ANATOMICAL STUDIES IN VITIS AND ALLIED GENERA
I. DEVELOPMENT OF THE FRUIT
II. FLORAL ANATOMY

by

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INTRODUCTION

In the growing and breeding of grapes little attention has been paid to anatomical characters of the fruit. In general, only the weight, size, color, etc., have been considered. In fact, rarely is a cross effected in which the anatomy of the parents differs sufficiently to make possible any comparison between them. However, on the other hand, where there are some differences between the berries of the parents it is possible to examine those of the hybrid not only for such superficial characters as smoothness, color, size, etc., but also for their fundamental anatomical structure. This is the basis for these superficial characters and therefore the critical point for attack by a genetical study.

With this in mind, a part of this study was carried on to compare the histology of the fruit of the F_1 hybrid (Golden Muscat) with those of its parents, Muscat Hamburg and Diamond grapes, with regard to (a) flesh development, (b) protective layers, and (c) anatomical structure associated with the readily separating skin of the Diamond grape and the F_1 hybrid.

Also an attempt was made to determine the probable relationship between the genus Vitis and allied genera by comparisons of their floral anatomy, since a wealth of

evidence obtained from many different groups of Angiosperms has shown that vascular anatomy of flowers provides valuable clues to phylogenetic relations.

MATERIALS AND METHODS

All of the plant breeders who have undertaken to improve native grapes have chosen as their chief task hybridization with the European grape to obtain a combination of the fruit characters of the European grape with the vine characters of the American grapes. With this in mind, the Golden Muscat was originated at New York Experiment Station in 1916 as a cross between Muscat Hamburg (a horticultural variety of Vitis vinifera L.) and Diamond (a horticultural variety of V. labrusca L.) (Dix 13).

The fruit of Muscat Hamburg is characterized--as far as this study is concerned--by its large size, nonreadily separating skin, and good handling quality. That of the Diamond is of medium size, readily separating skin, and poor handling quality. The hybrid fruit exhibits the large size together with the readily separating skin and the poor handling quality.

The material from the above varieties was collected from the Oregon State College vineyard at weekly intervals from the first appearance of the inflorescence until maturity of the fruit. Although several fixatives were

tested, a formalin-alcohol-acetic acid fixative* gave the most satisfactory results. After a period of 24 hours in this fixing reagent, the material was washed in 50% alcohol and then dehydrated and infiltrated by the tertiary butyl alcohol method (Johansen 20).

Since no fresh or preserved flowers of the other genera were available, their study was of necessity based entirely on preparations obtained from herbarium specimens.† These were given a softening treatment, slightly modified from the method of softening and restoring specimens recommended by Juel (23). The buds were first heated in water at slightly less than 100°C. for from one to two hours, then transferred to 1% potassium hydroxide for 24 hours. This treatment softened the flattened specimens and restored them to approximately their original size and shape. After the buds were rinsed thoroughly in running water the same technique for dehydration and embedding was followed as for the fresh material.

Following this softening treatment sections were obtained which compared favorably with those from freshly

*Commercial formalin 5 c.c.
Glacial acetic acid 5 c.c.
50% alcohol 90 c.c.

†The herbarium material was kindly provided by the curators of the Oregon State College, the University of Oregon, the University of California, and the Gray Herbarium to whom I wish to express my sincere appreciation.

fixed materials, the only difference being the shrunken appearance of the protoplasm.

The fruit material was sectioned at 20 microns and, following removal of the paraffin, placed in 1% chromic acid for a period of 12 hours. The slides were then washed in water and placed in a solution of 1% iodine-potassium iodide for another 12 hours. After washing in water a combination stain of crystal violet followed by orange (G) was used.

The floral material was sectioned at 15 microns and serial sections were mounted and stained by the above method for the fresh material, and by a combination of 1% aqueous solution of safranin followed by orange (G) for the herbarium material.

Free hand sections of about 50 microns thick from fresh fruits were used for microchemical tests. Pectic substances were tested by using 1:5000 solution of ruthenium red (Carré 8). A solution of iodine and potassium iodide was used in testing for cellulose (Johansen 21). Phlorogluein in a 5 per cent aqueous solution applied simultaneously with hydrochloric acid was used in testing for lignin (Chamberlain 9). For tannin material a solution of 10% ferric chloride was used (Rawlins 34). A one per cent alcoholic solution of Sudan III added to an equal volume of pure glycerine was used to test for cuticle

(Lee and Priestly 26).

The drawings, some of which are semi-diagramatic, were made with the aid of a Spencer camera lucida and then reduced to the magnifications noted in the figures.

HISTORICAL TREATMENT

The literature on the subjects of this study is very meager. Certain structural and developmental phenomena of the fruit of grape have been briefly mentioned in a few general sources.

Lewis (27) concluded that in its development, the berry increases slowly in size during the first four weeks, followed by a short period in which there is a very rapid increase in size. The rate of increase becomes gradually reduced as the grapes approach maturity. He believes that this rapid growth is due entirely to environmental conditions, mainly continuous rain-fall and lack of sunshine during this period of development. Vielliers (39) stated that the size of this fruit increases primarily by the expansion of the already existing cells. Lampe (25) said that cell division in the grape berry occurs only in the tangential plane. Eames and McDaniels (18) reported that there is no separation of cells at maturity in this fruit. McArthur and Butler (28) from a similar study of the development of the tomato fruit, arrived at the conclusions that the ovary size at anthesis

is associated entirely with cell number and not with cell size, while during the post-anthesis period it is associated chiefly with cell size. Sinnott (38) concluded from a study on cell size and fruit size in cucurbits that although growth takes place at first chiefly by cell multiplication, cell size also increases slowly. After a specific fruit size is reached, division ceases, and all further growth is by cell expansion.

In connection with the protective layers, Villiers (39) stated that in grape they include a cutinized epidermal layer with four or more rows of well lignified subepidermal cells. Lignification of the epidermal and subepidermal layers becomes intensified as the fruit matures. Eames and MacDaniels (18) reported that no stomata occur in the epidermis of this fruit. Bioletti (7) stated that in vinifera grapes the cuticle is a thin, continuous, translucent membrane covering the epidermis which is a single layer of flattened cells overlying the hypodermis, a layer of two or more rows of somewhat larger cells. Bell (6) concluded from a similar study on the protective layers of the apple fruit, that the outer protective region includes four layers of tissue. These are, the coating of epidermal hairs, the cuticle, the epiderm and the hypoderm. The cuticle increases in thickness at a uniform rate from

about the time of full blossom until the maximum thickness is reached, about two weeks before harvest. The epidermal cells change from the radially elongated type to the more plate-like tangentially elongated type and finally they become widely separated. The hypodermal cells multiply by an indefinite number of radial divisions during the period preceding full bloom. Very shortly after full bloom they become displaced, distorted, and in many cases crushed. Dorsey and Potter (15) stated that in peach the epidermal layer protects the fruit in early stages of development, but as growth and enlargement proceed, the deeper layers function with the epidermis as an additional protecting layer for the fruit.

The readily separating skin is reported by Robbins (36) to be a characteristic of the New World species of Vitis. The contrary is true of the Old World species. No work was reported in connection with the anatomical reasons behind this phenomenon as far as this genus is concerned. However, Addons, Nightingale, and Blake (1) stated that peeling of the skin in some peach varieties is caused by actual breaking of the walls of the outermost layers at maturity.

Adkinson (2) studying some anatomical features of the wood of the Vitaceae concluded that the genus Leea is the most primitive living representative of this family, while

Ampelopsis and *Cissus* appear to be less primitive than *Vitis*. His work was concerned with the anatomy of the vegetative and not with the reproductive organs.

I. THE DEVELOPMENT OF THE FRUIT OF GRAPE

A. FLESH DEVELOPMENT

The pericarp of this fruit consists of homogeneous fleshy layers throughout (Kraus 24). It is composed entirely of parenchymatous cells with two whorls of more or less equally spaced vascular bundles. The parenchymatous cells around the bundles are rather small with no intercellular spaces.

The development of the flesh was studied largely by counting and measuring the cells in the pericarp at many stages from the week-old flowers to the mature fruits. The results of this study will be presented with a comparison between the hybrid and its parents throughout the different stages.

Contrary to Villier's (39) statement that flesh development in this fruit is due merely to expansion of the already existing cells, it was found that there are three distinct periods of growth and development. The transition from one period to another is not sudden and complete. These are:

1. A period of six to seven weeks during which there are cell divisions with only slight cell expansion. This in turn is divided into two stages.
    a. The pre-anthesis stage of three to four weeks.
    b. The anthesis stage of two to three weeks.

2. A period of eight to ten weeks of cell expansion with only occasional cell divisions. This again is divided into two stages:

   a. The post-anthesis stage of six to seven weeks.

   b. The pre-maturation stage of three to four weeks.

3. A period of four to six weeks of almost no cell expansion or division. This is the maturation period.

THE PRE-ANTHESIS STAGE

This stage is characterized by a slow rate of division and very slight enlargement of small, non-differentiated, isodiametric cells. The cell walls are very thin, and most of the cells contain tannin materials. The vascular system is not well differentiated during this stage. Toward its end, the processes of pollination and fertilization take place.

The difference between the hybrid and its parents, during this stage, is mainly in the number of layers of cells which constitute the flesh, rather than in the sizes of these cells. The hybrid was intermediate in numbers of layers when compared with the parents. This number was 10, 12, and 16 layers with an average cell size of 10 microns in the first week for the Diamond parent (Fig. 1), the hybrid (Fig. 6), and the Muscat Hamburg parent

(Fig. 11); and 18, 20, and 24 layers with an average cell size of 16 microns in the fourth week (Figs. 2, 7 and 12).

THE ANTHESIS STAGE

During this stage the number of cells is increased rapidly by the successive divisions which occur largely in a tangential plane. This rapid division is due probably to stimulation resulting from the pollination and fertilization processes. The enlargement of cells is still very slight during this stage. Toward the end of this period the cells become more or less differentiated into either isodiametric cells, or cells which are tangentially elongated. The former form the central and larger part of the fleshy pericarp, while the latter are located next to the epidermis and the locule.

The vascular supply can now be seen clearly differentiated. It consists of two portions, an outer and an inner whorl of bundles, which unite at the base of the fruit and become continuous with the vascular supply of the pedicel.

The cell walls in the parenchyma are still thin, and the amount of tannin material is more or less the same as in the previous stage.

Here again the main difference between the hybrid and the parents is largely in cell number and to lesser

degree in cell size. The average number of layers at this stage in the hybrid is 40 (Fig. 8), while it is 34 in the Diamond parent (Fig. 3) and 45 in the Muscat Hamburg parent (Fig. 13). Cell sizes average from 19 to 25 microns in all three varieties.

THE POST-ANTHESIS STAGE

This is a stage of rapid increase in size of the berry, together with completion of cell differentiation into isodiametric and tangentially elongated cells (Figs. 4, 9, and 14). This rapid increase is due chiefly to expansion of the cells formed by division during the previous stage. The cells are, therefore, probably subjected to various forces of tension and compression, and the result of these forces together with the degree of elasticity of the cell walls, very likely determines their final shape. The increase in size of the berry subjects all cells at the outer edge of the pericarp to considerable tension in a tangential direction, and this would decrease towards the center of the berry, until the inner layers of the ovary wall are reached, where a similar effect on the cells near its boundary can be observed.

After differentiation, there occurs occasional division in some of the isodiametric cells, while the tangentially elongated cells stop dividing and their number

remains constant.

Increase in thickness of cell walls takes place and continues until the maturation period is reached. Intercellular air spaces appear toward the end of this stage. There is also a gradual decrease in the tannin material, progressing with age from the inner parts toward the outer layers, finally becoming restricted to the outermost cells at maturity.

THE PRE-MATURATION STAGE

This stage is typified by a decrease in rate of cellular expansion and growth is thereby slowed.

Although the hybrid, during this stage, as well as during the post-anthesis stage, is still intermediate in the number of cell layers which make up the fleshy body of the fruit, its average individual cell size exceeds that of the large fruited parent. This number is 46 layers for the hybrid (Fig. 10), 41 for the Diamond parent (Fig. 5), and 54 for the Muscat Hamburg parent (Fig. 15). The size cannot be represented by an average type here, but that of the large cells inside the first whorl of the vascular system, is 250 microns for the hybrid (Fig. 22), 150 microns for the Diamond (Fig. 20), and 200 microns for the Muscat Hamburg (Fig. 24).

The fruit of this hybrid, then, is intermediate between the two parents in number of cell layers, but because of the development of larger cells it attains in the same time the size of the large fruited parent. There is no difference in the chromosome number of the hybrid and its parents (Nebel 30), (Sax 37), and Negrul 31). This, then suggests that the process of flesh development in this case is possibly governed by two types of genes since environmental conditions also were equal. One of these types controls the rate of cell division and the other controls the rate of cell expansion. Their function is independent, and the former is of more pronounced effect during the first period of development while the latter is more active during the second period. The final size of the fruit at maturity is chiefly determined by the interaction of these two types of genes. This agrees with the working hypothesis advanced by McArthur and Butler (28) in their studies on size inheritance in tomato fruit.

MATURATION PERIOD

This is mostly a period of chemical changes which has been studied thoroughly by several investigators (Copeman and Frater 10), (Dalmasso 11), (Almida 3), and (Atkinson and Strachan 5).

The duration of this period is two to three weeks less in both the hybrid and the Diamond parent than in the Muscat Hamburg parent. In all of them, however, there is no increase in size or number of cells during this period as compared with the pre-maturation stage. The only apparent histological change is the decrease in the thickness of the cell walls in certain areas adjacent to the skin in the hybrid and its Diamond parent. The corresponding areas in the Muscat Hamburg fruits do not undergo these changes. The development of these thin-walled cells will be described in detail in connection with the discussion regarding causes of the separation of the skin.

B. PROTECTIVE LAYERS

The fruit of grapes is protected only by the epidermal layer during the first period of development; but as growth proceeds, other layers function with the epidermis in protection. These are: a thin layer of cuticle, a thick and heavily cutinized outer tangential wall of the epidermal cells, and the hypodermis. The development of these regions will be discussed individually below.

THE CUTICLE

The cuticle is a thin, continuous, superficial layer of fatty substances deposited upon cutinized lamellae. It

is difficult to distinguish these two layers in the first period of development (Fig. 16). The combined thickness of the two layers at this time is only about one micron in both the hybrid and its parents.

In the beginning of the second period of the developmental process, the differentiation between these two layers becomes less obscure and the cuticle appears in many cases as a wrinkled layer with an average thickness of less than one micron. This thickness does not increase much in later stages, a phenomenon which might be due to stretching.

THE CUTINIZED AREA

This is an area of cellulose lamellae impregnated with fatty deposits. Its thickness increases gradually from less than one micron at the first period of development to about 6.5 microns in the hybrid and the Diamond parent and 8 microns in the Muscat Hamburg parent at maturity. These measurements apply only to the thickness opposite the centers of the epidermal cells. The thickness of the cutinized layer in the region of the radial and cross walls is approximately the same during the early stages of development. (Fig. 17). Toward the end of the second period the thickness of the radial wall is increased resulting in V-shaped wedges between the epidermal cell (Fig. 18). This continues till finally, at maturity, the

thickness of the cutinized layer between the epidermal cells is two microns more than that in the points opposite the centers of the epidermal cells (Fig. 19).

Having both cuticle and cutinized layers in this fruit disagrees with the findings of Vielliers (39) who stated that there is only a cutinized layer, and with those of Bioletti (7) who reported that only cuticle is present.

THE EPIDERMIS

The epidermal cells of the fruit of this hybrid and its parents do not exhibit any kind of hairs or stomata throughout their life.

At the pre-anthesis stage, the epidermis is a layer of active thin-walled cells measuring, on the average, 9 microns tangentially and 12 microns radially (Fig. 16).

During the anthesis stage there occurs a rapid division of these cells mostly in the radial plane. This division is followed by an increase in cell size. The epidermal cells at that time average 11 microns tangentially and 15 microns radially. The epidermis is then a layer of closely fitting columnar cells which divide rarely and remains as such until the beginning of the post-anthesis stage when cell division is no longer observed.

At the pre-maturation stage the cells are more of a tabular shape with average measurement of 15 microns for the tangential dimension and 9 microns radially (Fig. 18). The tangential dimension increases and the radial one decreases until at maturity the average epidermal cell is 21 microns tangentially and 7 microns radially (Fig. 19). The above findings were almost the same for the hybrid and its parents.

THE HYPODERMIS

The hypodermis is composed of 8 or more layers of tangentially elongated cells with very thick walls. They are rather tightly fitted together with no intercellular spaces. This minimum number of 8 layers differs from that of 4 and 2 layers mentioned by Vielliers (39) and Bioletti (7) respectively.

As stated above, the cells of the hypodermis are similar in shape to the adjacent cells of the flesh until the post-anthesis stage (Fig. 17), when they become more and more elongated in the tangential plane (Fig. 18). Their average size increases from 10 microns for both the tangential and the radial width at the pre-anthesis stage to 24 microns for the former and 18 microns for the latter at the post-anthesis stage. Their wall thickness, which averages one micron at this time, then increases gradually

until maturity. Likewise there is an accompanying increase in size but there is no further increase in number. The increase in size is much less in the cells next to the epidermis than in those next to the flesh.

At the pre-maturation stage, the tangential width averages about 100 microns with 33 microns for the radial width in these cells next to the flesh. The cells next to the epidermis are about half this size. Their wall thickness is about 3 microns and does not increase in later stages.

At maturity the radial width of the hypodermal cells is decreased about 3 microns, and the tangential width is increased about 10 microns over corresponding measurements made in the previous stage.

As proved michrochemically, thickness of these walls is due to deposition of cellulose and not of lignin as stated by Vielliers (39).

C. SKIN SEPARATION

The skin of the mature berry consists of the protective layers together with 3 to 5 layers of cells adjacent to the flesh (Fig. 19). The physical characters of the skin, like those of the pulp, influence greatly not only the eating qualities of the grape but even more its keeping and handling qualities (Bioletti 7). The poor handling

quality of both the Diamond parent and the hybrid is due largely to the fact that the skin of these varieties is easily separated from the flesh when the fruit is subjected to slight pressure. This phenomenon, while not exhibited by the Muscat Hamburg parent, appears in the other two varieties near the beginning of the maturation period with gradual increase in ease of separation as the fruit matures.

A histological study of the skin at different stages of development seemed advisable because in this way it would be possible to arrive at a clear understanding of its structure as found at maturity. As stated above, the fruit in its first period of development consists of many small, tightly fitted cells with very thin walls. In the second period, the increase in size depends more and more upon the expansion of these cells. This enlargement is accompanied by an increase in thickness of cell walls. Only the protective layers become truely thick-walled, but the walls of the cells that constitute the flesh are perceptibly thicker than when the cells are first formed.

It is found that the changes which result in the ready separation of the skin occur mainly during the maturation period. Careful measurements under oil immersion by the use of ocular micrometer, as well as measurements of camera lucida drawings, show a gradual decrease in

the thickness of cell walls in the layers next to the skin in the hybrid (Figs. 22 and 23) and the Diamond parent (Figs. 20 and 21). This thickness was 1.2 microns for both of them at the pre-maturation stage, and then decreased to 0.5 micron at the end of the maturation period. This decrease in cell wall thickness was accompanied by the removal of pectic substances from these walls as proved by michrochemical tests. These changes did not occur in the corresponding cells of the Muscat Hamburg parent. Their cell wall thickness of 1.4 microns was approximately the same during the pre-maturation (Fig. 24), and the maturation period (Fig. 25).

Thus it is clear that the hydrolysis of pectic substances which occur during the maturation period in both the hybrid and the Diamond parent results in decreasing their strength. These layers of very thin-walled cells bordered, especially on the outer side, by layers of much more thickly walled cells are probably less resistant to pressure than are those of the above mentioned bordering cells. As a result, these thinner walled cells will break more easily when pressed than do the outer, stronger or more resistant layers of the skin. These outer, stronger layers of the skin, thereby are readily separated from the flesh.

In contrast, hydrolysis of the pectic substances was not complete during the maturation period in the Muscat Hamburg parent, consequently the cells were still firm, possessed thick walls, and probably their resistance to pressure does not differ much from that of the outer bordering area. Hence its skin is more adherent to flesh and is not affected by slight pressure as is that of the other two varieties.

II. FLORAL ANATOMY OF VITIS AND ALLIED GENERA

INTRODUCTION

The family Vitaceae is divided, according to Engler (19) and Wettstein (40), into two subfamilies, the Vitoideae and the Leeoideae. The former includes Vitis, Ampelocissus, Parthenocissus, Pterisanthes, and Cissus. The latter includes only the genus Leea. Rendle (35) and Pool (33) state that this family includes 11 to 12 genera, but they name only Vitis, Cissus, Parthenocissus, and Leea. According to Merril (29), and Wettstein (40), the genus Leea differs from the other members of the family, nearly all of which are vines climbing by tendrils, in the woody stem and the shrub or tree-like habit.

The small greenish flowers of this family are borne in compound dichasial inflorescences, or in panicles passing in the ultimate branches into dichasia. The flower, as described by the above investigators and also by Payer (32), possesses a calyx of 4 to 5 sepals usually only very slightly developed, and often forming a ring around the base of the corolla. The petals are 4 to 5 in number and may be united or free. The antipetalous stamens are free, except in Leea, where they are joined at the base to form a tube united to the base of the corolla (Engler 19, Rendle 35, and Wettstein 40). Inside the androecium is a

well developed glandular disc, surrounding the pistil. The ovary is superior with 3 to 8 united carpels in Leea, and 2 in other genera. Dorsey (14) reported that an increase in the number of stamens is associated with an increase of carpels in the genus Vitis.

The present study is intended to elucidate, by means of the floral anatomy, the probable relationship among certain genera of this family.

FLORAL ANATOMY OF THE GENERA STUDIED

Leea

Two species of this genus were studied, namely, L. indica (Burn.) Merr., and L. aculeata Ml. Since their vascular anatomy is quite similar, only the former will be described in detail.

The base of the pedicel shows a dissected siphonostele composed of five bundles (Pl. VI, Fig. 27). The xylem and phloem strands of some of these basal bundles are gradually separated leading to the formation of new bundles at higher levels in the pedicel (Fig. 28). This method of formation of new bundles at higher levels in the pedicel is also true with the genera to be described later.

At the base of the flower, five strong traces depart to the calyx at equal distances from each other on the circumference (Fig. 29). Usually, these traces remain solitary until well out in the calyx where each of them gives rise to two lateral branches (Fig. 30). The main traces with their lateral branches continue to the top of the calyx lobes which are well developed in this genus when compared with those of the other genera studied. Although numerous smaller laterals arise at frequent intervals, the above mentioned fifteen strands form the

basic vascular structure of the calyx in this genus. The lesser laterals and the original traces of the sepals anastomose to form a network of vascular tissue. The calyx as an independent whorl, is freed from the rest of the floral whorls at a low level (Fig. 32). These floral whorls are; the petals, the stamens, the glands, and the carpels. The petals are alternating with the sepals, the stamens are antipetalous, and the glands are inside the stamen whorl.

The traces to the petals are fused with those to stamens and glands when they first depart from the central stele. They appear as five strong bundles departing at a level slightly higher than that of the calyx traces and alternating with them (Fig. 30). Each one of these five strong bundles thus represents a complex of a petal, a stamen, and a gland trace. From this complex, the petal trace is first separated at a level slightly above the origin, while the stamen and the gland traces are separated from each other at a still higher level (Figs. 35-36).

After separation, the traces to the petals remain solitary until the petals are freed, and then anastomose in the way exhibited by the calyx (Fig. 41). The corolla, as an independent whorl, is freed from the fused stamens and glands at approximately the level of the base of the

style (Fig. 40). The petals in this genus, as well as in all the other genera studied, are not to be considered united anatomically, but their edges are fitted together in dovetail fashion (Fig. 43). Such a way of fitting exerts some degree of resistance to the separation of the adjacent petals, hence they are considered united morphologically.

After the petal traces are separated from the petal-stamen-gland complexes, the remainder of these complexes divide tangentially at a level slightly higher than that of the origin of the ventral carpellary traces (Fig. 36). The outer bundles resulting from this tangential division constitute the stamen traces. Each remains solitary and passes to the opposite filament. The inner bundles, on the other hand, are divided radially again and again at higher levels, and together with their branches, constitute the traces to the glands (Figs. 38-43). The traces do not pass to the upper ends of the glands, but usually terminate just below their centers (Fig. 26). This mode of the departure of the glandular traces indicates that the glands probably originated as inside branches from the bases of the stamens.

The lobes of the glands are equal in number to the members of any other whorl in the same flower, except the carpels. They are, in this genus, stamen-like structures.

Each is branched approximately half way up into two unequal branches which are almost on right angles to each other. They are fused almost to their tips. Their bases, combined with those of the stamens and petals, form a small tube which is also fused for a short distance with the ovary, while the fusion of their upper branches forms a cup-like structure (Fig. 26). Reflected downward into the cavity of this cup-like structure, are the upper ends of the filaments with their anthers. The anthers are then found inside this cavity in a reversed direction (Fig. 26). The edges of the adjacent anthers are fitted together in the dovetail fashion exhibited by the petals (Fig. 45).

There are from 3 to 8 united carpels in this genus. Each carpel has three traces; a dorsal and two ventrals. The dorsal traces depart first from the receptacular stele at a level just above that where the calyx is freed (Fig. 33), the ventrals higher up (Fig. 34). In their departure, the ventral traces are separate bundles with a number twice that of the dorsals. Higher up, the ventrals of the adjacent carpels are fused together, and then their number becomes equal to that of the dorsals (Figs. 36 and 37). They remain fused for a very short distance only and then separate again at the level where the ovary is freed from the glands (Fig. 38). The ventral bundles become inverted before they enter the carpels, the phloem being

being on the ventral side in the carpel, whereas it is on the dorsal side in the midrib. The dorsals and the ventrals form a ring of anastomosing bundles at the base of the style (Fig. 40). This ring disappears gradually on higher levels in the long style, until finally the extension of the dorsal and the ventral carpellary traces and their branches terminates just below the stigma.

The traces to the ovules are derived from the ventral bundles (Fig. 38). This is also true with the ovules in the genera to be described later.

Ampelocissus acapulunsis (H. B. K.) Planch.

The size of the flower in this genus, as well as in the other genera studied, is about half that of the genus Leea. The vascular structure of the pedicel is very similar to that of Leea in the way that the xylem and phloem strands of some of the basal bundles are separated, giving rise to more bundles on higher levels in the pedicel (Pl. VII, Figs. 48 and 49).

The calyx of Ampelocissus usually consists of five united and much reduced sepals. The traces to the sepals depart at the base of the receptacle (Fig. 50), and each trace soon branches at a higher level into two lateral traces which are weak in many cases (Fig. 51). The main traces with their laterals pass into the opposite sepals. They do not anastomose so much higher up in the sepals, as do those of Leea.

The complexes of the petal-stamen-gland traces appear at the level just below that where the calyx is freed from the other floral whorls (Fig. 51). They are five large bundles alternating with the calyx traces. From these complexes, the traces to the petals are separated soon after departing from the stele (Fig. 54). At higher levels, every petal trace is branched into lateral traces when well out in the petals. The petals themselves are freed before the stamens and the glands (Fig. 55).

After the petals are freed, the remainder of the petal-stamen-gland complexes are divided tangentially in much the same way as those of Leea. The outer bundles resulting from this division pass into the filaments which are almost straight in the genus. The anthers, are bent inward but not fitted together like those of Leea. The inner bundles are divided again radially and pass to the glands where they give rise at higher levels to some lateral branches (Figs. 55-57). Such lateral branches are much fewer than those exhibited by Leea. The traces to the glands do not extend to the upper ends of the lobes, but usually terminate at approximately the level where the ovary is freed from the glands (Fig. 61). The lobes of the glands are reduced in size, with complete loss of the upper branches found in Leea. They form a complete circle fused with the ovary except at the top where they are free (Fig. 47). Their bases are also fused with those of the stamens and the petals in a way similar to that of Leea.

The ovary is composed of two united carpels, the dorsal traces of which appear at the level where the stamens are freed (Fig. 56). They start to branch close to the base of the style (Fig. 61). The ventral carpellary traces depart at a level just above that of the dorsals (Fig. 57). They become inverted when they enter the carpels, a phenomenon which is also true with the ventral

bundles of other genera studied. The ventrals of the adjacent carpels do not fuse together at higher levels in this genus, but remain separate throughout the ovary (Figs. 57-61). The dorsals and the ventrals form a ring of anastomosing bundles at the base of the style, similar to that found in Leea (Fig. 62). This disappears gradually at higher levels in the long style leaving only the continuation of the ventral traces which extend further than the dorsals, but disappear usually below the stigma (Fig. 47).

Vitis

Two cultivated forms of V. vinifera L. and one of V. labrusca L. (V. landii prince.) were studied. These are Muscat Hamburg, Black Hamburg, and Diamond grapes respectively. The floral anatomy of the Muscat Hamburg grape will be described in detail, since the other forms are quite similar to it.

The calyx which is highly reduced in this genus, forms a ring around the base of the other floral parts. The main traces to the sepals are similar in their origin to those of the genera already described (Pl. VIII, Fig. 67). They differ only in the manner of branching at higher levels. Instead of having two lateral traces on both sides of the main trace, the latter is divided into two branches. When well up in the calyx, one of these is branched again and again while the other usually remains unbranched (Fig. 68).

The traces to the petals and stamens are fused when they depart from the stele (Figs. 70 and 71), but separate immediately thereafter (Figs. 72 and 73). The petals are freed before the stamens (Fig. 75).

The anthers are not curved inward as in the genera already discussed, but are almost straight along their full length (Fig. 64).

Traces to the glands do not appear in this genus. The lobes of the glands are highly reduced in size when compared with those of the genera already described (Fig. 64). They look like small fleshy protuberances forming a ring fused with the base of the ovary. They are also fused with the bases of the stamens and petals for a very short distance.

The dorsal and the ventral carpellary traces appear at the same level just above where the petal traces are separated from the petal-stamen complexes (Fig. 74). The dorsal traces remain solitary until higher up in the ovary where they give rise to several lateral branches (Fig. 80). The ventral bundles of the adjacent carpels are separate between the level of their origin and the level just below the top of the ovary (Figs. 74-81), where they fuse together for a short distance and then are separated again (Figs. 82-84). Some of the ventral traces are branched just above the level of their origin (Fig. 76) These branches are pushed far from the ventrals toward the outside until higher up it becomes difficult to distinguish between them and the branches of the dorsal bundles (Figs. 78-82). The dorsals, the ventrals, and their branches continue up into the short style and then disappear. The dorsal traces and the other branches disappear completely at a level below that of the ventrals.

The style in this genus is highly reduced in size when compared with those of Leea and Ampelocissus (Fig. 64).

Different stages of reduction from a higher toward a lower number of carpels were observed in this genus. A series of three fertile carpels (Fig. 89), of two fertile and one sterile (Figs. 90 and 91), and of two fertile carpels were found in different flowers.

The sterile carpel is completely inclosed in one of the fertile carpels and is attached only at the margins. It shows one dorsal and two ventral bundles in some cases (Fig. 90). In other cases the traces have disappeared before the loss of the carpel (Fig. 91).

Columella

Two species of this genus were studied; namely, C. (cogratiei) Japanica Werr. and C. mairei Lee. The floral anatomy of the two species is quite similar, hence the former only will be described in detail.

The flower, at least in the specimens studied, is usually 4 merous rather than 5 or 6 merous, except for the two united carpels. Its anatomy differs from that of the genera already described in the following respects.

After the departure of the four calyx traces from the stele, each of them is divided just before the calyx is freed into two branches which are almost at right angles from the main one (Fig. 94). A third branch or trace is barely visible. The two branches of the main trace, thus pass to the opposite sepal where they give rise to fewer and weaker laterals higher up in the sepal which is not very well developed in this genus (Pl. IX, Fig. 97).

The complexes of the petal-stamen-gland traces remain fused for a distance longer than that exhibited by the previous genera. In other words the petals traces do not separate immediately from these complexes after they depart from the stele, but their separation occurs at a level higher than that of Leea, Ampelocissus, and Vitis (Figs. 97-99).

As independent whorls, they follow the same pattern exhibited by the above genera, i.e. the petals are freed first, followed by the stamens, and then the glands (Figs. 99-104). Morphologically, the stamens resemble those of the genus Ampelocissus (Fig. 92).

The lobes of the glands are intermediate in shape and size between those of Leea and Ampelocissus. They differ from both of them, however, in the fact that each lobe exhibits a large cavity just below its upper end (Fig. 92). The attachment of these lobes to the adjacent whorls is similar to that of Ampelocissus. The traces to the glands appear clearly at a level just below that where the stamens are freed (Fig. 102). They behave in their separation from the stamen-gland complexes, and in their branching, in much the same way as those of Ampelocissus (Figs. 101-104). They terminate at a level where the cavities appear in the lobes of the glands (Fig. 106).

The two dorsal carpellary traces appear just below the level where the petals are freed (Fig. 98). The four ventral traces appear where the petals are freed (Fig. 99). The ventral traces of adjacent carpels are separated for a short distance (Figs. 100 and 101), and then become fused and appear as large inverted bundles (Fig. 102). They remain so until about the top of the ovary where they start to separate again (Fig. 105), and then pass separately

into the style (Fig. 106). The dorsals and the ventrals do not form a ring of anastomosing bundles at the base of the style. The dorsals do not go far in the long style, resembling Leea and Ampelocissus.

Ampelopsis cordata Mich. (Cissus ampelopsis Pers.)

The strong traces to the calyx appear at the base of the flower (Pl. X, Fig. 111). Higher up every trace gives rise to two branches (Fig. 112). These two branches and the main trace pass to the opposite sepal. Well out in the sepals, they give rise to weak laterals as shown in Columella.

Higher up, the petal-stamen-gland complexes appear, alternating with the calyx traces. The petals traces are separated from the complexes as soon as they depart from the stele (Figs. 115 and 116). The petals are freed before the stamens, which in turn are freed before the glands, as is the case in the previous genera.

At the level just below that where the stamens are freed, the traces to the glands appear in the same way exhibited by Columella and Ampelocissus (Fig. 117). These traces are branched soon after their departure and pass to the lobes of the glands (Figs. 119-121). They disappear higher up in the lobes at the level where the ovary is freed from the glands (Fig. 123). The lobes of the glands themselves are smaller in size than those of Ampelocissus, but larger than those of Vitis. They adhere to the adjacent whorls in much the same way as in Ampelocissus (Fig. 109).

The dorsal and the ventral carpellary traces depart from the stele at the same level. This level is just above that where the traces to the glands appear (Fig. 119). The dorsals start to branch at higher levels where the ovary is freed from the glands (Fig. 123). They pass with their lateral branches into the style at the base of which a ring of anastomosing bundles appears in a manner similar to that of Leea, Ampelocissus and Vitis (Fig. 124). The dorsals together with the lateral branches terminate higher up in the style at a level below that of the termination of the ventral traces.

Soon after the ventral traces depart from the stele, the two ventrals from the adjacent carpels approach each other gradually, and finally become fused (Figs. 120-122). They remain fused until very high in the style and then separate again (Figs. 122-125). They terminate below the stigma.

The style here is rather long and resembles those of the previous genera, except Vitis.

Parthenocissus quinquefolia Planch. (Ampelopsis quinquefolia Mich.)

The floral morphology of this genus resembles that of Vitis more than any other of the genera already described.

In its anatomy, the pedicel of the flower is similar to those of the previous genera, both at lower and higher levels (Pl. XI, Figs. 127 and 128). The traces to the calyx appear departing at the base of the flower (Fig. 129), and each one is branched rapidly in the way exhibited by Ampelopsis (Fig. 130).

The petals and the stamens are freed from the glands at the same level (Fig. 136), differing from the other genera where the petals are freed before the stamens.

The traces to the glands are less strong than those of the other genera (Fig. 136) except Vitis where they do not appear. They become weaker at higher levels and might be confused with the branches of the dorsal and ventral traces which appear at similar levels in Vitis (Fig. 137). Their origin, however, indicates that they are glandular traces and not branches from the dorsal and the ventral carpellary traces. Such branches do appear also in this genus at higher levels in the ovary (Figs. 139-141).

The lobes of the glands in this genus are similar in size, shape, and the method of attachment to the adjacent whorls, to those of Vitis (Fig. 126).

The dorsal carpellary traces depart at a level just below that of the ventrals (Fig. 133). The ventrals depart separately from the stele (Fig. 134). They remain separate for a very short distance along which the ventrals from the adjacent carpels approach each other (Figs. 135 and 136). Finally, they fuse together and remain fused until they pass into the style (Figs. 137-141). They are separated again higher up in the style (Fig. 143). Both the dorsals, the ventrals, and their branches disappear below the stigma in the same manner of the previous genera.

The style is rather short and similar to that of Vitis.

Modification of the floral description of the Vitaceae

According to the present study, the two subfamilies of the Vitaceae, namely, Vitoideae and Leeoideae might still be distinct in the matter of carpels. The stamen tube, which has been supposed to be present in Leea, and absent in other genera, actually is absent in all the genera studied including Leea. The attachment of the bases of the petals, stamens, glands, and carpels with each other is more or less the same in all of them. The floral morphology of this family might be described as follows.

The calyx is composed of very small and united sepals. The number of the sepals corresponds exactly with that of the petals, stamens, and the lobes of the glands respectively. This number differs from three to seven with five most prevalent.

The petals which appear to be united morphologically, are merely fitted together in a dovetail fashion and are not to be considered united in any of the genera studied.

The stamens are antipetalous. They are free along the entire length of their bodies, except for the fusion at their bases with the adjacent petals and glands. The anthers are either straight or curved inward. They are free in all genera studied, except in Leea, where they are fitted together in the fashion exhibited by the petals, a

characteristic which might be considered in the separation of the Leeoideae from Vitoideae. The number of the stamens is not associated with that of the carpels either in Vitis or in other genera, contrary to Dorsey (14).

The glands are inside the whorl of the stamens. They originated by tangential splitting of the stamens. They are united except at their tips, and fused at their bases with both stamens and carpels. Their shape is exhibited by a stamen-like structure in Leea, a disc-like structure in Vitis and Parthenocissus, and by intermediate stages in other genera.

The carpels are united. Their average number is two in most of the genera studied except in Leea, where there are 3 to 8 carpels.

The style is simple and long in all genera studied, except in Vitis and Parthenocissus where it is rather short.

The probable evaluation and relationship among the genera studied.

Before definite conclusions can be drawn as to the phyletic status of any plant, evidence from all fields must be considered. The above anatomical study, however, should cast some light on the probable evaluation of certain genera of the Vitaceae.

According to Eames (17(, the most important evalutionary changes in the structure of the flower are those involving the fusion of parts and their consequent greater or lesser submersion as individual parts in the united mass; and those of reduction, either attendant upon cohesion and adnation, or due to definite direct loss as individual organs. A flower which exhibits a greater degree of fusion and reduction, is thus considered less primitive than otherwise.

On the basis of the above assumptions, the genus Leea would be considered as the most primitive among the genera studied. Its primitive characters are: higher degree of separation of the ventral bundles.of the adjacent carpels, a higher number of carpels, and non-reduction in the size of the glands and the style.

It is very probable that the genera already described, as indicated by their floral structures, were originated from a common ancestor of the following hypothetical nature.

The androecium of this ancestor possessed a whorl of antipetalous stamens. During its evolutionary course, each stamen was split tangentially into two branches at the base. The inner branches gave rise to the glands as indicated by their traces. The traces to these glands are found in all genera studied except in Vitis where they are lost. The vascularization of the glands in some genera and its absence from other genera of one family was also found by Dawson (12) in the Polemoniaceae, and Douglas (16) in the Primulaceae.

The ancestral gynoecium was probably composed of 8 or more united carpels with non-fused ventral traces, and with a rather long style. An evolutionary step in this family is a process of reduction in number of carpels and size of the style, accompanied in some cases by different degrees of fusion of the adjacent ventral bundles. The loss of one or more carpels, in this case, was accompanied by complete loss of their dorsal and ventral traces. This agrees with the views of Arber (4) and Joshi (22) that the vascular tissue is not more conservative than the organ it supplied. In some cases the traces to the sterile carpel are lost before the carpel itself as in Vitis.

Every new form originated from the above supposed ancestor possesses a mixture of some advanced and some primitive characters; in other words, the evolution of a

given floral whorl is independent from that of the others.

According to the importance of their different characters, the relationship of the genera studied may be arranged in the following way. Leea, as previously shown, is the most primitive of this group. Ampelocissus which differs from Leea in possessing lower number of carpels, but which does not exhibit any greater or lesser degree of fusion in its ventral bundles, will come next to Leea. Vitis with some fusion of its ventral bundles, a shorter style, and reduced lobes of glands together with the loss of the traces to these lobes, is to be considered more advanced than Ampelocissus. Columella and Ampelopsis may be considered to be at about the same level as Vitis, but the styles and the glandular lobes are longer, while traces to these lobes are also present. Parthenocissus showing a higher degree of fusion in the ventral bundles together with some advanced secondary characters such as the short style and glandular lobes, is to be considered more advanced than the above genera and consequently the most advanced genus in this group.

SUMMARY AND CONCLUSIONS

I. 1. The process of flesh development of the grape berries of the Diamond, Muscat Hamburg and their hybrid (Golden Muscat) is divided into three periods.

a. The first period of six to seven weeks is characterized by cell divisions with slight cell expansion. This period is again divided into pre-anthesis stage with a slow rate of cell divisions, and an anthesis stage with rapid cell divisions. The duration of the former is about four weeks, of the latter about three weeks.

b. The second period of eight to ten weeks is characterized by cell expansion with only occasional cell divisions. It is divided into a post-anthesis stage with rapid cell expansion, and a pre-maturation stage of slight cell expansion.

c. The third period or the maturation period is of four to six weeks in duration, and includes almost no cell expansion or divisions.

d. The cell number of the hybrid berry is intermediate between that of the two parents, but its cell sizes are larger than those of the large fruited parent (Muscat Hamburg).

1. The protective layers of the grape berry are a thin layer of cuticle, a thick and heavily cutinized

outer tangential wall of the epidermal cells, and the hypodermis.

a. The cuticle is a thin, continuous, superficial layer of fatty substances deposited upon cutinized lamellae. Its average thickness at maturity is close to one micron.

b. The cutinized layer is an area of cellulose lamellae impregnated with fatty deposits. Its thickness increases gradually from less than one micron at the beginning of development to about seven microns at maturity.

c. The epidermis does not exhibit any kind of hairs or stomata. They attain a polygonal shape at early stages of development. Later, their tangential dimensions increase and their radial ones decrease until at maturity, the average epidermal cell is twenty-one microns tangentially and seven microns radially.

d. The hypodermis is composed of 8 or more layers of tangentially elongated cells. The thickness of their walls increases from less than one half micron at early stages of development to three microns at maturity.

3. The skin of the mature berry consists of the protective layers together with 3 to 5 layers of cells adjacent to the flesh. The changes which result in the

ready separation of the skin in both the hybrid and the Diamond parent occur during the maturation period. This separation is due to the continuous decrease in cell wall thickness of the layers next to the skin during the maturation period. This decrease in thickness is accompanied by the removal of pectic substances from these walls. Such changes do not occur in the Muscat Hamburg parent where the skin is more adherent.

II. The floral anatomy of nine species representing six genera from the Vitaceae is described. This study modifies the description of the floral morphology of the family to a certain extent. It was determined that the glands in this family originated by tangential splitting of the stamens.

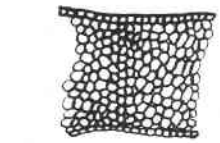
The relationship among those genera is probably as follows: Leea is considered the most primitive genus in this group, Ampelocissus is next to Leea, Vitis is to be considered more advanced than Ampelocissus, and probably on this same level of advancement would be Columella and Ampelopsis. Parthenocissus is considered as the most advanced genus in the above group.

It is very probable that a step in the evolutionary course of those genera, as indicated by their floral structures, is a process of gradual reduction and fusion of some organs from a common ancestor similar in some way to the genus Leea.

Plate I

Process of flesh development in the Diamond grape (a horticultural variety of Vitis labrusca L.) as shown by transverse sections through the pericarp.

1. One week old. 45X.
2. Four weeks old, pre-anthesis. 45X.
3. Five weeks old, anthesis. 45X.
4. Eight weeks old, post-anthesis. 15X.
5. Ten weeks old, pre-maturation. 15X.



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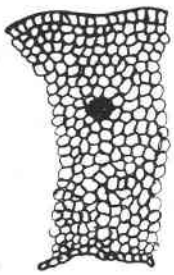

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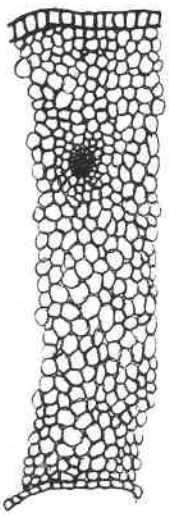

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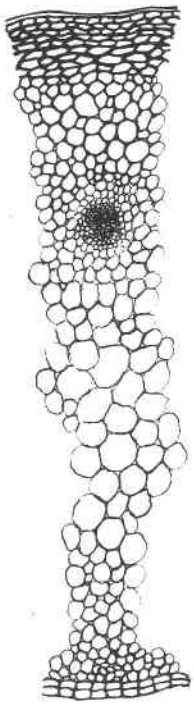

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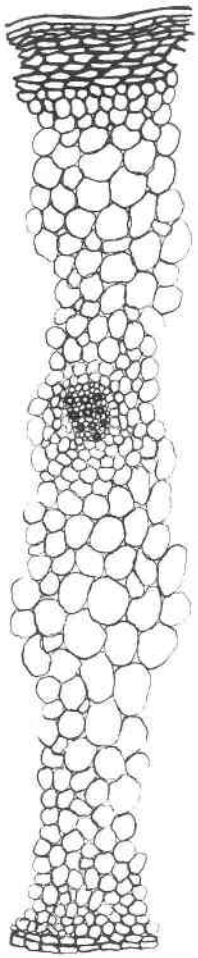

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Plate II

Process of flesh development in the Golden Muscat grape (a hybrid between Diamond and Muscat Hamburg) as shown by transverse sections through the pericarp.

6. One week old. 45X.

7. Four weeks old, pre-anthesis. 45X.

8. Five weeks old, anthesis. 45X.

9. Eight weeks old, post-anthesis. 15X.

10. Ten weeks old, pre-maturation. 15X.

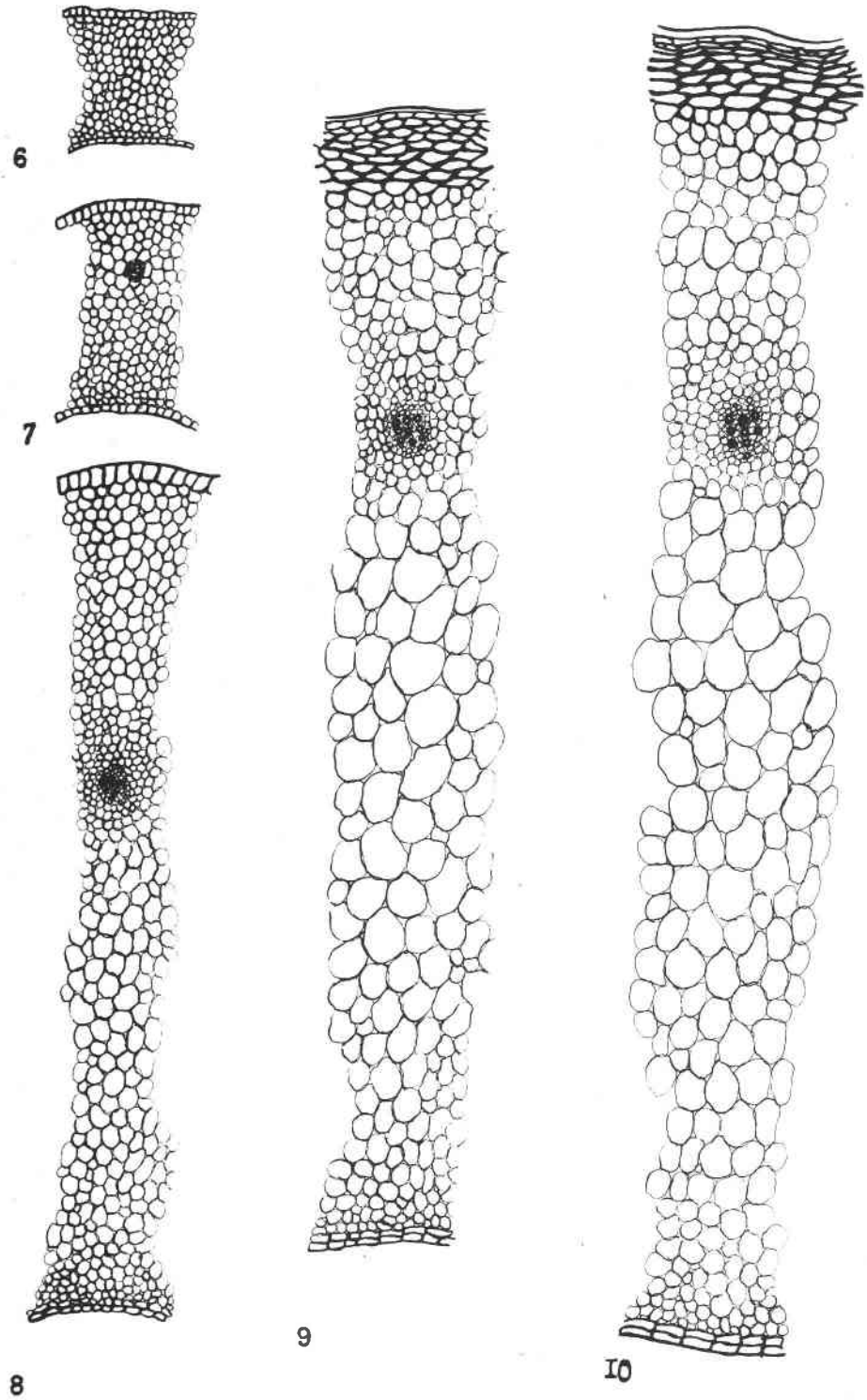
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Plate III

Process of flesh development in the Muscat Hamburg grape (a horticultural variety of Vitis vinifera L.) **as indicated by transverse sections through the pericarp.**

11. One week old. 45X.

12. Four weeks old, pre-anthesis. 45X.

13. Five weeks old, anthesis. 45X.

14. Eight weeks old, post-anthesis. 15X.

15. Ten weeks old, pre-maturation. 15X.

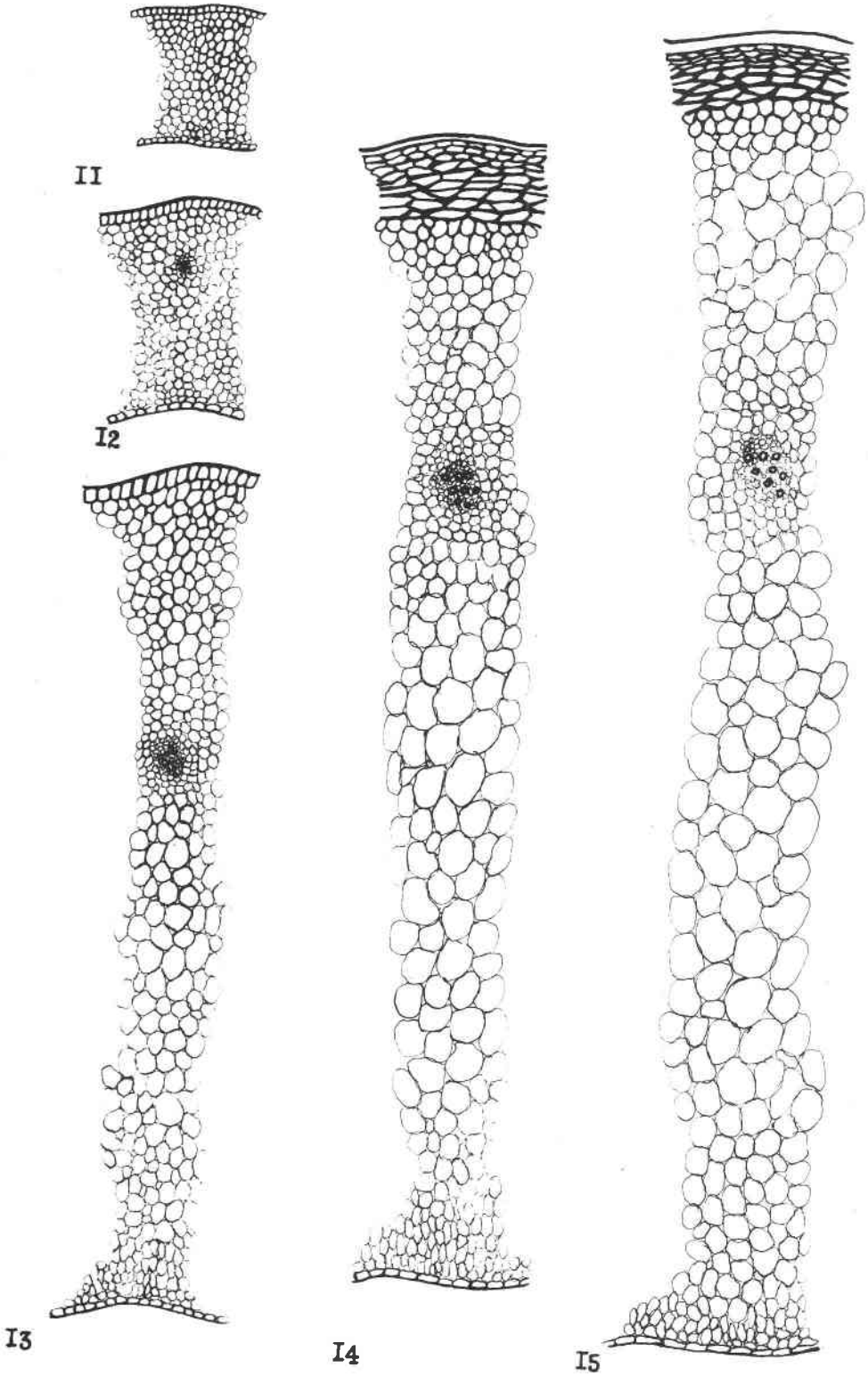
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Plate IV

Developmental process of the protective layers of the Golden Muscat grape as shown by transverse sections.

c = cuticle ct = cutinized layers

ep = epidermal cell Hp. = hypodermis

F = adjacent cells from the flesh

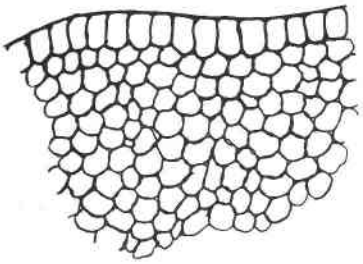
16. One week old.

17. Six weeks old.

18. Nine weeks old.

19. Twelve weeks old.

All figures 180X.



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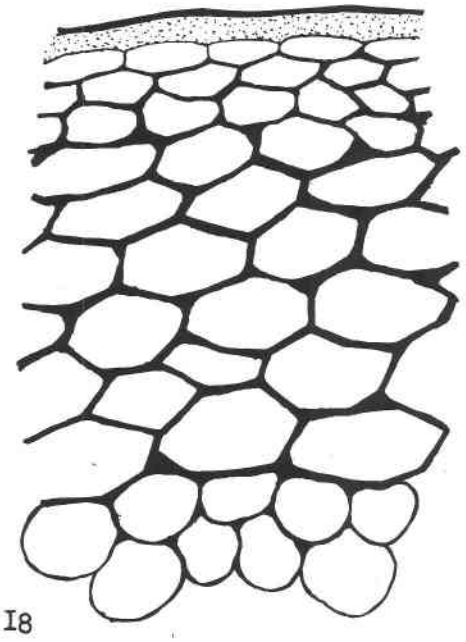

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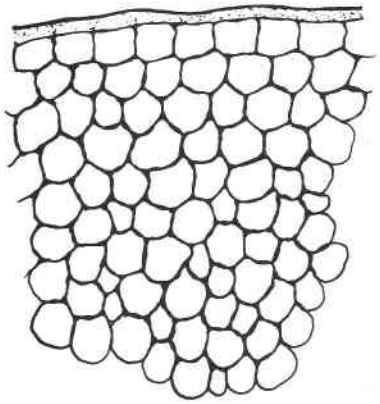

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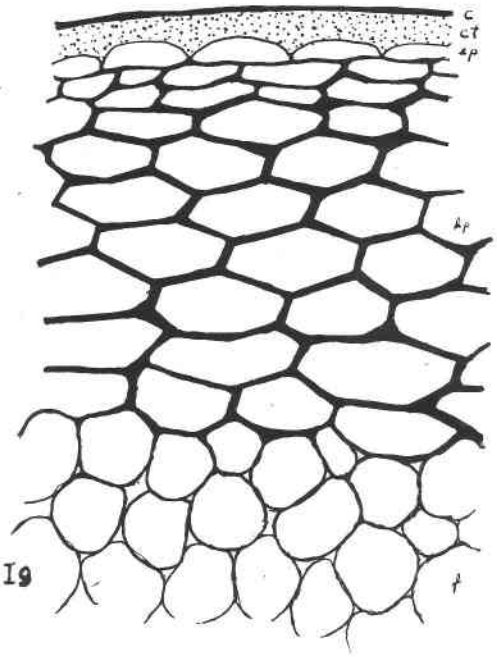

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Plate V

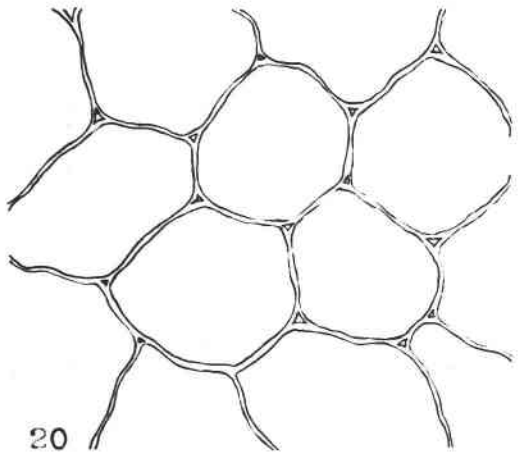
Comparison between the thickness of cells next to the skin in the Diamond, Golden Muscat, and Muscat Hamburg grapes during the pre-maturation periods respectively.

20 & 21. Diamond.

22 & 23. Golden Muscat.

24 & 25. Muscat Hamburg.

All figures 350X.



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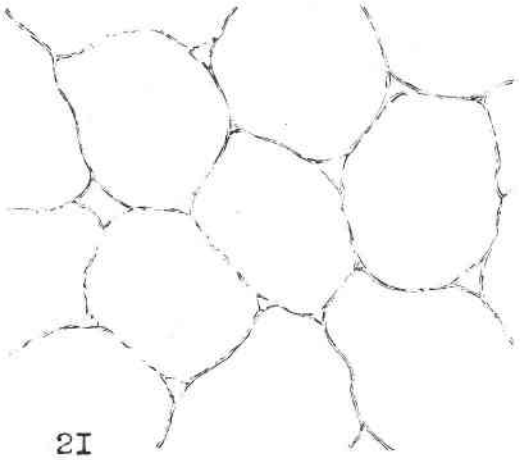

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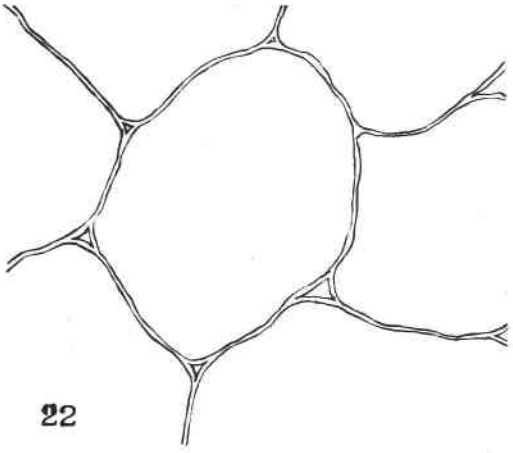

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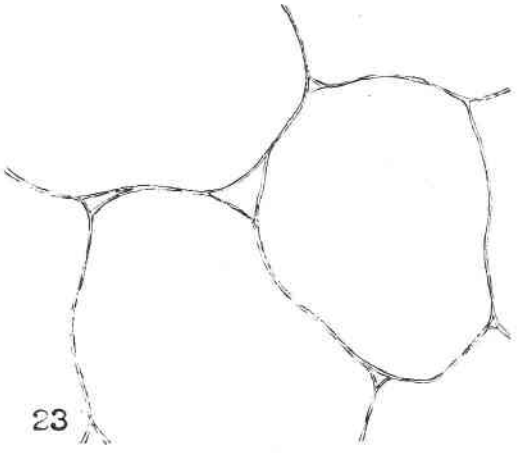

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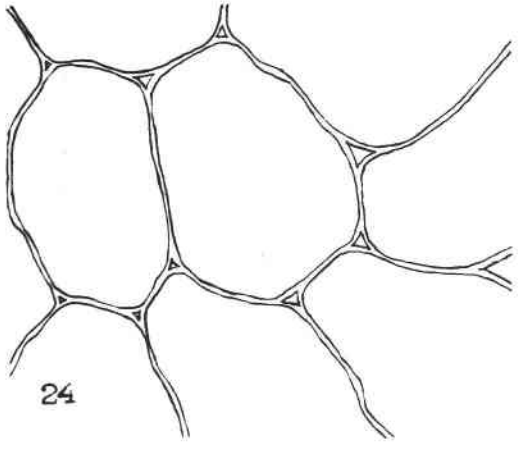

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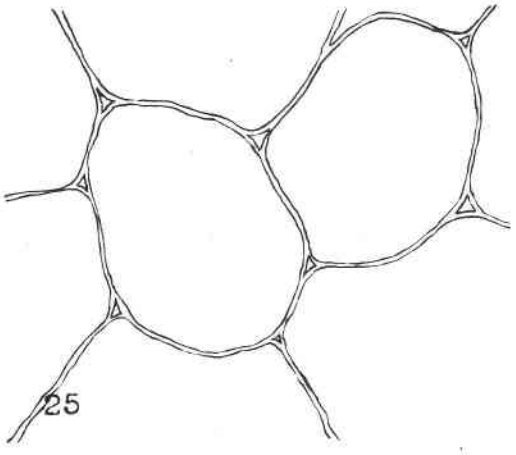

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Plate VI

Diagrams showing the floral structure of Leea indica (Burn.) Merr.

The numbers on the longitudinal section diagram indicate the levels on the cross-section diagrams with the same numbers. The letters S, P, St, G, DC, and VC. indicate sepal, petal, stamen, gland, dorsal carpellary and ventral carpellary bundles respectively.

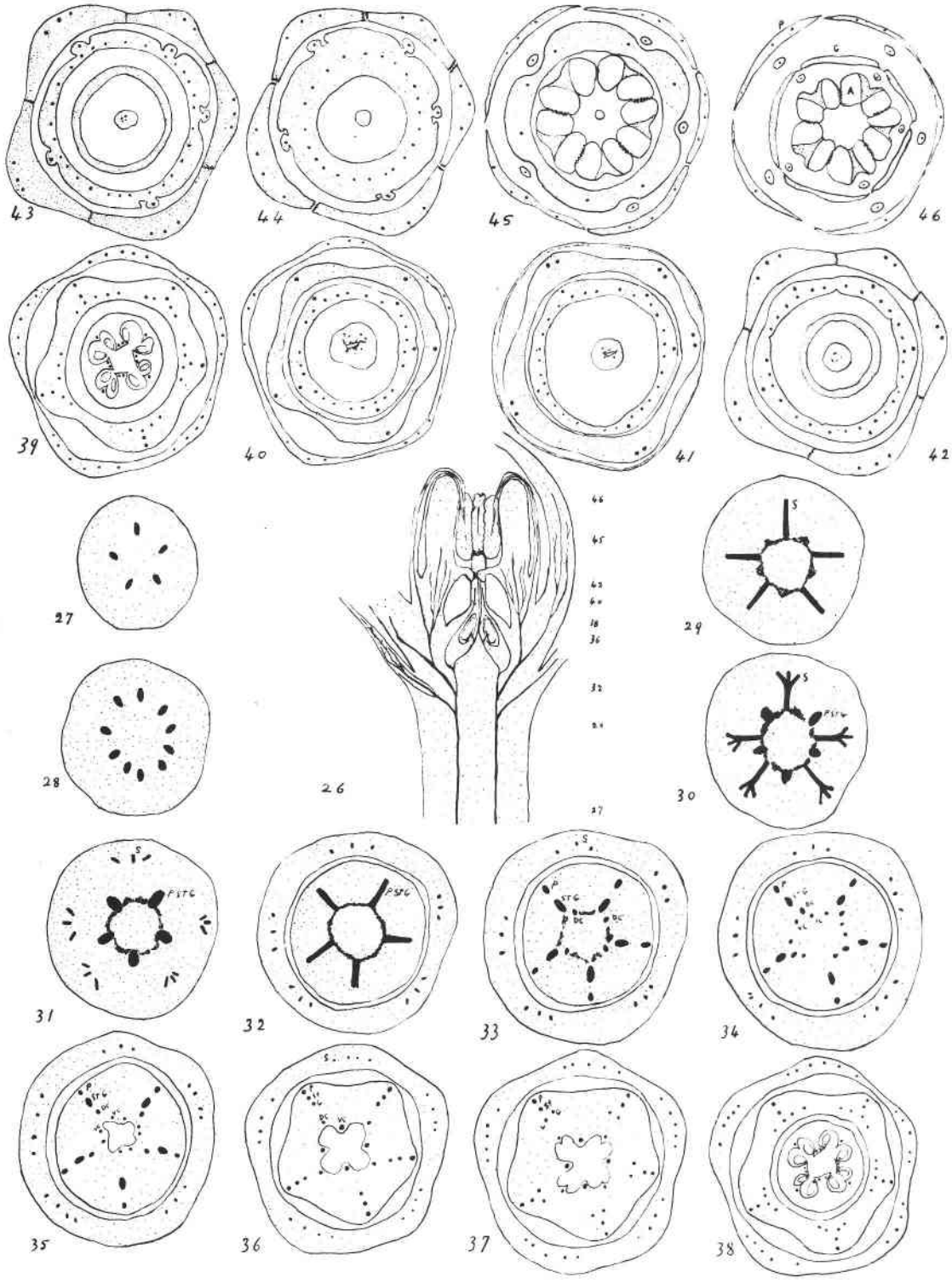
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Plate VII

Diagrams showing the floral structure of *Ampelocissus acopulunsis* (H. B. K.) Planch.

The numbers on the longitudinal-section diagram indicate the levels on the cross-section diagrams with the same numbers. The letters S, P, St, G, DC, and VC indicate sepal, petal, stamen, gland, dorsal carpellary and ventral carpellary bundles respectively.

Plate VII

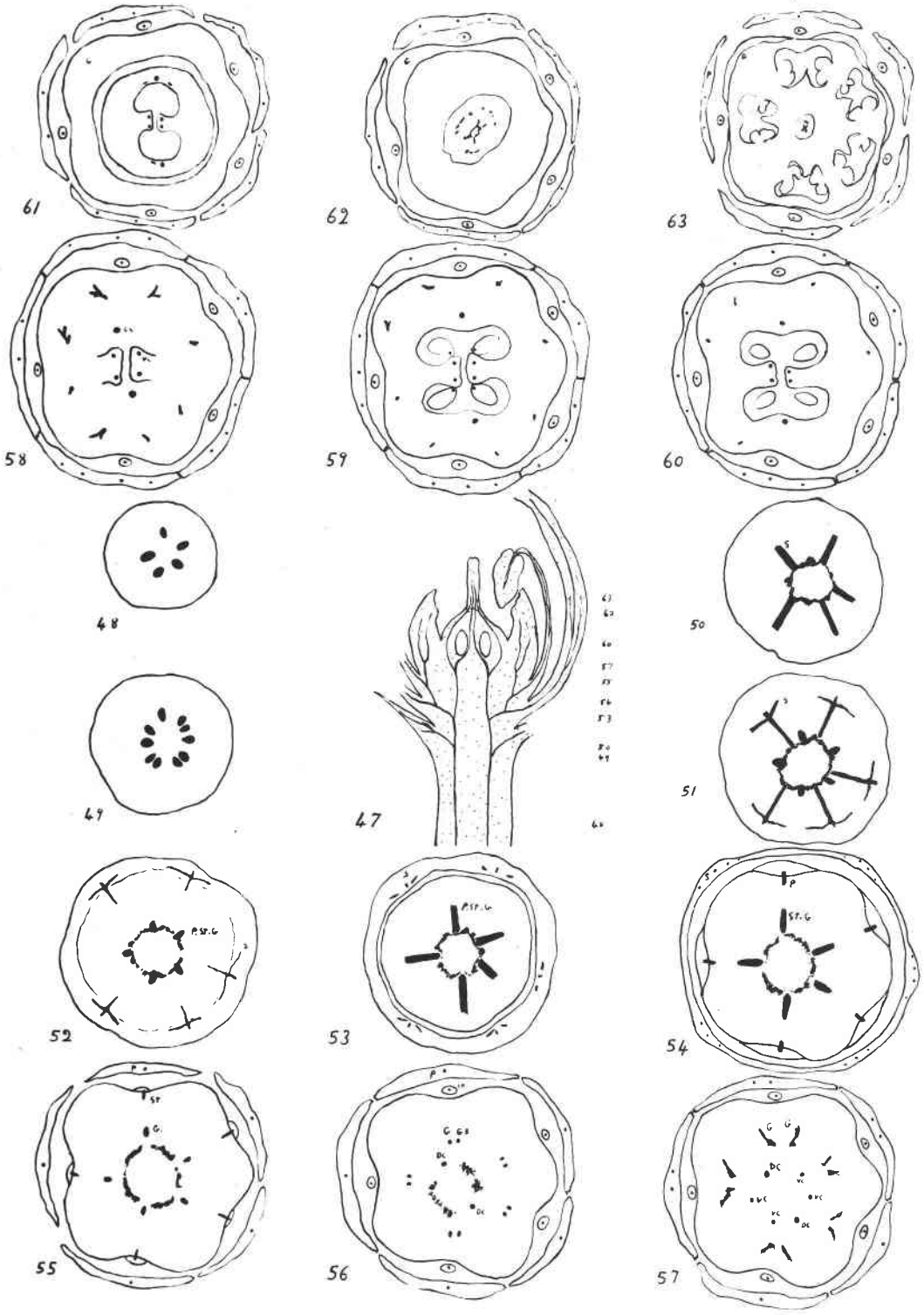

Plate VIII

Diagrams showing the floral structure of Muscat Hamburg grape (a horticultural variety of Vitis vinifera L.).

The numbers on the longitudinal-section diagram indicate the levels on the cross-section diagrams with the same numbers. The letters S, P, St, DC, DB, VC, and VB indicate sepal, petal, stamen, dorsal carpellary, branches of the dorsal carpellary, ventral carpellary, and branches of the ventral carpellary bundles respectively.

Petals and stamens are omitted from Figs. 87 and 88.

89. An ovary with three fertile carpels.

90. An ovary with two fertile carpels and one sterile. The sterile carpel shows its dorsal and ventral bundles.

91. An ovary with two fertile carpels and one sterile. The sterile carpel does not show any traces.

Plate VIII

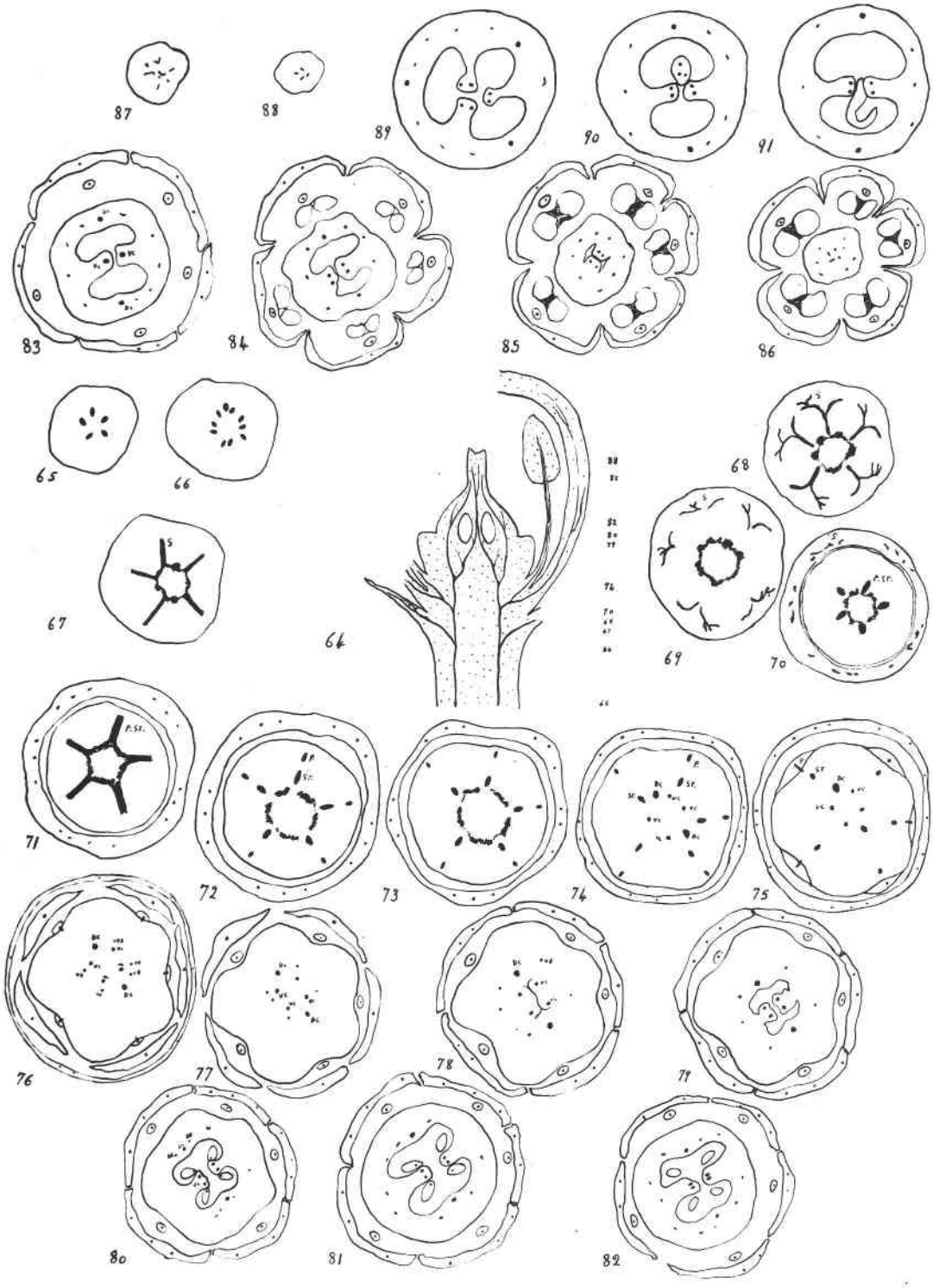
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Plate IX

Diagrams showing the floral structure of Columella (cogratiei) Japonica Werr.

The numbers on the longitudinal-section diagram indicate the levels on the cross-section diagrams with the same numbers. The letters S, P, St, G, DC, and VC indicate sepal, petal, stamen, gland, dorsal carpellary and ventral carpellary bundles respectively.

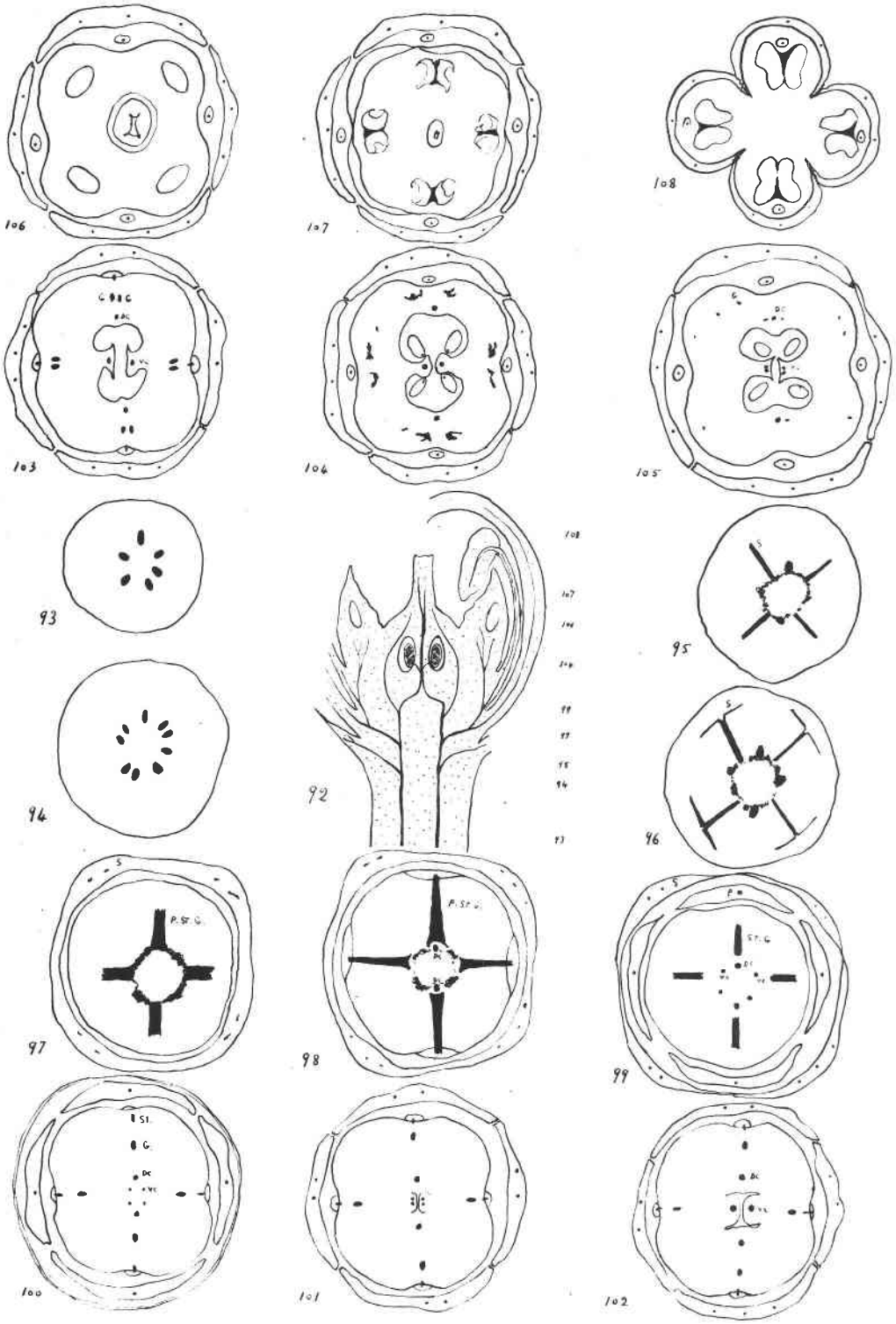
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Plate X

Diagrams showing the floral structure of *Ampelopsis cordata* Mich. (*Cissus Ampelopsis* Pers.).

The numbers on the longitudinal-section diagrem indicate the levels on the cross-section diagrams with the same numbers. The letters S, P, St, G, DC, and VC indicate sepal, petal, stamen, gland, dorsal carpellary and ventral carpellary bundles respectively.

Plate X

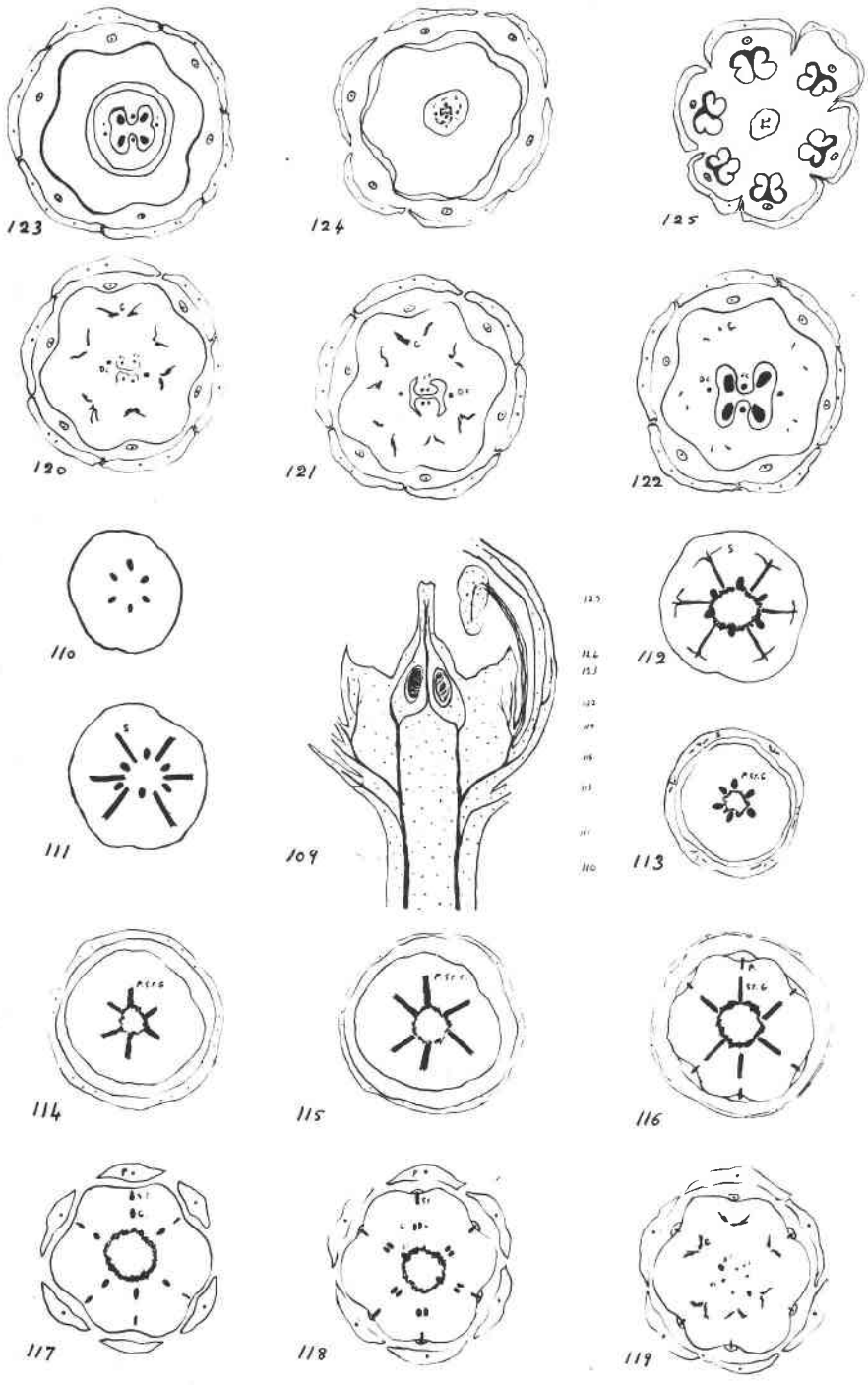
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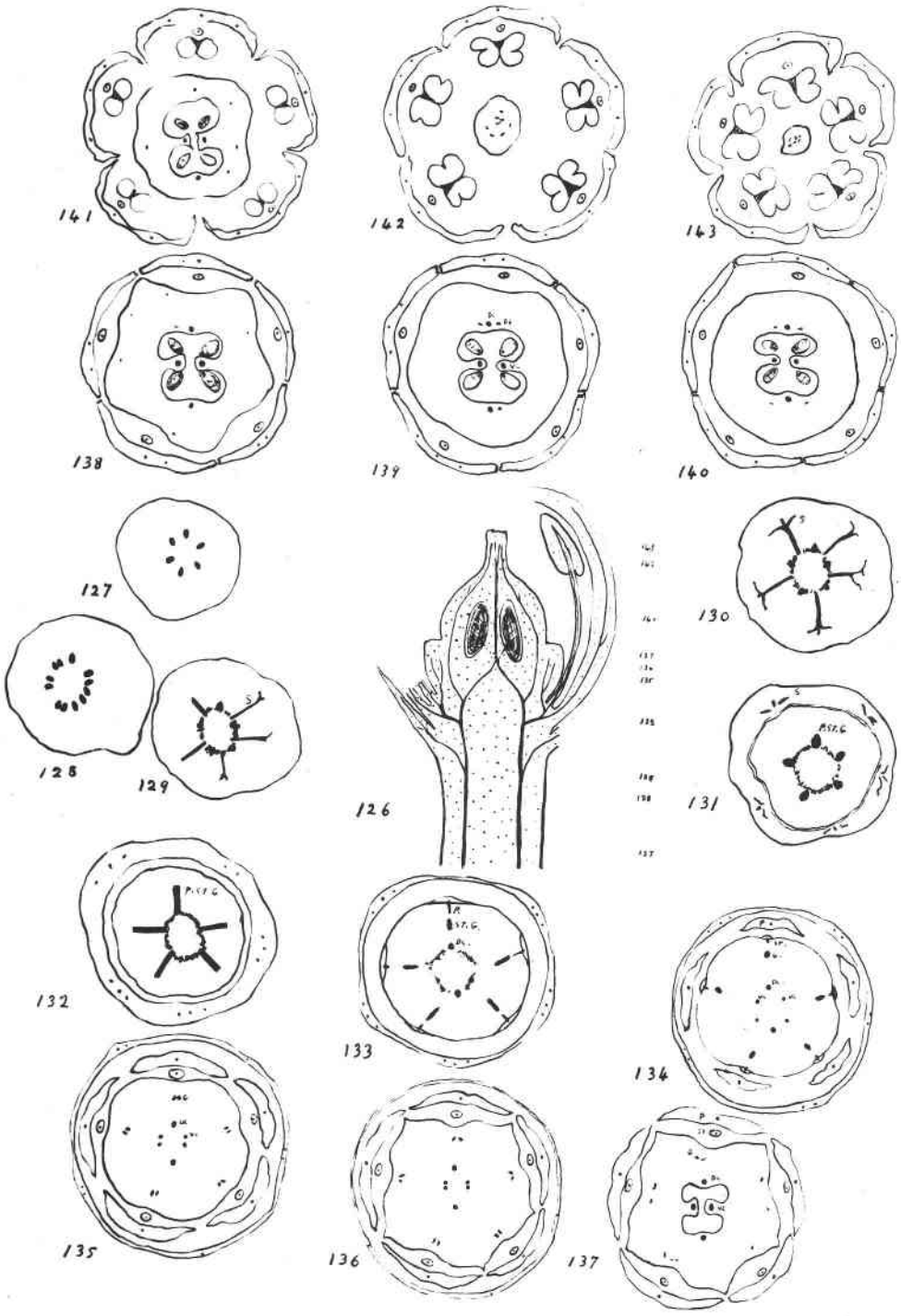
Plate XI

Diagrams showing the floral structure of *Parthenocissus quinquefolia* Planch. (*Ampelopsis quinquefolia* Mich.).

The numbers on the longitudinal-section diagram indicate the levels on the cross-section diagrams with the same numbers. The letters S, P, St, G, DC, and VC indicate sepal, petal, stamen, gland, dorsal carpellary and ventral carpellary bundles respectively.

Plate XI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