STUDIES IN THE ORDER PIPERALES

V. A Contribution to the Study of Floral Morphology of Some Species of Piper^{1, 2}

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Introduction

Johnson (1902) was perhaps the first to investigate *Piper (P. medium)* and report an 8-nucleate, *Adoxa*-type of embryo-sac developing directly from an archesporial cell. This was confirmed by him in 1910 from his study of *P. betel* var. *monoicum*, and by Fisher (1914) from his study of *P. tuberculatum*. However, Schnarf (1931) from a close scrutiny of the diagrams suspected that the embryo-sac should be other than the *Adoxa*-type. That this suspicion was well founded, was shown by Swamy (1944) who, on a reinvestigation of *P. betel*, found the development to follow *Fritillaria*-type. In the same year Joshi reported the same type of embryo-sac development in *P. longum*.

Some difference of opinion also exists regarding the number of carpels in *Piper* gynæceum. Whereas Baillon (1874) considered it as monocarpellary, Eckardt (1937) regarded the same as psudomonomerous and tricarpellary.

The present of the series of papers deals with the floral anatomy of 12 species and embryology of one species of *Piper*.

MATERIAL AND METHODS

Preserved material of *P. Gaudichaudianum* and *P. Tucumanum* was obtained from Dr. T. Meyer of Argentina; that of *P. betle* from Mr. Y. K. Murty; *P. Schmidtii* from Mr. A. N. Rao; *P. nigrum* and *P. longum* from Prof. P. Maheshwari; *P.* spp. from Dr. K. M. Silberschmidt of Brazil and *P. subrubrispicum* from Prof. V. Puri and paraffin embedded material of *P. obtusilimbum*, *P. unguiculatum* and *P. nigrescens* from Dr. O. Hagerup.

¹ Based on a portion of a thesis accepted for a Ph.D. Degree of the Agra University.

² Research contribution No. 18 from the School of Plant Morphology, Meerut College, Meerut.

terial of P. longum and P. subrubrispicum was also collected by the author m Saharanpur and Dehra Dun respectively. Serial transverse and longinal sections, 10-12 microns thick, were cut and stained with crystal violet lerythrosin.

OBSERVATIONS

The flowers may be unisexual (P. Schmidtii, P. Wightii, P. nigrum, longum) or bisexual (P. Gaudichaudianum, P. Tucumanum, etc.) and occur leaf opposed cylindrical spikes. With unisexual flowers the plants are ecious. Occasionally the female spikes of P. nigrum and the male spikes P. Longum were observed with some bisexual flowers. The male spikes general are narrower, longer and more compact than the female ones ept in P. Schmidtii where they are shorter.

Each flower is subtended by a peltate bract, which has a prominent stalk Gaudichaudianum and P. obtusilimbum). The bract of P. nigrum is nate to the inflorescence axis with which it forms a minute cup round the ary. Hooker (1885) probably mistook this cup to be bracteoles. Often P. Gaudichaudianum the stamens are adnate to the ovary wall for about f way up. In P. Tucumanum, however, they separate only just below the ma, while in P. longum the fusion of the flowers is so complete that it olves all parts except the stigmas and apices of bracts which are free and ich project out from the surface of the spike (Fig. 1).

The flowers are many, sessile, naked and arranged spirally on the axis. ile, female and bisexual flowers are sometimes found in one and the same cies as P. longum. The male flower has two (P. Schmidtii) or three longum, P. unguiculatum, etc.) stamens and a pistillode, while the female wer has a tricarpellary gynæceum with three sessile stigmas and two Wightii, Fig. 2) or three (P. nigrescens) staminodes. In the hermaphroflowers there are two (P. subrubrispicum) or three (P. Gaudichaudianum i P. Tucumanum) stamens. The filaments are long and jointed in Gaudichaudianum and P. Tucumanum. In the latter species the constriction just above the point of its separation from the ovary wall.

Ordinarily a single ovule occupies the ovarian cavity, but in one instance, ond rudimentary ovule was observed in *P. Wightii* (Fig. 3). The fruit is ine-seeded drupe with a hard endocarp.

Development of the Bract.—The development of the bract in general similar to that in Peperomia (Murty, 1958). The bract arises as a small tuberance caused by the activity of the sub-epidermal cells of the apex the inflorescence axis. This protuberance elongates towards the apex

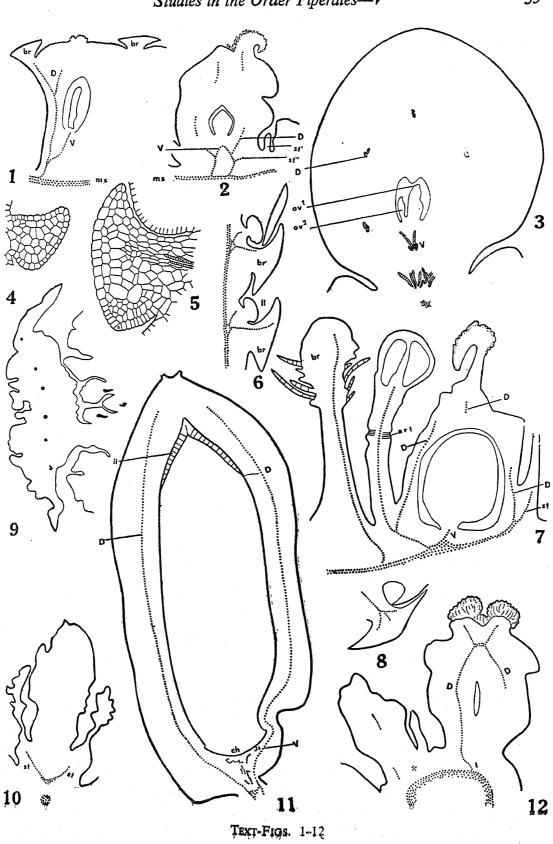
of the inflorescence as a result of the activity of sub-marginal cells (Fig. 4). Some anticlinal divisions of the cells on the lower side bring about elongation of this side of the bract towards the base of the inflorescence also (Fig. 5). Though in earlier stages the upper lobe of the bract appears to be longer (Fig. 6), in older flowers the lower lobe elongates faster and becomes equal to it. In both transverse and longitudinal sections the bract of *P. Gaudichaudianum* looks like a club reaching the height of the anther and stigmas (Fig. 7). Oil cells occur in the mesophyll while stomata are found in the middle of the disc (shield); and hydathodes and multicellular hairs (trichomes) on the surface of the bract.

VASCULAR ANATOMY

The Inflorescence.—The structure of the inflorescence axis in male, female and hermaphrodite spikes is just the same. It consists of two rings of collateral and open bundles, an outer of 10 (P. betle) or more (P. Schmidtii, P. Gaudichaudianum, P. nigrum, etc.) and an inner of about five (P. longum, P. betle, P. nigrum, P. unguiculatum, etc.). While those of the outer ring are embedded in thick-walled tissue (P. Gaudichaudianum, P. Wightii, P. Tucumanum and P. obtusilimbum) a bundle sheath is seen round the bundles of the inner ring in P. Gaudichaudianum.

The Flower.—Vasculature of the flower in the different species studied is essentially similar. Whatever differences have been observed are due to variations in the number of stamens, presence or absence of pistil or pistillode and occasionally also due to the fusion of bract or stamens or both with the ovary wall. Hence, the floral supply in the bisexual flower is described in detail and attention will be drawn to the differences in other flowers whenever necessary.

A single branch diverges out somewhat obliquely or horizontally from the parent stele of the inflorescence axis and branches somewhere in the middle of the cortex into a bract and floral supply. In some of the male flowers of *P. Schmidtii*, it was observed that these branches separate off very close to the point of their origin from the parent stele (Fig. 6). However, in the female flowers of *P. longum*, which show complete fusion between bracts and axillant flowers and also between adjacent flowers, the bract trace appears to remain adnate to one of the abaxial bundles in the ovary wall and separates from it only at the level of the micropyle (Fig. 1). Generally the bract trace after bending slightly enters the organ and passes through the upper half of its stalk (Fig. 7). Within the disc (shield of the bract) it divides into two or more (Figs. 8, 9) branches,



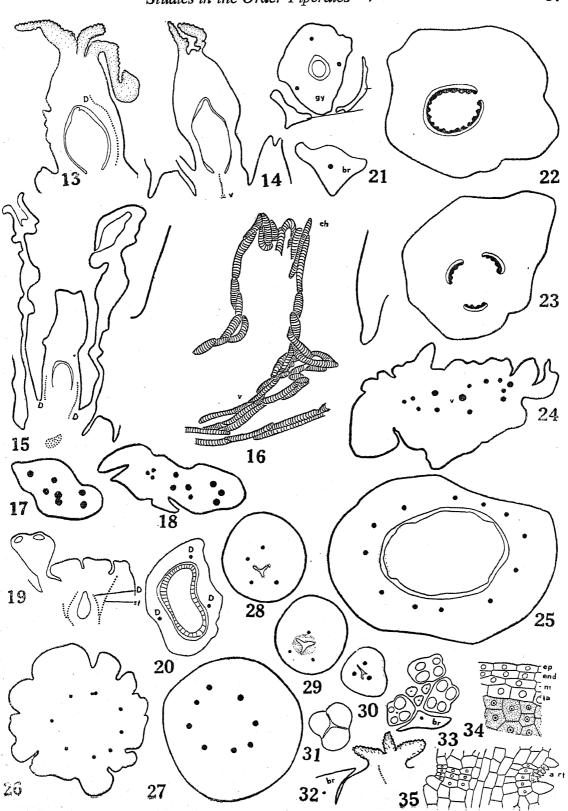
The floral supply reaches the base of the flower where it gives out laterally a trace each to the two stamens [P. Schmidtii, P. betle, P. subrubrispicum (Fig. 10), P. unguiculatum, P. Gaudichaudianum] and sometimes as in the case of female flowers to two (P. Wightii, P. nigrum) or three (P. nigrescens) staminodes, and then reaches the base of the ovary to supply the gynæceum. The trace that enters the stamen or staminode remains undivided throughout and reaches the connective (Fig. 7). However, in those female flowers (P. Schmidtii, Fig. 11) where there are no staminodes the floral supply reaches directly the base of the ovary. Generally in P. Tucumanum and, sometimes, in P. Gaudichaudianum (Fig. 7) where a certain degree of fusion between the stamens and ovary wall is seen, the stamen traces separate only at a higher level.

The supply to the gynæceum divides at its base into four branches of which one is central and the other three are peripheral as in P. sp., P. Gaudichaudianum (Fig. 7), P. longum (Fig. 12), and P. subrubrispicum (Figs. 13, 14 15). The central bundle reaches the chalaza and is more or less completely used up in furnishing a single ovular trace (Fig. 14). This bundle forms a cup of tracheids at the base of the chalaza in P. Wightii and P. Schmidtii (Fig. 11). The tracheids making up this branch were in one instance seen negotiating a bend (Fig. 16), somewhat similar to that in Peperomia incana and Peperomia comarapana (Murty, 1958). But in P. Schmidtii the central bundle gets separated from one of the peripherals (Figs. 17, 18).

The three peripheral bundles which may or may not branch supply the ovary wall. But in those species where the stamens are adnate to the ovary wall for some distance as in *P. Gaudichaudianum* and *P. Tucumanum* they are compound bundles, *i.e.*, the outer one supplies a stamen while the inner, the ovary wall (Figs. 7, 19).

Except in *P. Schmidtii*, *P. Wightii* and *P. nigrum* the three bundles passing through the ovary wall do not show any branching (Figs. 20, 21) and reach the stigmas where they disappear. They are placed equidistantly. However in *P. longum* these three bundles fuse forming a sort of plate of tracheids from which three small bundles are given off one for each of the three stigmas (Figs. 12, 22, 23).

In the three species mentioned above, e.g., P. Schmidtii, P. Wightii and P. nigrum all the three peripheral bundles divide further so as to give rise to about a dozen bundles (13 in P. Schmidtii). As was described earlier one of these in P. Schmidtii occupies a central position (Figs. 17, 18) and it supplies the chalaza. Thus in all 9-12 bundles are observed to be arranged in the ovary wall almost uniformly about the level of the chalaza (Figs. 24, 25).



TEXT-Figs. 13-35

These bundles are placed almost equidistantly from one another. Their number decreases gradually towards the apex of the ovary and only three of them are seen to persist below the level of the stigmas (Figs. 26–30). These continue into the sessile stigmas which are separated by a triradiate stylar canal that appears between them (Figs. 29–32).

The vascular supply in the pistillodes of the male flower, though rudimentary, confirms to the pattern given above (Fig. 33).

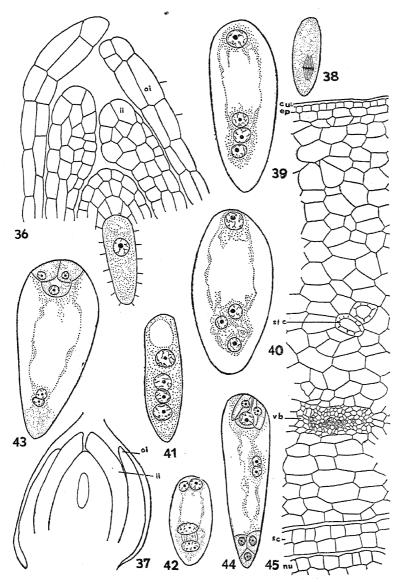
The Microsporangium and the Male Gametophyte.—The development of the microsporangium has been studied in P. Schmidtii, P. Gaudichaudianum, P. longum and P. unguiculatum. The anther has four microsporangia (Fig. 33) and a wall consisting of four layers (Fig. 34). The innermost layer, tepetum, remains uninucleate. The sporogenous cells take up a deep stain and develop into two-celled pollen grains. At maturity endothecium becomes fibrous and the middle layer is completely crushed.

It is very interesting to note that the stamens of the P. Gaudichaudianum, P. Tucumanum and P. unguiculatum show a circular constriction about $\frac{2}{3}$ the height of the filament. About 3-4 layers of cells at this region appear to be meristematic (Fig. 35). The constriction becomes more prominent as the stamen matures and the filament breaks off at this point. This special mechanism of separation of the anther may probably have some significance in the method of shedding of the pollen. It has also been used as a character in delimiting the species of Piper.

The Megasporangium and the Female Gametophyte.—Though the female gametophyte in P. Gaudichaudianum alone could be worked out, some stages observed in P. Tucumanum have also been recorded. The tricarpellary gynæceum is unilocular with a single bitegmic orthotropous ovule at the base. The outer integument is 2-layered while the inner is 3-layered below and 4-layered at the apex. Though in earlier stages the outer integument is longer than the inner (Fig. 36), finally the two become equal and the micropyle is formed by the inner integument only (Fig. 37).

A megaspore mother cell is formed as a result of a periclinal division of the primary archesporial cell. Even before the nucleus of the megaspore mother cell undergoes the first division the parietal tissue becomes 2-3-layered in thickness (Fig. 36), and at the 8-nucleate condition it becomes 4-layered in P. Gaudichaudianum. In P. Tucumanum it is, however, 5-layered at the primary 4-nucleate stage. The megaspore mother cell is much longer than broad (Fig. 36). Its nucleus is centrally situated though it moves to the chalazal end just before it divides (Fig. 38). No vacuole is formed

at this stage and there is no cell-plate formation either. After the second meiotic division all the four nuclei are somewhat towards the chalazal end at the beginning but soon the upper nucleus moves towards the micropylar end, while the other three remain in a linear row at the lower end (Fig. 39) being separated from the upper nucleus by a large vacuole (Fig. 40). A linear row of four nuclei was also observed in *P. Tucumanum* (Fig. 41).



Text-Figs. 36-45

A third division of the nuclei appears to result in a secondary 4-nucleate stage (Fig. 42). Although this particular embryo-sac is very small, the triploid nature of its chalazal nuclei is apparent. Besides, the 1+3 arrangement at the primary 4-nucleate stage cannot be reasonably

explained in any other way. It is significant to note that the divisions of these nuclei are seldom simultaneous. In some cases it is the nucleus at the micropylar end that divides first while in others those in the chalazal end may have the lead. One more division in all the four nuclei brings about an 8-nucleate embryo-sac which is broadest on the micropylar side (Fig. 43). The two polars meet each other either in the middle of the embryo-sac (Fig. 44) or towards the chalazal end (Fig. 43). The egg apparatus and the antipodal cells are organized in the usual manner (Figs. 43, 44). The development of the embryo-sac in this species, therefore, follows the *Fritillaria*-type.

The ovary wall at the 8-nucleate stage is about 10 cells thick and is not differentiated into definite regions. Hydathodes and oil cells occur abundantly.

The Fruit Wall.—This has been studied in P. Schmidtii, P. Wightii and P. nigrum. Cooper (1909) described the fruit wall of P. nigrum. In all of them the fruit wall is thick and many layered. This is differentiated into three regions. The outer one is fleshy and several layered and is bounded on outside by a layer of epidermis. The epidermal cells have thickened outer walls covered by a thick layer of cuticle. Inner to the epidermis there are 1–3 layers of hypodermis where cells are small and somewhat thick-walled. In P. nigrum these cells are elongated at right angles to the surface and often show a narrow central lumen. Next to the hypodermis there are 14–20 layers of parenchyma in which are scattered groups of stone cells (Fig. 45). The second region consists of 3–4 layers of small cells and the vascular bundles traverse through this region. The third one has about 6–8 layers of cells. In P. Schmidtii only parenchyma cells occur while in P. Wightii it contains thick-walled cells that are somewhat elongated parallel to the surface. This region contains oil cells scattered here and there.

The seed-coat shows 2 (P. nigrum) or 3 (P. Wightii) layers. The outer one is completely crushed and in its place there remains a dark layer without any differentiation of its cells. The perisperm cells are very prominent with numerous starch grains in the vacuoles.

DISCUSSION AND CONCLUSIONS

The course of the vascular supply to the bract and its axillant flower is fundamentally same in all the flowers studied. From the position and course, the three peripheral bundles at the base of the ovary are to be interpreted as the carpellary dorsals and the one that supplies the chalaza as the ventral (Placental) strand which is consumed entirely in supplying the single ovular trace. Additional bundles observed in the ovary wall of *P. Schmidtii*,

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P. nigrum and P. Wightii appear to constitute secondary laterals. However, such a typical plan of vascular construction is modified as a result of adnation of bract or stamens.

In the female flower of *P. longum* not only the bract is fused to the ovary wall for quite a long distance, even its bundle shows fusion with one of the carpellary bundles running on the abaxial side, separating only at about the level of the micropyle. Such a fusion of the bract with its axillant flower has been reported in *Juglans* (Manning, 1940), *Lonicera* (Wilkinson, 1944) and especially in the genera showing inferior ovaries. Occasionally in *P. Gaudichaudianum* and generally in *P. Tucumanum* where the stamens arise somewhat above the base of the ovary and at the level of the stigmas respectively the carpellary dorsals and the stamen traces separate only at this level. Such an adnation of the stamen and carpellary traces (or bundles?) has also been observed by the author in *Houttuynia* (Murty, 1956) and in *Chloranthus* (Swamy and Bailey, 1950). As the flowers are naked, it is difficult to say whether such a condition should be described as semi-inferior (*P. Gaudichaudianum*) and inferior (*P. Tucumanum*).

The Number and Position of Carpels.—On the basis of the number of stigmas the Piper ovary is generally interpreted as 2–5 carpellary (Rendle, 1938, Lawrence, 1951). Baillon (1874), however, interpreted it as monocarpellary and the three stigmas as three lobes but at the same time he admitted that occasionally there may be flowers with two or more carpels. Eckardt (1937) also discussed at some length the pseudomonomerous condition of the ovary.

As far as the author is concerned there is little doubt that the *Piper* gynæceum consists of three carpels. This is supported by the fact that there are, in the ovary wall, three dorsal bundles which continue either directly or after forming a ring (*P. longum*) into the three stigmas. There is no justification, whatsoever, to interpret the three stigmas as merely lobes of a single one. They are definitely three stigmas representing three carpels.

Joshi (1944) described the gynæceum of *P. longum* to be bicarpellary as he observed four bundles in the ovary wall; two of which he interpreted as dorsals and the other two as fused ventrals. The present observations on the same species did not reveal such a condition. It appears, that Joshi mistook the bract bundle which separates from one of the dorsals at a higher level as a carpellary bundle. Actually there are only three dorsals which traverse the ovary wall. The placental strand formed by the fusion of the ventrals is consumed more or less completely in furnishing a single ovular trace. The

three stigmas at the top of the ovary too are quite evident (Fig. 32). Hence in *P. longum* also there are three carpels.

Not only all the species studied agree in the number of carpels, but they also show the same pattern in their arrangement. Out of the three dorsals two are always found to be antero-oblique and the third posterior. The stigmas which are carinal also occupy the same positions. The solitary ovule apparently belongs to one of the carpels.

The Placentation.—The solitary ovule is often described as basal. Baillon (1874) described it as sub-basillar. In Peperomia some anatomical evidence has been brought forward to show that the single apparently basal ovule has been derived from lateral position (Murty, 1952). Although no such evidence exists in Piper there is little doubt that the condition here too is the same as in Peperomia and that the basal position of the ovule is a derived one. The formation of the ventral strand from the carpellary dorsals in P. Schmidtii, the presence of a bend in one instance in the course of the ventral strand of P. longum seem to confirm such a belief. A rudimentary second ovule like the one reported in Peperomia Peirescifolia (Murty, 1956, 1958) has been observed in P. Wightii but it will not be advisable to speculate on this count.

The Megasporangium and the Female Gametophyte.—Unlike the condition in Peperomia, the Piper anthers are four-locular and the ovules are bitegmic. Generally as has been described by Johnson (1910) and Joshi (1944) the micropyle is formed by the inner integument alone though Johnson (1902) described and figured a much larger outer integument in P. medium. Such a difference in closely related species is according to Joshi (1944) unlikely. The difference may probably be due to a difference in the stages of the ovules examined. As was described earlier the condition in a young ovule is different from that in a mature one.

The 1 + 3 arrangement of the megaspore nuclei, the presence of three nucleoli in the chalazal nuclei at the secondary 4-nucleate stage and then the subsequent divisions and the ultimate formation of 8-nucleate embryosac showing an egg apparatus with 2 synergids, 2 polars and three antipodals observed in *P. Gaudichaudianum* lead to the conclusion that the embryosac in *Piper* belongs to the *Fritillaria*-type and not to the *Adoxa*-type as was believed by Johnson (1902, 1910), Fisher (1914), etc. This conclusion is in agreement with that of Swamy (1944) and Joshi (1944) regarding *P. betel* and *P. longum* respectively.

SUMMARY

The vascular anatomy of the flower in general is uniform in all the species of *Piper* studied. A flower is always supplied by a single branch that gives out first a trace to the bract. The remaining vascular supply gives out traces to the stamens or staminodes when present and then supplies the gynæceum. Only in some species like *P. Tucumanum* adnation of the stamen traces and in the female flowers of *P. longum* of the bract trace with the carpellary dorsals, has been observed. The gynæceum supply splits up at its base into three dorsals and one ventral strand. Secondary laterals are observed only in three species. In *P. longum* the dorsals are seen fusing below the stigmas otherwise they directly supply them.

Embryology in *P. Gaudichaudianum* has been studied and it is concluded that it follows *Fritillaria*-type as in other species of *Piper*.

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EXPLANATION OF TEXT-FIGURES

Figs. 1–12. Fig. 1. Part of a longitudinal section of female spike of *P. longum* showing adnation of bract to the ovary, and bract trace with the carpellary dorsal, × 13. Figs. 2 and 3. Two flowers of *P. Wightii* cut longitudinally. Note the staminode and its trace in Fig. 2 and an extra ovule in Fig. 3, × 13. Figs. 4 and 5. *P. Schmidtii* showing stages in the development of bract, × 133. Fig. 6. Part of longitudinal section of a young male spike of *P. Schmidtii* showing the arrangement of bracts and vascular supply to the flower and bract, × 13. Fig. 7. Semi-diagrammatic longitudinal section of a flower of *P. Gaudichaudianum* showing vascular supply to bract and different organs of flower. Note the articulation on the filament and adnation of stamen and carpellary dorsal for some distance, × 53. Fig. 8. A bract of *P. Schmidtii* showing the branching of the bract bundle in the shield of the bract, × 13. Fig. 9. Bract of *P. nigrum* showing many bundles within its shield, × 30. Fig. 10. Flower of *P. subrubrispicum* in longitudinal section showing vascular supply to the two stamens, × 133. Fig. 11. Female flower of *P. Schmidtii* in longitudinal section showing the ventral strand and carpellary dorsals. Fig. 12. Cross-section of a spike of *P. longum* showing the course of two carpellary dorsals, × 30.

art., articulation; br., bract; ch., chalaza; D., carpellary dorsal; fl., flower; ii., inner integument; ms., main vascular supply of the inflorescence axis; ov^1 and ov^2 ., fertile and rudimentary ovules; st., stamen trace; St'., staminode; St''., staminode trace; V., ventral strand.

Figs. 13-35. Figs. 13-15. Flowers of P. subrubrispicum in longitudinal sections showing vascular supply to the ovary, \times 133. Fig. 16. A well-developed ventral strand in P. longum showing a bend in its course, \times 53. Figs. 17 and 18. Cross-sections of female flower of P. Schmidtii showing the formation of ventral strand, carpellary wall bundles, \times 30. Fig. 19. Longitudinal section of a flower of P. Tucumanum showing the vascular supply to the stamens. Note the adnation of stamen traces and carpellary dorsals for some distance, \times 30. Fig. 20. Cross-section of an ovary of P. Gaudichaudianum showing the three carpellary dorsals, \times 13. Fig. 21. Cross-section of a flower of P. subrubrispicum showing bract, two stamens and gynæceum, \times 58. Figs. 22 and 23. Cross-sections of an ovary of P. longum showing the formation of a ring of vascular tissue below the stigma region (Fig. 22) and its division into

indles (Fig. 23) that supply the three stigmas, \times 30. Figs. 24 and 25. Cross-sections of ovary P. Schmidtii and P. nigrum respectively showing 12 wall bundles. Note the ventral strand in ig. 24, \times 30. Fig. 26. P. Wightii and Figs. 27-29. P. Schmidtii. Cross-sections of ovary lowing reduction in the number of wall bundles to three towards the apex. Fig. 26, \times 13. igs. 27-29, \times 30. Figs. 30 and 31. Cross-sections of the apex of the ovary of P. nigrum, showing the formation of stigmas and the disappearance of traces, \times 30. Fig. 32. Apex of the ovary of P. longum showing the three stigmas, P 30. Fig. 33. Cross-section of male flower of P. longum towing the position of bract, three stamens and three stigmas, P 30. Fig. 34. A part of coss-section of anther of P. Schmidtii showing the wall layers and sporogenous cells, P 533. ig. 35. Shows the arrangement of cells at the place of articulation on the filament of P Gaudichaudianum, P 53.

art., articulation; br., bract; ch., chalaza; D., carpellary dorsal; end., endothecium; ep., pidermis; gy., gynæceum; m., middle layer; St., stamen trace; ta., tapetum; V., ventral trand.

Figs. 36-45. Figs. 36, 38-40, 42-44. *P. Gaudichaudianum* and Figs. 37 and 41. *P. Tucumanum*. Fig. 36. Upper part of a young ovule showing the two integuments, megaspore mother cell nd parietal tissue, × 533. Fig. 37. Ovule with two integuments. Note the inner integument s longer, ×133. Fig. 38. Megaspore mother cell with its nucleus undergoing division, × 567. Figs. 39 and 41. Show the arrangement of nuclei at the primary 4-nucleate stage of the embryo-ac. Figs. 39 and 40, × 567; Fig. 41, × 533. Fig. 42. Embryo-sac showing secondary 4-nucleate condition. Note the number of nucleoli in the two nuclei on the chalazal side, × 567. Fig. 43. Embryo-sac with egg apparatus and two polar nuclei, × 567. Fig. 44. 8-nucleate embryo-sac, × 567. Fig. 45. Part of a cross-section of fruit wall of *P. Wightii*, × 133.

Cu., cuticle; ep., epidermis; ii., inner integument; nu., nucellus; Oi., outer integument Sc., seed-coat; Stc., stone cell; Vb., vascular bundle.