

# DEVELOPMENT AND ANATOMY of the Pistillate Flower of some Cucurbitaceous Species

by

LÊ - TUỆ - QUANG

## INTRODUCTION

The Cucurbitaceae is an important horticultural family and includes plants grown for edible fruits and for ornamental vines. For centuries certain species have been associated with civilizations. Species of **Cucurbita** are among the most ancient of cultivated plants in the Americas. The archeological evidence recorded by Erwin (1931) indicates the pre-columbian use of **Cucurbita pepo** and **Cucurbita moschata** in North America. **Cucurbita ficifolia** is known archeologically from coastal Peru at about 3000 B.C. (Cutler and Whitaker, 1961). The watermelon was a favorite for the ancient Egyptians. De Candolle (1882) mentioned that the cucumber has been cultivated in India for at least 3000 years. Remains of the gourd **Lagenaria**, used as utensils have been found in Egyptian tombs at about 2400 B.C. and in New World sites dated at least 3000 B.C. (Cutler and Whitaker, 1961).

In addition to their interest for students of archeology and agriculture, the Cucurbitaceae offer suitable materials to morphologists, physiologists and plant breeders. Many works have appeared dealing with their physiology and genetics. Relatively little has been done, however, on development and anatomy of their flowers. As a result,

the family is still a center of controversy in the fields of taxonomy and morphology.

Robert Brown, De Candolle and Naudin placed the Cucurbitaceae among the perigynous polypetalous families. This view was adopted by Bentham and Hooker (1861), who put the family in the order Passiflorales between the families Passifloraceae and Begoniaceae. Hutchinson (1926) placed it under the order Cucurbitales comprising the Cucurbitaceae, Begoniaceae, Datisceae and Caricaceae whereas Rendle (1959) was of the opinion that the Cucurbitaceae, Begoniaceae and Datisceae should constitute an order, the Peponiferae.

Engler, on the other hand, placed the Cucurbitaceae among the sympetalous groups. He treated it as an independent family under the order Cucurbitales next to the order Campanulales.

Another view maintained by Vuillemin (1923) is that the Cucurbitaceae and the Begoniaceae must be related to the apetalous families Balanophoraceae, Rafflesiaceae, Nepenthaceae and Aristolochiaceae.

Concerning the phylogenetic position of the Cucurbitaceae Whitaker (1962) wrote « Rarely do any two authorities agree as to where it should be placed with respect to other families and orders. Until much more is known about the floral anatomy, embryology, cytology and comparative morphology of this large and homogeneous family, it would appear unprofitable to speculate about its position in relation to other dicotyledonous families ».

The family consists of approximately 100 genera and 700 species almost equally divided between the New and Old World tropics. A few species have ranges extending into the temperate zones. The number of stamens, the degree of fusion in the androecium, the elaboration of the anther-thecae which may be straight, flexuous or variously twisted, and the orientation of the ovules, have served as bases for subdivisions of the family. Bentham and Hooker (1861) subdivided the Cucurbitaceae into eight tribes. Cogniaux (1881) also divided the family into eight tribes, but later reduced it to five (Cogniaux and Harms, 1924). According to Pax and Mueller (1889), the family is divisible into five tribes. Recently Jeffrey (1961) proposed a new classification of the family into two subfamilies, the Cucurbitoideae and the Zanonioideae. The former contains seven tribes and the latter, one tribe.

A review of the literature shows that detailed anatomical and ontogenetic studies of the cucurbitaceous flowers are relatively few. Consequently, certain morphological problems such as the nature of the inferior ovary and the type of placentation are not yet clearly understood.

Considering the inferior ovary in the Cucurbitaceae, Naudin (1855) expressed the view that the wall of the ovary is entirely receptacular.

Payer (1857), Kirwood (1905) and Judson (1929), on the basis of ontogenetic study of some cucurbitaceous flowers, also regarded the ovary wall as axial. Eames (1931), on the other hand, had demonstrated by anatomical evidence that the inferior ovary in almost all families results from the adnation of the outer floral whorls to the gynoeceum. In certain cases, however, vascular anatomy has given convincing proof that the ovary is partly immersed in receptacular tissue: the vascular strands go up along the ovary wall for some distance and after giving off traces to the peripheral organs they bend inward and downward to supply the carpels. Such recurving or recurrent traces have been reported in the Calycanthaceae (Smith, 1928), Santalaceae (Smith and Smith, 1942), Cactaceae (Sharma, 1949) and certain members of the Rosaceae (Jackson, 1934). The floral cup in these cases is believed to have been formed by a process of sinking or invagination of the floral axis. In view of the fact that the ovary wall of the Cucurbitaceae has been interpreted as receptacular without the benefit of evidence from floral anatomy, a study of the vascularization of the female flower to determine whether recurrent traces are present is critical.

Much confusion still exists with regard to the type of placentation in the Cucurbitaceae. Naudin (1855) stated that the placentation is apparently parietal, but actually it is an « exaggerated » axile placentation. Le Maout and Decaisne (1876) and Warming and Potter (1932) described it as spuriously trilocular. Hayward (1938) regarded it as axile whereas Lawrence (1951) considered it parietal. Rendle, (1959) without precisely stating the type of placentation, wrote, « the edges of the carpels meet in the center of the ovary and then curve outward across the middle of each chamber bifurcating near the circumference and bearing the ovules on the two incurving edges ». Puri (1954), having noted a great variation in the mode of ovular supply in some species, made this statement, « the placentation in the Cucurbitaceae is still in a fluid state and nothing is finally fixed as yet ». His work described ten species and thus can serve as an introduction and a basis for future study.

In this investigation both ontogeny and vascular anatomy of the female flowers were studied with the hope that more information on the subject would be forthcoming. Much work needs to be done before this family is better known in all its various morphological aspects. The present investigation was undertaken in an attempt to fill some of this gap.

## MATERIALS AND METHODS

Thirteen species representing eleven genera were studied. They are *Sioimatra amazonica* Cogn., *Melothria* sp., *Cucurbita maxima* Duch., *Cucurbita moschata* Duch., *Lagenaria leucantha* (Duch.) Rusby, *Sicana*

*odorifera* Naud., *Benincasa hispida* (Thumb.) Cogn., *Trichosanthes anguina* L., *Momordica charantia* L., *Luffa acutangula* (L.) Roxb., *Luffa cylindrica* (L.) M. Roem., *Sechium edule* Sw., *Cyclanthera pedata* Schrad. They were fresh materials except *Siolmatra amazonica* which was obtained from herbarium specimen.

Mature flowers were fixed in F.A.A., whereas buds of different stages for ontogenetic study were preserved in Crafi I (Sass, 1958). Since the buds and flowers are very pubescent, a suction pump was used to remove air bubbles; in this way rapid fixation and infiltration were secured. They were then examined and dissected under the binocular microscope to study their general pattern of development and their gross structure.

The materials were dehydrated in tertiary butyl alcohol, ethyl alcohol or normal butyl alcohol. Normal butyl alcohol proved to be the most satisfactory for young flowers. Transverse and longitudinal serial sections of buds of various stages of development were cut at 7-10 microns and stained with tannic acid, ferric chloride and safranin according to Foster's method (1934). Mature flowers were cut at 10-15 microns and stained in safranin and fast green. Free hand sections of fresh mature flowers and sections obtained by means of a hand microtome were cleared in a solution of sodium hypochlorite and stained with iodine green and carmin-alum according to the schedule given by Dop and Gautié (1928). Herbarium specimens were heated in water almost to boiling and transferred to a 3 % solution of NaOH. A second method consists of soaking the specimens in a solution of sodium lauryl sulphate. In either method, when the flowers swelled and rounded up, which took from two to several days, they were washed in water and then dehydrated and embedded as with fresh materials. Since the sections of herbarium specimens had a tendency to become detached from the slides during staining, they were coated in a 1 % solution of celloidin according to Johansen's method (1940). This treatment made the sections adhere firmly to the slides.

For determining the courses of vascular bundles from the pedicel to different floral whorls, flowers previously preserved in F.A.A. were washed in water for several hours and then transferred to lactic acid. The bottles containing these materials were tightly closed and kept in the oven at 63°C. After two to four days, depending on the size of the flowers, the clearing process was complete, with cellular tissue transparent and vascular bundles opaque. The cleared specimens were then dissected and studied under a binocular microscope.

Drawings were made in a dark room by the use of a microprojector. A camera lucida was used in certain cases.

### ONTOGENY

The flowers of the species studied are unisexual. Female flowers are epigynous. The pistil usually consists of three carpels. Four carpels

were found in some flowers of *Cucurbita maxima*. Staminodes are present in many species.

The ontogeny of the female flowers of *Cucurbita maxima*, *Trichosanthes*, *Momordica*, *Luffa cylindrica* and *Cyclanthera* was followed from early stages. Special attention was paid to the development of the carpels.

The primordium of the flower is found in the axil of a young leaf. It appears as a small protuberance whose cells are densely cytoplasmic and darkly stained. As a result of active cell divisions the flower primordium elongates and broadens. The floral apex soon loses its convexity and becomes concave. Subsequent growth results in the formation of a ring of tissue surrounding the central apical depression. From five equidistant points on this ring, five protuberances arise which are the sepal primordia. The primordia of the petals appear shortly after those of the sepals. They form a whorl within the sepals and alternate with them. Meristematic activity in the sepals and petals as well as growth at their common bases cause their upward extension and increase the depth of the central cavity within which the staminodia and carpels develop.

The staminodia soon arise on the flank of the central cavity below the petals. In *Trichosanthes* and *Momordica* three staminodia are found, two are large and the third one is smaller. In *Cucurbita maxima* the two large staminodia are so bilobed that the primordia appear to be five in number. In *Luffa cylindrica* there are five primordia. Growth stops very soon in the staminodia.

The carpels are the last organs to appear. Usually there are three carpels in the species studied. Occasionally four carpel primordia are found in *Cucurbita maxima*. A cross section of the floral bud at the stage of initiation of the carpels shows three lobes (plate 1,A ; plate 2,A) which grow toward the center of the ovary. As they come into contact a triradiate cavity is formed (plate 1,B ; plate 2,B). Meristematic activity in the wall of the ovary and in the lobes especially at their margins causes the expansion of the triradiate cavity so that in a transverse section of older buds the ovary appears to be divided into three parts by a triradiate fissure with T-shaped extremities (Plate 1,B ; Plate 2,B). The ovules arise on the edges of the placental lobes (Plate 1,D ; Plate 2,C). In *Cucurbita maxima* three or four rows of ovules develop on each placental edge. In *Trichosanthes* and *Momordica* there is only one row of ovules on each placental edge. The carpels grow up to form the style and stigma.

It was found that in the young buds of *Cucurbita*, *Momordica* and *Trichosanthes* the triradiate fissure exists throughout the entire ovary ; however in older buds and in mature flowers fusion has taken place resulting in a solid central core which isolates the three locules (figs.

1, D, E; figs. 2, C, D). In *Cucurbita*, and *Trichosanthes* the solid central core exists only in the basal region of the ovary; in *Momordica* the core extends further up.

Serial transverse sections of young female buds of *Luffa cylindrica* show three arc-shaped cavities separated by a solid central core (fig. 4, D). Each cavity contains one placental lobe on the edges of which the ovules will develop. In the uppermost part of the ovary three fissures originating from the middle of the arc-shaped cavities gradually converge toward the center (fig. 4 E). As they meet each other in the center, a triradiate fissure with T-shaped extremities is formed (fig. 4 F). Higher up the tangential T-shaped cavities gradually disappear, only the triradiate central fissure persists (fig. 4 G).

In *Cyclanthera* at the stage of initiation of the carpel only one lobe projects into the central cavity of the flower (fig. 4 A). As growth takes place this lobe elongates and differentiates into a basal narrow part and an expanded upper part (fig. 4 B). The ovules arise on the reflexed margins of the placental lobe (fig. 4 C).

#### VASCULAR ANATOMY

*Cucurbita maxima*, *Cucurbita moschata*, *Lagenaria leucantha*, *Benincasa hispida* and *Sicana odorifera* are described together since their vascular anatomy differs only in minor details. The pedicel of the flower is five-angled in *Cucurbita maxima*, *C. moschata* and *Lagenaria* and more or less circular in *Benincasa* and *Sicana*. It contains 15-20 bicollateral bundles arranged in two rings in the former group and in one ring in *Benincasa*. In *Sicana* the bundles are disposed at different distances from the epidermis. In *Lagenaria* the internal phloem may invade the pith. Patches of collenchyma under the epidermis constitute the strengthening system of the pedicel. Each vascular bundle is capped by an arc of perivascular fiber (fig. 1A). The collenchyma and perivascular fiber disappear at the top of the pedicel. Concomitantly the bundles divide and give off branches which invade the pith, anastomosing and forming a vascular network (or vascular plate) at the base of the flower (figs. 1, B, C). The main bundles move out to the periphery and extend upward to supply the floral envelopes. During their course they branch repeatedly so that in a cross section of the ovary there are about twenty large bundles and numerous small ones at the periphery. At the narrow neck of the flower these bundles give off branches which enter the style and finer strands which go to the nectary tissue.

The carpels are supplied by two vascular sources. The first consists of numerous strands, « the median cylinder », lying in the dorsal region of the carpels. These strands originate from the vascular plate or from the peripheral bundles. The second source of carpellary supply, the central bundles, extends through the central region of the ovary,

and is also made up of branches from the vascular plate. In *Lagenaria*, *Sicana*, *Benincasa* and *Cucurbita moschata* vascular strands from the vascular plate go up to the center of the ovary without diverging, whereas in *Cucurbita maxima* many branches from the vascular plate after ascending the wall of the ovary for some distance, bend inward and downward, then follow an almost horizontal course at the base of the carpels, on reaching the center of the ovary they extend upward (fig. 3K). Some of these branches supply the lowermost ovules.

In all species, when the three locules begin to appear, vascular strands from the vascular plate are joined by branches from the median cylinder. These strands from the two sources form a triradiate plate with a prominent bundle or vascular plexus in the center (fig. 1 D). The vascular plexus soon splits into three inverted bundles which lie in the angles of the triradiate central cavity (figs. 1, E, F). The three ventral bundles go up to the style and ramify in the stigma. During their course they send branches right and left to the ovules (fig. 1 F). The ovules are also supplied with vascular strands from the median cylinder: the strands from the median cylinder diverge almost horizontally inward the septum and after traversing the septum they curve to follow the contour of the placental lobes to reach the ovules (fig. 1F). Thus ovular supply is derived from both the median cylinder and the ventral bundles. The ovules are numerous. In the upper part of the ovary the tangential parts of the T-shaped cavities gradually disappear. In the style only a triradiate fissure persists (fig. 1G).

### ***Trichosanthes anguina.***

At the base of the pedicel there are ten vascular bundles surrounded by a ring of perivascular fiber (fig. 1I). Beneath the epidermis is a two- or three-celled layer of collenchyma. Higher up, the number of bundles increases to about twenty larger and numerous smaller ones. From these bundles branches invade the pith (fig. 1J), but no vascular plate is formed at the distal part of the pedicel. The main peripheral bundles are sepal, petal and dorsal carpellary bundles. At the base of the ovary at least six bundles become prominent in the center of the section (fig. 1K). These six bundles merge with each other and then divide into three inverted ventral bundles. Each ventral bundle is clearly bilobed (fig. 1L). Ovular supply is derived chiefly from the ventral bundles. Occasionally vascular strands from the dorsal carpellary region contribute to the ovular supply. The ovules are relatively few. In the style the ventral bundles are joined by the dorsal carpellary bundles. All these bundles form a nearly closed ring around the triradiate cavity (fig. 1M). Placentation is more or less similar to that of the previous species: a solid central core separates the three locules at the base of the ovary; higher up three fissures originating from the tangential cavities converge toward the center of the ovary until they reach each other. As a result a triradiate central cavity is formed (fig. 1L).

### **Momordica charantia**

A cross section of the pedicel shows eight bundles surrounded by a ring of sclerenchyma (fig. 2A). Beneath the epidermis are patches of collenchyma. As the pedicel increases in size, the bundles give off branches which are scattered over the section (fig. 2B). When the three locules appear, vascular strands from the peripheral region enter the placentae to form six small bundles (fig. 2C). These bundles supply the lowermost ovules. The central core of the ovary is supplied by one bundle (fig. 2D) which divides later into three inverted bundles. As usual, the ventral bundles stand in the angles of the triradiate cavity. The ovules in the upper region of the ovary receive their supply from both the ventral bundles and branches from the peripheral region. In the style the dorsal carpellary bundles, which are given off by the petal bundles at the narrow neck of the flower form three arc-shaped strands (fig. 2F); meanwhile each ventral bundle divides tangentially into two (fig. 2F). All these bundles end blindly in the six stigma lobes. Each sepal and petal receives one bundle which constitutes the midvein.

### **Luffa acutangula.**

The pedicel contains ten bundles (fig. 2G) which later increase to about twenty. Ten of them migrate out, each standing in the ribs of the flower; they are the traces for the sepals and petals. The bundles left behind divide, anastomose and form a vascular plate (fig. 2H). Higher up, most of the branches from the vascular plate move out to form the median cylinder in the dorsal carpellary region (figs. 2, I, J). One big bundle remains in the center (figs. 2 I, J). This central bundle contributes little to ovular supply which derives mostly from the median cylinder (fig. 2J). Throughout the entire fertile region there is a solid central core separating the three locules (fig. 2J). Only in the uppermost part does the ovary become unilocular, the closed carpels gradually opening up (fig. 2K). Concomitantly the central bundle divides into three inverted bundles (fig. 2K) which go up to the style (fig. 2L). Fig. 2M represents a longitudinal section of the flower.

### **Melothria.**

Melothria is interesting in the vascular supply to the carpels. The carpel traces arise from the peripheral bundles at a level much higher than that of the origin of the carpels. The carpel traces, on leaving the peripheral bundles, bend inward and descend the ovary wall (fig. 3A). At the base of the carpels they turn upward to enter the central region of the ovary (fig. 3A). Both cleared specimens and serial transverse sections of the flowers permit one to determine the origin of the carpel traces. In the pedicel there are 4-5 bundles surrounded by a ring of sclerenchyma (fig. 3B). The distal part of the pedicel is constricted.



A little above this constriction the bundles branch, anastomose (fig. 3C) and give rise to 9-10 bundles (fig. 3D). When 9 bundles are present, one bundle later divides into two. The ten bundles constitute the midveins of the calyx and corolla lobes. At the base of the carpels vascular strands suddenly appear in the pith (fig. 3D). In examining the serial transverse sections of the flower it was found that these strands are connected with the peripheral bundles at a higher level. They are the carpel traces. Usually there are three carpel traces. As has been stated earlier these carpel traces on leaving the peripheral bundles bend inward and downward. At the base of the carpels they turn upward (fig. 3A) and before entering the carpels they fuse into one bundle (fig. 3A) so that in a cross section at the base of the ovary one can find a big central bundle surrounded by three small bundles (fig. 3E). The central bundle soon splits into three inverted ventral bundles, each standing at the angle of the triradiate cavity (fig. 3F). Ovular supply is derived mostly from the ventral bundles.

#### ***Siolmatra amazonica.***

The pedicel of the flower contains eight bundles which later increase to ten; five bundles supply the petals and the alternating five supply the sepals. This species is interesting as there is little internal phloem. At the base of the flower three bundles divide tangentially to give rise to three inverted bundles (fig. 3G). These bundles move to the septa separating the three empty locules. There are only two ovules per locule borne in the upper part of the ovary (fig. 3H). Above the ovule-bearing region, three fissures gradually converge toward the center (fig. 3I) and separate the three septa from each other. A central triradiate cavity is formed in the stylar region (fig. 3J).

#### ***Sechium edule.***

The five to six bundles increase in number by branching at successively higher levels in the pedicel. At the distal part of the pedicel there are ten bundles arranged in two rings, the outer ring with five bundles, the inner one with five alternating bundles (fig. 5B). These bundles give rise to numerous branches which are scattered at the peripheral region (fig. 5C). At the base of the ovary phloem strands invade the pith which is composed of smaller cells than those of the peripheral region (fig. 5D). Higher up xylem elements appear next to the phloem strands to form tiny bundles.

When the central ovular cavity appears, these tiny bundles arrange themselves in the ring of small cells surrounding the ovular cavity (fig. 5E). A cross section through the middle of the ovary shows then numerous small vascular branches at the peripheral region, ten to eleven main bundles surrounding the ring of

small cells which in turn surround the central ovular cavity with a single ovule (fig. 5 E).

At the top of the ovary two main bundles send branches down to the pendulous ovule (figs. 5, F, G). The two bundles from which the ovular traces arise and two other opposite main bundles move inward. They are destined to go up to the style. These four bundles stand more or less equidistant from the central core of small cells, the central ovular cavity having been disappeared at the top of the ovary.

Higher up two other bundles move inward so that in the peripheral region there remains five bundles (fig. 5 H), each of which stands in the angle of the five-angled narrow neck of the flower (fig. 5 I). The bundles in the center go up to the style. During their course they arrange themselves in two arcs (fig. 5 I).

On approaching the base of the floral tube the five peripheral bundles branch, anastomose and form a siphonostele (fig. 5 J) from which five bundles go to the sepals, five alternating bundles go to the petals and numerous small branches go to the ten masses of nectarial tissue situated at the base of the petals (fig. 5 K). Each sepal and petal receives one bundle, the sepal laterals are formed by branching of the sepal bundle, the petal laterals are also formed by branching of the sepal bundles.

## DISCUSSION

### Epigyny

The problem of the nature of the inferior ovary has been debated for a long time. The literature dealing with the subject has been reviewed and discussed by Douglas (1944, 1957) and Puri (1952).

In the present investigation the vascular supply to the floral envelopes and gynoecium supports the appendicular nature of the ovary wall in most species. In the species studied each sepal receives one trace. Miller (1929) also reported the one-traced sepal in the cucurbitaceous species *Echinocystis lobata*. Among the dicotyledons, sepal having one trace instead of the usual three traces has been recorded in some cases, e.g. *Menispermum*, *Colpoon*, *Olea*, *Lycopersicum* and *Primula* (Puri, 1951). The lack of lateral veins is believed to be correlated with poor development of the mesophyll tissue.

Usually there are lateral veins in the sepals of the species investigated except *Cucurbita maxima*, *Melothria* which have narrow calyx lobes. The lateral veins of the sepals result from branching of the sepal or petal bundle. The petals are supplied by one midvein and several lateral veins. The midvein and two main lateral veins are most prominent.

The vascular supply to the calyx and corolla may be divided into two categories. In the first category which includes *Luffa* and *Momordica*, the two sepal laterals are formed by branching of the main sepal bundle at the top of the ovary. Each sepal lateral may dichotomize in the sepal lobe. The two main laterals of each petal lobe originate from the laterals of two adjacent sepal bundles (fig. 4 H). The fact that the petal laterals are adnate to the sepal bundle indicates a fusion of the calyx and corolla.

In the second category, represented by *Cucurbita moschata*, *Benincasa*, *Sicana* and *Lagenaria*, the two lateral veins of each calyx lobe originate from two adjacent petal bundles. Each corolla lobe is supplied by three bundles which come from the base of the flower (fig. 4 I). In addition they may receive vascular strands from the sepal bundles.

The wall of the ovary in all species is supplied by vascular strands from sepal and petal bundles and at the narrow neck of the flower sepal and petal bundles may give off branches which enter the style.

Thus the splitting of the sepal and petal bundles at the top of the ovary is an evidence of their composite nature and indicates that the ovary wall which they traverse is made up of appendicular tissue formed by adnation of the calyx and corolla to the gynoecium.

In *Cucurbita maxima* and *Melothria* however, the ovary wall in the basal part of the flower may be regarded as receptacular. As has been described for *Cucurbita maxima*, the ventral carpellary traces, after ascending the wall of the ovary for some distance, bend inward and downward to enter the central region of the ovary (fig. 3 K). In *Melothria* the ventral carpellary traces also have a downward course (fig. 3 A). The presence of such recurving bundles may be regarded as an evidence of the receptacular nature of the ovary wall up to their bending point.

### Placentation.

The placentation in the Cucurbitaceae has been described either as axile or parietal. On the basis that the placentae in the cucurbitaceous species he investigated were borne on the fused margins of adjacent carpels and that the ventral bundles lay on septal radii, Puri (1954) concluded that the placentation in the cucurbitaceae is parietal. According to Puri the apparent multilocular condition is due to « secondary fusion of adjacent placental ridges », and the inverse orientation of the ventral bundles is « a relict of past history ».

Eames (1951), referring to the problem of placentation in angiosperms, stated that lines between types of placentation do not exist; axile merges into parietal and into free central. Whether placentation

in a syncarpous ovary is parietal or axile depends upon the degree of infolding of the margins of the individual carpels and the degree of fusion of all the carpels to one another. When fusion of closed carpels to one another is complete, an axis-like central core is formed. If, near the top of the ovary, the margins of the carpels do not meet in the center and the margins of each carpel fuse only with those of contiguous carpels, placentation is parietal. The upper part of the ovary then exhibits parietal placentation while the lower part exhibits axile placentation. This condition is present in many families such as the Tiliaceae, Sarraceniaceae, Capparidaceae, Liliaceae and many other plants (Gundersen, 1939).

The same condition is found in many cucurbitaceous species investigated in this present study. In **Cucurbita**, **Lagenaria**, **Sicana**, **Benincasa** and **Trichosanthes**, in the basal region of the ovary, a solid central core provided with a vascular plexus (in **Trichosanthes** the central core is usually provided with 6 bundles) separates the three locules from each other (fig. 1 D). At higher levels, the closed carpels gradually open up (fig. 1 E). A cross section of the ovary shows, therefore, a triradiate cavity with T-shaped extremities (fig. 1 F). Concomitantly the central plexus splits into three inverted ventral bundles which lie in the angles of the triradiate cavity (fig. 1 F). Above the ovule-bearing region the tangential cavities gradually obliterate. Thus in the style only the triradiate styler canal persists (fig. 1 G). In **Momordica** the central core extends upward through about half of the ovary. In **Luffa** and **Siolmatra**, the solid central core extends almost to the base of the style. In **Luffa** the central core is provided with one bundle (fig. 2 J), whereas in **Siolmatra** there are three inverted bundles which stand in the septal region (fig. 3 H). Only at the base of the style do the margins of each carpel gradually become separate from each other (figs. 2 K, 3 I). As a result a triradiate open center is formed (figs. 2 L, 3 J). Thus it appears that the placentation is axile in **Luffa** and **Siolmatra**. In other species studied in the present investigation the basal region exhibits axile placentation while the upper part exhibits parietal placentation.

Ovular supply may be divided into three types. In the first type, represented by **Cucurbita**, **Lagenaria**, **Sicana**, **Benincasa**, **Trichosanthes**, it is derived both from the ventral bundles and vascular strands from the dorsal carpellary region. In the second type, represented by **Melothria**, the ventral bundles alone are the source of ovular supply. In the third type, represented by **Luffa**, the ovules receive their supply mostly from the dorsal carpellary strands.

The question which now arises is whether parietal placentation is derived from axile or vice versa. Puri (1952) wrote, « It is not so easy to decide whether axile or parietal placentation is more primitive ».

Some students considered that parietal placentation is derived from axile by withdrawal of the placentae from their original central

position ; this is achieved by a phylogenetic reopening of the previously closed carpels and retraction of their margins (Eames 1961, p. 235). The presence of inverted ventral bundles in certain families with parietal placentation, such as the Cruciferae, Capparidaceae, Papavera-ceae, Passifloraceae and the Moringaceae serves as evidence for Puri's view that in the ancestors of these families, the ovary exhibited axile placentation (Puri, 1952). Arber (1938), on the other hand, did not attach any importance to the inverted condition of the placental strands. Although Puri strongly favored the view that axile placentation preceded parietal, he admitted that there may exist an evolutionary trend from parietal to axile placentation which is yet to be proven (Puri, 1952, p. 626, fig 14).

Other students believed that parietal placentation is antecedent to axile placentation (Gundersen, 1939). In the Gentianaceae (Lindsey, 1940), Theaceae (Keng, 1962) and certain species of the Begoniaceae (Gauthier 1950, 1959) the upper region of the ovary has an open center whereas in the basal region a solid central core separates the locules. It was believed that fusion of the margins of the same carpel proceeds gradually upward resulting in axile placentation in the lower part whereas in the upper part, where the closure of the carpels is incomplete, the ovary retains its parietal placentation. Axile placentation in these cases were considered to be more advanced than parietal.

In the present investigation the results from ontogeny and comparative study are taken into account in an effort to decide between the two opposing views. As has been described in the young female buds of *Cucurbita*, *Momordica* and *Trichosanthes*, a cross section of the ovary shows three lobes with active meristematic activity (Plate 1A ; Plate 2A). These placental lobes expand laterally and grow toward the center. As they come into contact, a triradiate fissure with T-shaped extremities is formed (Plate 1B ; Plate 2B). The ovules are developed on the edges of the placental lobes (Plate 1D ; Plate 2C). Each placental lobe is the product of congenital fusion of the margins of two adjacent carpels, a criterion of parietal placentation. Evidence for such a fusion is seen in plate 3, figures A-D. These figures represent transverse sections of a bud of *Cucurbita maxima* from the base of the ovary upward.

It was found that in the young buds of *Cucurbita*, *Momordica* and *Trichosanthes* an open center exists throughout the entire ovary ; however in older buds and in mature flowers, the margins of each carpel have fused in the basal region of the ovary resulting in a solid central core which isolates the locules. Thus in the young bud the ovary is unilocular with parietal placentation, and in mature flowers it is multilocular with axile placentation in the lower part, whereas in the upper part fusion of margins of each carpel does not take place, the ovary retains its parietal placentation. If this represents a case in which ontogeny repeats phylogeny, then we must consider that

axile placentation, which involves fusion of margins of adjacent carpels as well as fusion of margins of the same carpel, is more advanced than parietal placentation.

Comparative study of some species of the Cucurbitaceae also supports the view that in the Cucurbitaceae axile placentation is more advanced than parietal placentation. In *Cucurbita*, *Sicana* and *Benincasa* only the basal region has axile placentation, most part of the ovary has parietal placentation. This condition is associated with the primitive many-seeded character. *Momordica*, in which axile placentation extends further up, has fewer seeds. In *Luffa* the entire fertile region exhibits axile placentation and the seeds are relatively few. In *Siolmatra* axile placentation extends to the base of the style and the seeds are very reduced in number.

In conclusion the results from ontogeny and comparative study suggest the fact that the primitive type of flower in the Cucurbitaceae is one with parietal placentation although parietal placentation may be advanced in other families.

### SUMMARY AND CONCLUSIONS

The ontogeny and vascular anatomy of the pistillate flowers of some cucurbitaceous species were studied in an attempt to determine the morphological nature of the inferior ovary and the type of placentation.

Vascular anatomy supports the appendicular nature of the ovary wall. The observations that the petal laterals arise from the sepal bundles and in many species the sepal laterals arise from the petal bundles at the top of the ovary indicate the composite nature of the sepal and petal bundles and hence of the tissue they traverse : it is made up of fused calyx and corolla bases. The wall of the ovary is supplied by vascular strands from sepal and petal bundles which at the narrow neck of the flower send branches to the style. Thus the dorsal carpellary bundles are adnate to the sepal and petal bundles. These vascular patterns are evidence of the fusion of the outer floral whorls to the gynoecium. In *Cucurbita maxima* and *Melothria* however, the outer wall of the basal region of the ovary may be regarded as receptacular, the ventral carpellary traces having a downward course in *Melothria* and in *Cucurbita maxima* many strands from the vascular plate ascend the wall of the ovary for a short distance and then they too bend downward to enter the center of the ovary.

Placentation is prevailingly parietal ; however, a solid central core separates the locules in the basal part of the ovary in most species. Ontogeny reveals that in the young buds the ovary is unilocular throughout from bottom to top but in later stages fusion between margins

of the same carpel has taken place so that a solid central core is formed at the base of the ovary. If ontogeny here recapitulates phylogeny, then parietal placentation in the Cucurbitaceae antedates axile placentation in the course of evolution. Comparative study also supports this view. In **Cucurbita**, **Lagenaria**, **Sicana** and **Benincasa** the central core exists only in the basal region of the ovary. The seeds are numerous in these species. In **Momordica** half of the ovary has axile placentation and the ovules are few. In **Luffa** the entire fertile region has axile placentation and the number of ovules is relatively reduced. In **Siolmatra** axile placentation extends to the base of the style; this character is accompanied by sterilization of most part of the ovary; the ovules are found only in the upper part of the ovary.

---

### LITERATURE CITED

- ARBER, A. 1938. Studies in flower structure. IV. On the gynaecium of **Papaver** and related genera. *Ann. Bot. (N.S.)*, 2 : 649-663.
- BENTHAM, G. and J.D. HOOKER. 1861. *Genera Plantarum*. I : 818-841. London.
- CANDOLLE, A. De. 1882. *Origine des plantes cultivées*. Germe Baillièrre, Paris.
- COGNIAUX, A. 1881. Cucurbitaceae. In *De Candolle's Monographia Phanerogamarum* 3 : 325-951.
- COGNIAUX, A. and H. HARMS. 1924. Cucurbitaceae. In *Engler, Das Pflanzenreich*, 88 (IV 275 II) : 1-246.
- CUTLER, H.C. and T.W. WHITAKER. 1961. History of the cultivated cucurbits in the Americas. *American Antiquity*, 26 : 469-485.
- DOP, P. and A. GAUTIE. 1928. *Manuel de technique botanique*. 2nd. Ed.
- DOUGLAS, G.E. 1944. The inferior ovary. *Bot. Rev.*, 10 : 125-186.
- DOUGLAS, G.E. 1957. The inferior ovary. *Bot. Rev.*, 23 : 1-46.
- EAMES, A.J. 1931. The vascular anatomy of the flower with refutation of the theory of carpel polymorphism. *Amer. Jour. Bot.*, 18 : 147-188.
- EAMES, A.J. 1951. Again : « The New Morphology ». *New Phyt.*, 50 : 17-35.
- EAMES, A.J. 1961. *Morphology of the Angiosperms*. Mc Graw Hill Book Co., N.Y. 650 pp.
- ERWIN, A.T. 1931. Nativity of the Cucurbitas. *Bot. Gaz.*, 91 : 105-108.

- FOSTER, A.S. 1934. The use of tannic acid and iron chloride for staining cell walls in meristematic tissue. *Stain Tech.*, 9 : 91-92.
- GAUTHIER, R. 1950. The nature of the inferior ovary in the genus *Begonia*. Univ. Montreal. *Inst. Bot. Contr.*, 66 : 1-93.
- GAUTHIER, R. 1959. L'anatomie vasculaire et l'interprétation de la fleur pistillée de l'*Hillebrandia sandwicensis* Oliv. *Phytomorphology*, 9 : 72-87.
- GUNDERSEN, A. 1939. Flower buds and phylogeny of the dicotyledons. *Bull. Torrey Bot. Club.*, 66 : 287-295.
- HAYWARD, H.E. 1938. *The structure of Economic Plants*. Mac Millan, N.Y.
- HUTCHINSON, J. 1926. *The families of Flowering Plants*. Vol. I, Dicotyledons.
- JACKSON, G. 1934. The morphology of the flower of *Rosa* and certain closely related genera. *Amer. Jour. Bot.*, 21 : 453-466.
- JEFFREY, C. 1961. Notes on Cucurbitaceae including a proposed new classification of the family. *Kew Bull.*, 15 : 337-371.
- JOHANSEN, D.A. 1940. *Plant Microtechnique*. McGraw Hill Book Co., N.Y.
- JUDSON, J.E. 1929. The morphology and vascular anatomy of the pistillate flower of Cucumber. *Amer. Jour. Bot.* 16 : 59-86.
- KIRKWOOD, J.C. 1905. The comparative embryology of the Cucurbitaceae. *Bull. N.Y. Bot. Gard.*, 3 : 313-402.
- KENG, H. 1962. Comparative morphological studies in Theaceae. *Univ. Calif. Pub. Bot.*, 33 : 269-383.
- LAWRENCE, G.H.M. 1951. *Taxonomy of vascular Plants*. The MacMillan Co., N.Y. 823 pp.
- LINDSEY, A.A. 1940. Floral anatomy in the Gentianaceae. *Amer. Jour. Bot.*, 27 : 640-652.
- LE MAOUT, E. and J. DECAISNE. 1876. *A general system of Botany, descriptive and analytical*. Engl. Trans. London.
- NAUDIN, C. 1855. Observations relatives à la nature des vrilles et à la structure de la fleur chez les Cucurbitacées. *Ann. Sci. Nat. IV. Bot.*, 4 : 5-19.
- PAX, F. and E.G.O. MUELLER. 1889. Cucurbitaceae. In Engler and Prantl «Die natürlichen Pflanzenfamilien» IV (5) : 1-39.
- PAYER, J.B. 1857. *Traité d'Organogénie comparée de la fleur*.
- PURI, V. 1951. The role of floral anatomy in the solution of morphological problems. *Bot. Rev.*, 17 : 471-553.
- PURI, V. 1952a. Floral anatomy and the inferior ovary. *Phytomorphology*, 2: 122-129.
- PURI, V. 1952b. Placentation in Angiosperms. *Bot. Rev.*, 18 : 603-651.



- PURI, V. 1954. Placentation in certain species of the Cucurbitaceae. *Phytomorphology* 4 : 278-299.
- RENDLE, A.B. 1959. The classification of Flowering Plants. Vol. II.
- SASS, J. E. 1958. Botanical microtechnique. 3rd Ed.
- SHARMA, D.N. 1949. Vascular anatomy of the flower of some species of the Cactaceae. Unpub. thesis, Agra Univ.
- SMITH G.H. 1928. Vascular anatomy of Ranalian flowers. II. *Bot. Gaz.*, 85 : 152-177.
- SMITH F.H. and E.C. SMITH. 1942. Anatomy of the inferior ovary of *Darbya*. *Amer. Jour. Bot.*, 29 : 464-471.
- VUILLEMIN, P. 1923. Recherches sur les Cucurbitacées. *Ann. Sci. Nat. X. Bot.*, 5 : 5-19.
- WARMING, M.E. and M.C. POTTER. 1932. A Hand-Book of Systematic Botany. 2nd. Ed.
- WHITAKER, T.W. and G.N. DAVIS. 1962. Cucurbits. Interscience Publishers, N.Y.

## Plate 1

- A.-D. Successive stages of the development of the placental lobes in *Momordica Charantia*.
- A. Transection of a very young bud showing the three placental lobes.
  - B. Later stage showing the formation of the triradiate cavity with T-shaped extremities.
  - C. Still later stage showing the closely appressed epidermal layers of the carpels.
  - D. Initiation of the ovules on the reflexed edges of the placental lobes.

# PLATE 1

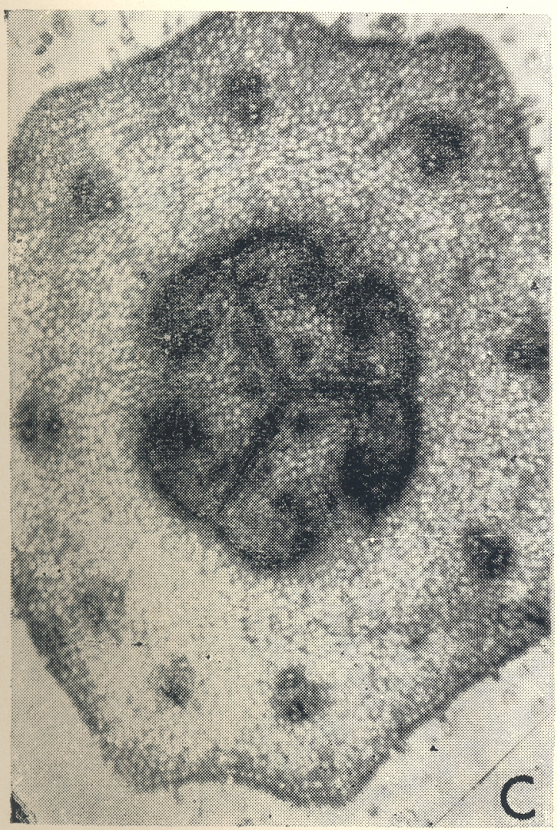
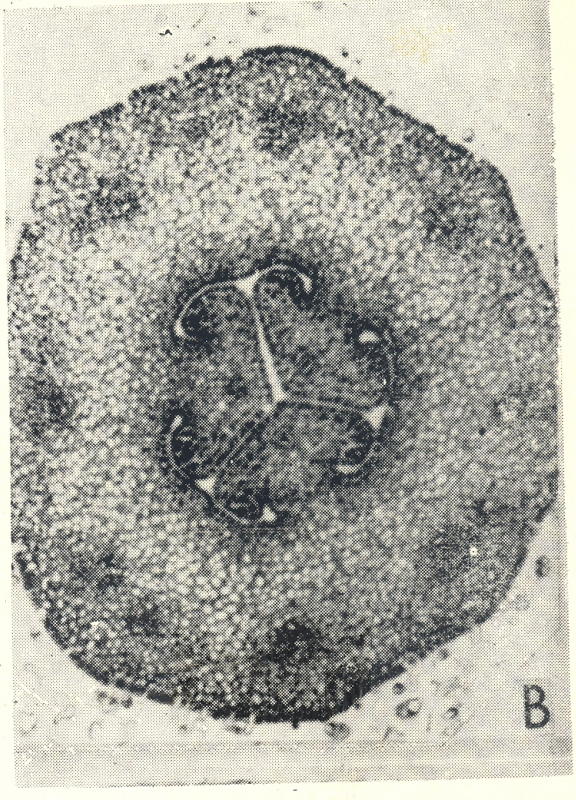
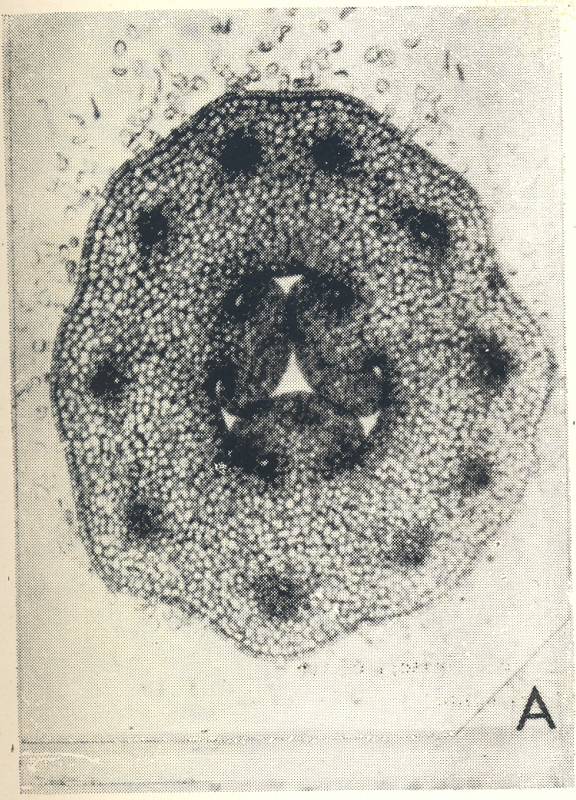
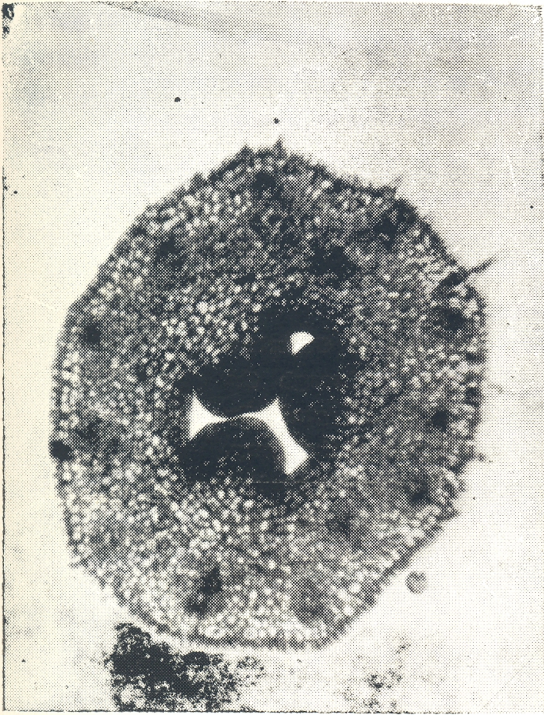


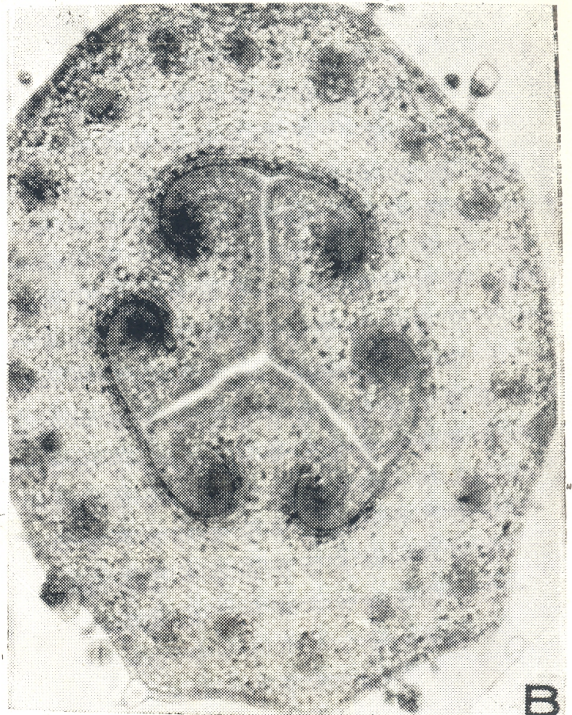
Plate 2

**A-C. Successive stages of the development of the placental lobes in *Trichosanthes*.**

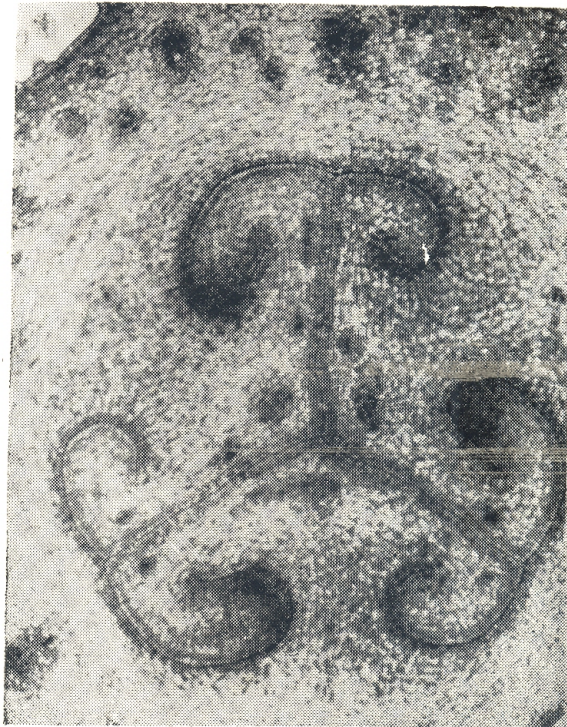
# PLATE 2



A



B

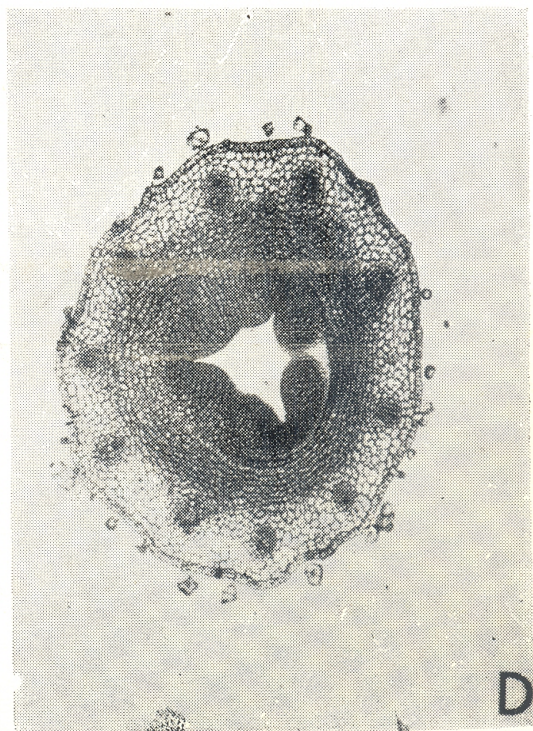
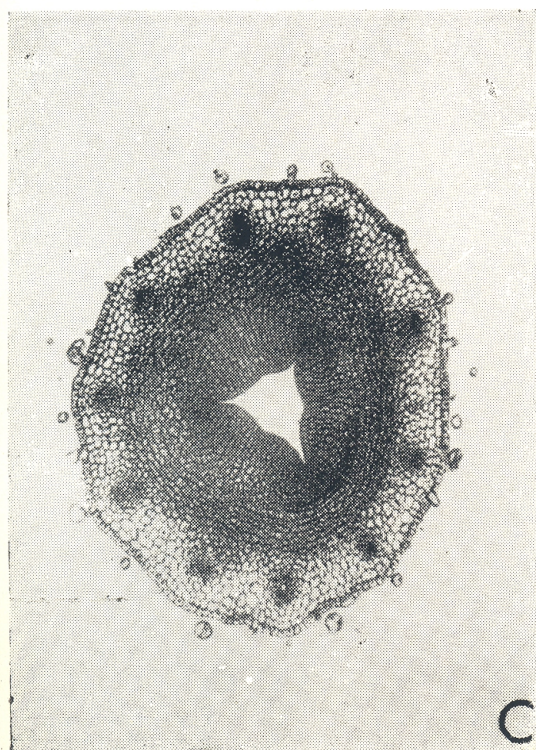
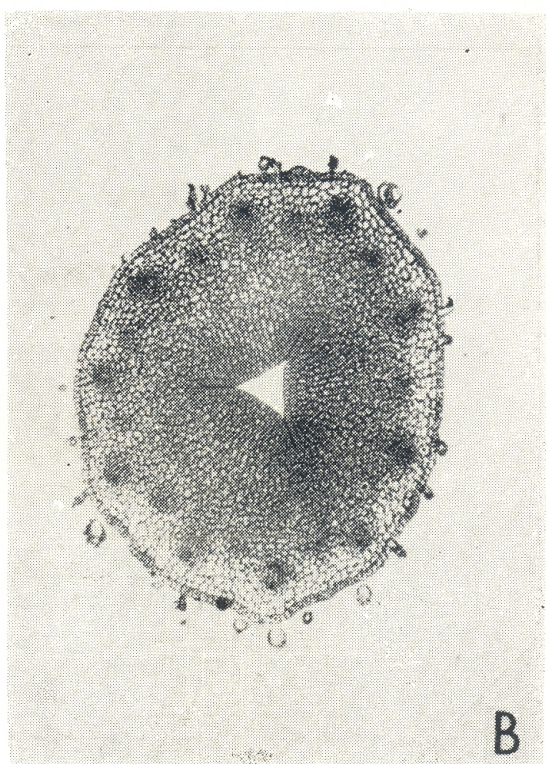
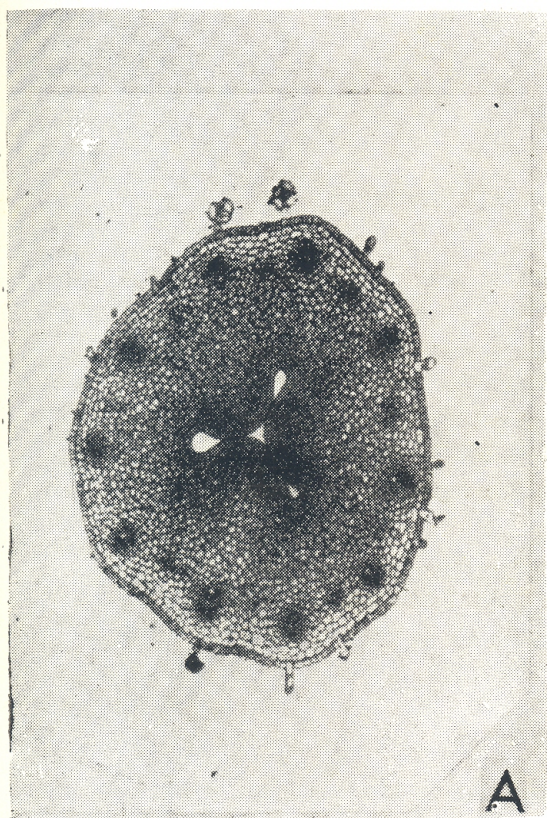


C

## Plate 3

A.-D. Transections of a young female bud of *Cucurbita maxima* at successively higher levels through the ovarian region. The placental lobes are gradually flattened and bilobed in the upper part of the ovary. Fig. D shows that each placental lobe is the product of fusion of the margins of two adjacent carpels. Note the horseshoe-shape of the carpels.

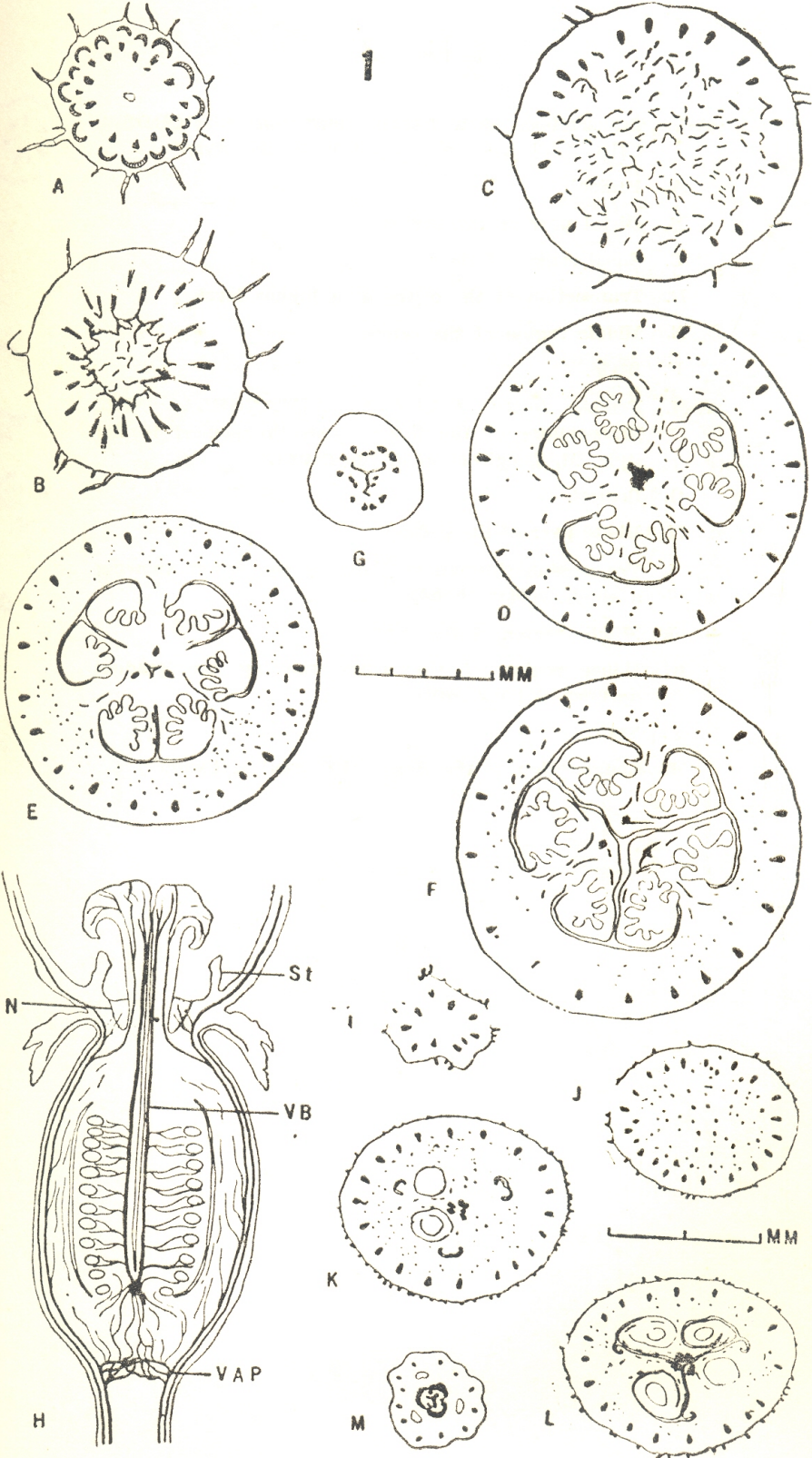
# PLATE 3



## Fig. 1

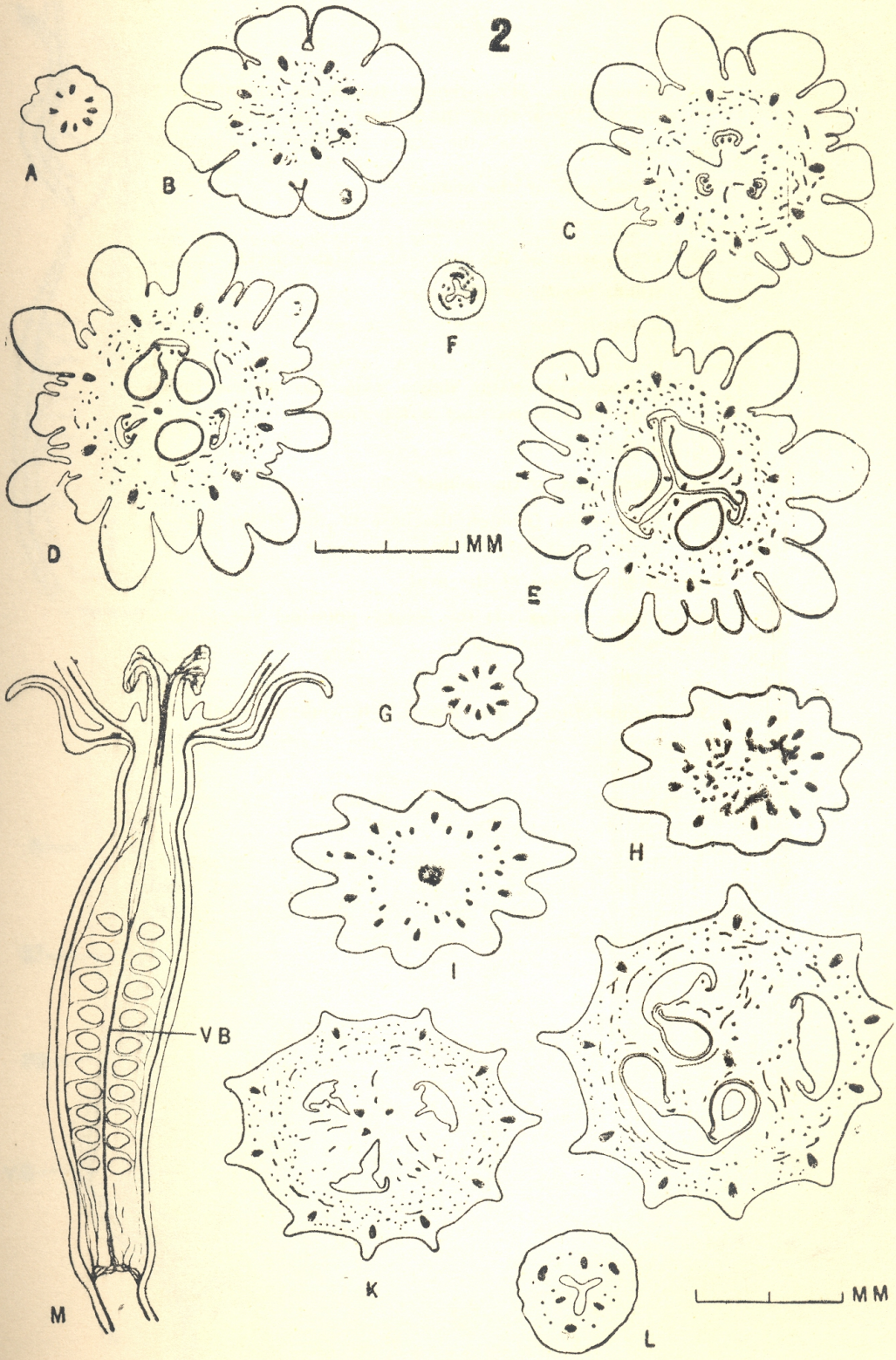
- A-H.** Female flower of *BENINCASA HISPIDA*.
- A.** Transection of the pedicel.
  - B,C.** Transections through the distal part of the pedicel showing the vascular plate.
  - D.** Transection through the basal region of the ovary showing the vascular plexus in the central core.
  - E.** Transection of the ovary at a higher level showing the gradual separation of carpellary margins.
  - F.** Transection through the middle region of the ovary.
  - G.** Styler region.
  - H.** Longisection of the flower. (N, nectary; St, staminode; VAP, vascular plate; VB, ventral bundle).
- I-M.** Transections of the female flower of *TRICHOSANTHES* from the pedicel to the style.
- I.** Pedicel.
  - J.** Distal part of the pedicel.
  - K.** Basal region of the ovary showing six ventral carpellary bundles in the center.
  - L.** Middle region of the ovary.
  - M.** Style.





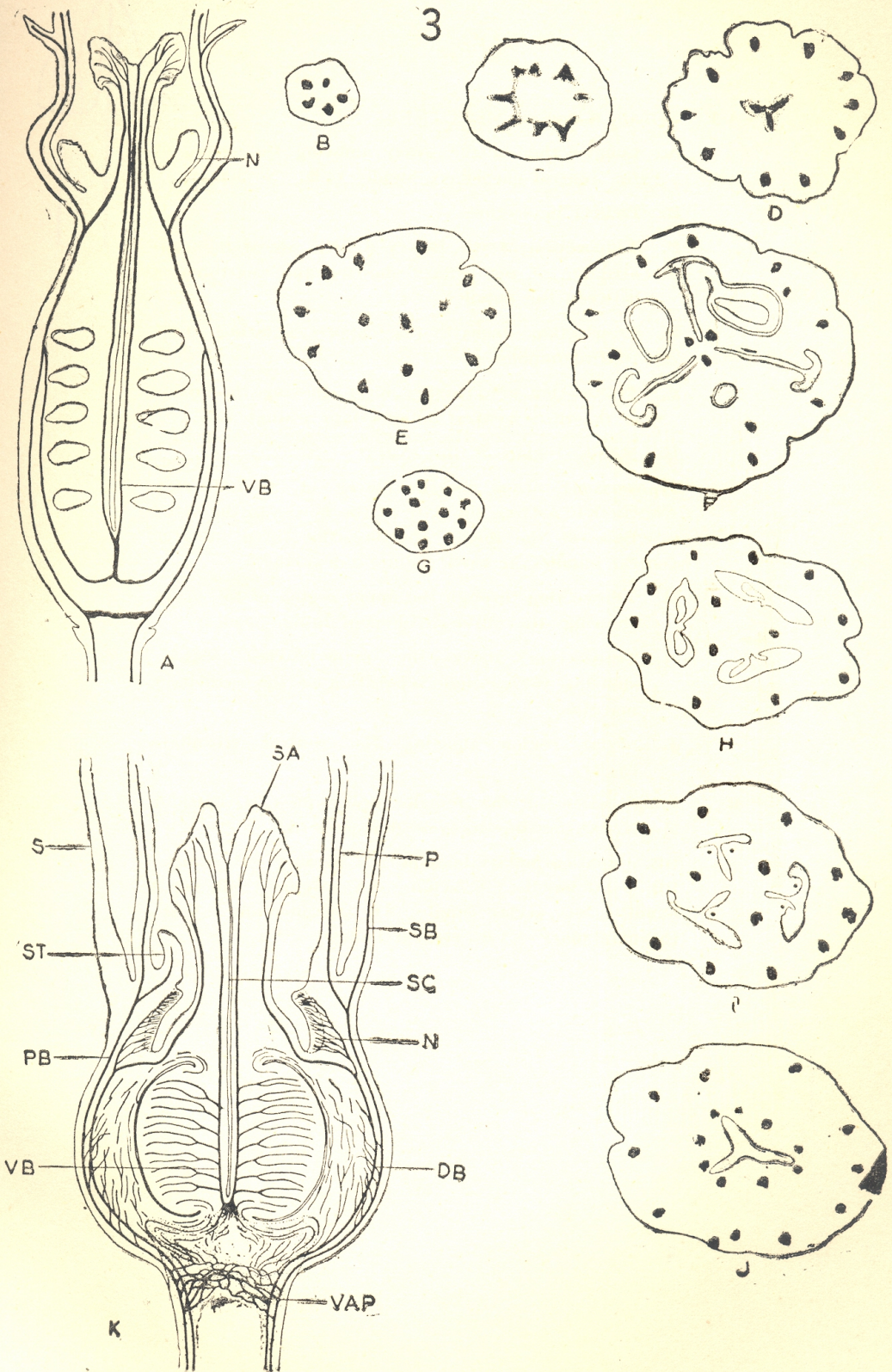
## Fig. 2

- A-F.** Transections of a female flower of *MOMORDICA CHARANTIA* from the pedicel to the style.
- A.** Pedicel.
  - B.** Distal part of the pedicel.
  - C.** Basal region of the ovary.
  - D.** Transection of the ovary at a higher level.
  - E.** Middle region of the ovary.
  - F.** Style.
- G-M.** Female flower of *LUFFA ACUTANGULA*. **G-L.** Transections of the flower from the pedicel to the style. **M.** Longisection of the flower.
- G.** Pedicel.
  - H.** Distal part of the pedicel.
  - I.** Transection through the base of the flower showing a single ventral bundle.
  - J.** Middle region of the ovary.
  - K.** Upper region of the ovary showing the gradual opening of the carpels.
  - L.** Style.
  - M.** Longisection of the flower. **VB,** ventral bundle.



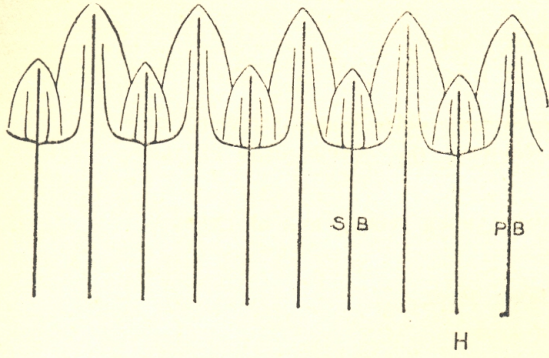
## Fig. 3

- A-F.** Female flower of *MELOTHRIA*.
- A.** Longisection of the ovary showing the origin of the ventral carpellary bundle (VB). N, nectary.
  - B.** Pedicel in section.
  - C.** Transection of the flower a little above the constriction of the pedicel showing the anastomoses between the bundles.
  - D.** Transection beneath the carpels showing three ventral bundles.
  - E.** Transection at a higher level showing the fusion of the three ventral bundles into a single one.
  - F.** Middle region of the ovary.
- G-J.** Transections of a female flower of *SIOLMATRA AMAZONICA* from the base of the flower to the style.
- G.** Base of the flower showing the three inverted ventral bundles at their point of departure.
  - H.** Transection through the upper region of the ovary showing the three ovule-containing locules.
  - I.** Transection above the ovule-bearing region showing the gradual separation of the carpellary margins.
  - J.** Stylar region showing the central triradiate cavity.
- K.** Longisection of the female flower of *CUCURBITA MAXIMA* showing its vascular pattern.
- DB, dorsal carpellary bundle ; N, nectary ; P, petal ; PB, petal bundle ; S, sepal ; SA, stigma ; SB, sepal bundle ; SC, stylar canal ; ST, staminodium ; VAP, vascular plate ; VB, ventral bundle.

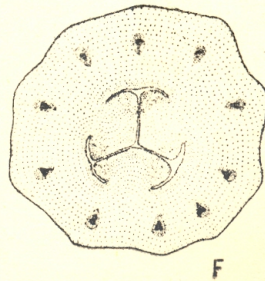
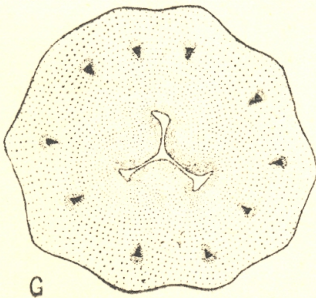
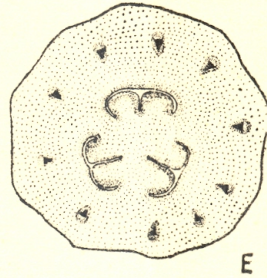
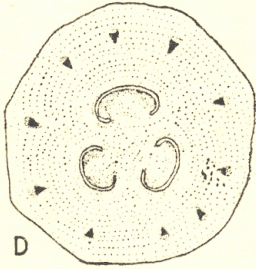
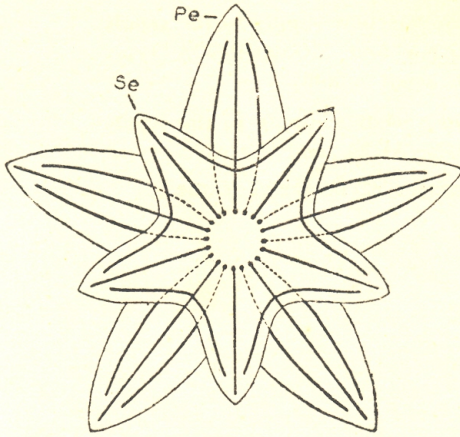
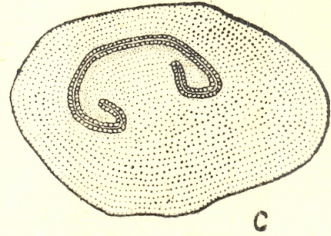
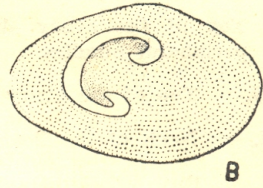
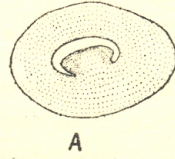


## Fig. 4

- A-C. Transections of successively older buds of *CYCLANTHERA PEDATA* showing the development of the carpel.
- D-G. Transections of a very young female bud of *LUFFA CYLINDRICA*.
- D. Middle of ovary.
- E. Upper region of ovary.
- F-G. Transections of the ovary at higher levels.
- H. Diagram representing the vascular supply to the sepals and petals in the *LUFFA* and *MOMORDICA* type. PB, petal bundle ; SB, sepal bundle.
- I. Diagram representing the vascular supply to the sepals and petals in the *LAGENARIA* and *SICANA* type. Pe, petal ; Se, sepal.



4



1mm

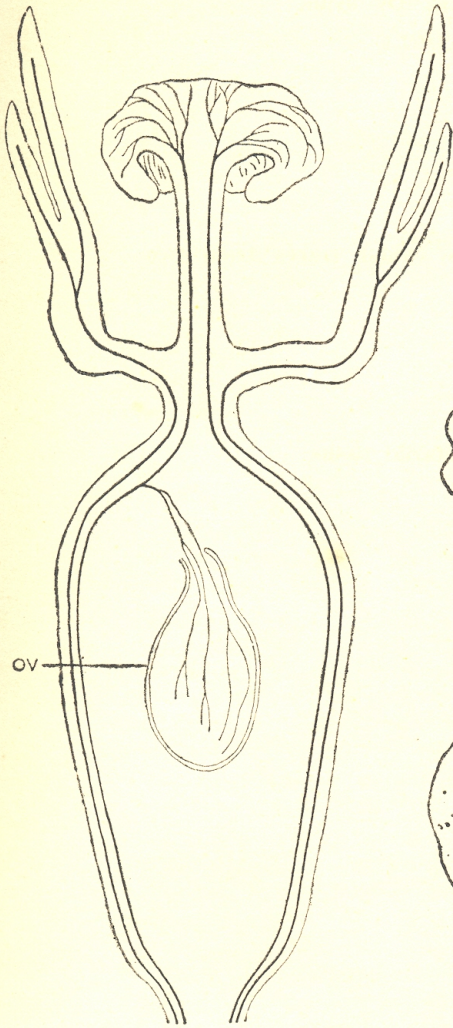
1mm

## Fig. 5

- A. Longisection of the flower of SECHIUM EDULE. Ov. ovule.
- B-J. Transections of a female flower of SECHIUM EDULE.
- B. Distal part of the pedicel.
  - C. Base of the ovary.
  - D. Base of the ovary at a higher level.
  - E. Middle of the ovary.
- F-G. Top of the ovary showing the origin of the ovular traces from two peripheral bundles.
- H. Top of the ovary at a higher level.
  - I. Neck of the flower.
  - J. Base of floral tube.
- K. Base of floral tube showing ten masses of nectarial tissue.

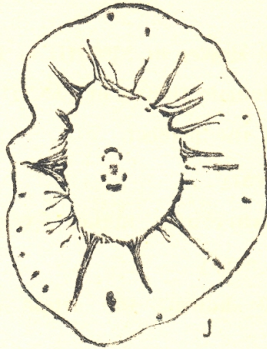


5

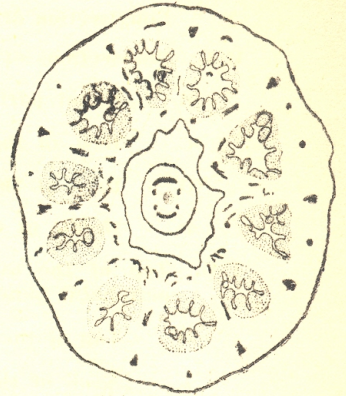


A

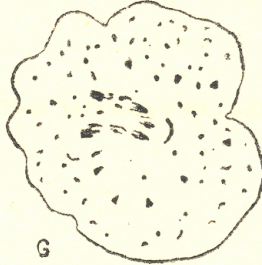
MM 5



J



K



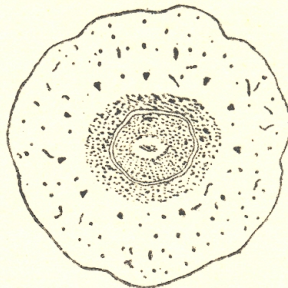
G



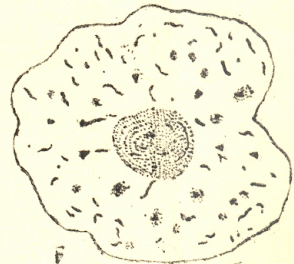
L



I



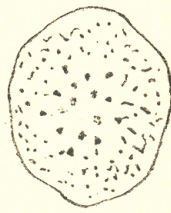
E



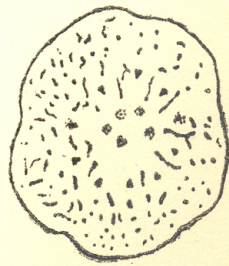
F



B



C



D