ovary where abortive loculus shows a tendency to reduce in size in comparison with fertile one. In addition, this conclusion is also supported by the following respect: *Symphoricarpos* and *Linnaea* having globose ovary are suggested to be primitive in this tribe from the other features of floral anatomy as well as the floral morphology (Fukuoka, 26). An intermediate form between the two types is found in *Kolkwitzia* whose ovary has a long sterile neck.

In the way of separating the fertile ovular supply, this tribe has two types: one is found in *Linnaea* whose fertile ovular supply separates from central bundle at the base of ovary (pl. 9-1), and the other is found in all the other genera whose fertile ovular supply becomes distinct at the level nearly the same as or slightly lower than the attachment of fertile ovule. A fertile ovule is supplied by double strands in *Sym-*

phoricarpus, and by a single one in the other members.

Peripheral bundles arrange at the dorsal portion of carpels and the radii of septa. Two bundles near the latter portion show a tendency of fusing to each other. As the result of fusing as well as the reduction of carpel, the number of peripheral bundles decreases. From this feature *Abelia* is suggested to be most advanced and *Linnaea* most primitive.

There are two types of the separation of calyx supplies: the calyx supplies are derived from all the peripheral bundles, or a lobe of calyx is supplied by a strand branched from a peripheral bundle as in *Zabelia*. After the separation of calyx supplies, peripheral bundles become ten in number in *Symphoricarpus*, nine in *Dipelta*, *Linnaea*, *Kolkwitzia*, and *Abelia*, and eight in *Zabelia*. They are corolla and stamen supplies, so the number of bundles is correlated with that of corolla lobes and stamens.

The bractlet is supplied by three bundles in the primitive stage as in *Linnaea* and probably in *Dipelta*. In derived one, a single bundle enters to the bractlet as well as bract in the other members.

Tribe Diervilleae — In the tribe Diervilleae, Wilkinson (15) observed the floral anatomy of *Diervilla lonicera*, *D. sessilifolia*, *Weigela floribunda*, *W. florida*, and *W. japonica*. I have reexamined on *D. lonicera* and *W. japonica*, and the observations were newly added concerning the species as follows: *Macrodiervilla middendoriana*, *W. coraensis*, *W. decora*, *W. hortensis*, and *W. maximowiczii*.

In this tribe, the elongated ovary has long sterile neck at the upper part and consists of two carpels showing involute closure. The degree of the fusion of these involute carpels is more or less different for each genera as mentioned in the following pages.

In *Macrodiervilla* the enlarged placentae are circular in outline and convex at the center in cross section at the lower half of ovary (pl. 10-7). The convex margins of each carpel separate from each other at the upper half of ovary, where the margins are close to those of the opposite carpels (pl. 10-8). Each of the enlarged carpellary margins bears ovules spirally three- to four-seriate at the lower half (pl. 10-7~8), and two seriate at the upper half (pl. 11-1). In the sterile neck there is a split in the center (pl. 11-2).

In *Diervilla* the carpellary margins fuse to each other at the lower half of ovary, and they separate as in *Macrodiervilla*. At the lower half the placenta extends to the wall of ovary at right angles to the true septum and fills most of the cavity of the loculus where is not occupied by ovules (pl. 11-4). Each of the carpellary margins divides into two lobes bearing ovules at the lower half (pl. 11-4), but does not divide at the upper half (pl. 11-5). Therefore, the ovules arrange in four rows in each loculus at the lower half and in two rows at the upper half.

The inrolled carpels of *Weigela* fuse to the margins of the opposite carpels forming the septa. Each of the carpellary margins extends at the right angles to the wall of ovary, though the two margins of the same carpel extending in parallel do not fuse even at the lower part of ovary (pl. 11-8). All of the four extending margins of carpels bear ovules at the apex (pl. 11-8).

In this tribe the vascular bundle in pedicel forms a loop in cross section. When the ovary has the bract, each bract is supplied by a bundle given off from the receptacular stele at the ranges from receptacle in *Macrodiervilla*, *Weigela*, and *Diervilla*, to the level slightly above the bottom of loculi in some cases of *Diervilla* (pl. 11-3). Such differences in the level at the separation of the bract supply is correlated with the portion to which the bract attaches.

At the receptacle of *Macrodiervilla* in cross section, there are observed eight to ten bundles, though they are decurrenting to the neighbouring ones like as *Triosteum* (pl. 10-4). At the further upper level, a pair of three bundles proceed to the periphery faced to the dorsal portions of carpels, and then at the level slightly above the bottom of loculi a pair of two bundles in radii of septa become distinct (pl. 10-6). In the pattern of the separation of the peripheral bundles, *Diervilla* and *Weigela* resemble *Macrodiervilla*. In *Diervilla*, however, the radial division of a vascular ring occurs at the upper level than *Macrodiervilla*. Namely, the bundles in the radii of septa remains broad linear or crescent in the shape even at the level above the bottom of loculi, and then these bundles divide radially and centripetally (pl. 11-3).

When the peripheral bundles are less than nine in number, one or two of them are divided into two at the ranges from the base of ovary to the middle level (pl. 11-7). In all the genera of this tribe, therefore, there are ten peripheral bundles at the upper level of ovary as well as sterile neck (pl. 10-8, & 11-1~2, 4~5 & 8). Among them, every other five are located to the slightly inner portion of the sterile neck and supply to the corolla. Each of the other five gives off centrifugally a calyx supply (pl. 11-9), and then enters to the stamen in *Macrodiervilla*, *D. lonicera*, and *Weigela*. In *D. sessilifolia*, according to Wilkinson (15), all the ten peripheral bundles give off the calyx supply as in *Leycesteria*. In *D. lonicera* the corolla bundle gives off occasionally the small calyx supply which often divides into two and disappear at the base of calyx-tube. Each of the calyx supplies divides into and fuse together in *Macrodiervilla*. The main calyx bundle of *D. lonicera* gives off one or two short traces. In *Weigela*, on the other hand, each of the calyx supplies branches into two to three at the base of calyx-lobe.

At nearly the same level as the separation of calyx supplies, the peripheral bundles separate centripetally branches which join together to form a thin cylinder there in the tribe Diervilleae (pl. 11-6 & 9). This cylinder seems to consist of the bundles given off from all the peripheral bundles in *Macrodiervilla*, *Diervilla*, and most of *Weigela*, though the bundles given off from five outer bundles are small in size. In *W. hortensis*, on the other hand, bundles composing the cylinder are not given off from five outer bundles but from five inner corolla ones. The centripetal vascular ring joins with a corolla bundle at the uppermost portion of sterile neck (pl. 11-9). This corolla bundle becomes large in size at the level where the vascular ring disappears and style become distinct. This large bundle supplies to the glandular protuberance whose base fuses to the ventral side of corolla tube, and then gives off centrifugally a bundle entering to the ventral side of corolla.

After the separation of the peripheral bundles, eight to ten alternative bundles

decurrenting to the center at the base of receptacle remain in their place or proceed towards the center at the ranges from receptacle to the level slightly above the bottom of loculi. In *Macrodiervilla* a pair of two bundles faced to the dorsal portion of carpels remain in the center of receptacle. These bundles and the bundles faced to the radii of septa arrange as if they draw a loop (pl. 10-5), and then a pair of two separate from the margins of the latter. These bundles fuse to each other and form V-shape or nearly so in cross section (pl. 10-6). At the level further above a pair of large bundle remain in the septa after the separation of the peripheral bundles at the radii of septa (pl. 10-6). At the lowermost level of placenta where the ovules are, the central bundle is complicated, for the ovular supplies are successively given off from the portion near the corner of V-shaped bundle. At the further upper level, the central bundle becomes two in number and forms V-shape closed against the septa (pl. 10-7). Each of the arms of V-shaped bundles gives off successively the ovular supplies. Each of the lower V-shaped bundles divides into two as the result of the separation of ovular supplies, and the each arm fuses to that of the opposite carpel together with a remaining solitary bundle between them forming a V-shaped bundle in cross section. The upper V-shaped bundles gradually reduce in size in the upper level of ovary, and become broad linear bundles. These bundles divide again into several strands which arrange along the split of placentae (pl. 11-1). At the sterile neck the central bundles reduce to two or four small ventral strands as the result of supplying to the ovules. They run up to style along the split of the sterile neck (pl. 11-2).

In *Diervilla* several strands proceed towards the center at the ranges from receptacle to the level slightly above the bottom of loculi (pl. 11-3). They fuse to form a large round bundle. This bundle divides into two at the level where carpellary margins extend in loculi. In this genus the central bundle gives off the ovular supplies at the lower level than the attachment of ovules (pl. 11-4). They run up in the middle portion of extending carpellary margin to the same level as the attachment of ovule where ovular supply extends horizontally and divides into two, each of which extends to the two ends of carpellary margins. In *Weigela*, on the other hand, eight to ten strands proceeding center become together to form a thin cylinder below loculi (pl. 11-7). This cylinder becomes a large round bundle at the level above loculi in cross section, and is gradually to form two V-shaped bundles at the level where carpellary margins extend into loculi as the result of the extending of bundle along the carpellary margins (pl. 11-8). Both the ends of the V-shaped bundle successively separate branches which extend horizontally and supply to ovule. After the separation of ovular supplies the central bundle becomes two to four small ventral strands running up to style in *Diervilla* and *Weigela* (pl. 11-9).

Evolutionary trend. From the floral anatomical features the tribe Diervilleae are characteristic in two carpels, many ovules in a single loculus, the presence of centripetal vascular ring at the uppermost part of long sterile neck. However, the genera differ from each other in the features found in placenta as follows: each of the enlarged carpellary margins bears spirally the ovules three- to four-seriate at the

lower half of ovary and two-seriate at the upper half, i.e. each of loculi has ovules in six to eight rows at the lower half and in four rows at the upper half, in *Macrodiervilla*; in putatively advanced one each of the carpellary margins divides into two lobes whose apex bears ovules at the lower half and does not divide at the upper half, i.e. each of loculi are in four rows at the lower half and in two rows at the upper half, in *Diervilla*; and in the most extreme form each of the carpellary margins bears ovules one-seriate throughout the fertile parts of loculi, i.e. in two rows, in *Weigela*.

Concerning the separation of the ovular strands, there are two types. In one type the ovular strands are given off from the central bundle at the lower level than the attachment of ovules, as seen in *Macrodiervilla* and *Diervilla*; and in the other probably derived type the ovular strands are separated at nearly the same level as the attachment of ovules and extend horizontally to ovules as in *Weigela*.

Two types of the derivation of the centripetal ring are recognized as follows: in a type which seems to be primitive, each of ten peripheral bundles gives off the strands composing the centripetal ring; in the other the centripetal ring is derived from the five corolla supplies. The former is found in *Macrodiervilla*, *Diervilla*, and most of *Weigela*, and the latter in *W. hortensis*.

Calyx supplies are usually given off from five peripheral bundles, though in some of *D. lonicera* the corolla bundles branch the small calyx supplies as well as the calyx-stamen ones.

Leycesteria ——— I have reexamined the floral anatomical features of *L. formosa* which is already described by Wilkinson (15) in detail. I will summarize here the important features among them.

As one of the characters to define the subgenus *Paralestera* based on *L. gracilis*, Airy-Shaw (32) valued the number of the loculi in each ovary. Hara (33) studied the variation of the number of the loculi in each ovary of this species, and concluded that *L. gracilis* had usually five-celled ovary and that this subgenus could not be distinguished from the other having five-celled ovary in many cases.

Wilkinson (15) described that *L. formosa* had usually five-celled ovary (pl. 12-1). However, the ovary of this species has often four loculi which are four-merous in the other floral parts, i.e. lobes of calyx and corolla, corolla glands, and stamens (pl. 12-2).

At the lower half of the loculi the carpellary margins fuse to each other (pl. 12-2), though at the upper half they are separated at the end being anchor-shaped in cross section (pl. 12-1). The end of the anchor-shaped carpellary margin bears the many pendulous ovules (pl. 12-1). There is the slender sterile neck.

In the five-merous flower ten peripheral bundles proceed centrifugally from the vascular ring which may divide into about ten bundles radially just below the loculi. They run up through the wall of the ovary to the top. The stamen-calyx bundles lie in the radii of the septa, and the corolla-calyx bundles lie in the radii of the loculi (pl. 12-1~2). Smaller and larger bundles are alternately at the periphery of the sterile neck. Smaller ones are the calyx-corolla bundles and larger the calyx-stamen ones. All of them may give off tangentially one or two calyx strands which may

unite into a vascular ring of less thickness (pl. 12-3).

Separating the peripheral bundles, about ten small strands remain in the center. They may be grouped into five and each of these five moderately proceeds to the septum. According to Wilkinson, in the radii of the loculi there are one or two traces which seem to supply directly to the lowermost ovules. The strands situated at the end of the septa give off a number of the ovular traces, extending to the ovules along the arm of the anchor-shaped carpellary margins (pl. 12-1). Among five ventral strands one is extinguished and four others usually extend to the style. Wilkinson (15) observed that two ventral strands were tapered and became extinct above the loculi in one specimen with the five-celled ovary.

In the four-merous flower, on the other hand, there are four loculi, eight peripheral bundles and four ventral strands extending to the style (pl. 12-2~3).

Lonicera ——— As the important key characters to define the infrageneric taxa of *Lonicera*, Rehder (34) took up the floral anatomical features, i.e. the number of the loculi in one ovary and whether a pair of the ovaries being connate or distinct.

Wilkinson (15) minutely observed the floral anatomical features of *Lonicera* for twelve species belonging to two subgenera and three sections in Rehder's system. Based on her own study she proposed some taxonomic opinions. Subgen. *Caprifolium* seems to be highly evolved comparatively with Subgen. *Lonicera* with respect to the peripheral bundle. Sect. *Coeloxystoeum* is more generalized than Sect. *Isika* which seems to be greatly specialized. I made detailed anatomical observations of the ovary of *L. alpigena* var. *glehni*, *L. chamissoi*, *L. gracilipes*, *L. harae*, *L. japonica*, *L. maackii*, *L. mochidzukiana*, *L. morrowii*, *L. ramosissima*, *L. sempervirens*, *L. standishii*, *L. tschonoskii*, and *L. vidalii*, in addition to a preliminary study on some other species.

Rehder (34) placed the value to the number of the loculi for each ovary as one of the characters to define the subsections of Sect. *Isika*, though the feature was fairly variable even in a single individual. However, we can safely describe the number of the loculi for every species. According to Rehder (34), five-celled ovary is found in monotypic Subsect. *Calcaratae* of Sect. *Nintooa*; three-celled one in Subsect. *Spinosa* of Sect. *Isoxystoeum*, Subsects. *Pileatae*, *Vesicariae*, *Chlamydocarpi*, *Fragrantissimae*, *Bracteatae*, *Pyrenaicae*, *Oblongifoliae*, *Alpigenae*, and *Rhodanthae* of Sect. *Isika*, Subsects. *Breviflorae* and *Longiflorae* of Sect. *Nintooa*, and Subgen. *Caprifolium*; and two-celled one in Subsects. *Purpurascens*, *Coeruleae*, and *Cerasinae* of Sect. *Isika*. In the members of Subsect. *Microstylae* of Sect. *Isoxystoeum*, on the other hand, there are two- or three-celled ovary. The ratio of the occurrence of these two forms is not different. *L. vidalii* belongs to Subsect. *Alpigenae* in Rehder's system, though it shows usually two-celled ovary as had been mentioned by Nakai (35).

Each of the loculi consists of a single carpel closed from each other by means of the septa at the lower half of ovary (pl. 12-4, 6 & 8), though the septa are free at the upper half (pl. 12-9). The carpellary margins show anchor-shape or nearly so in cross section as in *Leycesteria*. The end of the anchor-shaped margins bears the pendulous ovules. According to Wilkinson (15), however, the union of the septa in *L. oblongifolia* extends to almost entire length of the loculus.

The pair of the ovaries show a tendency of fusing to each other. Free ovaries are found in most of Subgen. *Caprifolium* and of Sect. *Nintooa*, Subsects. *Coerulea*, *Pileatae*, *Chlamydocarpi*, *Bracteatae*, and *Distegiae* of Sect. *Isika*, Sect. *Co eloxysteleum*, some of Subsect. *Microstylae* of Sect. *Isoxysteleum*, some of Subsects. *Purpurascens*, *Alpigenae* and *Rhodanthae* of Sect. *Isika*. Fused ovaries in various degree are found in Subsects. *Cerasinae* and *Fragrantissimae* of Sect. *Isika*, some of Subsect. *Microstylae* of Sect. *Isoxysteleum*, of Subsects. *Purpurascens*, *Alpigenae* and *Rhodanthae* of Sect. *Isika*, and Subsect. *Calcaratae* of Sect. *Nintooa*. I observed actually that the pair of the ovaries of *L. calcarata* fused highly to each other even at the sterile neck. In *L. tschonoskii* of Subsect. *Rhodanthae* the pair of the ovaries fuse to each other at the base or in rare cases still free. In *L. alpigena* and *L. vidalii* of Subsect. *Alpigenae*, there are intermediate forms between those partially united and highly fused. From these facts we can conclude that the union of the ovaries occur in parallel along various phyletic courses of this genus.

In the common peduncle of the pair of the flowers, according to Wilkinson's observation, the steles show a tendency to fuse into a single stele. In primitive evolutionary stage there are a pair of the circular stele derived from a pair of flowers. This is found in *L. syringantha*, most of *L. xysteleum* and *L. morrowii*, and some of *L. canadensis* and *L. tatarica*. In more advanced one the stele is elliptical in cross section as the result of the fusion of the two steles. In the peduncles of this stage two adaxial peripheral bundles of a single flower may arise either as four separate bundles or two large ones. In latter form each of these two larger bundles is formed by the fusion of a pair of adjacent bundles. The former is found in that of some of *L. morrowii*, and there are observed various evolutionary stages in the latter. One or both of the pairs of the adaxial peripheral bundles may be united in *L. standishii* and *L. oblongifolia*. The union may occur only in the lower half of the ovary as seen in *L. fragrantissima* and *L. standishii*, or it may reach the upper part of the ovary as in *L. oblongifolia*.

In my observation, however, this evolutionary trend is obscure in most of the species treated, because the stele divides into two or four after the separation of the bract and bractlet supplies. *L. affinis* has two distinct ovaries and its stele shows a elliptic ring at the pedicel, though the stele forms two open semicircular rings sometimes circular in outline or still remains in open semicircular form. In *L. mochidzuki-ana* and *L. vidalii*, adaxial peripheral bundles scarcely fuse or unite at the very base of the ovary. One or two pairs of the adaxial peripheral bundles fuse to each other at the base in *L. harae* and *L. standishii*, and at the lower half in *L. tschonoskii* (pl. 12-8).

Peripheral bundles become distinct at the level of receptacle and below loculi. When the pair of ovaries are distinct or they fuse to each other only at the base, eight to ten bundles proceed to the periphery of ovary at receptacle. In case the ovaries fuse to the opposite ones not only at the base but the other portion, on the other hand, the division of the peripheral bundles is rather indistinct, especially in bundles in adaxial side (pl. 12-6). In the latter case, the adaxial bundles proceed slightly bending to the abaxial sides along the wall of the ovary dividing into a few bundles.

The number of the peripheral bundles for each ovary counts eight to thirteen. In Subgen. *Caprifolium*, according to Wilkinson (15), there are twelve to thirteen

peripheral bundles. Some of them are smaller and often unite to the neighbouring larger bundles after the separation of the sepal strands, so that the peripheral bundles become ten in number. In my own observation on *L. sempervirens* of this subgenus, however, there are ten to eleven peripheral bundles (pl. 12-4). She also reported that Sects. *Isoxylosteum* and *Isika* have nine to ten bundles and Sect. *Coeloxylosteum* eight. According to my observation, however, the number of peripheral bundles at the middle level of the ovary is variable within a species. Therefore, we can not distinguish the infrageneric taxa of this genus by the difference in the number of the peripheral bundles. When the peripheral bundles are less than ten in number at this portion of the ovary, one or each of the two of them divides into two, or three even in the most extensive specimen of *L. tschonoskii*. In case there are more than eleven peripheral bundles, on the other hand, two or more of them unite into one. At the sterile neck of ovary the peripheral bundles are generally ten in number, or rarely nine or eleven.

At the uppermost level of the sterile neck the peripheral bundles separate the branches centrifugally supplying the strands into the calyx. There are two types of the separation of these calyx strands in this genus as follows: in *L. sempervirens*, *L. harae*, *L. standishii*, *L. morrowii*, *L. mochidzukiana*, *L. vidalii*, *L. vesicaria*, every peripheral bundles give off a calyx strand; in *L. japonica*, *L. gracillipes*, *L. chamissoi*, and *L. tschonoskii*, on the other hand, five calyx strands are separated from every other peripheral bundles which then supply to the stamens. According to Wilkinson (15), the former is found in *L. coerulea*, *L. sempervirens*, *L. fragrantissima*, *L. tatarica*, *L. korolkovii*, *L. morrowii*, *L. standishii*, and *L. dioica*, and the latter in *L. syringantha*, *L. canadensis*, *L. oblongifolia*, and *L. xylosteum*. Each of the calyx strands usually extends periclinally and forms a loop at the base of the calyx.

After the separation of the calyx strands, ten bundles run up centripetally according as the ovary becomes small in volume. All of them supply to the corolla to which the filaments fuse at the base. Among ten bundles, every other five are corolla supplies and others supply to the stamens. The former is further divided and larger as compared with the latter.

Just below the level of the separation of the calyx strands, I have newly observed that several of the ten peripheral bundles give off centripetally the traces which approach horizontally the center of the sterile neck and fuse to the ventral strands only in following two species. In *L. japonica* two to four peripheral bundles separate these traces whose neighbouring ones sometimes fuse to each other until they reach the ventral strands. In only one specimen of *L. chamissoi*, in which no carpellary trace is usually separated from the peripheral bundles in the sterile neck, only one trace fusing to a ventral strand is given off from a peripheral bundle (pl. 12-7).

The ventral and ovular strands separate variously in *Lonicera*. In the species with distinct ovary, it is observed that the receptacular stele is at the center of receptacle forming a loop in cross section. In *L. gracillipes* this vascular cylinder has several gaps after the separation of the peripheral bundles and becomes a large round and closed bundle running up in the center of the solitary ovary. In the distinct ovary

of *L. sempervirens*, about ten distinct bundles remain in the center just below the loculi as the result of proceeding of ten peripheral bundles from the vascular ring. In *L. japonica*, on the other hand, the separation of the ventral and ovular strands differs distinctly from those two species. In one specimen among four observed ones each of the two peripheral bundles gives off a trace. These two traces fuse to each other and approach horizontally the center where the fused trace runs up. In another specimen a single trace approaching the center is given off from receptacular stele at the same portion where the receptacular stele divides radially into peripheral bundles. In the level ranging from the bottom of loculi to near the upper extreme, every peripheral bundle except for the three bundles faced to the dorsal side of loculi gives off successively several ovular strands and probably ventral one (pl. 12-9). These strands extend horizontally to the middle portion of the septa and run up in that portion at the lower half of ovary, and gradually approach the inner portion of the septa upward (fig. 7-B). Though the floral anatomy of *L. calcarata* is observed by paraffin sections of the materials from dried specimen, I confirm that the peripheral bundles lying in the radii of the septa separate the spiral elements extending the center along the septa horizontally as in the case of the ventral and ovular strands of *L. japonica*.

In the connate ovaries of this genus, on the other hand, the central bundle is derived from the receptacle and the periphery of ovary. At the receptacle one or a few strands are given off centripetally from semicircular bundle. At the portion upwards and below the loculi as well in most of the species with united ovaries except for *L. chamissoi*, the peripheral bundles near the radii of the septa separate some bundles which approach the center (pl. 12-6). Often these peripheral bundles are still imperfectly divided into distinct bundles at this level of ovary. These bundles derived from the peripheral bundles are indistinct just after the separation of them, though they seem to group together into three bundles in three-celled ovary and into two in two-celled one in the inner side of ovary and below loculi. In *L. chamissoi*, however, the central bundle seems to consist of those decurrented into at various levels of ovary. At the receptacle one or a few strands are separated from and approach the center of semicircular bundle. At the upper portion and below loculi, these bundles remain in the center. In addition to these bundles, each of the two peripheral bundles in the radii of the septa usually separates centripetally a bundle approaching to the center along the septa at the level where three loculi appear (pl. 12-6).

In three-celled ovary of this genus except *L. mochidzukiana*, all of these are united into three groups which again fuse to form a triangular bundle at the lower level of ovary and three-lobed in cross section at the upper level. All the central bundles of *L. mochidzukiana* are united into a single thin bundle at the level between just below the loculi and the lower portion of them. The central bundle is round, elliptical, or two-lobed in cross section at the lower half of two-celled ovary. At the upper half, the central bundle divides into two in two-celled ovary and into three in three-celled one in accordance with the separation of carpellary margins. The central bundles gives off ovular strands which proceed to the ends of extending carpellary

margins at the upper portion of ovary.

In *L. coerulea*, according to Wilkinson (15), the two ventral bundles of each ovary are cut off centripetally below the attachment of the lowermost ovules, and are situated in the wall of ovary. These bundles give off ovular traces from their position. She also reported that the placentae of *L. dioica* are parietal (fig. 7-A).

Evolutionary trend. As mentioned above there are various forms of the floral anatomy in *Lonicera*, though we have not as yet enough information to generalize the evolution of this feature. However, an evolutionary trend of the floral anatomical features may at present be interpreted as follows.

The number of the carpels shows a trend of reduction, from five through three to two. The five-carpellate ovary is found only in monotypic Subsect. *Calcaratae* of Sect. *Nintooa*; three-carpellate one in Subgen. *Caprifolium*, most of Sects. *Isika* and *Nintooa*; and some of Sect. *Isoxylosteum*; and two-carpellate one in some of Sects. *Isika* and *Isoxylosteum*. Such a tendency of reduction in the number of carpels seems to occur in parallel along various phyletic courses in this genus, because there are two- or three-carpellate ovary even within a single species as well in the two species belonging to two distinct sections.

The pair of the ovaries show a tendency of fusion to each other. Free ovaries are found in most of Subgen. *Caprifolium*, of Sects. *Isika* and *Nintooa*, some of Sect. *Isoxylosteum*, and all of Sect. *Lonicera*. There are various intermediate forms between the free ovaries and partially connate ones, or partially connate ovaries and highly united ones, even within a single species. The connate and free ovaries are generally found in most of the taxa of this genus. By these facts we can speculate that the fusion of the ovaries has developed independently in various taxa.

The same kind of fusion of the ovaries is found in the vascular bundles of ovaries. On the two pairs of the adaxial peripheral bundles in the connate ovaries, one or two pairs of the adjacent bundles in different ovaries fuse to each other in various degree in accordance with that of the ovaries themselves. This fusion is scarcely observed in all the materials of distinct or partially connate ovaries, and sometimes in highly united ones as in Subsects. *Fragrantissimae* and *Alpigenae* of Sect. *Isika*.

There are two types of the placentations of *Lonicera*. In the primitive type the placentae are axile at the lower half (fig. 7-C) and parietal at the upper half as in most of this genus (fig. 7-D), and in derived one parietal as in *L. coerulea* and *L. dioica* (fig. 7-A). The ovular and ventral strands are given off at the level of receptacle in most of species treated, though in some ones they are separated from one or a few of the peripheral bundles at the level above the bottom of loculi.

In *L. japonica* and *L. calcarata*, on the other hand, the ventral and ovular strands are successively traced from the peripheral bundles and the receptacular stele at the level of receptacle and in the ranges from the bottom of loculi to near the upper extreme of them (fig. 7-B). Though a few peripheral bundles give off the lateral and ventral strand respectively at the sterile neck, these peripheral bundles primarily are not carpellary supplies but the calyx-stamen or calyx-corolla ones. Such separation of the ovular and ventral strands from peripheral bundles seems to have evolved

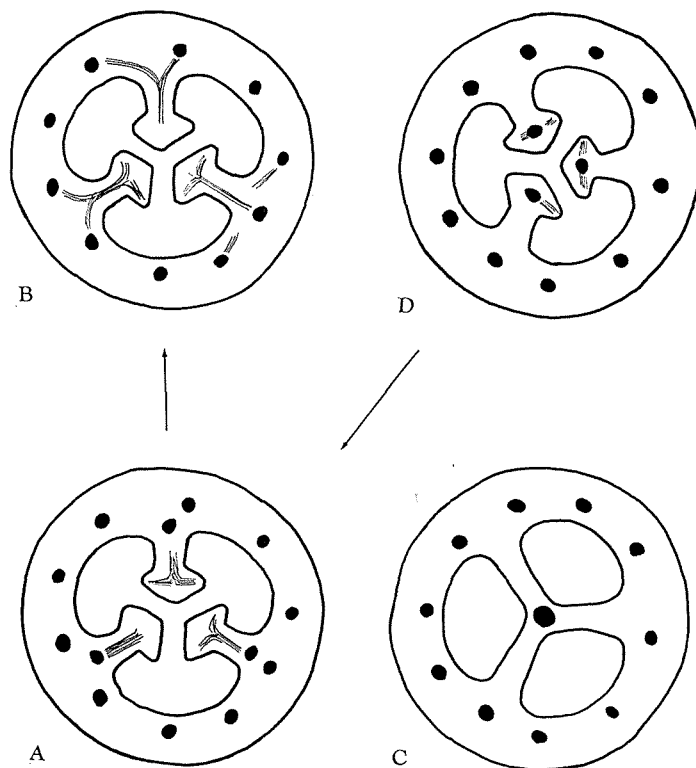


Fig. 7. Diagram showing an evolutionary trend of placentation in *Lonicera*. A: parietal placentation, in which ventral bundle is situated to the wall of ovary as in *L. coerulea* and *L. dioica*; B: placentation of *L. japonica*, in which ventral and ovular bundle seems to fuse to peripheral bundle supplying to calyx, corolla, and stamen; C: at lower half of ovary as in most of this genus, showing axile placentation; D: at upper half of ovary, in which ventral bundle becomes free to each other and are situated at apex of placenta. Explanation in text.

as follows: the placentation of *L. japonica* is parietal in its ancestor, i.e. the ovular and ventral strands are situated in the wall of ovary and the portion near the radii of septa like as *L. coerulea* and *L. dioica*; and each of these strands fuses to the calyx-stamen or calyx-corolla bundles near the radii of septa (fig. 7). This speculation is supported by the observation that the ovular and ventral strands fuse to the peripheral bundles at the lower half of ovary as in *L. chamissoi* and others.

Concerning the separation of calyx strands from the peripheral bundles, there are recognized two types. In a type which seems to be primitive, each of the ten peripheral bundles gives off a single calyx strand as in Subgen. *Caprifolium*, Sect. *Nintooa*, most of Sect. *Lonicera*, and some of Sect. *Isika*. In the other, putatively

advanced one, the calyx strands are separated from every other five peripheral bundles among ten. This is observed in one species of Sect. *Lonicera* and some of Sect. *Isika*. These two types are observed in different species in a single subsection of Rehder's system, Subsect. *Ochranthae* of Sect. *Lonicera*. Judging from these cases the reduction of the number of the calyx strands seems to have occurred in parallel in various phyletic groups in this genus.

In *Lonicera* the presence of the lateral ventral strands has not yet been reported. However, there are the lateral ventral strands which are separated from the peripheral bundles at the sterile neck in *L. japonica* of Sect. *Nintooa* and *L. chamissoi* of Sect. *Isika*.

Style and Stigma

As de Candolle (1) noted the variation of the style as one of the key characters to divide the family into two tribes of him, there are two distinct types, the elongated style and the short or very short and nearly absent style. The former is found in the tribes Diervilleae, Lonicereae, Linnaeae, and *Triosteum* of Viburneae. In these members the length of the style is generally correlated with that of the corolla tube. In the latter *Viburnum* of Viburneae has the very short style even in the elongate corolla tube as in *V. carlesii*, and the style of *Sambucus* is hardly recognizable (pl. 3-4).

There are two types in the shape of the stigma: the capitate stigma as in Diervilleae, Lonicereae, Linnaeae except some of *Symphoricarpos*, and *Triosteum*; and the slightly lobed stigma as in *Viburnum*, *Sambucus*, and some of *Symphoricarpos*.

As noted above, the form of the style in this family is correlated with that of the stigma in outline. As pointed out by some of authors, these features do not support a current opinion that *Triosteum* and *Viburnum* belong to a single tribe Viburneae. Hutchinson (13) actually separated *Triosteum* as a distinct tribe.

Corolla

The corolla is gamopetalous for all the species of this family, though the shape is much variable according to species. The actinomorphic corolla is seen in *Sambucus*, most of *Viburnum*, *Symphoricarpos*, *Leycesteria*, and some of *Lonicera*. On the other hand, typically zygomorphic one is known in *Dipelta*, *Kolkwitzia*, *Abelia*, *Diervilla*, most of *Zabelia* and *Lonicera*, and *Triosteum*. The corolla of *Linnaea*, *Macrodierilla*, *Weigela*, and some of *Viburnum* and *Zabelia*, and *Lonicera* seems to be transitional forms between the two types. In such case, the corolla of the tribe Linnaeae and the genus *Lonicera* shows the various forms between typical actinomorphic and zygomorphic corollas.

The lobes of the corolla usually count five, rarely four or three. Four-lobed corolla is found in *Sambucus gaudichaudiana* and most of *Zabelia*, and three-lobed corolla only in *S. australasica*. In some species, on the other hand, the lobes of the corolla vary in number even in a single individual: four to six in *Sambucus*, and four to five in *Leycesteria formosa*, *Lonicera angustifolia*, *L. cerasina*, and others. In most of them the number of corolla-lobes is correlated with the number of other parts of flower. According to Fukuoka (26), four-lobed corolla of *Zabelia* is interpreted as the result

of the fusion of two dorsal lobes (see his fig. 1).

The aestivation of corolla-lobes is mainly imbricate (pl. 1-9), except in Sects. *Ebulus* and *Scyphidanthé* of *Sambucus*, who have the valvate corolla-lobes (pl. 1-8).

Floral nectary

No floral nectary is observed on any portion of the corolla of *Sambucus* and *Viburnum*. In the rest of the family, however, the corolla is densely glandular hairy on the interior parts of the adaxial surface. The nectaries form linear to oblong zones along vascular bundles supplying to the corolla in *Symphoricarpos*, *Linnaea*, *Abelia* Sect. *Vesalea*, *Zabelia* Sect. *Zabelia*, and some of *Lonicera*. On the other hand, cushion-shaped nectary is found in *Triosteum*, *Dipelta*, *Kolkwitzia*, *Abelia* Sect. *Abelia*, *Leycesteria*, and most of *Lonicera*. In the tribe Diervilleae the glandular protuberance is club-shape with four glooves.

The nectary on each corolla varies five to one in number: five in most of *Symphoricarpos*, *Lonicera* Sect. *Isoxylosteum*, and *Leycesteria*; three in *Abelia* Sect. *Vesalea*, and some of *Lonicera*; and one in most of *Lonicera*, *Linnaea*, *Dipelta*, and others (pl. 9-6).

As noted in my previous paper (Fukuoka, 26), an evolutionary trend seems to be traceable concerning the arrangement and number of the floral nectary in Linnaeae based chiefly upon the number and arrangement of vascular bundles, stamens, and nectaries on each corolla. In the most primitive stage, five nectaries are nearly equal in size and arrange in regular order as found in most of *Symphoricarpos*. In further advanced one the nectaries are three in number, one lying ventral side and two lateral as in *Abelia* Sect. *Vesalea*. The size of these three nectaries is nearly equal in *Abelia floribunda*, and in *A. coriacea* the lateral two are smaller and sometimes almost reduced. In most of advanced one each corolla has only one nectary as the result of extinction of the two lateral nectaries as in the rest of this tribe, differing in the shape of the nectary. Such an evolutionary trend in the structure of the nectaries seems to be correlated to the evolutionary stage of symmetry of the corolla and is also found in the nectaries of *Lonicera*.

Stamen

To distinguish the tribe Viburneae from the tribe Sambuceae, Fritsch (3) took up the difference in the anthers, extrorse or introrse. The former is found only in *Sambucus* and the latter in the rest of the family. In *Sambucus*, however, I have actually observed introrse anther as in *S. javanica* subsp. *javanica* and *chinensis* and *S. hookerii* of Sect. *Scyphidanthé* (pl. 1-8). On the other hand, another herbaceous section *Ebulus* like as *S. adnata*, *S. ebulus*, and *S. wightiana* has extrorse anther as well as the arboreous representatives (pl. 1-9).

The number of the stamens is three to five: three only in *Sambucus australasica*; four in *Sambucus gaudichaudiana*, *Linnaea*, *Dipelta*, *Kolkwitzia*, *Abelia*, most of *Zabelia*, and some of *Leycesteria formosa*, *Lonicera cerasina*, and *L. angustifolia*; and five in the rest of the family. In the tribe Linnaeae the flower with four stamens seems to be derived from that with five stamens by extinction of one of them at the dorsal side

of corolla (pl. 9-6 & fig. 1 in Fukuoka, 26). In five-merous members of *Sambucus*, the anthers count occasional four or six in accordance with four- or six-merous flower (pl. 3-6). In this genus, thus, the number of anthers agrees with that of other parts of flower.

In *Macrodiervilla* and *Weigela maximowiczii* the anthers are coherent to each other, because they are densely pilose hairy and the hairs are entangled at the surface. In *Weigela*, except for *W. maximowiczii*, however, the pilose hairs are rather sparsely, and the anthers are not coherent. The coherent anthers is, therefore, no distinct character at all to recognize the phylogenetic relationship.

Fruit

There are a variety of fruits in the Caprifoliaceae. Nakai (5) took up the difference in fruit as the discriminative feature to segregate the tribe Diervilleae from Lonicereae. Troll & Weberling (20) enumerated the resemblance of fruit structure as one of the features to support their opinion that *Symphoricarpos* belonged to the tribe Lonicereae.

Two types of fruits may be recognized in this family: fleshy and dry. The former is further divided into two subtypes. In one form the fruit is referred to drupe having hard endocarp as in *Sambucus*, *Viburnum*, *Triosteum*, *Symphoricarpos*, and *Linnaea*. The detailed structures are different from each other generally in accordance with the difference in floral anatomy, especially in the structure of endocarp and the number of seeds in a single drupe. The other form is berry with several to many seeds as in *Leycesteria* and *Lonicera*.

The dry fruits are dehiscent or indehiscent. The former is found in *Macrodiervilla*, *Diervilla*, and *Weigela*, whose two-valvate capsule contains many seeds. The latter is further distinguished into two forms from the difference in the hardness of endocarp. The fruit of *Dipelta*, *Abelia*, and *Zabelia* is achene with one or two seeds. In *Kolkwitzia* the endocarp becomes hard, so its fruit seems to be regarded as nut with a seed.

As noted above, there are various types of fruit in the tribe Linnaeae: drupe, nut, and achene. As studied by Pfeiffer (36), the fruit of *Symphoricarpos* is not berry as typical in the tribe Lonicereae but drupe. In this respect, therefore, this genus does not belong to the tribe Lonicereae.

Conclusion

The circumscription of the Caprifoliaceae is rather obscure even at present, and there are several genera which are included in or excluded from this family. Airy Shaw (9, 10, 12) segregated *Alseuosmia* and *Memecylanthus* (including *Pachydiscus*) as the Alseuosmiaceae, and *Carlemannia* and *Silvianthus* as the Carlemanniaceae. From the study on the inflorescence Troll & Weberling (20) mentioned that all of these genera did not seem to belong to the Caprifoliaceae. On the other hand, Kern & van Steenis (11) included *Carlemannia* and *Silvianthus* in this family. Subse-

quent to them, Wargenitz (8) placed these two in the tribe Diervilleae, but Hutchinson (13) in the tribe Viburneae. Concerning the taxonomic position of *Carlemannia* and *Silvianthus*, these different opinions are resulted from the differences in evaluating the features of them. I can not give here my conclusive opinion for the circumscription of the Caprifoliaceae in general, though the taxonomic position of *Carlemannia* and *Silvianthus* proposed by Wagenitz (8) and Hutchinson (13) are briefly reexamined as follows.

To place *Carlemannia* and *Silvianthus* in the tribe Viburneae, Hutchinson (13) takes up much importance on the actinomorphic corolla not saccate at the base. Hutchinson's opinion is not supported by any other features. According to Hooker's (37) figure and Hutchinson's description, *Carlemannia* and *Silvianthus* have two-celled ovary bearing many ovules, two stamens, and elongated calyx-lobes. In these respects these two genera do not relate to *Viburnum* which is characterized by the ovary consisting of a fertile loculus with a single ovule and two abortive ones with some ovules, five stamens, and minute calyx-lobes. Indicated by the above features, it may be better to exclude *Carlemannia* and *Silvianthus* at least from the tribe Viburneae. On the other hand, Wagenitz (8) placed these genera in the tribe Diervilleae, because they had two-celled ovary with many ovules and drupe with many seeds. According to Hooker (37) and Hutchinson (13), *Carlemannia* and *Silvianthus* are characteristic in globose capsule dehiscent five-valves between the calyx-lobes in the former or loculicidally two-valves in the latter, and in two stamens, although the tribe Diervilleae have the elongated ovary with long sterile neck, cylindrical to spindle capsule dehiscent septically two-valves, and five stamens. Thus, *Carlemannia* and *Silvianthus* differ from the tribe Diervilleae in the structure of ovary and fruit which are the most important characters to define the tribes of the Caprifoliaceae. Accordingly, *Carlemannia* and *Silvianthus* do not seem to belong to the tribe Diervilleae, though we need further investigation of the floral anatomy of these genera.

Fritsch (3, 4) placed *Triosteum* in the tribe Viburneae indicated by the loculi each containing a single ovule, though he was not sure on the affinity between *Triosteum* and *Viburnum*. He (4) noted that *Triosteum* might be at the status between the tribes Viburneae and Lonicereae. Some of the recent botanists as Wagenitz (8), Ferguson (38), and others, also doubted to include *Triosteum* in the tribe Viburneae. Recently Hutchinson (13) separated *Triosteum* taxonomically as a distinct tribe. The separation has previously been proposed by Wilkinson (18) who concluded from the viewpoint of floral anatomy and morphology that this genus should be segregated into a distinct tribe. By the study on the morphology of the inflorescence, Troll & Weberling (20) suggested the relationship between *Triosteum* and the tribe Lonicereae.

The differences between *Triosteum* and *Viburnum* will be summarized as follows: 1) in *Triosteum* the habit is herbaceous, but in *Viburnum* it is woody or shrubby; 2) in the former the inflorescence is terminal or axillary cyme whose partial florescence consists of one or three flowers, but it is terminal panicle or corymb in the latter; 3) *Triosteum* has the large calyx each of whose lobes is supplied by three conspicuous bundles, and *Viburnum* has small calyx with each lobe supplied by a single minute

trace; 4) the former has zygomorphic corolla slightly saccate at the base, and the latter has actinomorphic one without spur, except the neutral flower whose corolla is slightly zygomorphic; 5) the style is elongated in *Triosteum* and very short in *Viburnum*; 6) in the floral anatomical features *Triosteum* differs from *Viburnum* chiefly in number of carpels, the pattern of the division of the central bundles and the peripheral ones at receptacle, that of fertile ovular supplies and the ventral strands, axile placentation, the absence of free dorsal strands and lateral one from the peripheral bundles at the upper level of ovary, the presence of long sterile neck of ovary, and the fibrous tissues surrounding each of the loculi. On the other hand, the presence of abortive carpel shows the similarity of these two genera. Comparing the abortive carpel of the former with that of the latter in detail, we observe that they differ from each other especially in the shape, the number of the peripheral bundles running up in the dorsal portion of abortive loculus, bi-lobed carpellary margins, and no separation of abortive ventral strand from a central bundle. The presence of abortive carpel can not be regarded as the evidence of the affinity between both the genera. From the facts noted above, *Triosteum* has no actual relation to *Viburnum*.

Wilkinson (18) pointed out that *Triosteum* was related to *Sambucus* in floral anatomical features, differing in morphological and taxonomical features. The affinity between them is supported by the following features: number of carpels, each loculus bearing a single ovule, the pattern of the division of the vascular bundles at receptacle, the division of the central bundle at the attachment of ovules, the presence of the abortive carpel found rarely in *Sambucus canadensis*, and the herbaceous habit, herbaceous representatives of *Sambucus* found in Sects. *Ebulus* and *Scyphidanthè*. *Triosteum* differs from *Sambucus* in the presence of long sterile neck of ovary, the fibrous tissues of ovary, the absence of free dorsal strand and lateral one, extensive calyx and its supplies, inflorescence, zygomorphic and tubular corolla being saccate at the base, long filaments, elongated style, larger seed, and leaf. As mentioned by Wilkinson (18), it should be evident that *Triosteum* never belongs to the tribe Sambuceae.

Weberling (23) noted that the leaf of *Triosteum* resembled that of *Lonicera* Subgen. *Caprifolium*, whose opposite leaves were often connate with each other at the base. Troll & Weberling (20) pointed out that *Triosteum* belonged to the tribe Lonicereae from the morphology of inflorescence. As noted both by Wilkinson (18) and by Troll & Weberling (20), this conclusion is supported also by elongated style, tubular corolla, the long sterile neck of ovary found in *Leycesteria*, and number of carpels. From these respects, except the number of carpels, *Triosteum* resembles also the tribe Diervilleae. From the floral anatomical features, *Triosteum* differs from the tribe Lonicereae as follows: the presence of the abortive carpel, the number of ovules in a single loculus, the fibrous tissues of ovary, and no elongation of the carpellary margins at the upper half of ovary. In addition, the former is distinguished from the latter in herbaceous habit, dry drupe with three stones, and the seed with thick and hard endocarp derived from the fibrous tissues of ovary. Thus, *Triosteum* does not belong to the tribe Lonicereae, and is scarcely related to any other genera of the Caprifoliaceae. Concerning the taxonomic position of *Triosteum*, therefore, I support

Hutchinson's opinion that this genus is distinct to warrant a monotypic tribe.

Hutchinson (13) unites the tribes Linnaeae and Diervilleae to the tribe Lonicereae, for he has made much importance to the resemblance of zygomorphic corolla, elongated style with a capitate stigma, and woody habit of them. In the Caprifoliaceae, zygomorphic corolla can be observed in parallel along the various phyletic lines. The length of style is correlated with that of corolla tube and elongated style is also found in another distinct tribe Triosteae. As mentioned below, the tribes Viburneae and Sambuceae can not be distinguished from each other by these features.

In the floral anatomical features, the tribe Linnaeae are clearly distinguished from the tribes Lonicereae and Diervilleae by the following features: the presence of two abortive carpels with several minute ovules, fertile one with a single ovule, and not extending carpellary margin. In addition, the tribe Linnaeae differ from the tribe Lonicereae in some taxonomic features as follows: inflorescence is raceme to cyme in the former, and raceme in the latter; in the former corolla is actinomorphic to slightly zygomorphic, and in the latter actinomorphic to distinctly bilabiate; floral nectary is slightly saccate in most of the former but forms distinctly spur in some of *Lonicera*; and the fruit of the former is regarded as drupe, nut, or achene, and that of the latter as berry with several to many seeds.

The affinity between the tribes Diervilleae and Lonicereae is suggested on the basis of the following features: extending carpellary margin, each loculus bearing many ovules longitudinally in the tribe Diervilleae and *Leycesteria*; the tubular corolla with more or less regular lobes in *Macrodiervilla*, *Weigela*, *Leycesteria*, and some of *Lonicera*; the long sterile neck of ovary in Diervilleae and *Leycesteria*; and the testa of seed being reticulate and scaly in Diervilleae and in some of *Lonicera* and fine reticulate in *Leycesteria* and most of *Lonicera*, differing the seed with wing as in *Macrodiervilla* and *Weigela*. On the other hand, the differences between these tribes are summarized as follows: the spindle to cylindrical fruit is the bi-valvate capsule with many seeds in Diervilleae, and the subglobose to globose berry with several to many seeds in Lonicereae; the shape of ovary is spindle to cylindrical in the former, and globose to subglobose in *Lonicera* in which a pair of ovaries show a trend to unite; the former has the centripetal vascular ring entering to nectary at the upper part of sterile neck, and Lonicereae lack this ring; inflorescence is cyme in the former and raceme in the latter; nectary is club-shaped in the former and that of the latter forms linear to oblong zone along corolla bundle or cushion-shaped; and the former has not earlap-like appendage at the base of leaf, but in the latter this appendage is sometimes observed.

Thus, the tribes Linnaeae and Diervilleae resemble the tribe Lonicereae in some respects, though these tribes are distinctly distinguished from each other by many taxonomic important features. The members within each tribe are allied closely, and all of these tribes are sufficiently warranting their ranks as such.

Wilkinson (18) has separated *Sambucus* and *Viburnum* widely from the other members of this family. The reason on which he has stood is that both of these genera are distinguished from the others of this family by many features which are common

to these genera as follows: rotate corolla without floral nectary, small and rotate or dentate calyx, short or absent style with lobed stigma, paniculiform or corymbiform inflorescence, and drupe. This conclusion is also supported by floral anatomical investigation as follows: the presence of free lateral and dorsal carpellary traces, loculi of ovary continuing beyond the position of the attachment of calyx, i.e. not completely inferior ovary, and the absence of the sterile neck of ovary.

As noted by Wilkinson (18), *Sambucus* and *Viburnum* differ from each other in many respects, and in one distinct case Fritsch distinguished *Viburnum* as a distinct tribe separated from the tribe Sambuceae. Recently, Airy Shaw (10, 12) regarded it as an appropriate opinion that *Sambucus* should be segregated as to form a distinct family. According to Moissl (39), the mode of development of embryo sac is regarded as *Adoxa*-type in *Sambucus* and as *Polygonum*-type in the other members of this family. According to Metcalf & Chalk (19), *Sambucus* differs from the others in wood anatomical features as follows: the occurrence of crystal-sand in the cortical region of petiole, the presence of narrow, thick-walled pericyclic fibres in stem, secondary xylem grouped in a tangential pattern, moderately short vessel members, scanty paratracheal parenchyma, and fibres with simple pits. Leaf is pinnately compound in *Sambucus* and simple or lobed in *Viburnum*. Anthers are extrorse or rarely introrse in the former and introrse in the latter. From these features, *Sambucus* is distinctly different from the other member of the Caprifoliaceae. In addition, both genera differ altogether in the floral anatomy as follows: the placentation is axile in *Sambucus* and parietal in *Viburnum*; in *Sambucus* carpels are usually fertile or rarely abortive as in one specimen of *S. canadensis* whose abortive carpel does not reduce distinctly in size and bears a single abortive ovule, and *Viburnum* has always one fertile and two abortive carpels which are situated above a fertile one and bear a few minute ovules respectively; at the stylar canal vestigial ovule does not observed in *Viburnum* but in *Sambucus*; the ventral supply of abortive carpel separated from a central bundle just below the attachment of a fertile ovule shows a trend to reduce in *Viburnum*, but this lacks in *Sambucus*; there are seven to ten peripheral bundles in *Sambucus*, and those of *Viburnum* show a trend to reduce ten to five in number as the result of the fusion of neighbouring bundles; in the latter are found various evolutionary stages from the large and circular placenta to rudimentary one, and the placenta of the former does not show such a trend; and the evidence of the double supplies to a fertile ovule remains clearly in *Viburnum* and lacks in *Sambucus*.

Thus, *Sambucus* and *Viburnum* are widely segregated from the other members of the Caprifoliaceae, though the difference between them seems to be more distinct than the differences among the other tribes of this family.

As discussed in details in this paper, the system of the Caprifoliaceae is here summarized and enumerated as:

Tribe **Sambuceae** H. B. K. ex DC. Prodr. 4: 321, 1830.

Sambucus L.

Tribe **Viburneae** FRITSCH in Nat. Pflanzenfam. 4-4: 163, 1891.

Viburnum L.

Tribe **Triosteae** HUTCHINSON, Gen. Flow. Pl. 2: 84, 1969.

Triosteum L.

Tribe **Linnaeae** FRITSCH, l.c. 164.

Symphoricarpos DUHAMEL, *Linnaea* L., *Dipelta* MAXIM., *Kolkwitzia* GRAEBNER, *Abelia* R. BROWN, and *Zabelia* (REHDER) MAKINO ex HISAUCHI et HARA.

Tribe **Diervilleae** C. A. MEYER in Bull. Phys.-Math. Acad. Sci. St. Pétersb. 2, 13: 216.

Macrodiervilla NAKAI, *Diervilla* MILLER, and *Weigela* THUNBERG.

Tribe **Lonicereae** R. BROWN ex DC. Prodr. 4: 329, 1830.

Leycesteria WALL., *Lonicera* L., and ? *Heptacodium* REHDER.

Key to the tribes and genera of the Caprifoliaceae

Concluding the above discussion, the classification of the Caprifoliaceae is revised as in the systematic list given on pages 52~53. An artificial key to all the tribes and genera is given below. The genus *Heptacodium* is excluded from the following key, because it is still obscure whether this genus belongs to the tribe Lonicereae or Linnaeae.

- 1A. Inflorescence corymbiform or paniculiform; ovary semi-inferior, without sterile neck; style short or nearly absent; stigma lobed; corolla actinomorphic, rotate, campanulate, or tubular, without nectary; bark with lenticel 2.
- 2A. Ovary three- to five-celled, each of loculi containing a fertile and a rudimentary ovules, abortive carpel absent, or very rarely present; anthers extrorse or rarely introrse; leaf pinnately compound; drupe with three to five stones Tribe Sambuceae, *Sambucus*.
- 2B. Ovary three-celled, a fertile loculus occupying nearly entire length of ovary and bearing a large ovule, and two abortive ones mostly situating to the portion just above or at nearly the same level as attachment of calyx; anthers introrse; leaf simple, lobed, or pinnate with stipular-like leaflets; drupe with a single stone Tribe Viburneae, *Viburnum*.
- 1B. Inflorescence not corymbiform nor paniculiform; ovary inferior, with or without sterile neck; style elongated; stigma mostly capitate, or rarely lobed; corolla actinomorphic to zygomorphic, with nectary inside; bark without lenticel, but often splitting longitudinally 3.
- 3A. Ovary composed of fertile carpel with a single ovule and abortive one; fruit indehiscent with less than three seeds 4.
- 4A. Herb; fertile loculi three in number, surrounded with fibrous and hard tissues, an abortive one compressed in shape; carpellary margins never free to each other; anthers five in number; drupe with three stones, with thick and hard endocarp Tribe Triosteae, *Triosteum*.
- 4B. Shrub; fertile loculi one or two, without fibrous tissues, abortive ones always two, containing several minute ovules; carpellary mar-

- gins free to each other at upper level of ovary; anthers five or four and didynomous; drupe, achene, or nut, with less than two seeds Tribe Linnnaeae.
- 5A. Corolla actinomorphic with five nectaries or rarely one; anthers five, or rarely four; calyx-lobes scarcely elongated; ovary four-celled, without sterile neck; drupe globose to subglobose, with two stones; inflorescence racemose *Symphoricarpos*.
- 5B. Corolla zygomorphic, with one or rarely three nectaries; anthers four and didynomous, or rarely five; calyx-lobes elongated; ovary three- or rarely four-celled, sterile neck elongated or rarely not; inflorescence cymose 6.
- 6A. Ovary subglobose, smaller, less than 1.5 mm long, sterile neck scarcely developed, three-celled, embraced by two large bractlets covered with glandular hairs; inflorescence bearing a pair of flowers on a long peduncle; trailing subshrub *Linnaea*.
- 6B. Ovary slender ovoid to cylindrical, with long sterile neck, more than 3 mm long; cyme without long peduncle; shrub erect, suberect, or rarely creeping on ground 7.
- 7A. Ovary four-celled, enclosed by a pair of large and round bractlets, or rarely not; stalk of a flower longer, more than 1 cm long, with subulate bracts at the base; achene with two seeds *Dipelta*.
- 7B. Ovary three- or rarely four-celled, not enclosed but subtended by small bracts and bractlets; fruit with a single seed or rarely two 8.
- 8A. Ovaries adnate to each other, densely covered with long bristle hairs; calyx-lobes five in number; nut subglobose at the base, with slender sterile neck at the apex, endocarp hard; stalk of flower longer with subulate bracts at the very base *Kolkwitzia*.
- 8B. Ovaries free to each other, without long bristle hairs; calyx-lobes five to two; achene not subglobose, but cylindrical and flattened, endocarp never hard; stalk of flower shorter, less than 0.5 cm long 9.
- 9A. Corolla campanulate- or rarely tubular-infundibuliform, lobes five in number; calyx-lobes five to two; branch

- not so thickened at node, old bark not splitting so deeply in six rows, but shallowly and irregularly *Abelia*.
- 9B. Corolla tubular-infundibuliform, lobes four or five; calyx-lobes four or five; base of petiole fusing to branch, so node much thickened; old bark deeply splitting longitudinally in six rows *Zabelia*.
- 3B. Ovary composed of only the fertile carpels with more than several ovules; fruit indehiscent or dehiscent, with several to many seeds 10.
- 10A. Ovary two-celled, with many ovules; capsule spindle, slender ovoid, or cylindrical, dehiscent into two valves, with many seeds; corolla slightly zygomorphic, with a club-shaped nectary; calyx-lobes elongated and sometimes fusing to each other; inflorescence cymose; opposite leaves never fusing to each other at the base Tribe Diervilleae.
- 11A. Each loculus bearing ovules in six to eight rows at the lower half of ovary and in four rows at the upper half; capsule spindle in shape, two valves splitting longitudinally along sterile neck, more than 5 mm in diameter; lenticular seed with broad linear wing developed on both ends; calyx persistent; cyme without a terminal flower at the apex; anthers coherent to each other *Macrodiervilla*.
- 11B. Each loculus with ovules in less than four rows even at lower half; capsule slender ovoid or cylindrical, less than 5 mm in diameter; seed with or without crest-like wing 12.
- 12A. Each loculus with ovules in four rows at lower half and in two rows at upper half; capsule slender ovoid, valves splitting longitudinally along sterile neck; seed without wing; calyx persistent; anthers free to each other; cyme with a terminal flower *Diervilla*.
- 12B. Each loculus with ovules in two rows throughout; capsule cylindrical, valves breaking at the base of sterile neck; seed with crest-like wing; calyx deciduous; anthers free to each other or rarely coherent; cyme without a terminal flower *Weigela*.
- 10B. Ovary two- to five-celled, with several to many ovules; berry globose, subglobose, or slender ovoid, with several to many seeds; corolla actinomorphic to zygomorphic and distinctly bilabiate, nectary never forming club-shape; calyx-lobes elongated or

dentate; inflorescence racemose; opposite leaves sometimes fusing to each other at the base Tribe *Lonicereae*.

13A. Ovary four- to five-celled, with long sterile neck, free to each other; corolla actinomorphic, with four to five nectaries; calyx elongated; fruit slender ovoid with many seeds, each of them smaller less than 1.2 mm long *Leycesteria*.

13B. Ovary two-, three-, or rarely five-celled, without sterile neck, pairs of ovaries sometimes connate to each other; corolla actinomorphic to zygomorphic, often bilabiate, with one, three, or rarely five nectaries, often gibbose at the base; calyx dentate; fruit globose to subglobose, with several seeds, each of them larger, more than 1.5 mm long *Lonicera*.

Acknowledgements

The present investigation has been carried out mainly in Kyoto University. I am especially indebted to Professors S. Kitamura and M. Tagawa for their advice and supervision on this work. In the last several years, my study has been made at Shoei Junior College. I wish to express my deep gratitude to the staff members of our college, especially to Mr. N. Kurosaki and Miss. H. Sawada who have kindly offered me the cooperations.

For this study, I have examined the specimens preserved in the Herbaria of Kyoto University, of University of Tokyo, of National Science Museum, Tokyo, of Arnold Arboretum, of the Royal Forest Department, Bangkok, and of the Botanic Gardens, Singapore. Many plants cultivated in the Botanical Gardens of Kyoto University, of University of Tokyo, of Osaka City University, and of Kyoto Prefecture were extremely valuable for my floral anatomical investigation. I will show my best gratitude to the directors and the curators of those herbaria and botanical gardens. My thanks are also due to the colleagues in the laboratory of plant taxonomy, Kyoto University, who are kind enough to provide me valuable materials including many living plants.

This study is supported partly by the Grant in Aid of Scientific Research of the Ministry of Education.

References

- 1) De Candolle, A. P., *Caprifoliaceae*, *Prodromus Plantarum* **4**: 321-340, Paris, 1830
- 2) Hooker, J. D., *Caprifoliaceae* in Bentham & Hooker, *Genera Plantarum* **2**: 1-7, London, 1873
- 3) Fritsch, K., *Caprifoliaceae* in *Die Natürlichen Pflanzenfamilien*. **4-4**: 156-169, Leipzig, 1891
- 4) Fritsch, K., *Die Gattung der Caprifoliaceen und demonstrierte Vertreter dieser Gattungen in Herbar-Exemplaren*. *Bot. Centralbl.* **50**: 137-139 & 168-170, 1892
- 5) Nakai, T., *Tentamen systematis Caprifoliacearum Japonicum*. *Jour. Coll. Sci. Tokyo Imp. Univ.* **42** (2): 1-139, 1921

- 6) Meyer, C. A., Einige Bemerkungen über *Diervilla*, *Weigela*, *Calysphyrum*, und eine neue, mit ihnen verwandte Gattung. Bull. Phys.-Math. Acad. Sci. St. Pétersb. 2, **13**: 216–220, 1855
- 7) Diels, L., Caprifoliaceae, Engler's Syllabus der Pflanzenfamilien 11th ed. 361–362, Berlin, 1936
- 8) Wagenitz, G., Caprifoliaceae, Melchior, Engler's Syllabus der Pflanzenfamilien 12th. ed. **2**: 473–475, Berlin, 1964
- 9) Airy Shaw, H. K., On a new species of the genus *Silvianthus* Hooker f., and on the family Carlemanniaceae. Kew Bull. **1965**: 507–512, 1965
- 10) Airy Shaw, H. K., Willis's Dictionary of the flowering plants and ferns 7th ed., Cambridge, 1966
- 11) Kern, J. H. & C. G. G. J. van Steenis, Caprifoliaceae, van Steenis, Flora Malesiana 1. **4**: 175–194, Bogor & Leyden, 1951
- 12) Airy Shaw, H. K., Diagnoses of new families, new names, etc., for the seventh edition of Willis's 'Dictionary'. Kew Bull. **1965**: 249–250, 1965
- 13) Hutchinson, J., Caprifoliaceae, The genera of flowering plants, Dicotyledons **2**: 81–89, Oxford, 1969
- 14) Rehder, A., Caprifoliaceae, Sargent, Plantae Wilsonianae **2**: 617–619, 1916
- 15) Wilkinson, A. M., Floral anatomy and morphology of some species of the tribe Lonicereae of the Caprifoliaceae. Amer. Jour. Bot. **35**: 261–271, 1948
- 16) Wilkinson, A. M., Floral anatomy and morphology of some species of the tribes Linnaeae and Sambuceae of the Caprifoliaceae. Amer. Jour. Bot. **35**: 365–371, 1948
- 17) Wilkinson, A. M., Floral anatomy and morphology of some species of the genus *Viburnum* of the Caprifoliaceae. Amer. Jour. Bot. **35**: 455–465, 1948
- 18) Wilkinson, A. M., Floral anatomy and morphology of *Triosteum* and of the Caprifoliaceae in general. Amer. Jour. Bot. **36**: 481–489, 1949
- 19) Metcalfe, C. R. & L. Chalk, Caprifoliaceae, Anatomy of the dicotyledons **2**: 752–758, Oxford, 1950
- 20) Troll, W. & F. Weberling, Die Infloreszenzen der Caprifoliaceen und ihre systematische Bedeutung. Abh. Acad. Wiss. Lit. Mainz, math.-naturw. Kl. **1966**: 455–605, 1966
- 21) Metcalfe, C. R., Notes on the anatomy of *Heptacodium*. Kew Bull. **1952**: 247–248, 1952
- 22) Weberling, F., Zur systematischen Stellung der Gattung *Heptacodium* Rehder. Bot. Jahrb. **85**: 253–258, 1966
- 23) Weberling, F., Morphologische Untersuchungen zur Systematik der Caprifoliaceen. Abh. Acad. Wiss. Lit. Mainz, math.-naturw. Kl. **1957**: 1–50, 1957
- 24) Cross, G. L., A comparative histogenetic study of the bud scales and foliage leaves of *Viburnum opulus*. Amer. Jour. Bot. **25**: 246–258, 1938
- 25) Fukuoka, N., Inflorescence of Linnaeae (Caprifoliaceae). Acta Phytotax. Geobot. **23**: 153–162, 1969
- 26) Fukuoka, N., Phylogeny of the tribe Linnaeae. Acta Phytotax. Geobot. **23**: 82–94, 1968, in Japanese
- 27) Schwerin, F., Monographie der Gattung *Sambucus*. Mitt. Deutsch. Dendrol. Ges. **18**: 1–56, 1909
- 28) Fukuoka, N., *Sambucus* and *Viburnum* of Thailand. Acta Phytotax. Geobot. **22**: 163–174, 1967
- 29) Clarke, C. B., Caprifoliaceae, Hooker, Flora British India **3**: 1–17, London, 1880
- 30) Rehder, A., The *Viburnum* of Eastern Asia, Sargent, Trees and Shrubs **2**: 105–116, Boston & New York, 1908
- 31) Billings, F. H., Caprifoliaceae, Beiträge zur Kenntnis der Samenentwicklung, Flora **1901**: 303–304, 1901
- 32) Airy Shaw, H. K., A revision of the genus *Leycesteria*. Kew Bull. **1932**: 161–176, 1932

- 33) Hara, T., Caprifoliaceae, The Flora of Eastern Himalaya, 317-321, Tokyo, 1966
- 34) Rehder, A., Synopsis of the genus *Lonicera*. Rep. Missouri Bot. Gard. **14**: 27-232, 1903
- 35) Nakai, T., A new classification of the genus *Lonicera* in the Japanese empire, together with the diagnoses of new species and new varieties. Jour. Jap. Bot. **14**: 359-376, 1938
- 36) Pfeiffer, N. E., Morphology of the seed of *Symphoricarpos racemosa* and the relation of fugal invasion of the coat to germination capacity. Contr. Boyce Thomps. Inst. **6**: 103-122, 1934
- 37) Hooker, J. D., *Silvianthus bracteatus* Hook. f., Hooker, Icones Plantarum **3**, **1**: t. 1048, 1868
- 38) Ferguson, I. K., The genera of Caprifoliaceae in the Southeastern United States. Jour. Arn. Arb. **47**: 33-59, 1966
- 39) Moissl, Vergleichende embryologische Studien über die Familie der Caprifoliaceae. Österr. Bot. Zeitsch. **90**: 153-212, 1941

Explanation of plates 1~12

Plate 1. Flowers of *Sambucus javanica* subsp. *chinensis* (1~8) and *S. canadensis* (9).

Fig. 1. Cross section of pedicel in which vascular bundles group five in number ($\times 50$). Fig. 2~3. Showing separation of peripheral bundles below loculi ($\times 50$). Fig. 4. At middle level of ovary ($\times 50$). Fig. 5. At upper level of ovary and base of corolla to which base of filaments fuses, showing a central bundle dividing into three ovular supplies and three ventral strands, carpellary supplies given off from peripheral bundles (periphery of ovary), stamen bundle (S), and corolla bundle dividing into three (arrow) ($\times 50$). Fig. 6. At further level than that, showing carpellary supplies ($\times 50$). Fig. 7. Calyx and its supply ($\times 100$). Fig. 8. Valvate corolla-lobes and introrse anther ($\times 50$). Fig. 9. Imbricate corolla-lobes and extrorse anther ($\times 50$).

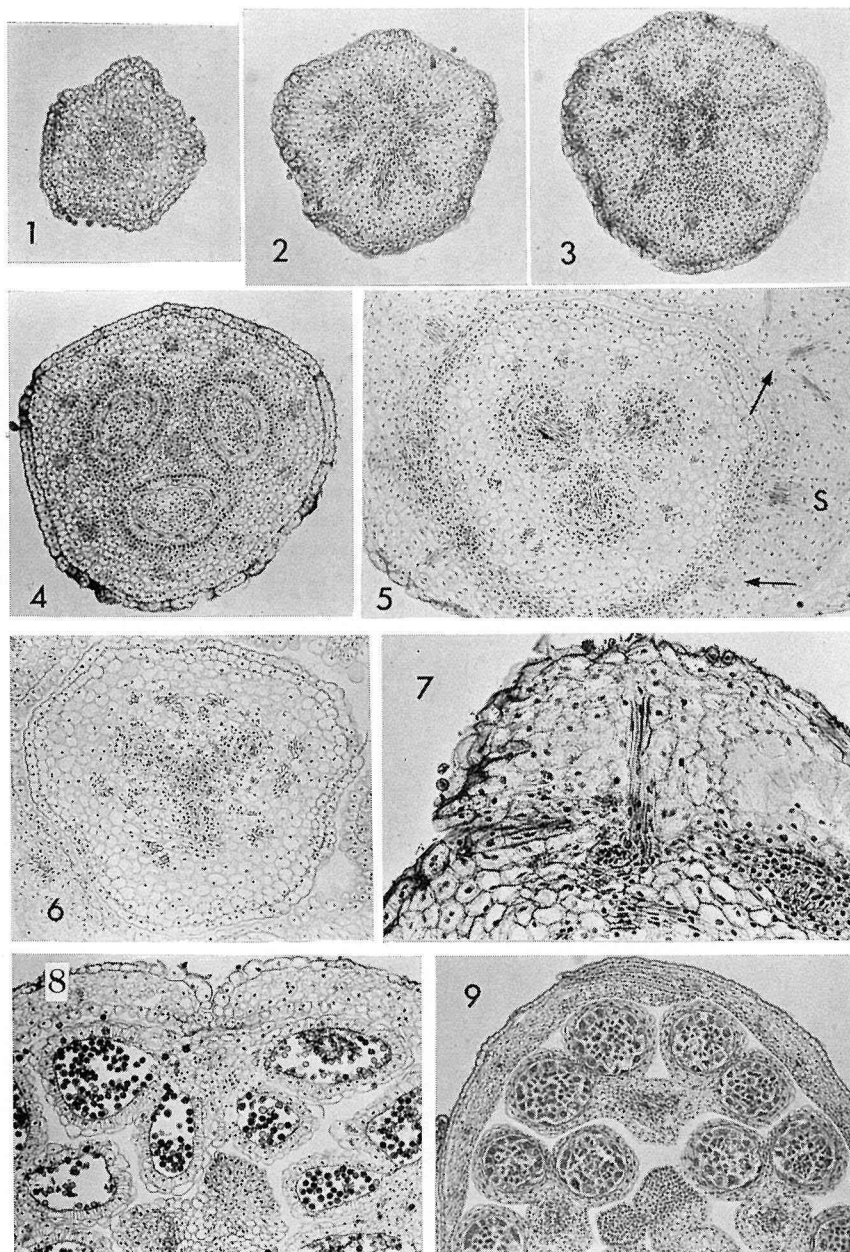


Plate 2. Flowers of *S. canadensis* (1~6) and *S. racemosa* subsp. *sieboldiana* (7~9).

Fig. 1. Cross section at upper level of receptacle, showing three distinct ventral traces (center) and ten peripheral bundles ($\times 50$). Fig. 2. At middle level of ovary, showing four fertile carpels and an abortive one (arrow) ($\times 50$). Fig. 3. At upper level than that, whose abortive carpel contains a large abortive ovule (arrow) ($\times 100$). Fig. 4. At middle level, showing ventral traces (arrow) which do not fuse to a central bundle ($\times 100$). Fig. 5. At level of attachment of ovules, showing four strands supplying to ovules and four ventral strands (arrow) extending toward wall of ovary along septa ($\times 100$). Fig. 6. Rudimentary ovules and carpellary supplies ($\times 100$). Fig. 7. Cross section of receptacle where bundles are five in number ($\times 50$). Fig. 8. At level of bottom of loculi, showing bundles in center not yet fusing together ($\times 50$). Fig. 9. At middle level of ovary, showing separation of lateral ventral strands (arrow) from peripheral bundles ($\times 50$).

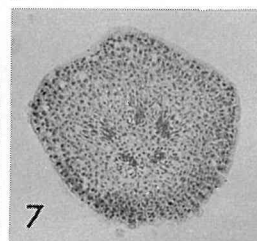
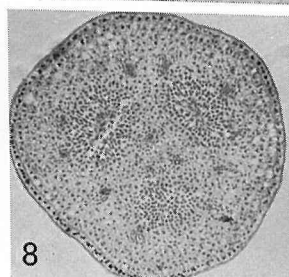
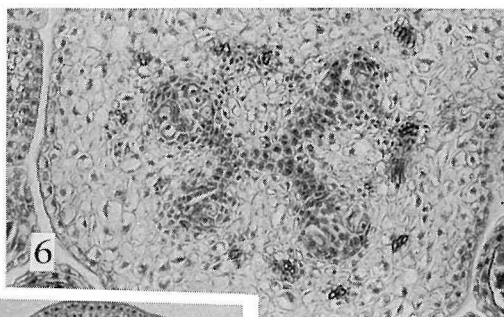
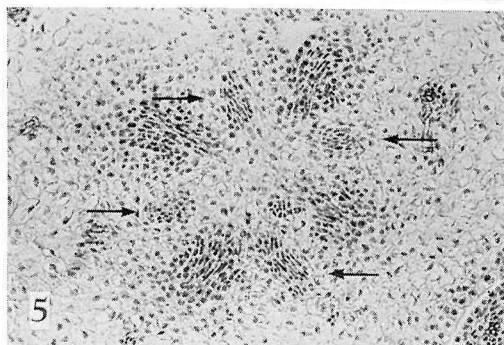
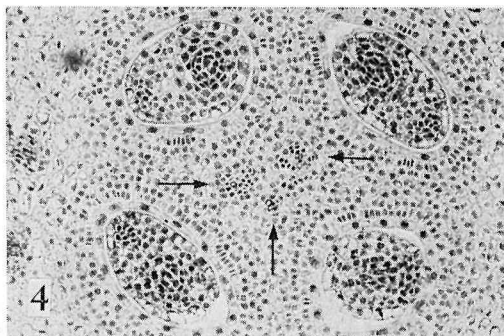
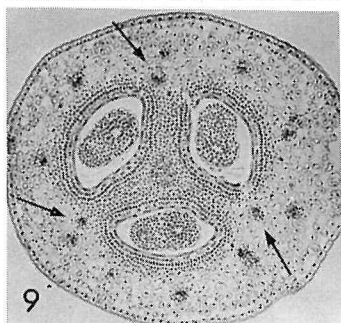
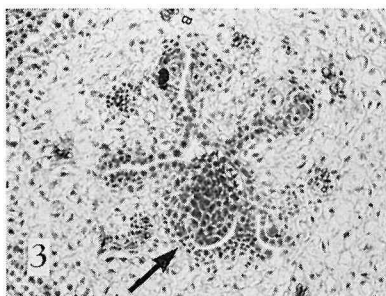
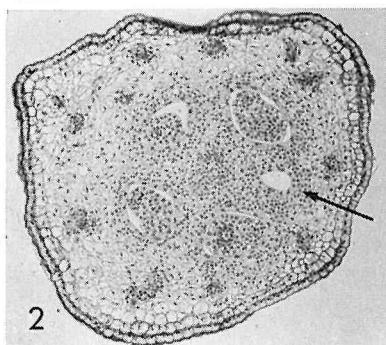
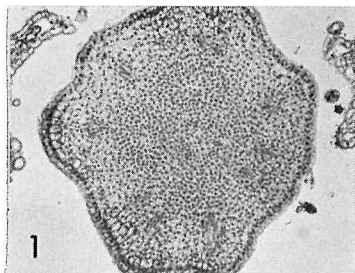


Plate 3. Flowers of *S. racemosa* subsp. *sieboldiana* (1~4) and *S. nigra* (5~7).

Fig. 1. Longitudinal section of two rudimentary ovules ($\times 100$). Fig. 2. Cross section of a rudimentary ovule and transmitting tissue ($\times 200$). Fig. 3. Cross section at uppermost level of ovary, showing three rudimentary ovules, three pairs of two ventral traces, and absence of dorsal one ($\times 50$). Fig. 4. Longitudinal section of semi-inferior ovary, showing transmitting tissue, rudimentary ovules, fertile ones, and central bundle ($\times 30$). Fig. 5. Cross section at middle level of two-celled ovary, showing separation of calyx and carpellary supplies (upper part) ($\times 50$). Fig. 6. At middle level of ovary in four-merous flower, showing three loculi and eight peripheral bundles ($\times 50$). Fig. 7. Cross section of four-merous flower ($\times 40$).

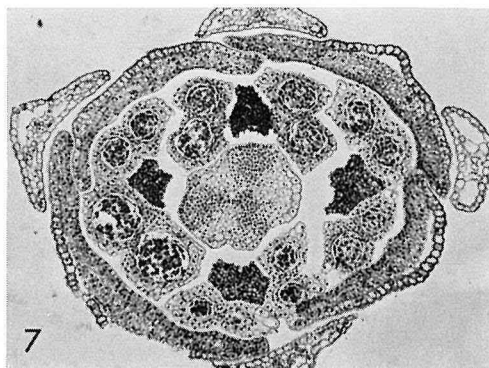
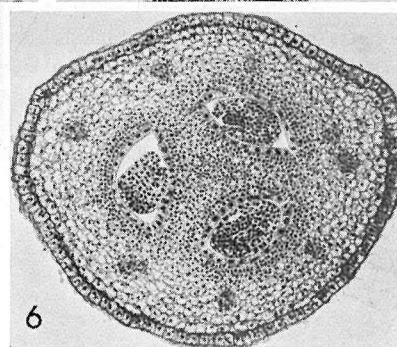
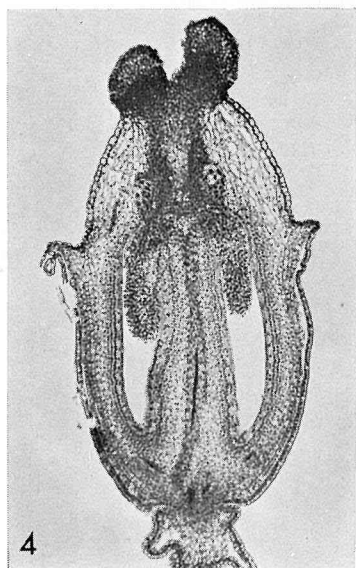
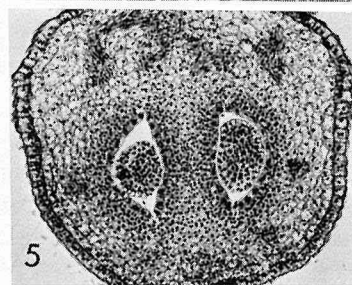
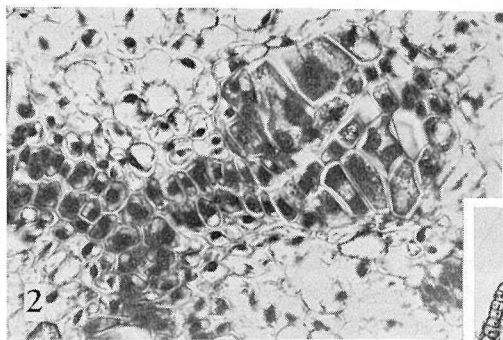
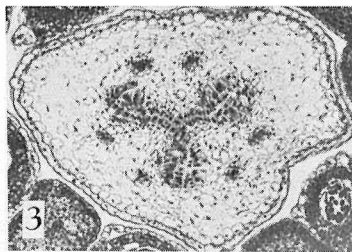
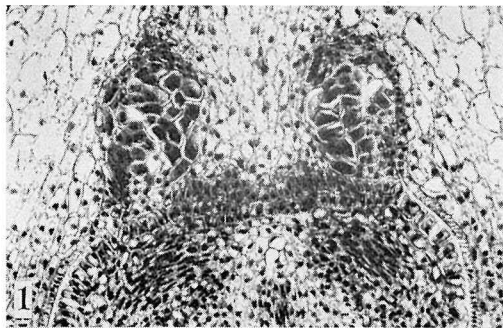


Plate 4. Flowers of *Viburnum sieboldii* (1~8).

Fig. 1. Cross section of receptacle, showing separation of central bundle from a peripheral bundle situating to ventral side ($\times 40$). Fig. 2. At lower level of ovary, whose fertile placenta is circular in outline ($\times 40$). Fig. 3. At middle level, showing linear-oblong placenta and five peripheral bundles without a dorsal trace of fertile locus ($\times 40$). Fig. 4. At upper level, showing V-shaped central bundle and elongation of peripheral bundles ($\times 40$). Fig. 5. At still upper level, showing two abortive loculi (arrow), central bundle dividing into four, a fertile ovular supply (F), a fertile ventral strand (V), and a pair of sterile ventral ones (A) ($\times 50$). Fig. 6. At upper level than that, showing ten peripheral bundles as a result of radial division and carpellary supplies (D—dorsal trace of abortive locus, FD—dorsal one of fertile locus, L—lateral and abortive ventral trace, and FL—lateral and fertile ventral trace) given off from peripheral bundles ($\times 40$). Fig. 7. Cross section of style, showing three dorsal supplies (D) and three pairs of ventral ones ($\blacktriangle$) ($\times 75$). Fig. 8. Longitudinal section of ovary, showing fertile locus and abortive one ($\times 30$).

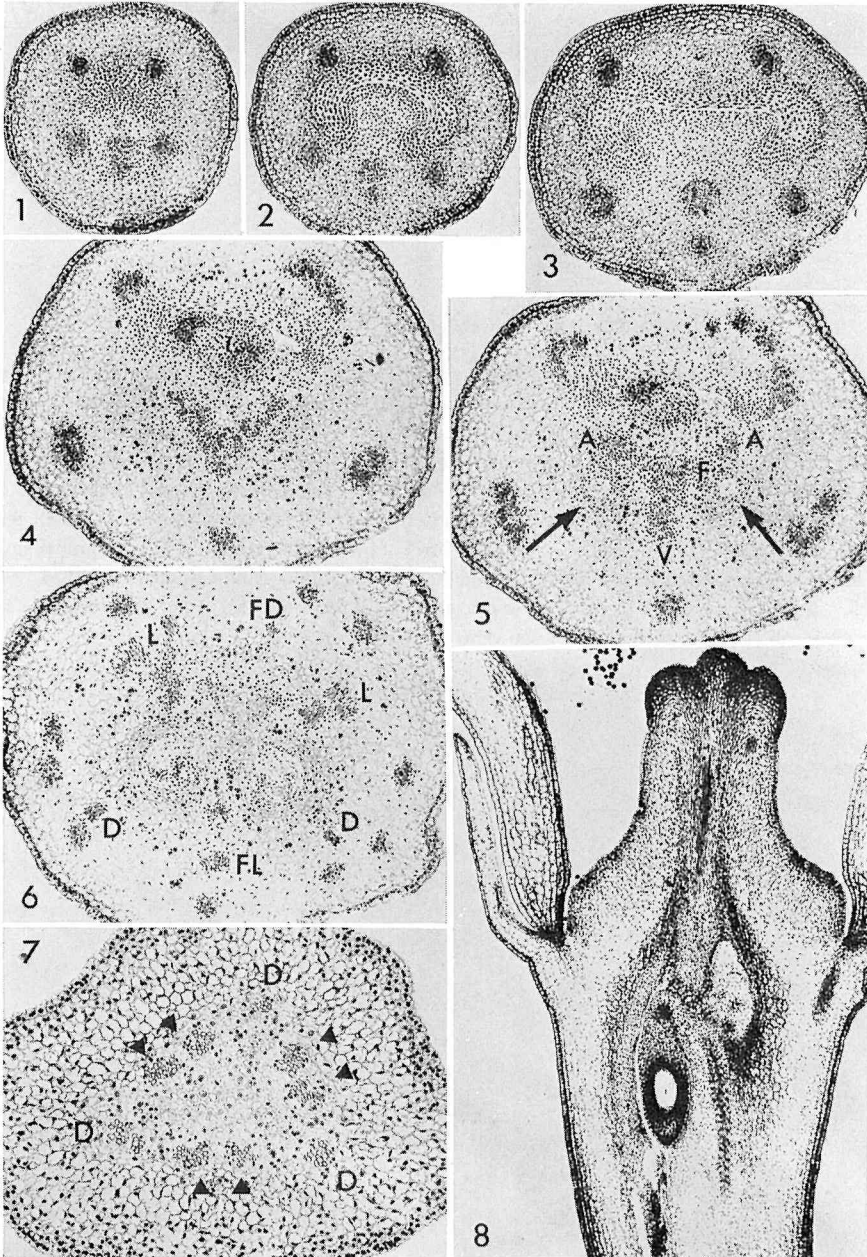


Plate 5. Flowers of *V. furcatum* (1~8).

Fig. 1. Cross section of receptacle, showing nine peripheral bundles ($\times 50$). Fig. 2. At lower level of ovary, whose peripheral bundles count ten as a result of radial division of a bundle situating at lower right of this figure ($\times 50$). Fig. 3. At middle level of ovary, in which placenta is raised ($\times 50$). Fig. 4. At still upper level, showing round central bundle and separation of calyx supplies ($\times 50$). Fig. 5. At upper level than that, where central bundle becomes deltoid in outline ($\times 50$). Fig. 6. Central bundle divides into two, a broad crescent fertile ovular supply and a small fertile ventral one (arrow) ($\times 50$). Fig. 7. At upper level of ovary, where broad crescent bundle supply to a fertile ovule, and peripheral bundles divide into corolla, stamen, and carpellary supplies ($\times 40$). Fig. 8. At still upper level, showing three dorsal traces of fertile loculus (FD), two dorsal traces of abortive loculi (D), and three pairs of two ventral traces (V) ($\times 50$).

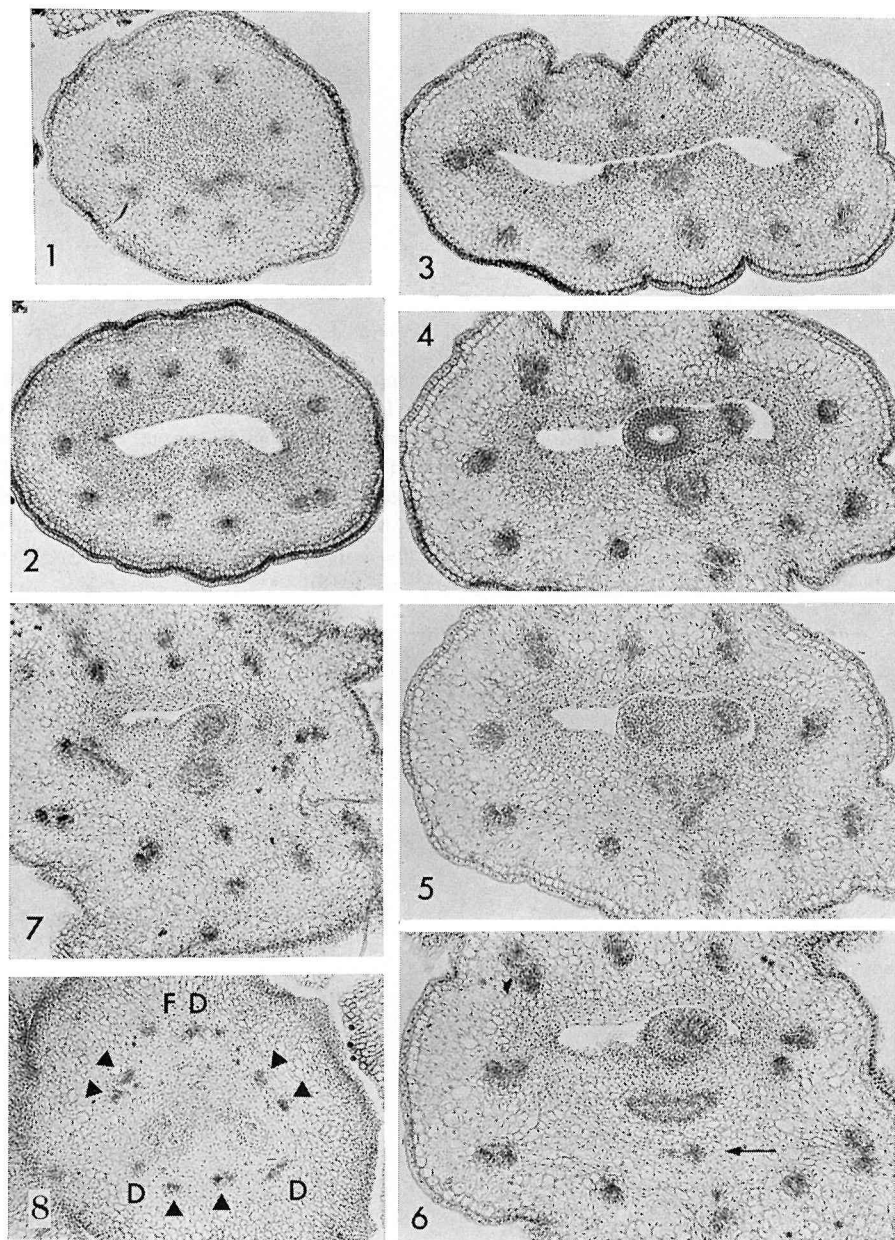


Plate 6. Flowers of *V. furcatum* (1~2) and *V. urceolatum* (3~8).

Fig. 1. Cross section of style, showing carpellary supplies ($\times 50$). Fig. 2. At upper level than that, showing three crescent-shaped bundles as a result of fusion ($\times 50$). Fig. 3~4. Cross section of receptacle, in which a central bundle is separated from a peripheral bundle at ventral side of ovary ($\times 60$). Fig. 5~7. Series showing division of central bundle at upper half of ovary ($\times 100$): 5—central bundle being deltoid in outline in cross section; 6—central bundle dividing into a larger bundle and a smaller fertile ventral strand; 7—the former branching into three, a fertile ovular strand and a pair of abortive ventral ones. Fig. 8. Cross section at upper level of ovary, showing two abortive loculi, separation of calyx supplies, and carpellary ones ($\times 40$).

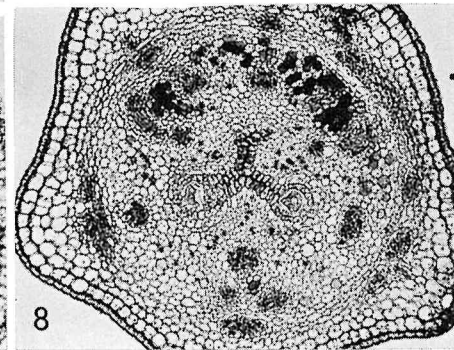
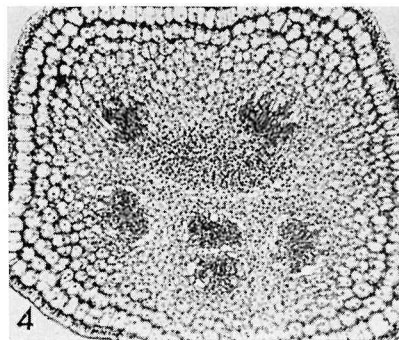
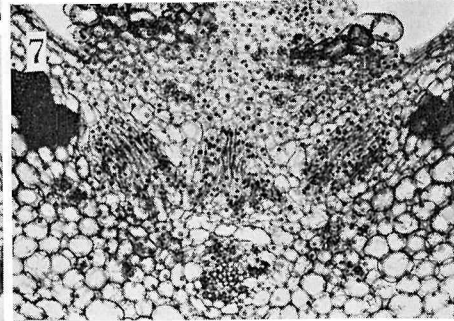
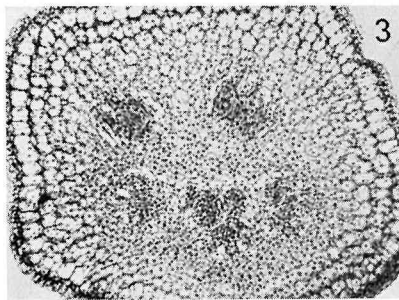
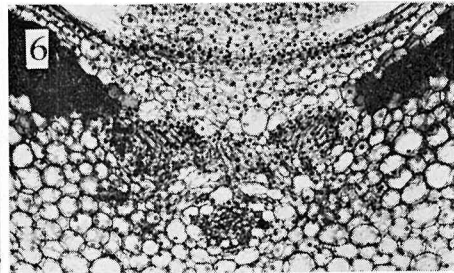
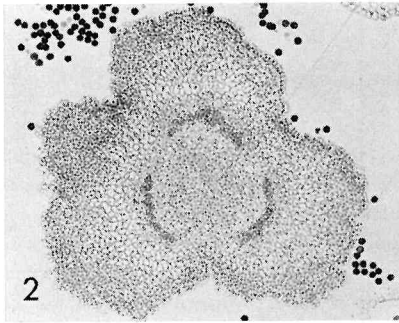
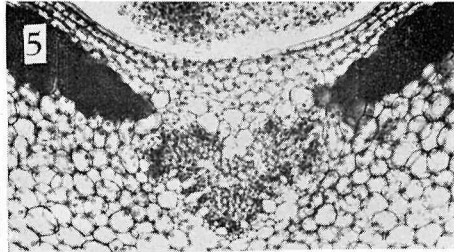
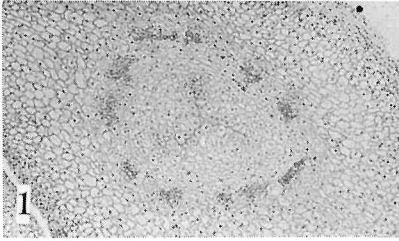


Plate 7. Flowers of *V. plicatum* (1~2), *V. opulus* var. *calvescens* (3), *V. tashiroi* (4), *V. odoratissimum* (5~7), and *V. suspensum* (8).

Fig. 1. Cross section at the upper extreme of ovary, showing parietal placentation and abortive ovules (arrow) ($\times 150$). Fig. 2. At slightly lower level than that in young fruit, abortive loculi containing ovules ($\times 50$). Fig. 3. Double fertile ovular supplies just after separation from central bundle ($\times 200$). Fig. 4. Cross section at middle level of ovary ($\times 50$). Fig. 5~7. Series of developing process from ovary to mature fruit: 5—ovary in bud in which loculus is occupied by placenta ($\times 50$); 6—enlarged one in young fruit ($\times 20$); 7—endocarp of mature fruit with a deep furrow corresponding to placenta ($\times 15$). Fig. 8. Cross section at lower level of ovary, showing separation of dorsal trace (arrow) of fertile loculus and circular placenta ($\times 50$).

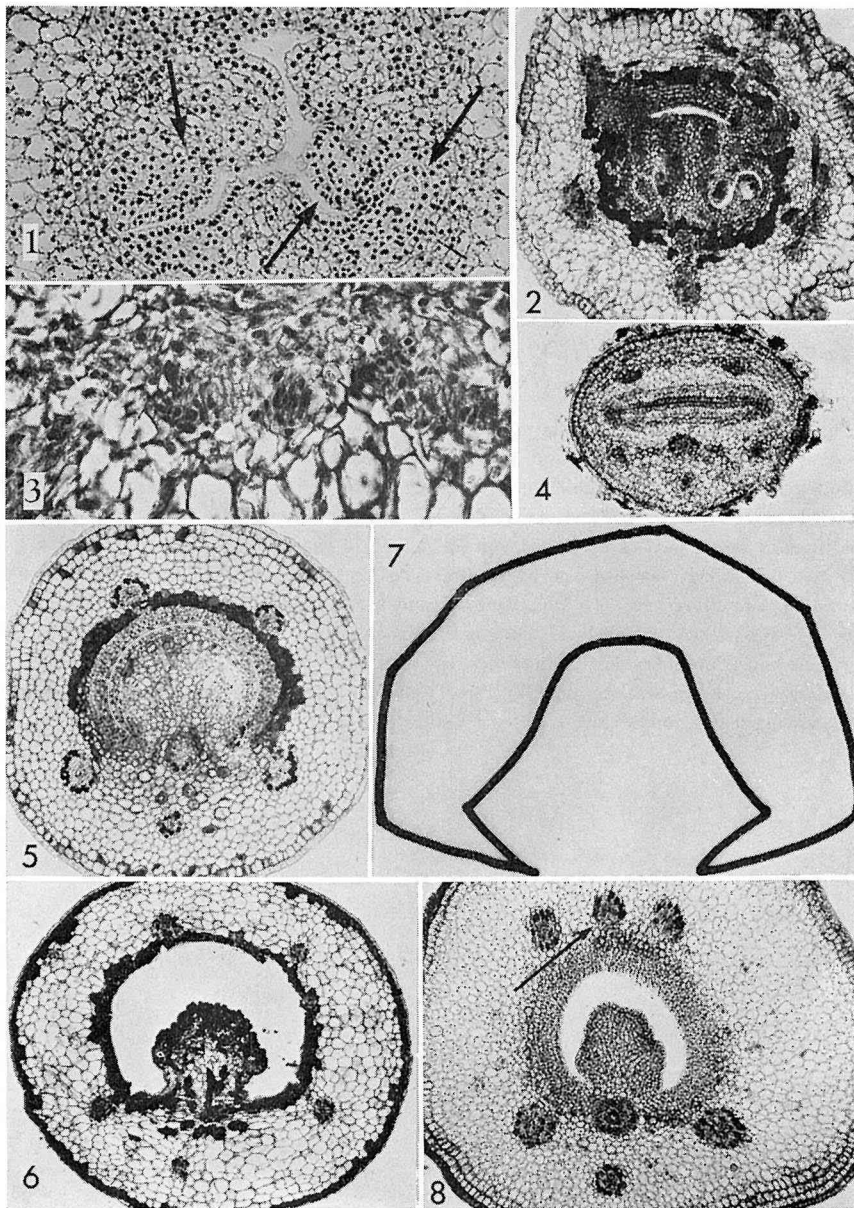


Plate 8. Flowers of *V. carlesii* (1), *V. tinus* (2), *Triosteum sinuatum* (3~5), *Symphoricarpos orbiculatus* (6), and *Linnaea borealis* (7~9).

Fig. 1. Cross section at upper level of ovary, showing a dorsal strand of fertile loculus (D) and separation of an abortive ventral strand (arrow) from a broad lanceolate bundle given off from central bundle ($\times 50$). Fig. 2. At middle level of ovary ($\times 40$). Fig. 3. Cross section of receptacle ($\times 20$). Fig. 4. At lower level of ovary, showing a central bundle and eight peripheral bundles whose three at upper part of this figure run up in wall of ovary faced to abortive loculus ($\times 20$). Fig. 5. At upper level, showing abortive loculus whose carpellary margins are bi-lobed, fertile one surrounding with fibrous tissues without cristal, and a fertile ovule supplied by a bundle ($\times 50$). Fig. 6. Cross section at middle level of young fruit, showing two fertile and abortive carpels ($\times 20$). Fig. 7. At upper level of pedicel, where there are six bundles ($\times 50$). Fig. 8. Cross section of receptacle, showing a bracteole supplied by three bundles ($\times 50$). Fig. 9. At uppermost level of ovary, showing separation of calyx supplies ($\times 40$).

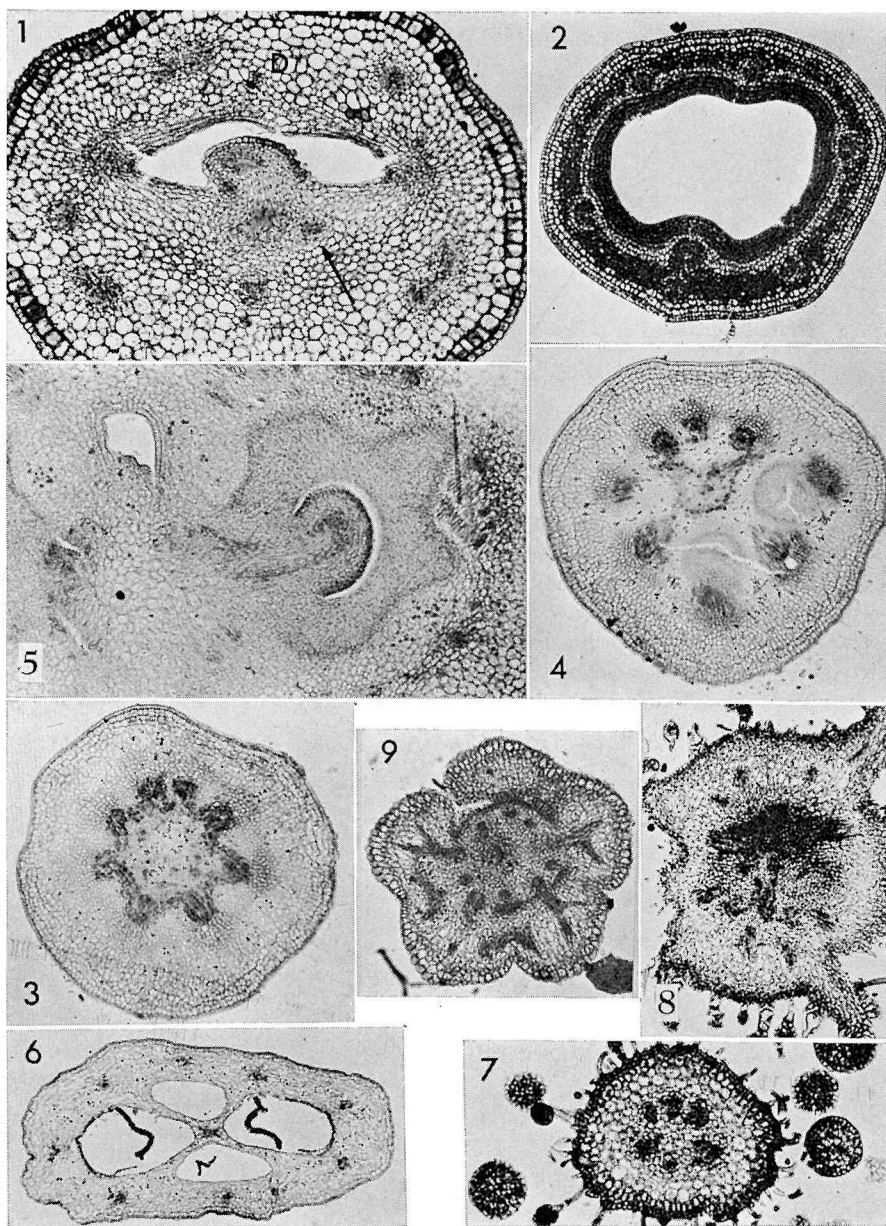


Plate 9. Flowers of *L. borealis* (1~6), *Abelia serrata* (7~8), and *A. tetrasepala* (9).

Fig. 1. Cross section at middle level of ovary embraced by bracteoles supplied by three bundles, showing two bundles in center of ovary ($\times 50$). Fig. 2. At upper level of ovary, a smaller bundle in center branching abortive ovular supplies ($\times 40$). Fig. 3. At still upper level, a larger bundle in center supplying to a fertile ovule in the whole, and a smaller one dividing into three ventral strands after separation of abortive ovular supplies ($\times 50$). Fig. 4. At upper level than that, where carpellary margins separate to each other ($\times 50$). Fig. 5. At further upper level, showing carpellary margins becoming close to each other ($\times 40$). Fig. 6. Cross section at base of flower, showing five calyx-lobes, a style, and base of corolla where five corolla bundles, four stamen ones (arrow), and a nectary are observed ($\times 40$). Fig. 7. Cross section at uppermost level of peduncle with a pair of flowers, showing bracts and bractlets, each of which is supplied by a single bundle ($\times 50$). Fig. 8. At receptacle, in which receptacular stele divides radially and centripetally ($\times 50$). Fig. 9. At middle level of ovary, showing a fertile loculus containing a larger ovule and two abortive ones with smaller ovules ($\times 40$).

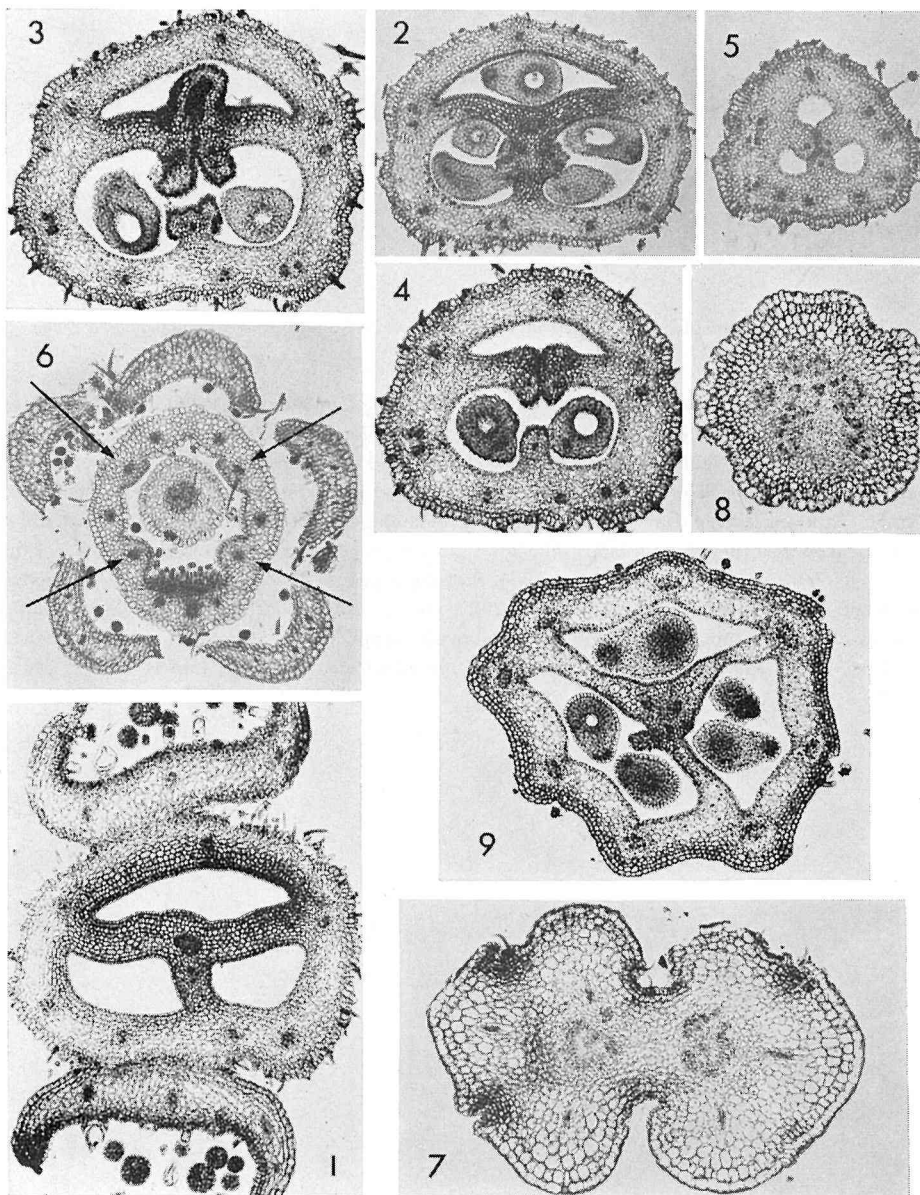


Plate 10. Flowers of *Zabelia integrifolia* (1~2), *Z. biflora* (3), and *Macrodiervilla middendoriana* (4~8).

Fig. 1. Cross section at upper level of pedicel, showing four bundles ($\times 100$). Fig. 2. Cross section of sterile neck, in which peripheral bundles fuse to form a ring in outline ($\times 50$). Fig. 3. Sterile neck, in which eight bundles are free to each other and each of every other four gives off a calyx bundle entering to each of four calyx-lobes ($\times 50$). Fig. 4. Cross section of receptacle ($\times 20$). Fig. 5. At lower level of ovary, in which bundles remaining in center and bundles faced to radii of septa arrange as if they draw a loop (this figure is arranged at right angles with other ones of this species) ($\times 50$). Fig. 6. At still upper level, showing a pair of V-shaped bundles closed against loculi and solitary ones in center of ovary ($\times 20$). Fig. 7. At level further above, central bundles form two V-shaped ones closed against septa and ovular supplies given off from apex of arm of these bundles ($\times 50$). Fig. 8. At middle level of ovary, in which placenta splits into two along center ($\times 20$).

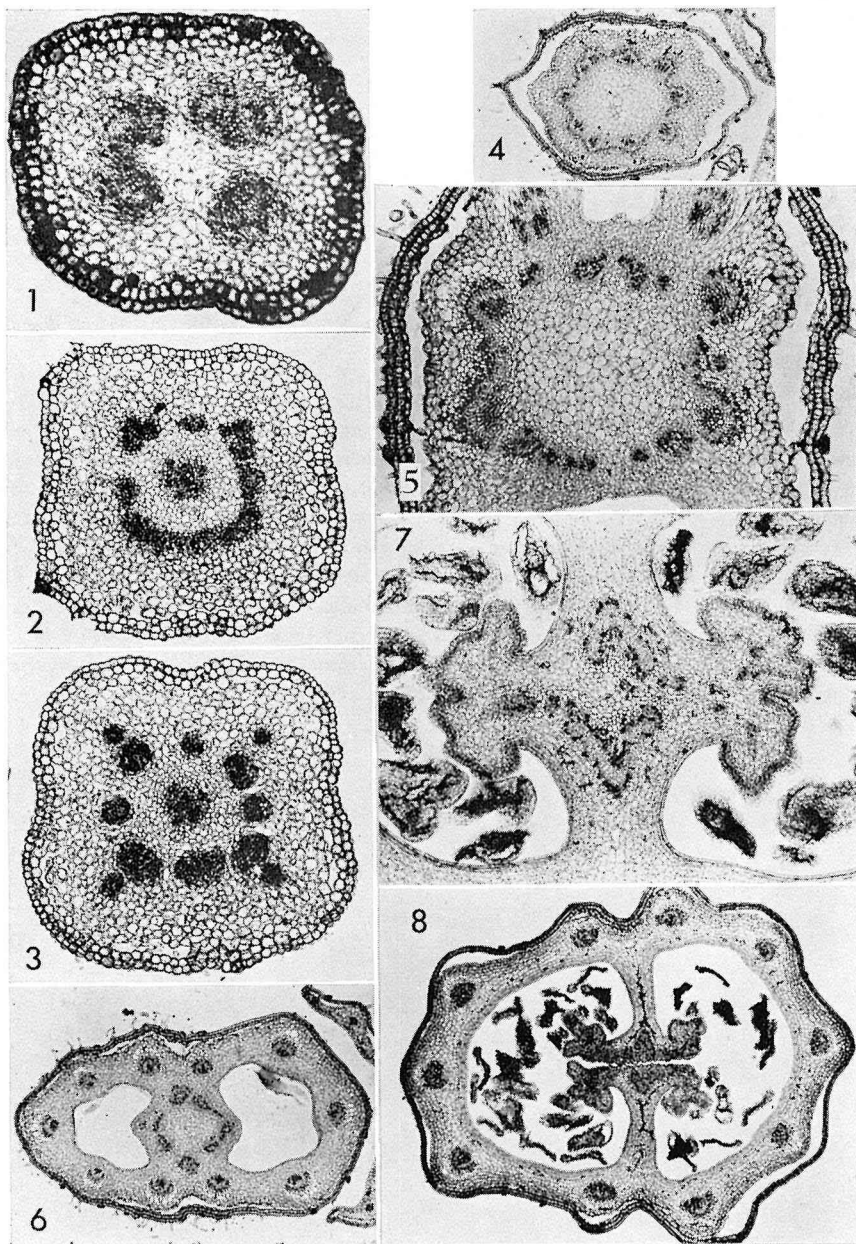


Plate 11. Flowers of *M. middendorffiana* (1~2), *Diervilla lonicera* (3~6), and *Weigela decora* (7~9).

Fig. 1. Cross section at upper level of ovary, in which central bundles divide into several ovular and ventral strands ($\times 20$). Fig. 2. Sterile neck, showing ten peripheral bundles and two ventral strands ($\times 20$). Fig. 3. At base of ovary, where peripheral bundles still remain to divide radially and a pair of bract supplies (arrow) are given off from these bundles (this section cutted slightly obliquely) ($\times 50$). Fig. 4. At middle level of ovary, each of carpellary margins divides into two ($\times 40$). Fig. 5. At upper level, each of carpellary margins does not divide ($\times 40$). Fig. 6. Longitudinal section of sterile neck, showing centripetal vascular ring (arrow) ($\times 40$). Fig. 7. Cross section at lower level of ovary, where peripheral bundles count eight and central bundles form a loop ($\times 40$). Fig. 8. At middle level, in which each loculus bears ovules in two rows ($\times 40$). Fig. 9. At uppermost level of sterile neck, showing four ventral strands in center, separation of calyx supplies (arrow), and a centripetal vascular ring joining with a corolla bundle ($\times 20$).

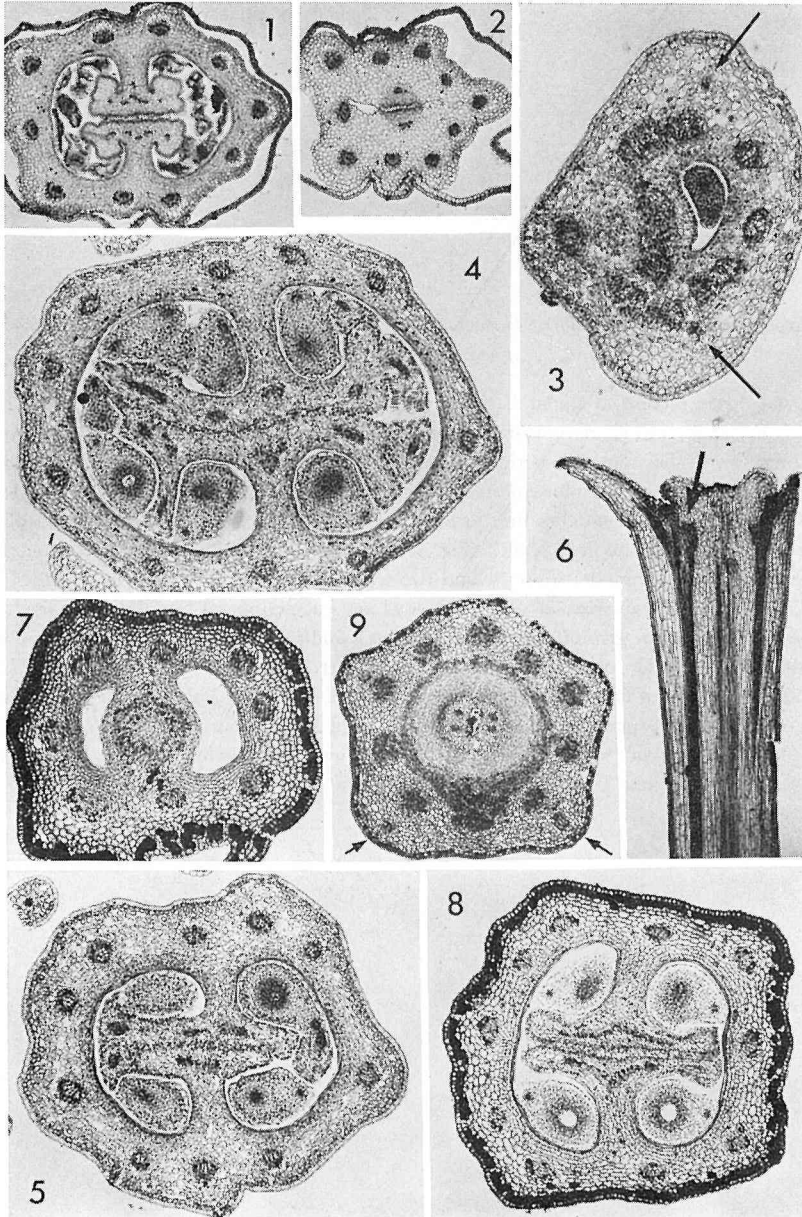


Plate 12. Flowers of *Leycesteria formosa* (1~3), *Lonicera sempervirens* (4), *L. chamissoi* (5~7), *L. harae* (8), and *L. japonica* (9).

Fig. 1. Cross section at upper half of ovary in five-merous flower, showing ten peripheral bundles, five carpels, and its margins free to each other ($\times 20$). Fig. 2. At lower level of ovary in four-merous flower, showing eight peripheral bundles, four carpels, and its margins fusing together ($\times 20$). Fig. 3. At uppermost level of sterile neck of four-merous flower, where calyx supplies given off from all the peripheral bundles fuse to form a ring ($\times 40$). Fig. 4. At lower half of ovary, showing ten peripheral bundles ($\times 40$). Fig. 5. At receptacle of highly fused ovaries, showing separation of bract and bractlet supplies, and two semicircular receptacular steles ($\times 20$). Fig. 6. At middle level of fused ovaries, in which a pair of adaxial peripheral bundles fuse together, and a few peripheral bundles give off ventral and ovular bundles ($\times 20$). Fig. 7. At upper level of ovary, showing separation of a lateral ventral strand (arrow) from a peripheral bundle ($\times 200$). Fig. 8. At lower half of fused ovaries, in which a pair of adaxial peripheral bundles (arrow) fuse to each other and each peripheral bundle is surrounded with tissues stained by safranin ($\times 20$). Fig. 9. At upper level of ovary, showing separation of ovular and ventral strands from peripheral bundles near radii of septa ($\times 40$).

