BOLUS LIBRARY
C24 0005 0790

B.Sc. Hons.

J. Mattatia

1965.

Floral morphology and vascular anatomy of some species of *Struthiola*.

The copyright of this thesis vests in the author. No quotation from it or information derived from it is to be published without full acknowledgement of the source. The thesis is to be used for private study or non-commercial research purposes only.

Published by the University of Cape Town (UCT) in terms of the non-exclusive license granted to UCT by the author.

University of Cape Town

Contents

Key for the symbols used for labelling diagrams.

The following symbols are used throughout the work:

A - Anther.

AB - Axillary bud.

Anst - Anastomosis of bundles derived from antisepalous and alternisepalous bundles.

Ax - Axis of flower bearing stem.

Alt S - Alternisepalous bundle, or bundles derived from it.

B - Bract.

BT - Bract trace.

Br - Bracteole.

BrT - Bracteole trace.

D - Hypogynous disc.

DC - Dorsal carpellary bundle of fertile, functional carpel.

sDC - Dorsal carpellary bundle of sterile, reduced carpel.

ES - Embryo sac.

F - Filament of stamen.

FT - Floral tube.

I Int - Inner integument.

N - Nucellus.

O - Ovary.

O Int - Outer integument.

Ov - Ovule.

OvT - Ovule trace.

P - Peduncle.

PS - Petaloid scale / vascular supply of petaloid scale.

R - Receptacle.

S - Antisepalous bundle (= sepal midrib) or bundles derived from it.

SL - Sepal lobe / vascular supply of sepal lobe.

ST - Stamen trace.

St - Style

VC - Ventral carpellary bundle.

T/S - Transverse section.

L/S - Longitudinal section.

T/L/S - Tangential longitudinal section.

Introduction.

The family Thymelaeaceae and its taxonomic position.

Members of the family Thymelaeaceae are usually shrubs with entire and exstipulate sessile leaves. The flowers are actinomorphic, seldom zygomorphic, usually bisexual, 4-5 merous. The calyx is usually petaloid, gamosepalous, forming a bowl-shaped or a cylindrical tube with free sepal lobes. Petal-like structures (or petaloid scales) are present in some genera, inserted at the mouth of the floral tube or sometimes lower down in the tube. The androecium is in most cases diplostemonous, or sometimes haplostemonous. The stamens are usually inserted in the upper part of the floral tube in two or one whorls. In the subfamily Thymelaeoideae the gynoecium is bicarpellary (apparently unicarpellary), unilocular, containing a single anatropous ovule attached near the top of the ovary. The style is simple, either terminal or laterally attached on top of the ovary. In the subfamily Aquilarioideae the gynoecium is usually 2-5 carpellary.

A constant anatomical character (which is absent only in one genus - Drapetes) is the presence of internal phloem in the vegetative as well as in the floral organs. (Metcalfe and Chalk, 1950).

When present, the petaloid scales show an enormous range of variation within the genera and in some cases even within the species. Within a single genus (e.g. Gnidia) they may range from large petal-like organs, similar in appearance to the sepal lobes, to small inconspicuous points, or they may be completely absent. In some species they are thin and membranous while in related species they are fleshy or filiform. The petaloid scales may be isomerous and alternating with the sepal lobes, or lobed and divided to their bases and appear as double or triple structures. In other cases, e.g. in Lachnaea and Cryptadenia various outgrowths are found lower down in the floral tube.

In spite of the variations in the presence and appearance of the petaloid scales, on the basis of the general morphology of the flower, as well as vegetative and anatomical characters, the Thymelaeaceae is regarded as a natural group. Its relationships, however, are very obscure. The taxonomic position of the family in various systems of classification is debatable and depends largely on the interpretation of the floral organs. There are three main points on which the views of authors diverge.

1. The gynoecium, which has been described as unicarpellary or bicarpellary.
2. The nature of the floral tube, which has been interpreted by various authors as a hollow receptacle, hypanthium or a calyx tube.
3. The true nature of the petaloid structures.

Those authors who regard the petaloid structures as petals and the floral tube as an extension of the receptacle, place the family among dialypetalous groups, like the Rosales and Myrtiflorae. Gilg (1895) included the family in the Thymelaeales, between the Parietales and the Myrtiflorae, and later included it in the Myrtiflorae. The same was done by Wettstein (1935) and other authors who followed Engler and Prantl's system, as Rendle (1963). Lawrence (1951) also included the Thymelaeaceae in the Myrtiflorae, although he regarded the floral tube as a hypanthium and not as a receptacle.

Other authors interpreted the petaloid scales as non-petal structures and therefore regard the Thymelaeaceae as apetalous and grouped the family with other groups as Penaeaceae, Elaeagnaceae, Geissolomataceae, proteaceae and Santalaceae. Meisner (1856) related the Thymelaeaceae to the Santalaceae. Bentham and Hooker (1883) included it in the Daphnales among monochlamydous groups. Bessey (1897) placed the Thymelaeaceae in the Celastrales with the Penaeaceae, Elaeagnaceae, Oliniaceae and Loranthaceae. Baillon (1880) regarded the petaloid structures as scales, but related the Thymelaeaceae to the Celastraceae, Rhamnaceae, Lythraceae and Onagraceae. Hutchinson (1959) who regards the petaloid scales as petals, included the Thymelaeaceae in the Thymelaeales in his division Lignosae, between the Bixales and the Proteales, together with the Aquilariaceae which he separated as a family, and with the Geissolomataceae, Penaeaceae and Nyctaginaceae. In the new edition of Engler's system (Melchior, 1964) the Thymelaeaceae are separated from the Myrtiflorae and included in the order Thymelaeales (between the Malvales and Violales), together with the Geissolomataceae, Penaeaceae and Elaeagnaceae. This is based on recent anatomical studies and on the view that the floral tube is a perianth and the unicarpellary ovary is really pseudomonomeric. The interpretation of the petaloid scales is still regarded as unsettled.

The Thymelaeaceae represent a specialized group which has undergone marked modification and reduction in the floral organs. It presents a case in which external morphology alone cannot yield adequate information, and the vascular anatomy is of great value for understanding and interpretation of the floral structures.

Studies in the floral anatomy of the

Thymelaeaceae have been carried out by Payer (1857), Leandri (1930), Eckardt (1937), Saunders (1939) and Heinig (1946, 1951). These will be considered in the discussion below.

In the present work, the floral morphology and vascular anatomy of 4 ~~number~~ species of Struthiola were studied in detail. The study concentrated on 4 major points.

1. The structure of the peduncle and the unit of inflorescence.
2. The gynoecium.
3. The nature of the floral tube.
4. The petaloid scales.

Material and methods.

The 4 species investigated were chosen so as to represent the 3 sections in the genus Struthiola (according to Gilg, 1895) thus showing all the possible variations in the number of petaloid scales.

Section Integrae Gilg. (4 petaloid scales).
S. striata Lam.
Section Bilobae Gilg. (8 petaloid scales)
S. dodecandra (L.) Druce (S. erecta Lam.)
S. ciliata (L.) Lam. (S. longiflora Lam.)
Section Trilobae Gilg. (12 petaloid scales).
S. martiana Meisn. (S. leiosiphon Gilg).

Fresh material was preserved in alcoholic formalin acetic acid (FAA), then dehydrated and embedded in paraffin. Both the chloroform method and the tertiary butyl alcohol method were tried (Johansen, 1940) The latter was found to be more suitable for the material. Serial transverse sections were cut 12 μ in thickness, then stained with crystal-violet and erythrosin (Jackson, 1926). This staining technique was found to be more suitable than safranin and fast-green (Johansen, 1940) as it shows better the xylem elements which in some cases are very small and only slightly lignified. At least 3. specimens of each species were sectioned, and in some cases also longitudinal sections which were used in conjunction with the transverse sections for reconstruction of the course of vascular bundles.

Several methods were tried for clearing the tissue in the upper part of the floral tube in order to observe the course of the bundles directly. The best results were obtained by 1. clearing with lactic acid, and 2. dehydrating in butanol series and clearing in xylol. No clearing or bleaching reagent was found to be effective for clearing the petaloid scales, which in *Struthiola* spp. consist in the outer layers of large, brownish tannin containing cells. Strong bleaching agents were tried, as H_2O_2 + NH_4OH in various concentrations but these caused maceration while the stained cells remained unbleached. For that reason it was found necessary to remove the petaloid scales from cleared flowers. The vascular bundles of the tube and sepal lobes were then traced with aid of a projection microscope. T/S diagrams were drawn with the aid of a camera lucida.

Terminology.

The terms used in the present work to designate floral organs and vascular tissue are used according to the definitions in Eames and MacDaniels (1951) and Eames (1961). The petal-like structures which are inserted at the mouth of the floral tube are termed petaloid scales. The vascular bundles of the floral tube which are opposite to the sepal lobes and those which alternate with them are designated as antisepalous and alternisepalous bundles respectively.

In describing divisions or branching of a vascular bundle, the terms tangential and radial division refer to the position of the line separating between the resulting bundles in relation to the centre of the floral tube, not to the position of the resulting bundle. The terms tangential and radial division are used in a similar manner as the terms periclinal and anticlinal divisions respectively are used in cell division, according to the definition in Esau (1960, P. 43).

The term hypanthium has been used by various authors to describe different structures and in some cases was used interchangibly with receptacular-cup and calyx-tube. To avoid confusion the terms suggested by Lawrence (1951), which are based on anatomical studies, will be used. Hypanthium is defined as a cup like structure inserted below the ovary, formed by fused bases of perianth segments and stamens. The hypanthium may surround the superior ovary, or may be fused to the ovary wall, in which case the ovary is inferior. But it does not consist of receptacular or stelar tissue. Hypanthium is thus distinguished from receptacular cup which is formed by extension and invagination of the receptacle, and therefore contains two cylinders of stelar bundle with the inner one inverted. (Eames and MacDaniels, 1951). Hypanthium is also distinguished from calyx tube which is formed by connate bases of sepals only.

The genus Struthiola.

Species of Struthiola are characterized by having spike-like inflorescences with sessile flowers, usually solitary, each subtended by a bract and two bracteoles. The floral tube is slender, circumscissile near the top of the ovary. Petaloid scales 4-12, free and fleshy, each surrounded by hairs. Struthiola is distinguished from Gnidia, to which it is closely related, by having 4 stamens (5 in the rare pentamerous flowers) alternating with the sepal lobes. The upper whorl of antisepalous stamens, which is present in other genera as Gnidia, Lachnaea, Cryptadenia and Daphne, is absent in Struthiola.

Description of the morphology and vascular anatomy of the flower based on serial sections.

1. Struthiola striata. (fig. 1-49). (p. 17-33).

The peduncle, bracts and floral receptacle.

A transverse section at a nodal region of the flower bearing stem shows a horse-shoe-shaped group of vascular bundles cut off the vascular cylinder of the stem and diverges laterally. The bundles increase in number and become arranged in form of a cylinder. It represents the cylinder of the peduncle plus its subtending bract which are congenitally fused. (figs 5-6. See also fig. 53-62 for S. martiana, and discussion on the nodal structure, p. 66)

On the abaxial side 3 traces diverge to the floral bract leaving a single gap, (i.e. a unilacunar node). (Fig. 5). Soon after entering the bract the traces divide to form many bundles. At a slightly higher level single traces diverge laterally from the peduncular cylinder to the two bracteoles on either side of it. (fig. 6). A minute axillary structure can be observed in some cases at the level of separation of the bracteoles from the peduncle. (fig 22). The ring of vascular bundles that is left after the divergence of traces to bracts and bracteoles represents the contracted pedicel of the sessile flower, or the receptacle.

The floral receptacle is very short. Slightly above the level of insertion of the bracteole, 8 traces diverge radially outwards to the base of the floral tube. The 8 bundles constitute the vascular supply of the floral tube (the hypanthium) and represent the fused bases of perianth members and adnated stamens. The 8 tube bundles are characteristic of most members of the Thymelaeaceae. Bundles from the remainder of the receptacular cylinder supply the ovary.

<u>The gynoecium and hypogynous disc.</u>

The ovary is borne on a short stalk or gynophore, which becomes distinguishable from the rest of the receptacular tissue as it is delimitted by large heavily staining epidermal cells. A small hypogynous disc divided in its upper part into irregular lobes can be observed surrounding the base of the ovary like a colar. (fig. 7-8. See also L/S fig. 4*). No vascular supply was observed to diverge towards the disc. The irregular disc lobes do not show any relationship in number or in

---

*Note: The L/S diagram is based on L/S of the flower and on reconstruction of the serial transverse sections. The horizontal lines and numbers correspond to the level of serial T/S fig. 7 - 21).

position to the tube bundles or to other floral organs.

At the base of the ovary 4 carpellary bundles can be observed (fig. 8-11). A single bundle at the dorsal side and 2 bundles arranged laterally near the ventral side represent the bundles of a fertile, functional carpel. They are designated as dorsal carpellary (DC) and ventral carpellary bundles (VC) respectively. The fourth bundle runs along the ventral side of the ovary. It represents the dorsal bundle of a sterile, abortive carpel (sDC). The ventral bundles of this carpel have either aborted and disappeared, or possibly fused with the ventral carpellaries of the fertile carpel. The dorsal carpellary bundle is not well differentiated at the base and lower part of the ovary and becomes more distinct at a higher level, first with unlignified and then with lignified xylem elements. (fig. 11).

The ovary is unilocular. It contains a solitary anatropous ovule which is laterally attached and almost pendulous from the ventral ovary wall near its top. The raphe is ventral and the micropyle facing up. The style is excentric, attached on the top of the ovary above the placental region. (fig 4.)

The 4 carpellary bundles run along the length of the ovary. The ventral bundles are slightly larger than the other. They run close to the sterile dorsal bundle (sDC) near the ventral side. A small branch from one of the ventral carpellary bundles was observed to diverge towards the ovule. (fig. 14). This branch constitutes the ovule trace (OvT) which runs down the funiculus and along the ventral raphe (fig. 11-13), and terminates at the chalazal region at the base of the ovary (fig 9-10) In the specimen described no connection between the other ventral carpellary bundle and the ovule trace could be seen with certainty. Near the top of the ovary above the placental region, both ventral bundles tend to move towards the dorsal side. The ventral bundle that supplied the ovule bifurcates into 2 branches that join again at a higher level and enter the laterally attached style together with the sterile dorsal carpellary bundle (SDC). (fig 15-20). These 2 bundles run along the style on either side of the stylar canal. The other carpellary bundles terminate at the top of the ovary. The slender style extends to about $\frac{2}{3}$ - $\frac{3}{4}$ of the floral tube and terminates in a capitate hairy stigma. (fig 2).

It appears that the vasculation of the ovary described above is not uniform in all the flowers of S. striata. In another specimen examined, a slightly different pattern was observed.* (fig. 22-25). The vascular supply of the ovary consisted of 3 traces. At the ventral end there were only 2 ventral bundles, and it appears that both supplied the ovary. Both ventral bundles entered the style.

The floral tube.

The long floral tube contains 8 conspicuous bundles. (fig. 21, 26). 4 of the bundles are opposite the calyx lobes, and are therefore designated as antisepalous bundles. Alternatively they can be called sepal midribs or sepal dorsal bundles (S). The other 4 bundles alternate with the first ones and with the calyx lobes, and can be

---

* It will be noted that both specimens were from the same collection and from the same clump of plants.

therefore designated as alternisepalous bundles. (Alt S).
The alternisepalous bundles are opposite to the 4 petaloid scales (ps) which are inserted at the mouth of the tube. The 4 stamens are situated on the alternisepalous bundles, and are therefore opposite to the petaloid scales and alternating with the sepal lobes. The stamens are inserted at the upper part of the tube below its mouth, so that the anthers are included. (See L/S diagram, fig. 2., T/S diagram, fig 13A)

Each of the 8 tube bundles consists of a central core of xylem more or less surrounded by internal phloem, external phloem and parenchyma. The internal phloem is somewhat less than the external phloem. Bundle caps of unlignified thick walled fibers are present on the external side of the bundles, mainly in the upper part of the tube.

The floral tube is circumscissile near the top of the ovary. The upper part is shed after anthesis, while its base is persistent and encloses the fruit. The line of abscission can be seen as a slight constriction in the walls of the tube. (fig. 4).
In L/S abscission zone can be seen (fig 48).

In the upper part of the tube, below the point of insertion of the stamens, each of the alternisepalous bundles divides tangentially to form an external and an internal bundle. (fig. 27).
The internal bundle is the stamen trace. It contains no observable differentiated xylem and appears to consist of phloem and parenchyma only. It enters the short filament, which is at first embedded in the tube tissue, and runs in the anther along the connective. (fig. 28-30). At the same level of separation of the stamen, or in some cases slightly higher, each of the alternisepalous bundles bifurcates by radial division to form 2 major branches (fig. 27). At middle level of the stamens

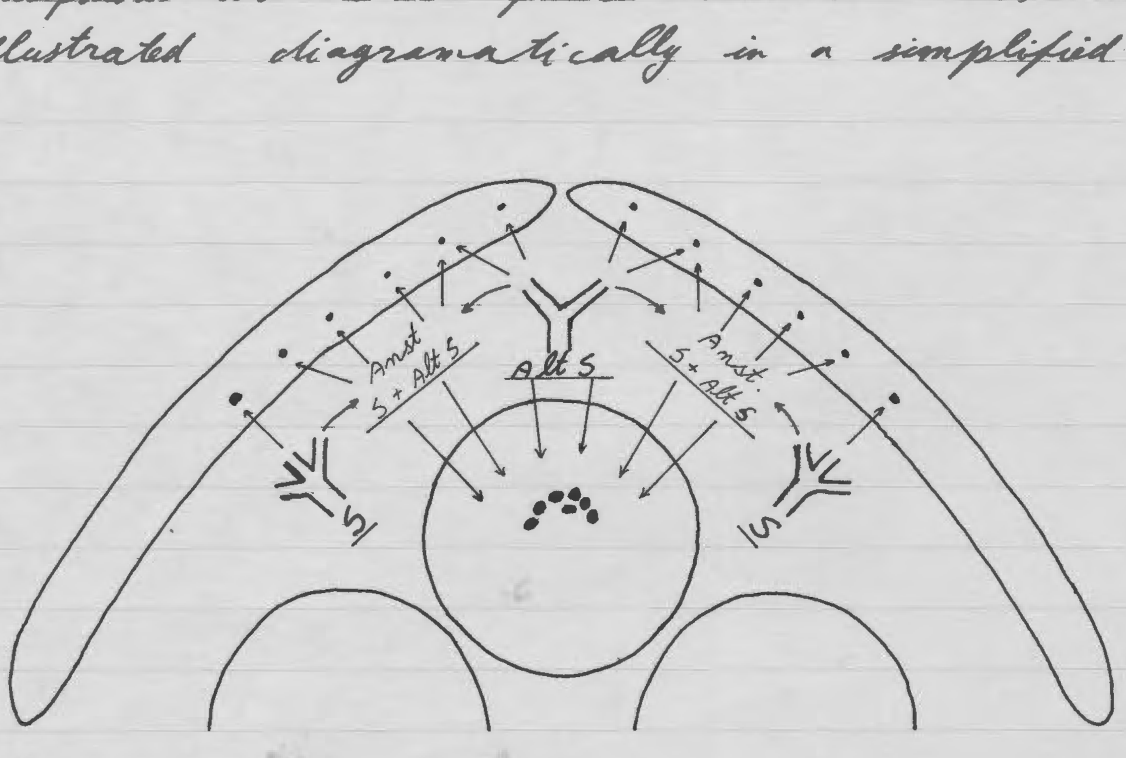
the tube bundles consist of 4 antisepalous bundles (S) alternating with 4 alternisepalous double bundles (Alt S) (fig 29).

The vascular supply of the petaloid scales and sepal lobes near the mouth of the floral tube.

Closer to the mouth of the tube below the base of the petaloid scales, the major branches of the alternisepalous bundles divide to form a number of strands that are spread laterally. The antisepalous bundles also divide, usually into 3 branches or groups of strands. (fig 31-33). The strands which mostly run obliquely or horizontally increase in number and become more scattered. Branches derived from antisepalous and alternisepalous bundles approach each other and form a more or less continuous net-work of vascular tissue, so that it becomes difficult to trace the identity of individual bundles. The ramifying branches form a complicated system of anastomoses near the base of the petaloid scales, just below the level of emergence of the petaloid scales and sepal lobes. Anastomoses occur between branches derived from the same bundles, or between branches of adjacent bundles. (The course of the bundles can be seen by observing carefully the diagram from cleared material, fig. 3, serial T/S diagrams fig. 30-39 and photomicrographs of T/S, fig 40-44 and tangential L/S, fig. 43-45, 47).

A generalized basic pattern as observed in serial T/S and checked by examining cleared material and L/S, is as follows: The median branch of an antisepalous bundle (S) continues into the sepal lobe as a midrib, which is only slightly more conspicuous than the other veins.

Lateral branches of antisepalous bundles approach neighbouring branches derived from the alternisepalous bundles. They form anastomoses that send traces outwards to supply the marginal parts of the sepal lobes and inwards to supply the petaloid scales. Other anastomosing branches derived from the alternisepalous bundles supply in a similar way the central portions of a petaloid scale and the margins of 2 adjacent sepal lobes behind it. The vascular supply of a sepal lobe is therefore derived (proceeding from the centre of the lobe to its margins): 1. From the sepal midrib. 2. From anastomoses of adjacent branches of antisepalous and alternisepalous bundles. 3. From branches of alternisepalous bundles. The vascular supply of a petaloid scale is derived from 1. Branches of the alternisepalous bundle in the centre. 2. Anastomosing branches of antisepalous and alternisepalous bundles. This can be illustrated diagramatically in a simplified way:



S - Antisepalous bundle.
Alt S - Alternisepalous bundle.
Anst. - Anastomosis between branches of adjacent antisepalous and alternisepalous bundles.

Before entering the petaloid scales, the vascular tissue appears like a network of xylem elements running obliquely and horizontally at the base of the scales. (fig. 37, 43). 4-6 conspicuous bundles can be seen at the level of separation of the scales from the floral tube. (fig 37-38, fig. 49). The vascular strands extend to about 1/4 - 1/3 of the total length of the petaloid scales. (fig. 49). The upper part of the scales consist of parenchymatous tissue of large cells containing heavily staining tannin sacs.

Struthiola striata (Fig 1 - 25, pp. 19-24).

Fig. 1. A flower.
" 2. L/S diagram.
" 3. Skeleton of the vascular tissue of the upper part of the flower.
" 4. L/S diagram of the lower part of the flower.
Fig. 5 - 21. Serial T/S through the lower part of the flower.
" 5-6. The peduncular cylinder. Divergence of traces to bracts and bracteoles.
" 7-8. The lower part of the floral tube and the base of the ovary. The lobes of the hypogynous disc appear as a colar around the base of the ovary.
" 9. The ovule trace (OvT) at its lowest point at the chalazal end of the ovary.
" 10. Termination of the ovule trace at the chalazal region.
" 11. T/S at middle level of the ovary, showing the 4 carpellary bundles and the ovule with 2 integuments. The ovule trace is seen in the ventral raphe.
" 12. T/S of the floral tube and the ovary.
" 13. The ventral part of the ovary showing the ventral carpellary bundles of the functional carpel (VC) and the dorsal bundle of a reduced, sterile carpel (sDC)
" 14. The ovary at the placental region. A branch from the ventral bundle diverges towards the ovule.
" 15-16. The ovary near the micropylar end, showing bifurcation of one of the ventral carpellary bundles.
" 17-19. Termination of the dorsal carpellary bundle (DC) and one of the ventral carpellaries (VC) at the top of the ovary.
" 20. The floral tube and the top of the ovary at the level of insertion of the style. A ventral bundle (VC) and the dorsal bundle of the abortive carpel (sDC)

enter the style.

Fig. 21 The floral tube and the style showing 2 bundles and the stylar canal.

Fig. 22-25. Serial T/S of the lower part of the flower. (a specimen with 3 carpellary traces).

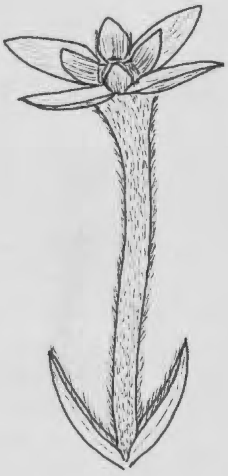
" 22. Divergence of traces to the bracteoles.

" 23. The floral tube and lower part of the ovary showing a dorsal carpellary and 2 ventral carpellary bundles. The ovule trace is seen arching over the base of the ovule in the chalazal region.

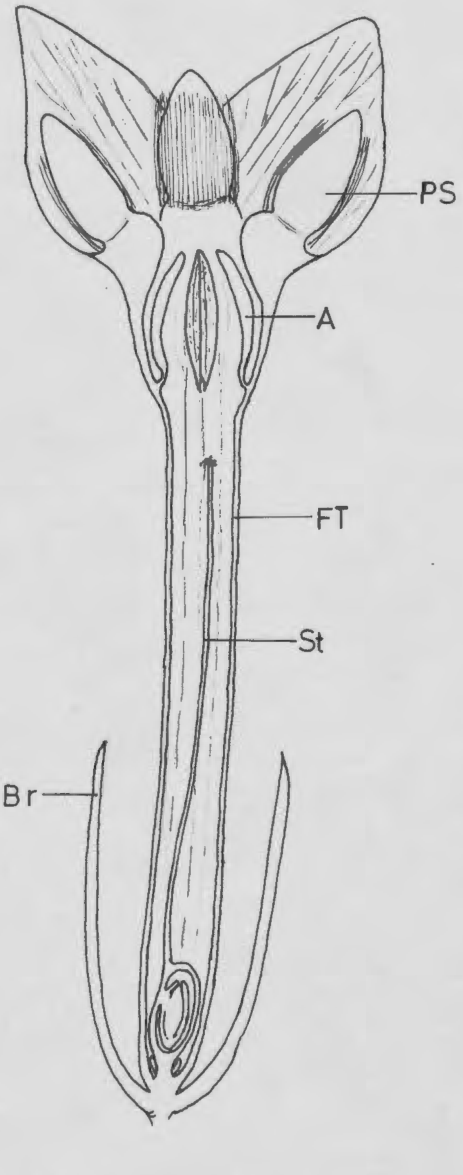
" 24. T/S at middle level of the ovary.

" 25. T/S at the placental region.

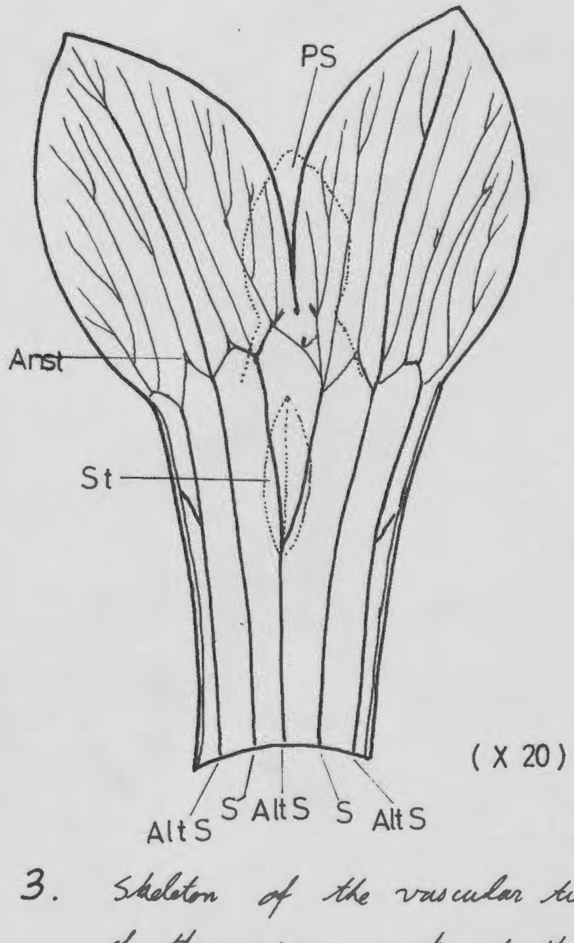
Struthiola striata.



1. A flower. (X 6)



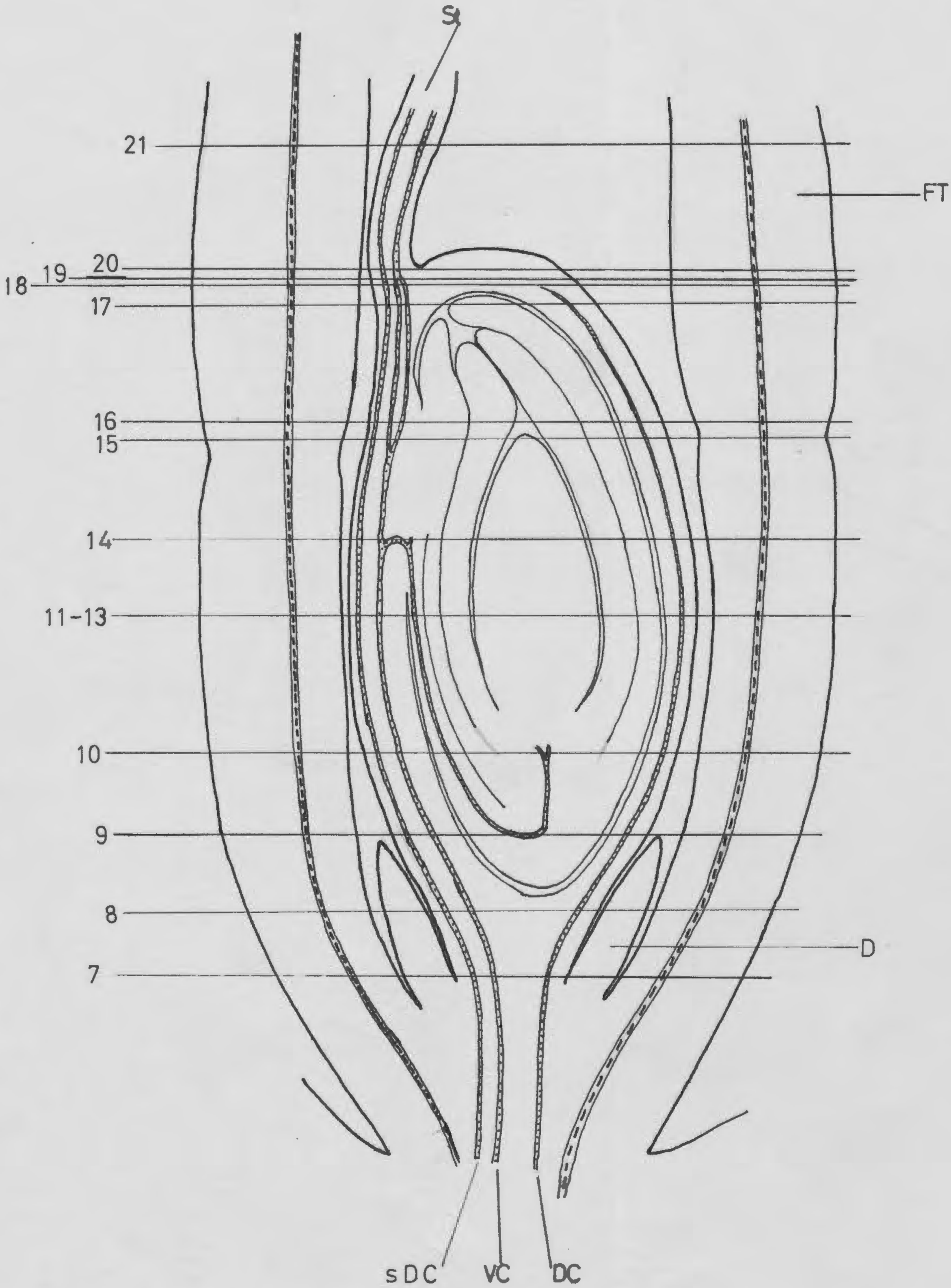
2. L/S diagram. (X 15)



3. Skeleton of the vascular tissue of the upper part of the floral tube and sepal lobes. (The petaloid scales and stamens were removed. Their position is shown in broken lines).

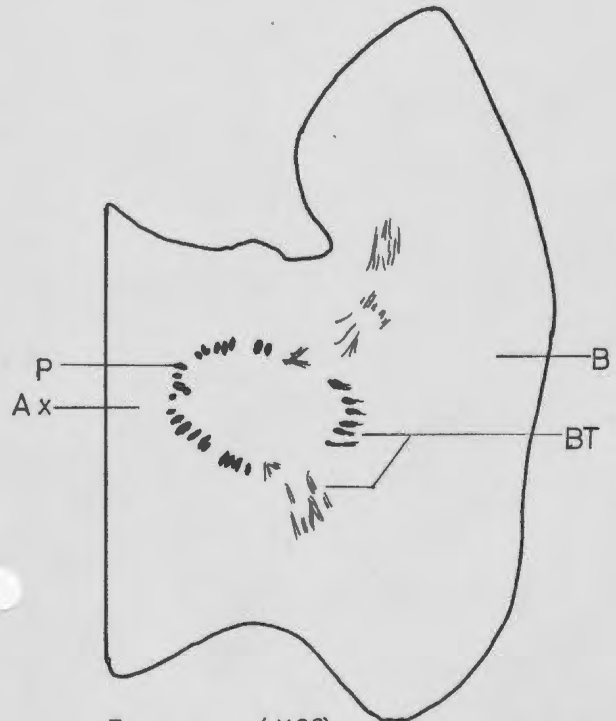
Struthiola striata

4. L/S diagram of the lower part of the flower.

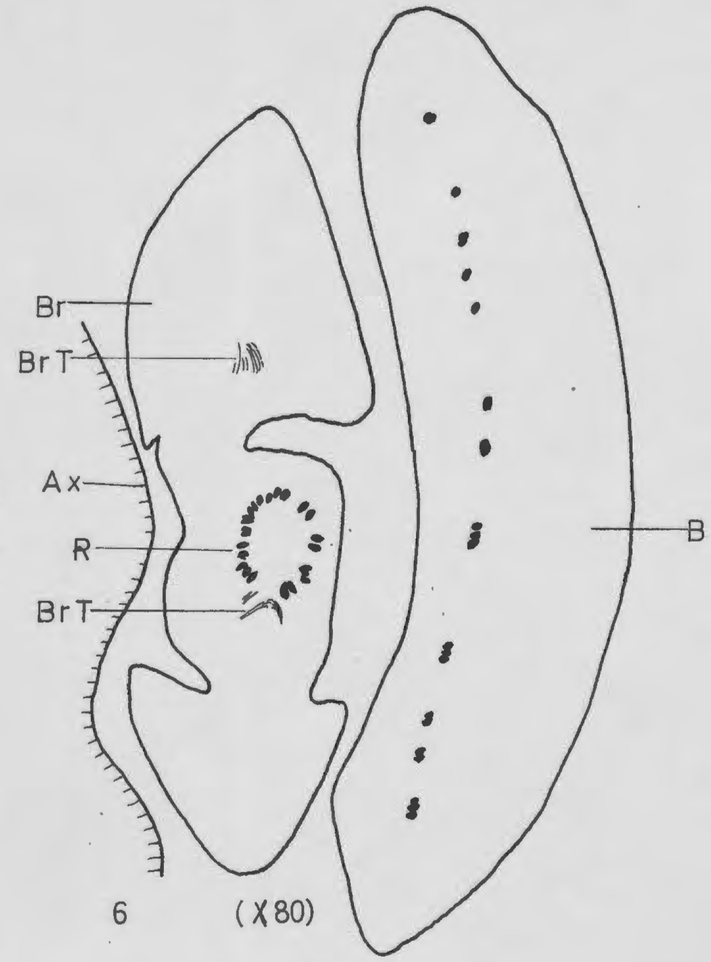


Note: The horizontal lines and numbers correspond to the level of serial T/S, fig. ~~7-21~~ 7-21.

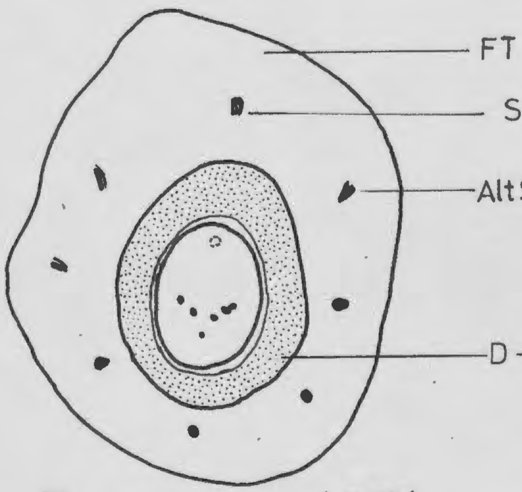
Struthiola striata.



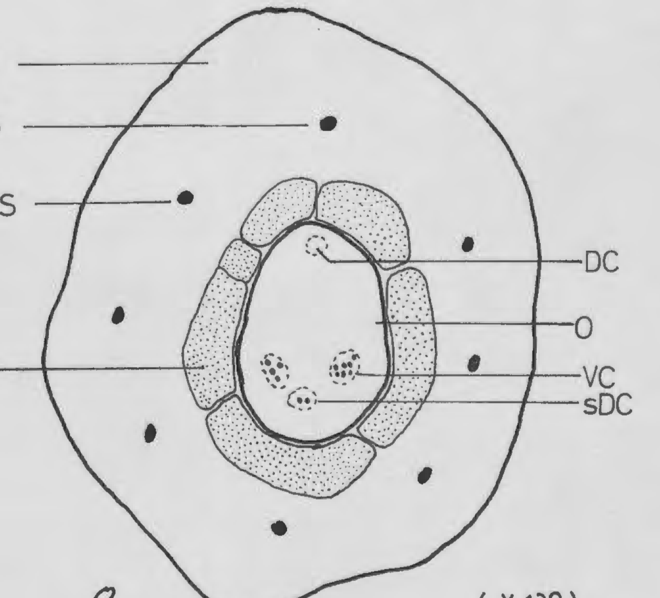
5 (X80)



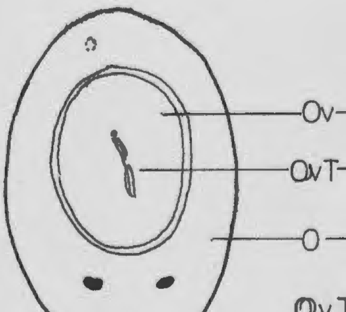
6 (X80)



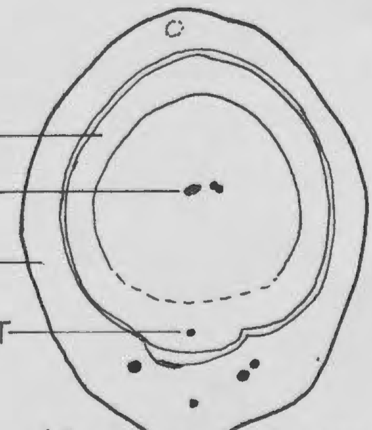
7. (X 115)



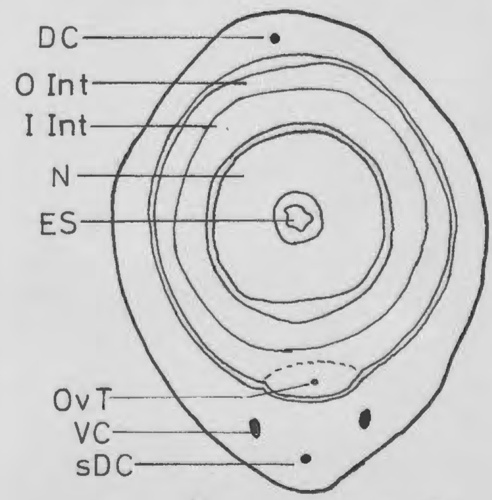
8. (X 130)



9. (X 160)

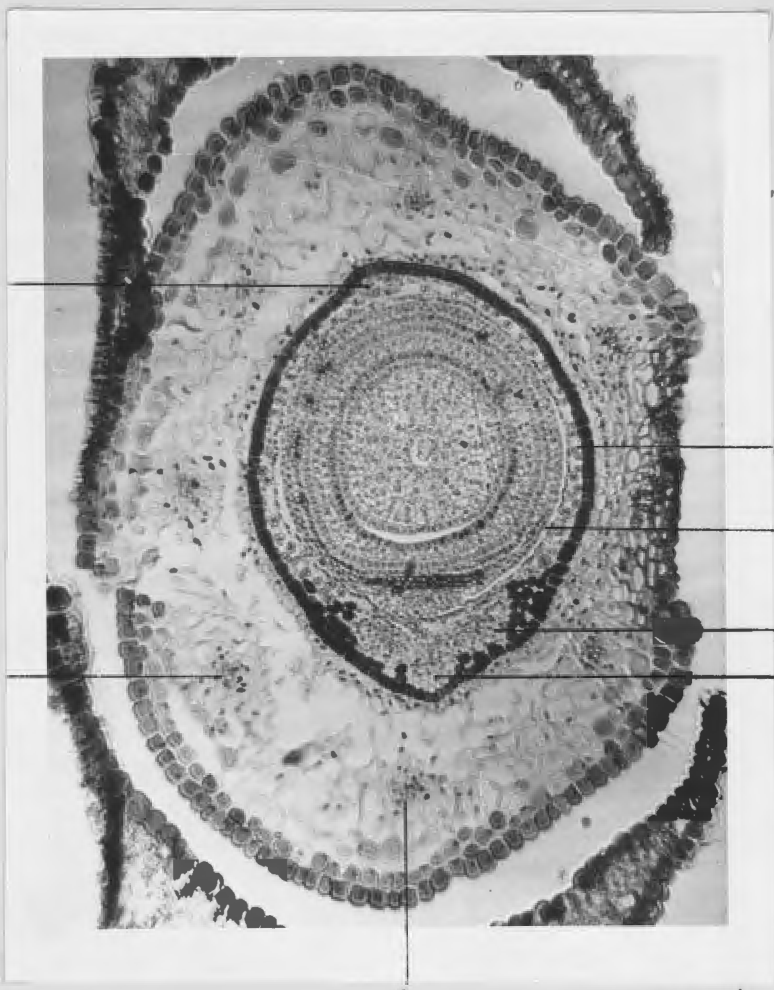


10. (X·160)

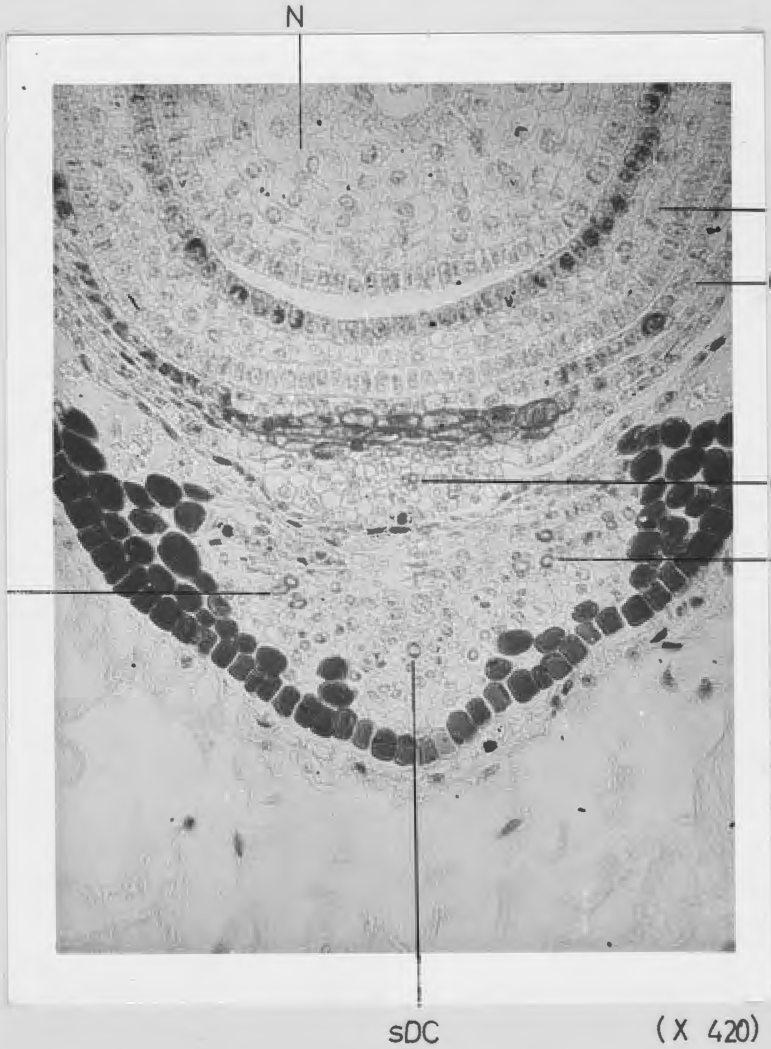


11. (X 160)

Struthiola striata

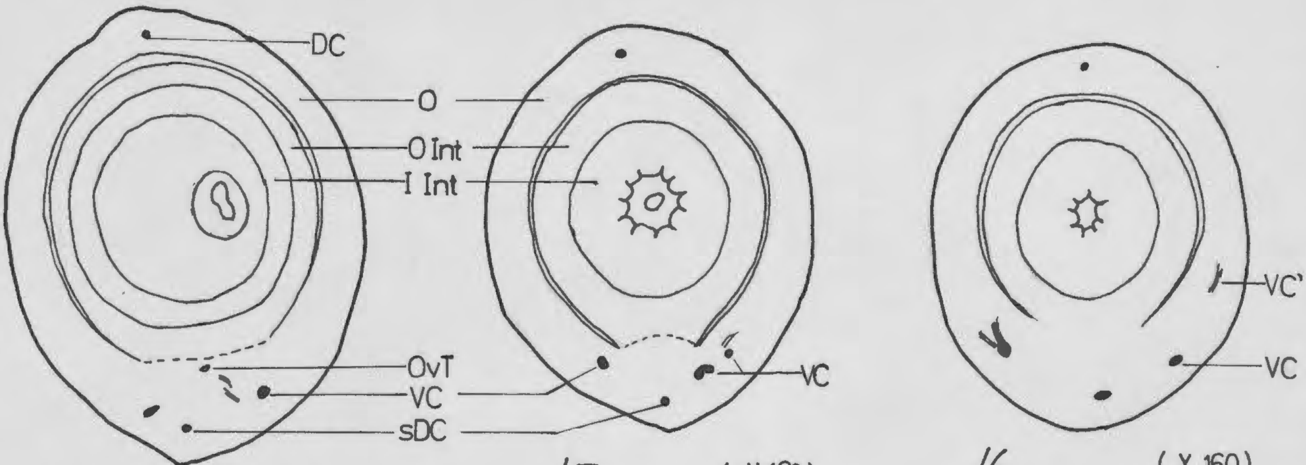


12 (X 150)



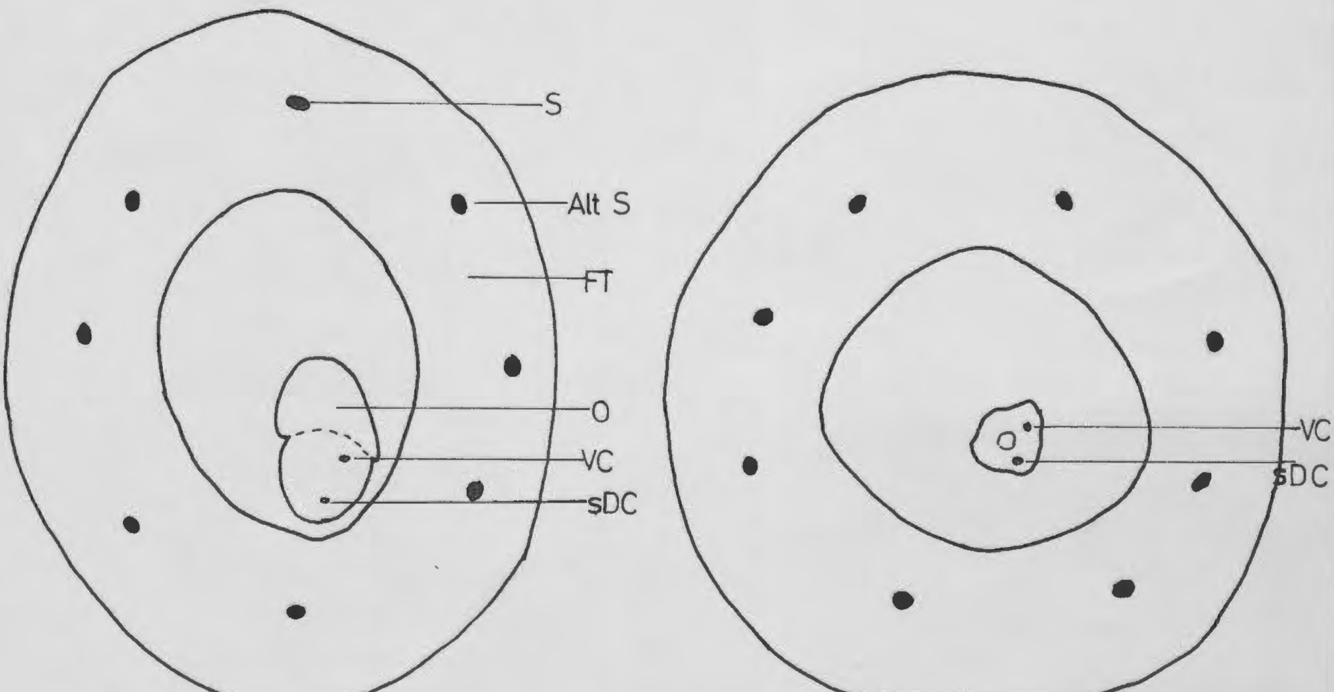
13 (X 420)

Struthiola striata



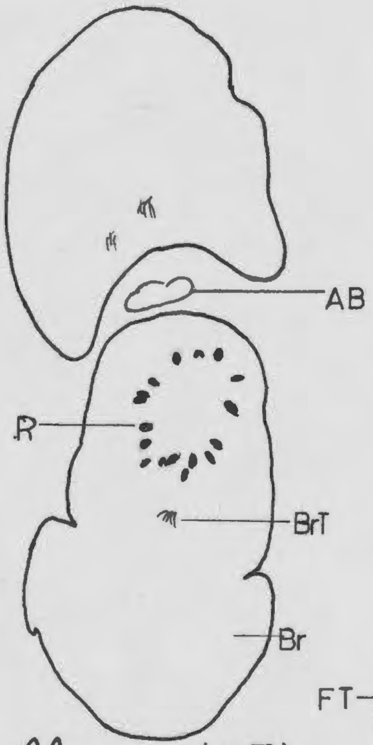
14. (X 160)   15. (X 160)   16. (X 160)

17. (X 160)   18. (X 160)   19. (X 160)

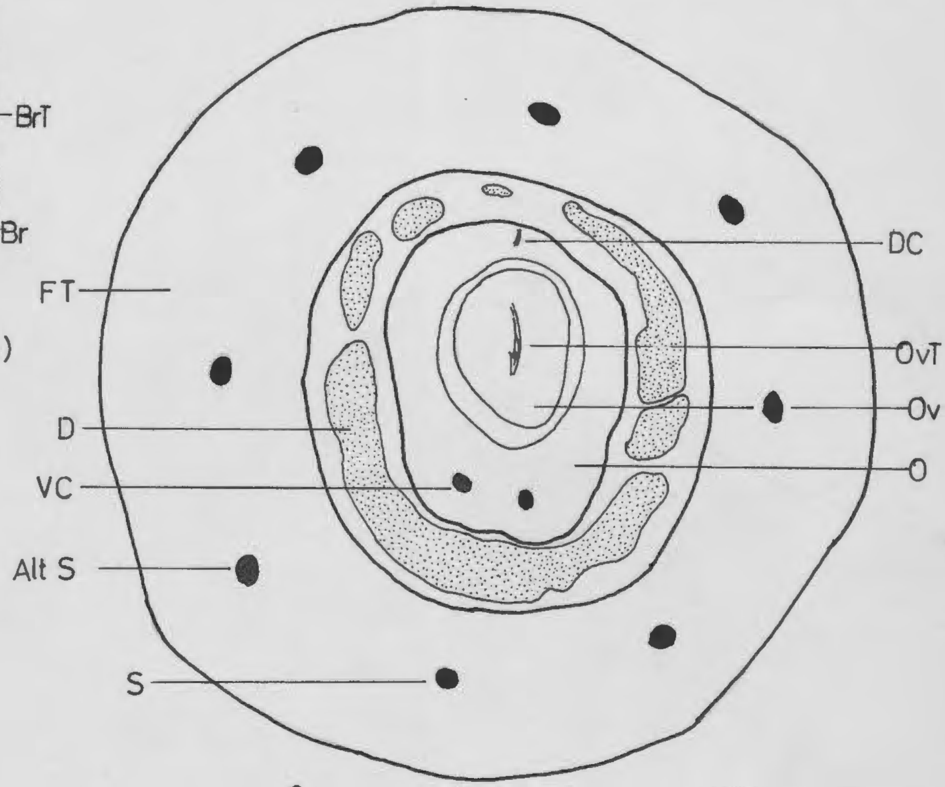


20. (X 130)   21. (X 130)

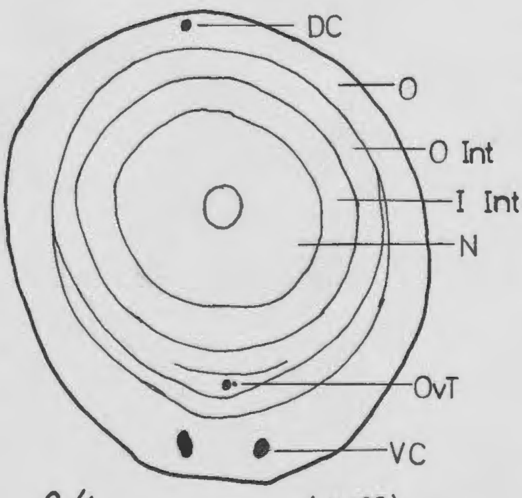
Struthiola striata



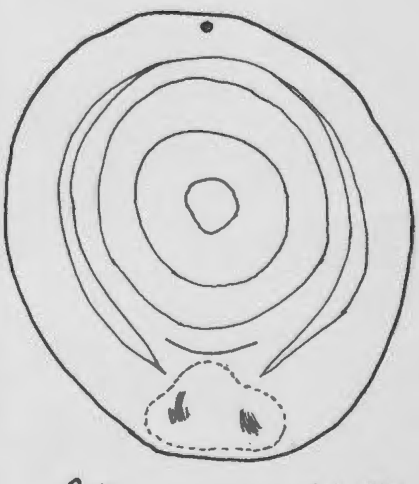
22. (X 78)



23. (X 180)



24. (X 180)



25. (X 180)

Struthiola striata. (Fig. 26-49, pp. 27-33).

Fig. 26 - 30. Serial T/S of the floral tube at the level of insertion of the stamens.

Fig. 26. The floral tube showing 8 bundles.

Fig. 27.- Tangential and radial division of the alternisepalous bundles. (Alt S).

Fig. 28. Separation of the stamens' filaments from the tissue of the floral tube.

Fig. 29 - 30. The floral tube at the middle level of the stamens.

Fig. 31-39. Serial T/S of part of the floral tube, close to its mouth. The sections (which are slightly oblique) show branching and anastomosing of bundles at the base of the petaloid scales, and the origin of vascular supply of the sepal lobes and petaloid scales.

Fig. 31-33. Antisepalous (S) and alternisepalous bundles (Alt S) branch repeatedly.

Fig. 34-35. Bundles derived from antisepalous and alternisepalous bundles approach each other. The margins of the sepal lobes are supplied by traces derived from the alternisepalous bundles.

Fig. 36. Branches of bundles (S + Alt S) anastomose and send traces outwards, to supply the margins of lateral portions of the sepal lobes, and inwards, to supply the petaloid scales.

Fig. 37. The network of vascular tissue at the base of a petaloid scale.

Fig. 38-39. Separation of the petaloid scales from the tube and sepal lobes.

Fig 40-49. Photomicrographs of T/S and TL/S – the upper part of the flower.

Fig. 40. T/S of the floral tube near the base of the petaloid scales. (PS) A branch derived from an antisepalous bundle on the right (S) and a branch derived from an alternisepalous bundle on the left (Alt S) approach each other to form anastomosis.

Fig. 41-42. Anastomosis of bundles (Anst) at the base of the petaloid scales. Vascular strands diverge from the anastomoses to supply the sepal lobe above. (SL).

Fig. 43. Network of vascular tissue at the base of a petaloid scale.

Fig. 44. The vascular tissue of a petaloid scale at the level of separation from the floral tube.

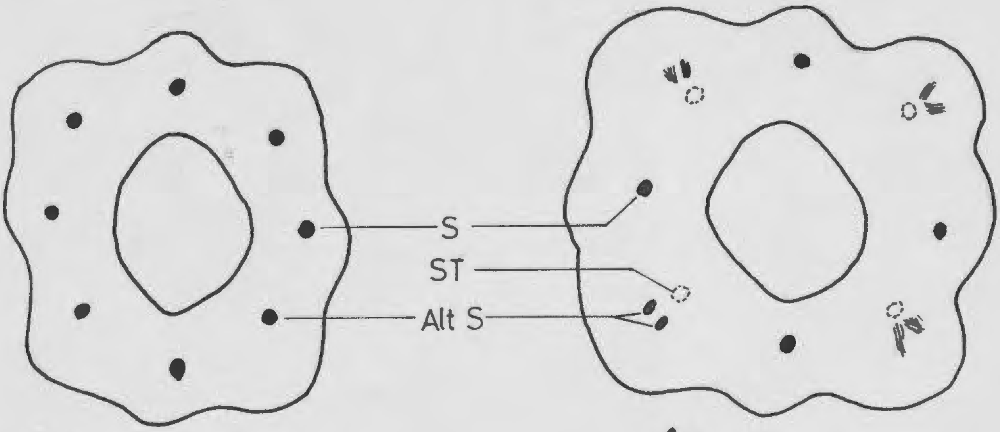
Fig. 45-47. Serial T/L/S near the mouth of the floral tube showing on the left an antisepalous bundle (S) divided into 3 main branches (S_1, S_2 and S_3), and on the right branches of an alternisepalous bundle. (Alt S). Adjacent branches derived from those bundles approach each other and anastomose (Anst). A network of anastomosing bundles can be seen at the base of the petaloid scales. (PS).

Fig. 48. TL/S of the lower part of the flower ~~near the top of the~~ showing the abscission zone around the floral tube near the top of the ovary.

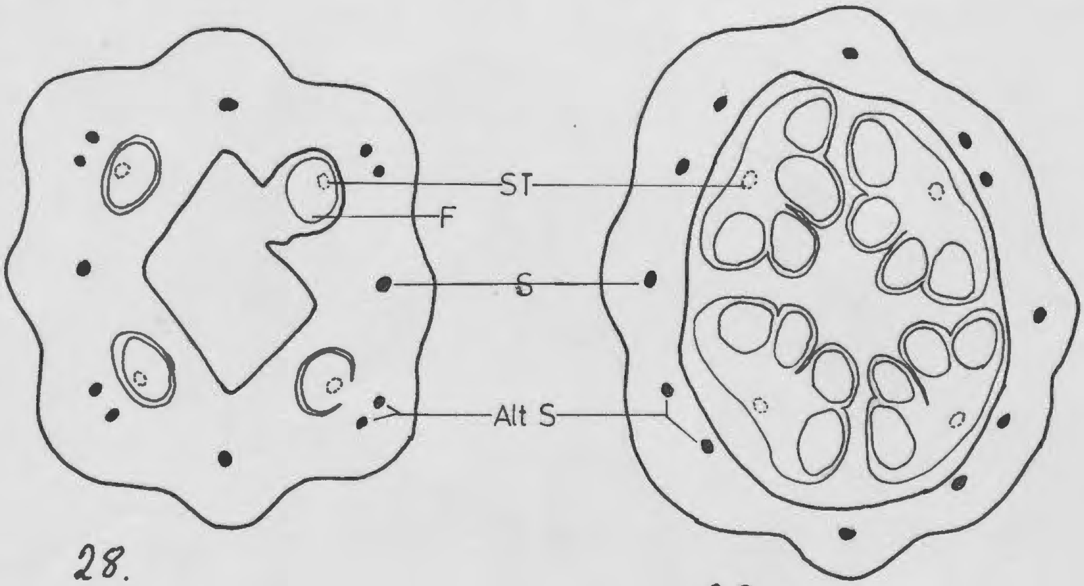
Fig. 49. L/S of a petaloid scale showing its vascular tissue.

Struthiola striata

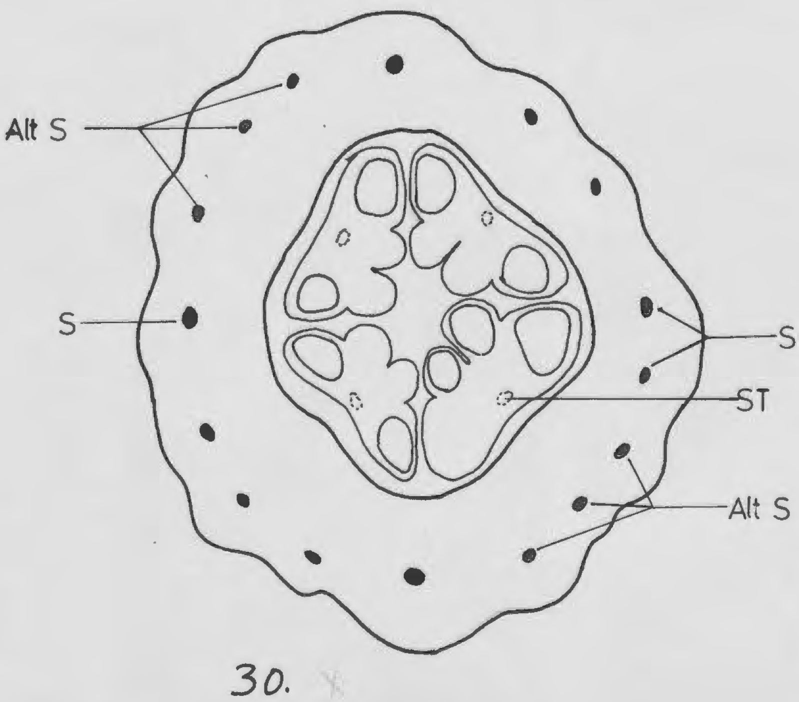
Fig. - 26 - 30(X 78)



26. 27.



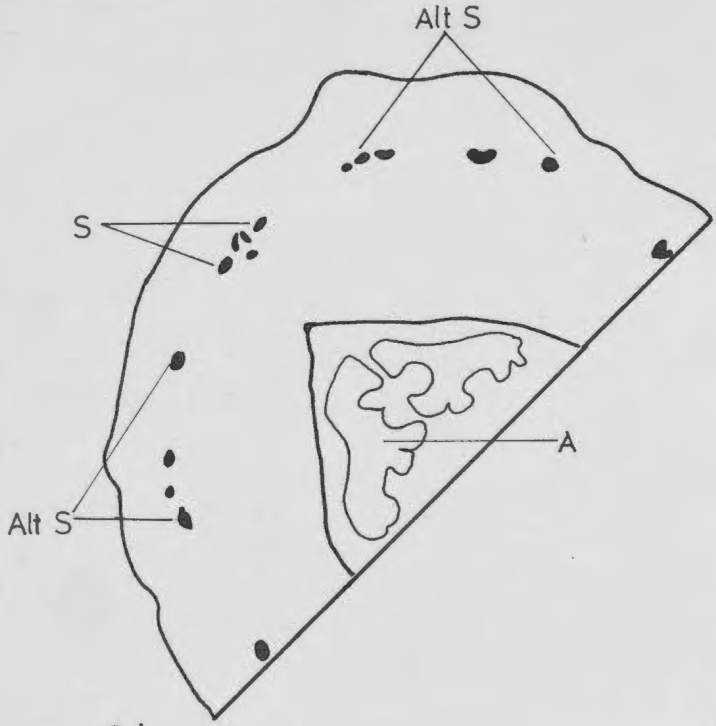
28. 29.



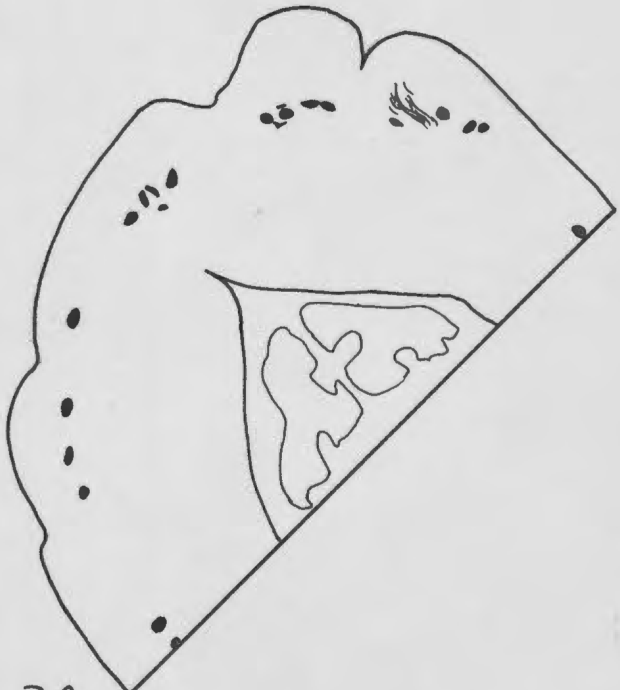
30.

Struthiola striata

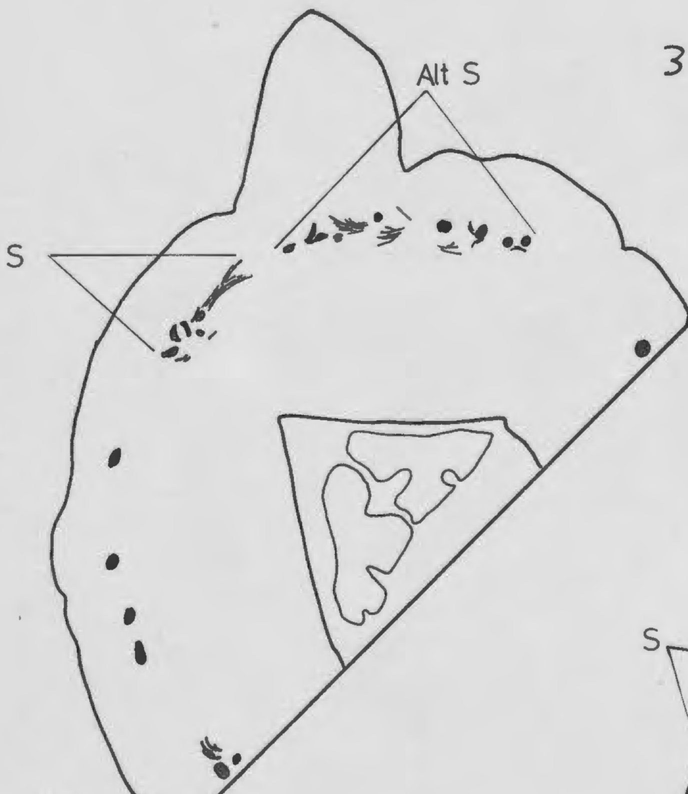
Fig. 31 - 34 (X 78)



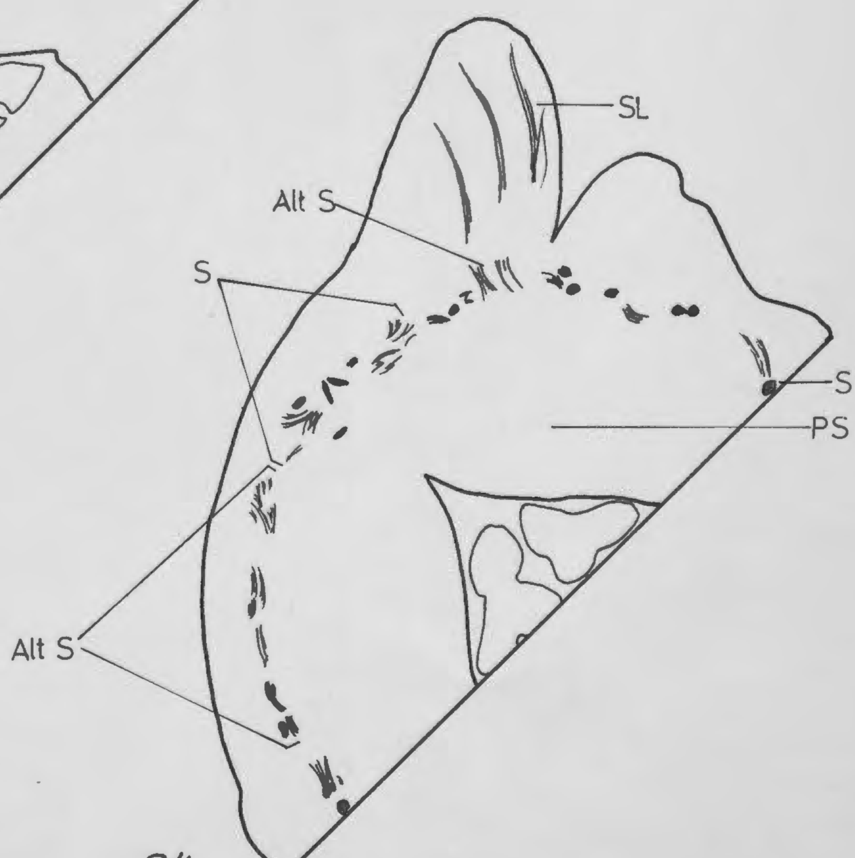
31.



32.



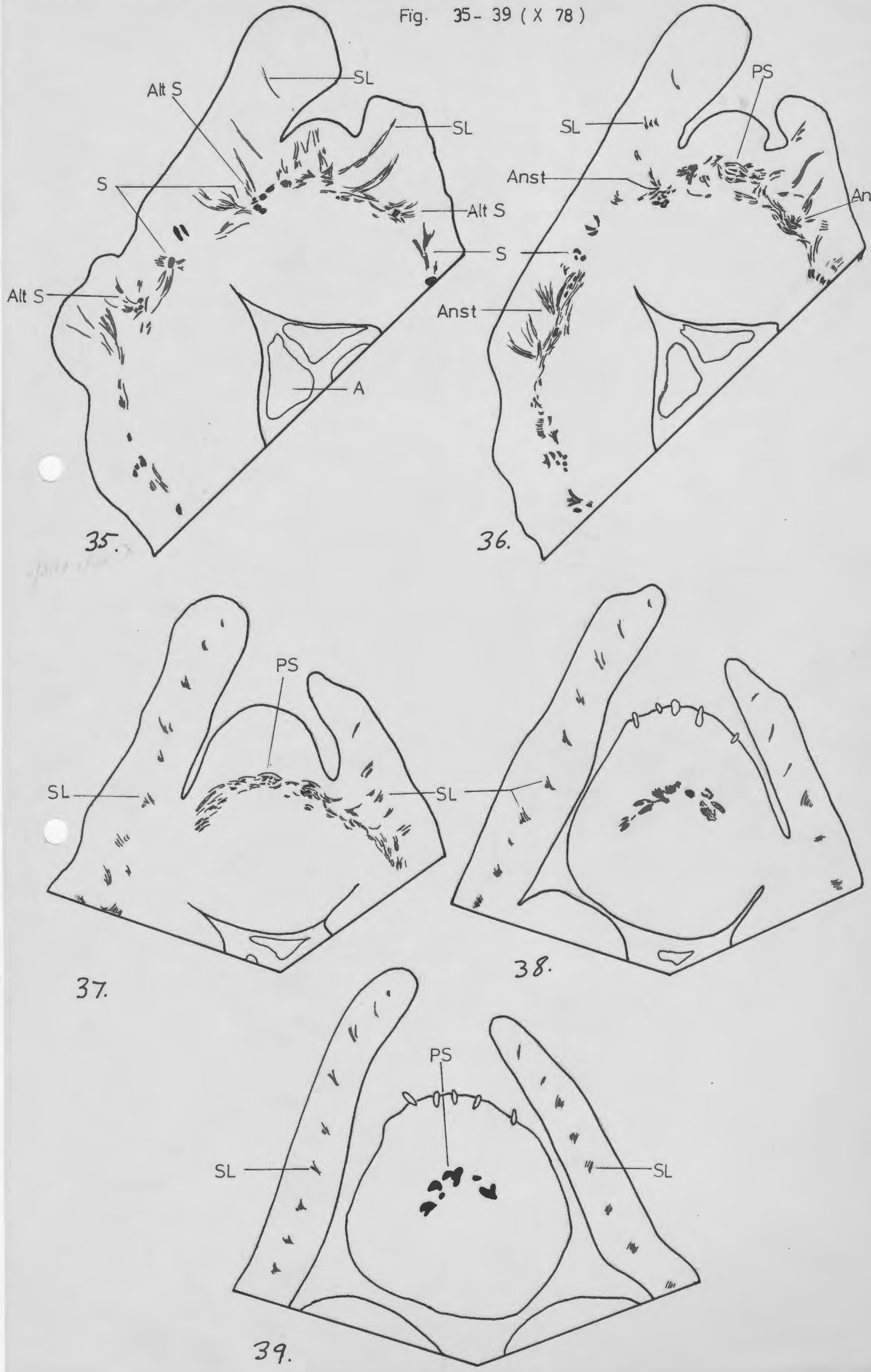
33.



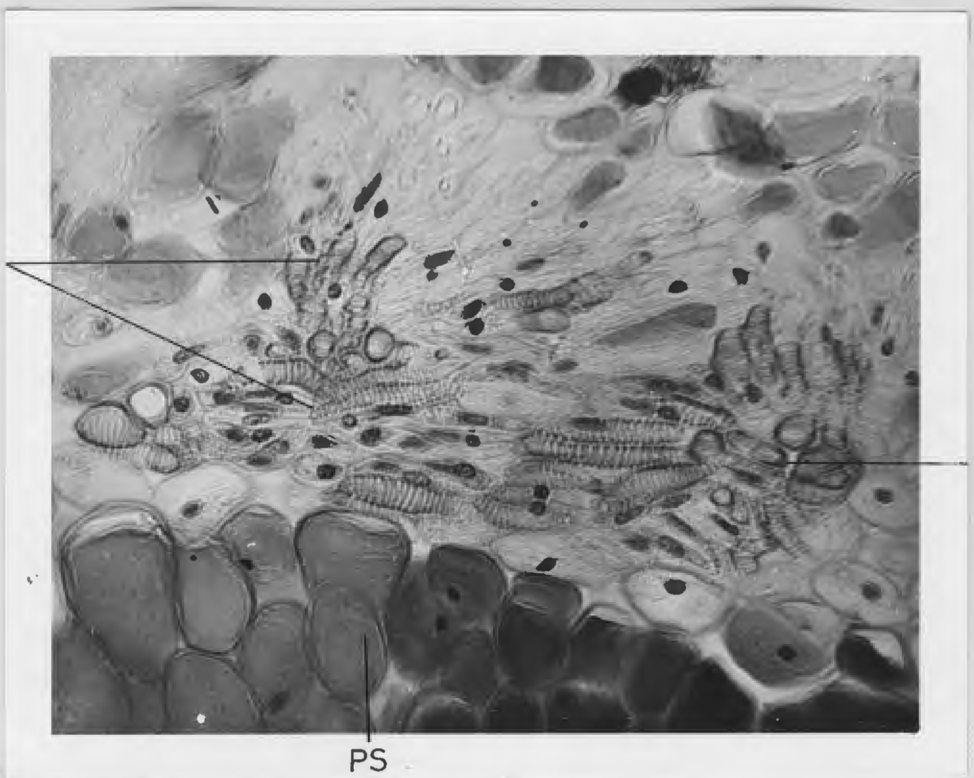
34.

Struthiola striata

Fig. 35- 39 (X 78)

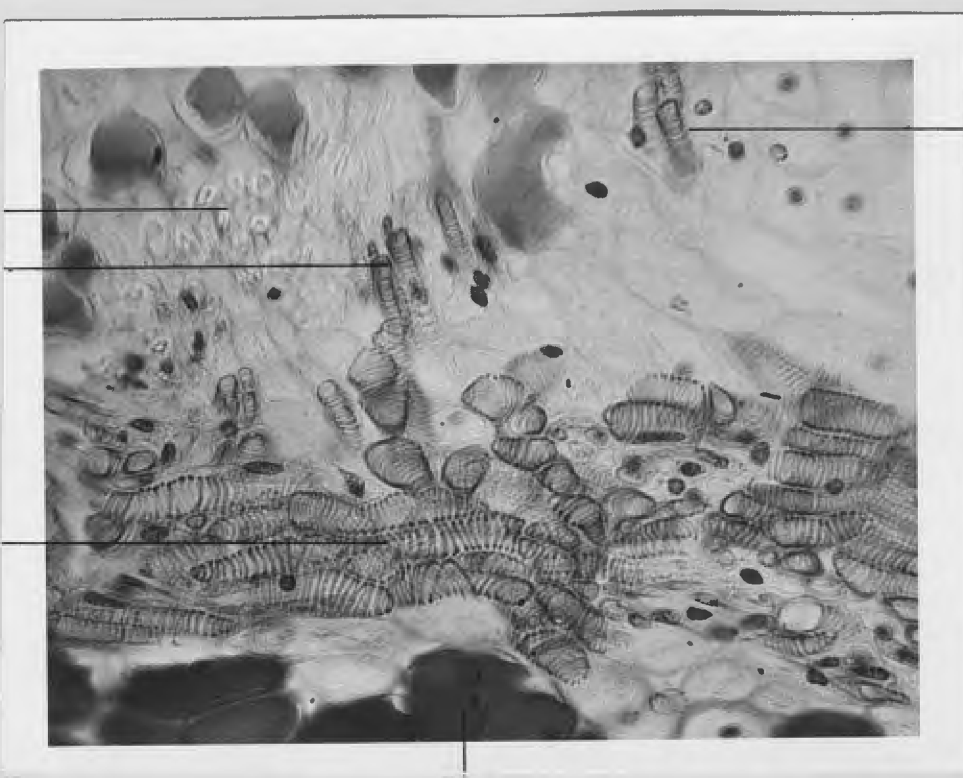


Struthiola striata.



40. (X 415)

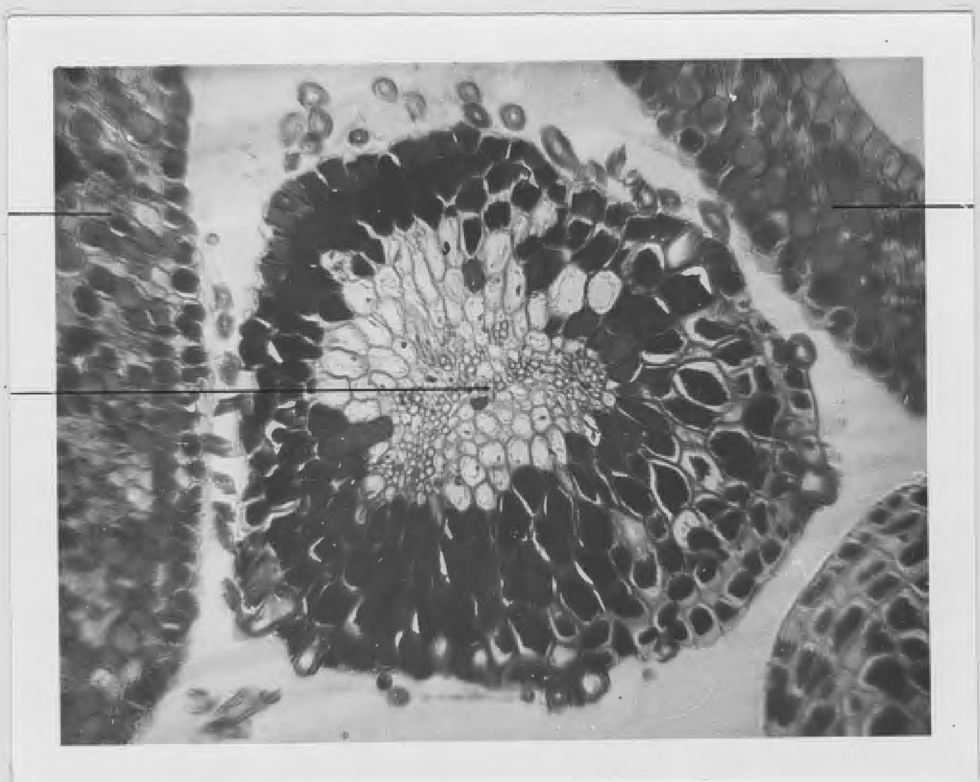
41. (X 415)



42. (X 450)

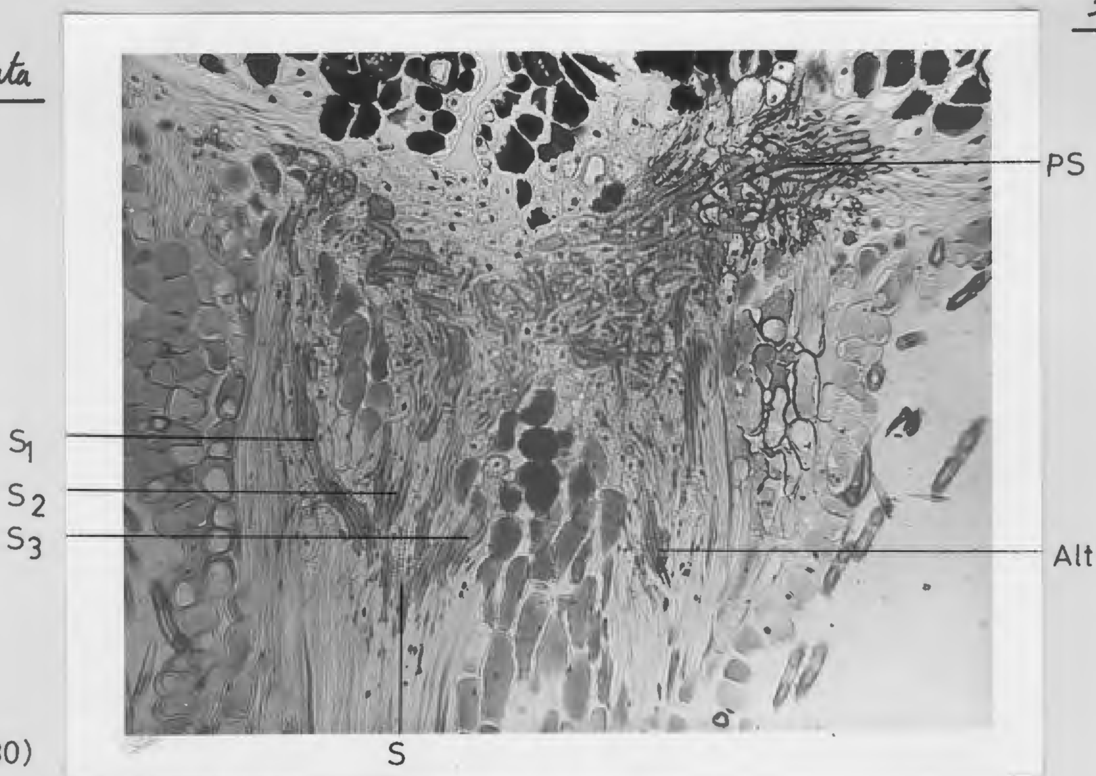
Struthiola striata.

43. (X 130)

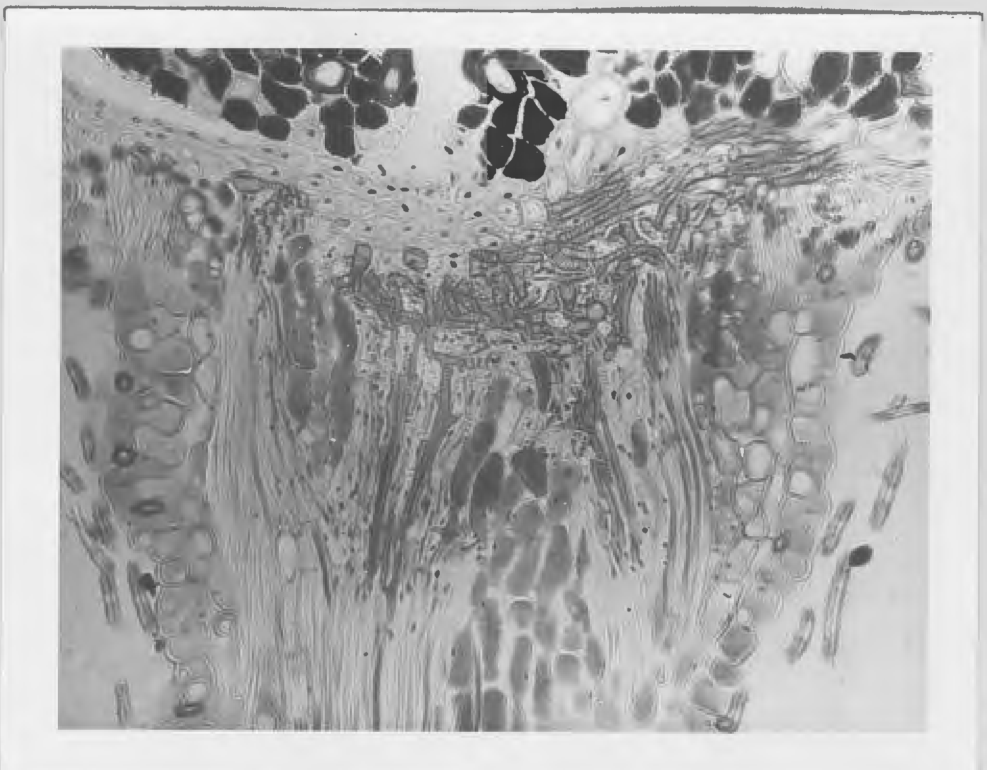


44. (X 120)

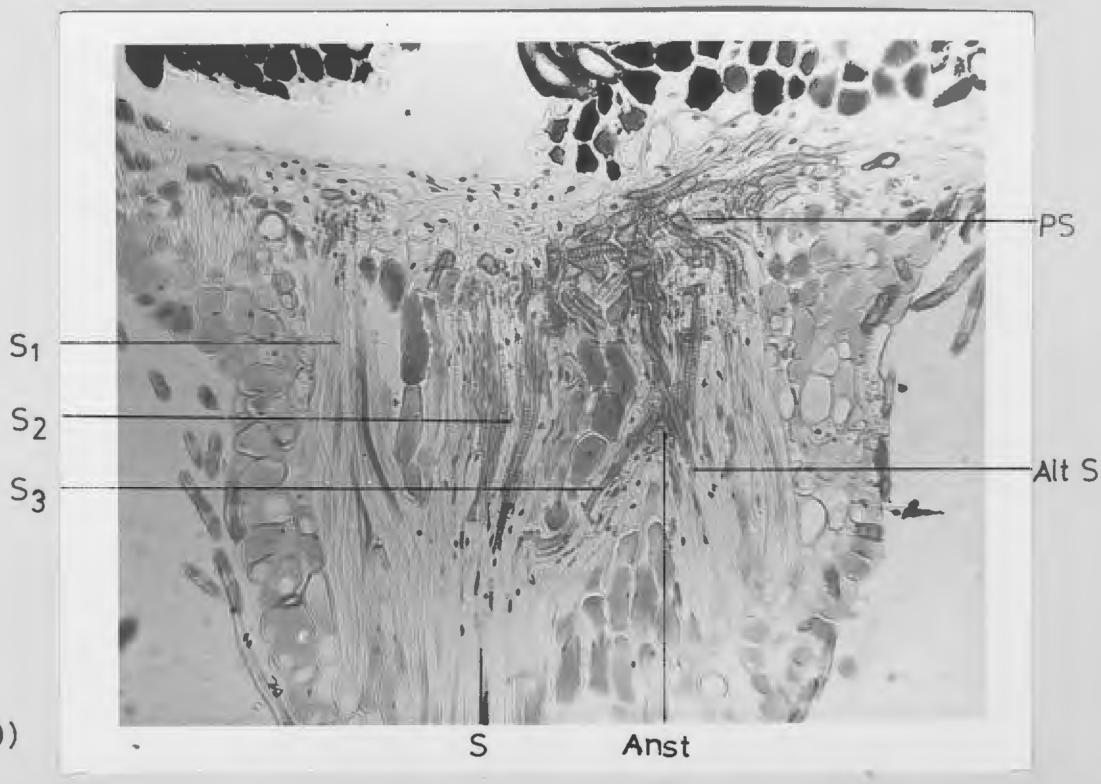
Struthiola striata



45. (X 130)

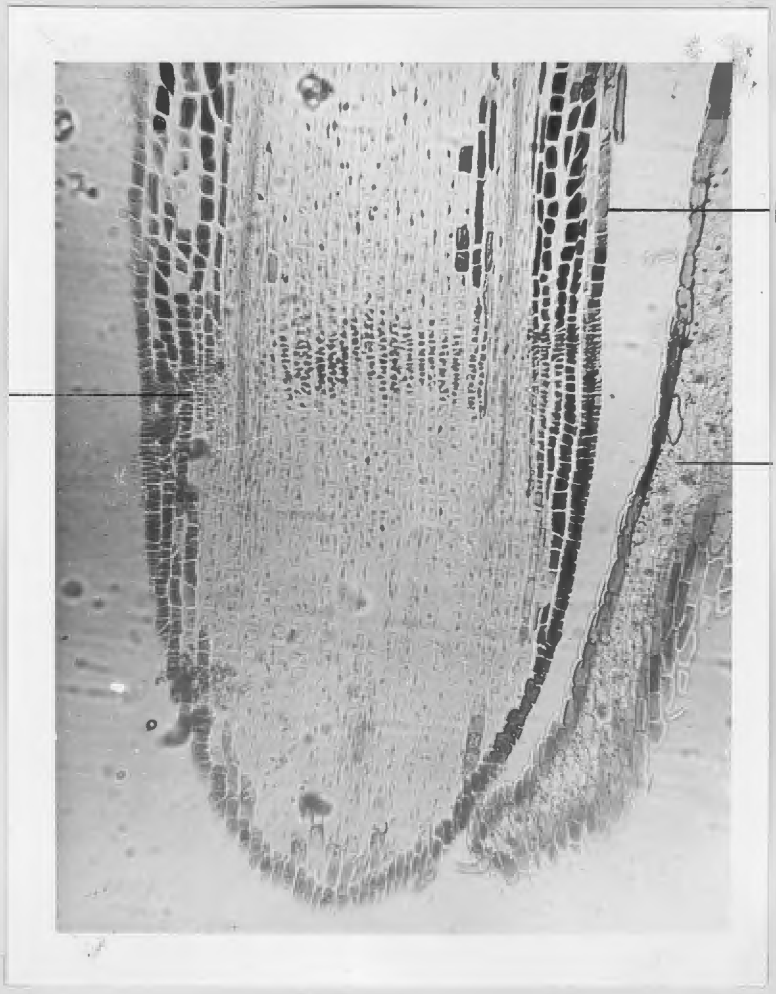


46. (X 130)



47. (X 130)

Struthiola striata



48. (X 120)

49. (X 90)

2. Struthiola martiana (Fig. 50-96, pp. 38-49).

The peduncle, bracts and floral receptacle.

The separation of the peduncular cylinder from the axis of the inflorescence and the divergence of traces to the bract and two bracteoles is as described for S. striata. (More detailed diagrams will be found in fig. 53-63).
An abortive axillary bud was observed in all the specimens of S. martiana sectioned. In some cases it is distinctly divided in its upper part into 3 lobes. It consists of small embryonic cells with dense content and large nuclei. (fig. 62-63). No vascular traces were observed to diverge to it.

At the base of the floral tube the 8 tube traces diverge outwards, leaving in the receptacular cylinder a rather large number of bundles. (fig. 64-65). Slightly at a higher level some of the bundles disappear, and the remaining bundles constitute the vascular supply of the ovary.

The ovary.

At the base of the ovary the dorsal carpellary bundle (DC) is not differentiated and therefore cannot be observed clearly. It becomes descernible at a higher level, first with unlignified and then with lignified xylem elements. The ventral carpellary bundles are rather scattered and arranged laterally. At a higher level they come closer to the ventral side. A small bundle at the ventral side can be observed at the base of the ovary (sDC, in fig. 67-68). It is possible that it represents the dorsal bundle of an abortive carpel as in S. striata. At a higher level this bundle diminishes and disappears, so that ~~that~~ the carpellary bundles at middle level of the ovary consist of a dorsal bundle and 2 larger ventral bundles near the ventral side. (fig. 70 - 73). Both ventral bundles supply the ovule. (fig 74 - 75). At a higher level they bifurcate. The two branches that face the dorsal side diverge dorsally and disappear at the top of the ovary. The other two bundles enter the lateral style and run along it on either side of the stylar canal. (fig. 76 - 78). The dorsal carpellary bundle arches over the top of the ovary and terminates (fig 79).

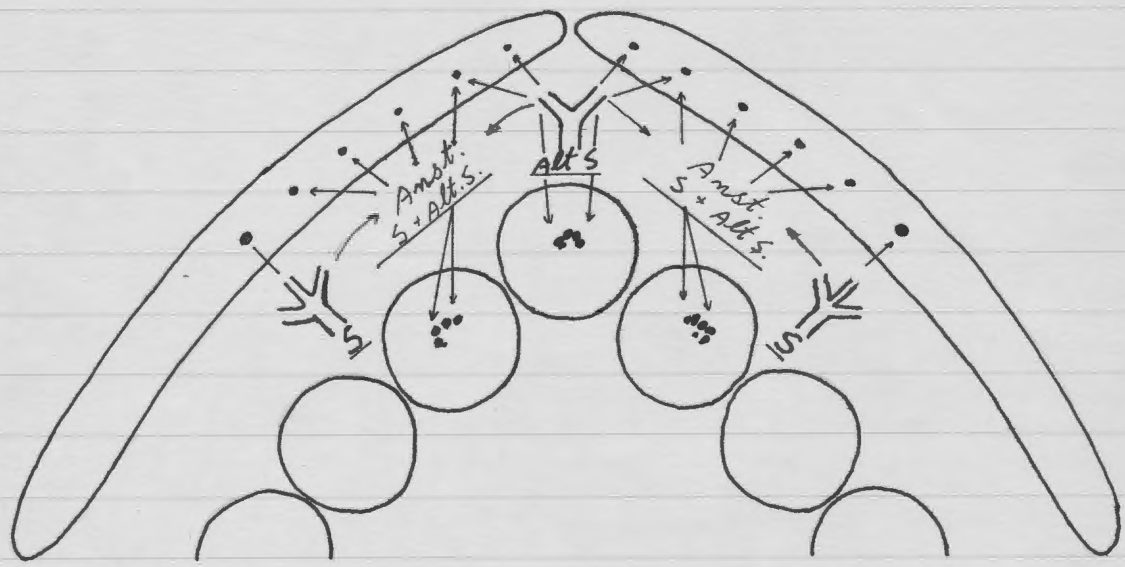
A peculiar feature was observed in the ovules of 2 specimens sectioned: the outer integument is separated from the inner integument for about 3/4 of its circumference at middle level of the ovule. (fig 73). In another specimen the structure of the ovule appeared normal. (fig 80 - 82). One of the ventral carpellary bundles appeared as a double bundle throughout the length of the ovary.

The vascular tissue at the mouth of the floral tube.

The structure and vascular pattern of the floral tube, as well as the insertion and vasculation of the stamens, is very similar to S. striata (fig 83 - 85). The vasculation of the petaloid scales and sepal lobes is also similar, in spite of the great difference in the number of scales. The 12 petaloid scales can be considered as 4 groups of 3 scales alternating with the sepal lobes. A group of 3 petaloid scales in S. martiana is equivalent to a single scale in S. striata, divided into 3 lobes to its base, as can be seen from the pattern of vasculation.

The branching of the antisepalous bundles to form

3 main bundles takes place very close to the mouth of the tube at the base of the petaloid scales, (fig 81), whereas the alternisepalous bundles bifurcate by radial division and branch at the same level of separation of the stamen trace (fig 52, 83). The central strands of an alternisepalous bundle (derived from 2 major branches of the alternisepalous bundle) supply the margins of 2 adjacent sepal lobes and the petaloid scale between them (the central petaloid scale in a group of 3). The central branch of an antisepalous bundle continues into the sepal lobe as a midrib. The intermediate portions of the sepal lobe between the midrib and the margins, and also 2 petaloid scales (the 2 laterals in a group of 3) are supplied by strands from anastomoses of branches of adjacent antisepalous and alternisepalous bundles. (fig. 87-94). A simplified diagramatic representation of the origin of vascular supply to the sepal lobes and petaloid scales :



By comparing S. martiana to S. striata (see diagram, p. 15) with regards to the position of the petaloid scales ~~in relation~~ in relation to the sepals and the origin of vascular supply of those organs, it becomes evident that 3 petaloid scales in S. martiana are equivalent to a single scale in *S. striata*.

The vascular strands in the petaloid scales extend up to a 1/4 of their total length. In their upper part the petaloid scales are purely parenchymatous.

Struthiola martiana (Fig. 50 - 82, pp. 40-45).

Fig. 50. A flower.
Fig. 51 L/s diagram of a flower.
Fig. 52 Skeleton of the vascular tissue of the upper part of the flower.

Fig. 53 - 82. Serial T/S through the lower part of the flower.
Fig. 53-56. Separation of the peduncular cylinder from the vascular cylinder of the stem.
Fig. 57-58. Divergence of traces to the bract.
Fig. 59-62. Divergence of traces to the bracteoles. Separation of the bract and bracteoles ~~from~~ the ground tissue of the peduncle. Note the small axillary bud in the axil of one of the bracteoles.
Fig 63. Axillary bud in axil of a bracteole. It represents an abortive branch of a dichasium. (see discussion, p. 67).
Fig. 64-66. The 8 tube bundles diverge from the floral receptacle to the base of the tube.
Fig. 67-68. The carpellary bundles at the base of the ovary. The dorsal carpellary bundle (DC) cannot be seen at this level. The small bundle at the ~~dorsal~~ ventral side, which represents the dorsal bundle of a sterile reduced carpel (SDC) disappears at a higher level.
Fig 69-70. T/S through the floral tube, the hypogynous disc and the base of the ovary.
Fig. 71. The ovule trace (Ov T) at its lowest point at the base of the ovary.
Fig. 72. Termination of the ovule trace at the chalazal end of the ovule.
Fig. 73. T/S at middle level of the ovary.
Fig. 74-75. The ovary at the placental region showing branches from the ventral carpellary bundles supplying

the ovule.

Fig. 76. Bifurcation of the ventral carpellary bundles (VC) above the placental region.

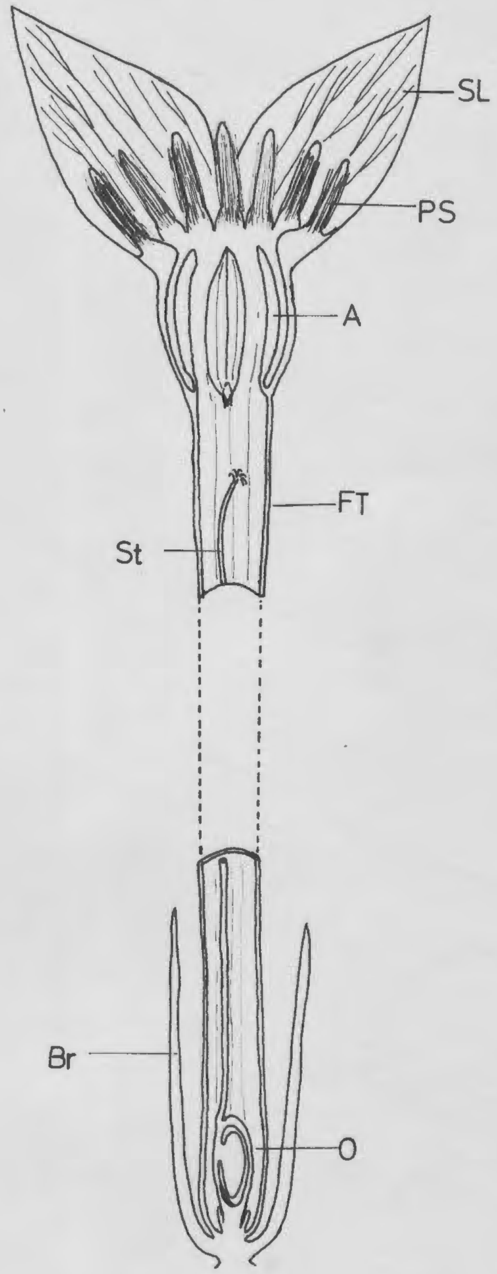
Fig. 77–78. The ventral carpellary bundles enter the style.

Fig 79. Termination of the dorsal carpellary bundle (DC) at the top of the ovary. The ventral carpellaries are seen in the style on either side of the stylar canal.

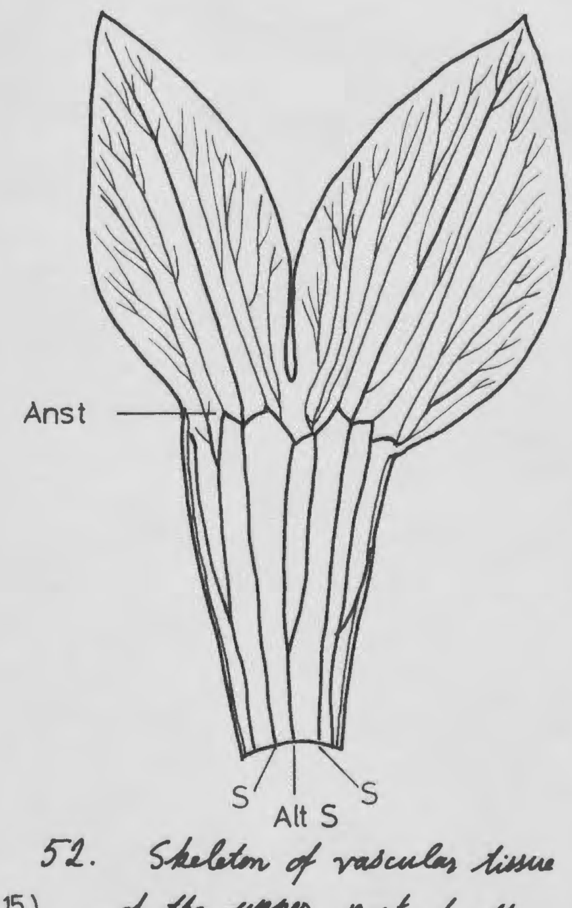
Fig. 80–82. T/S at the base and middle level of the ovary (in another specimen of S. martiana).

Struthiola martiana

50. A flower (X 3)



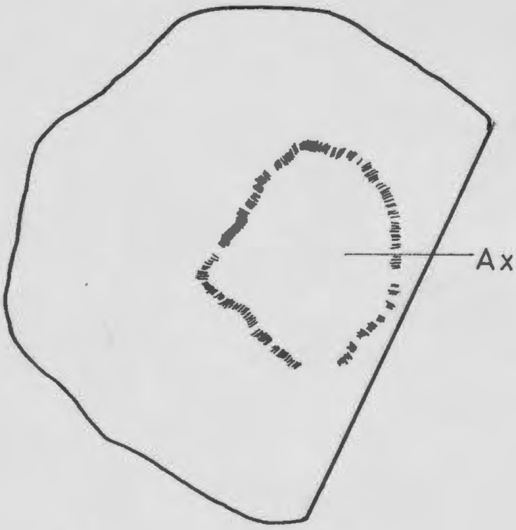
51. L/S diagram. (X 10)



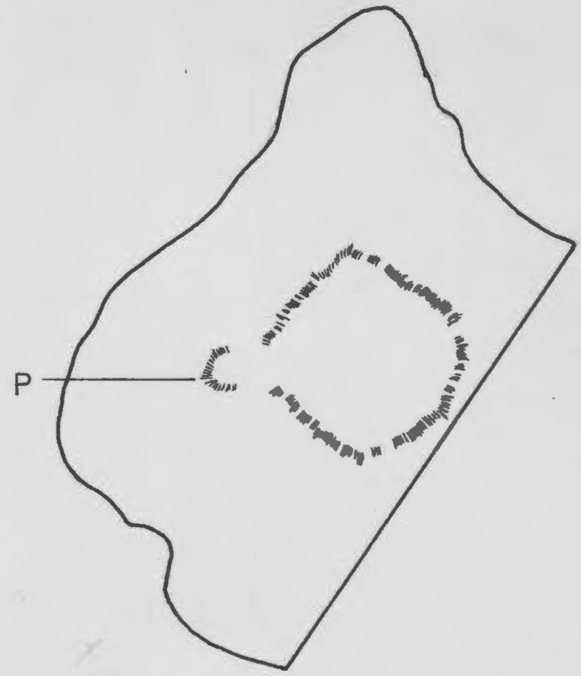
52. Skeleton of vascular tissue of the upper part of the floral tube and sepal lobes. (X 15)
(The stamens and petaloid scales were removed).

Struthiola martiana

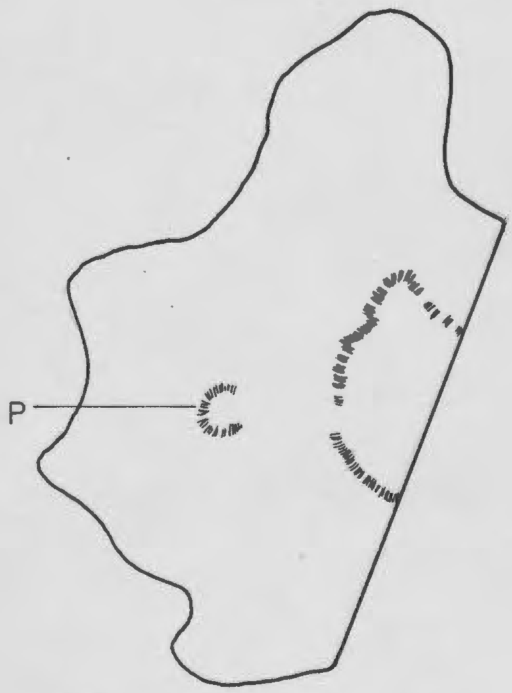
Fig. 53 - 58 (X 48)



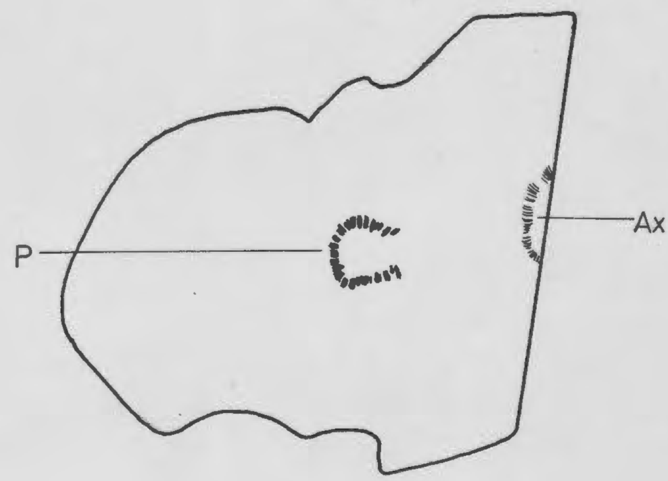
53.



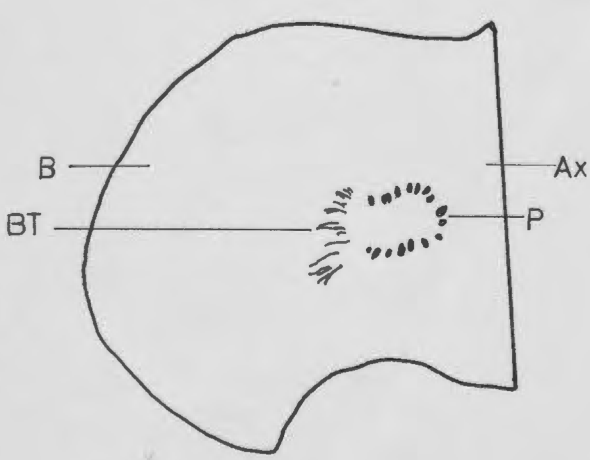
54.



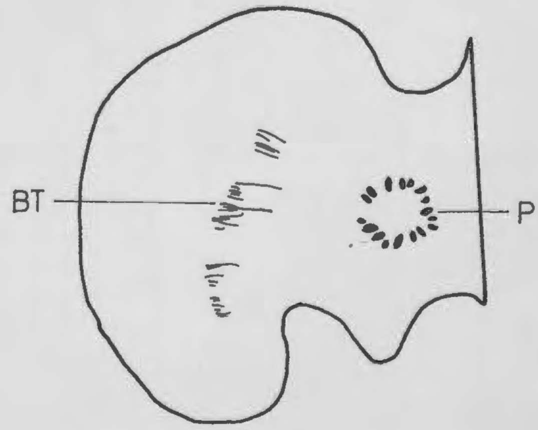
55.



56.



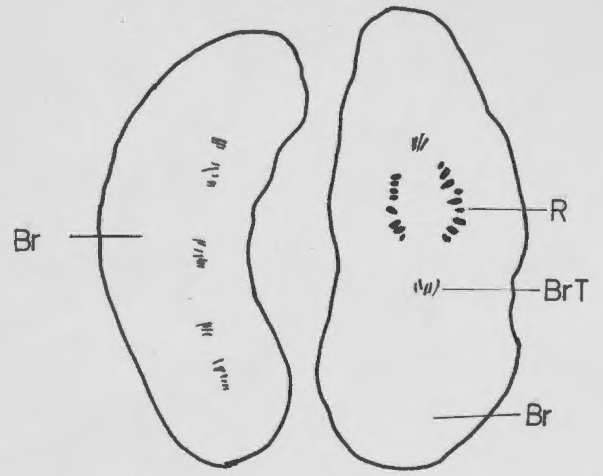
57.



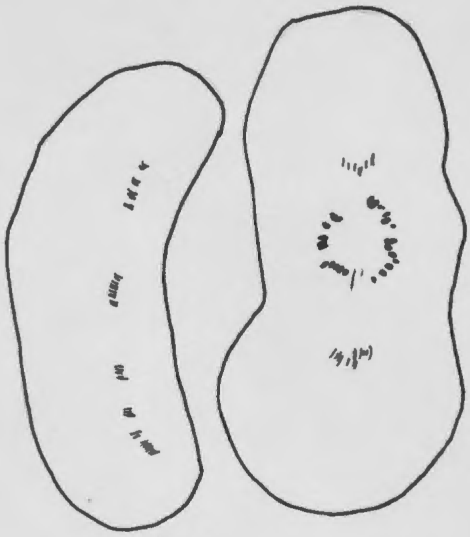
58.

Struthiola martiana

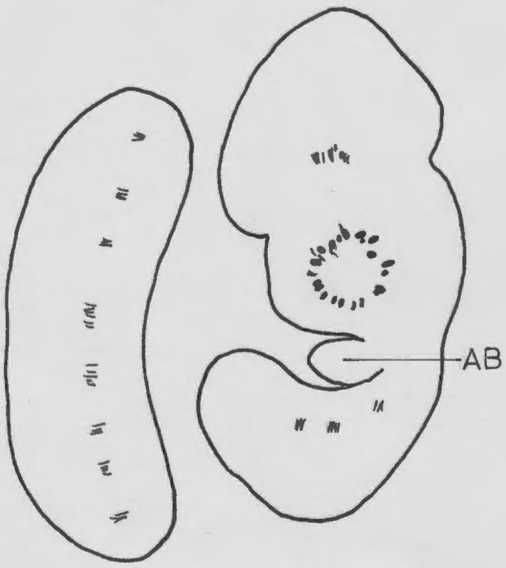
Fig. 59 - 62 (X 48)



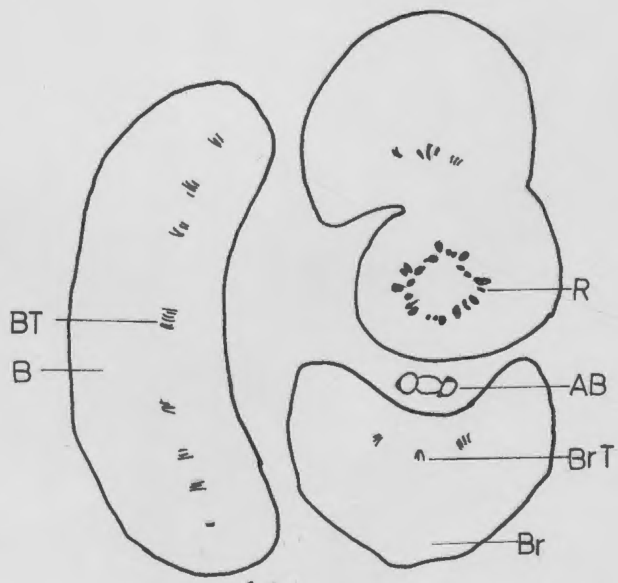
59.



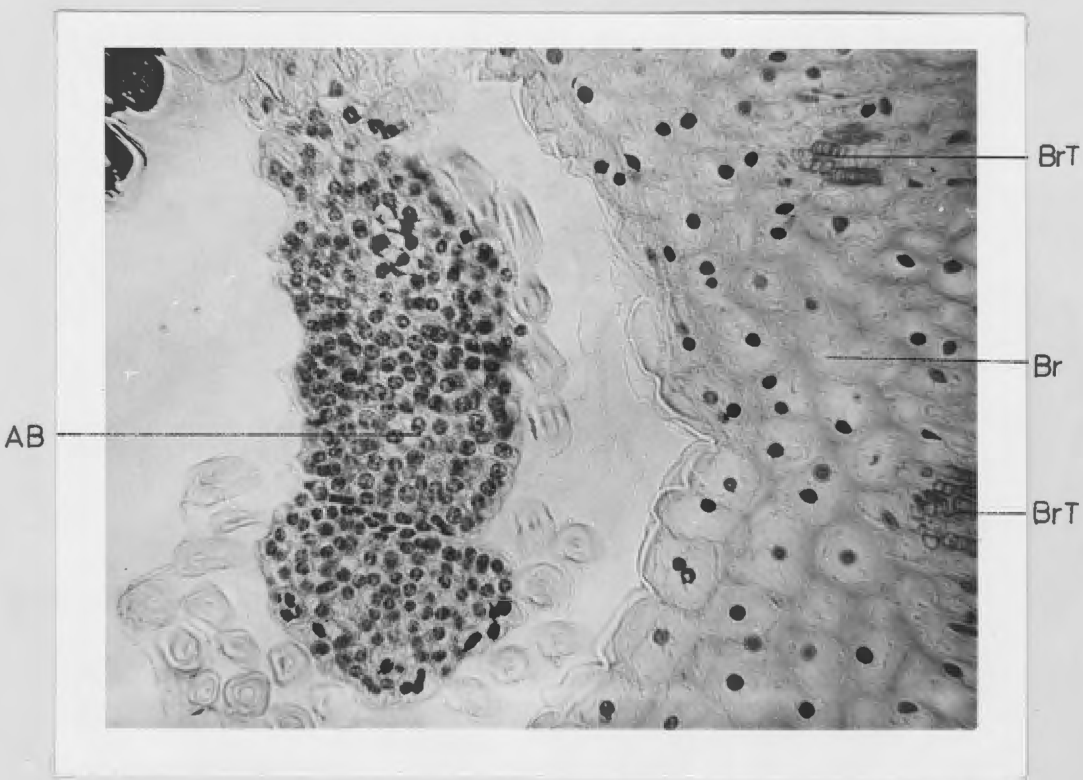
60.



61.



62.

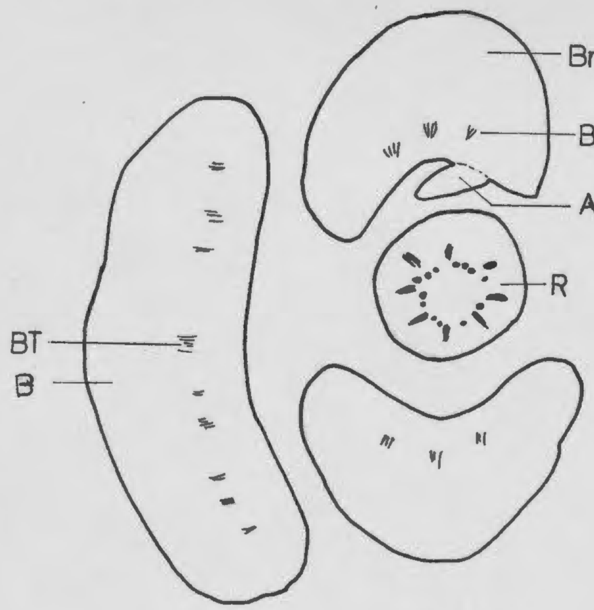


63.

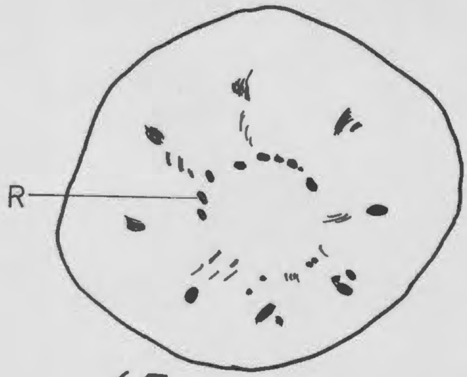
(X 400)

Struthiola martiana

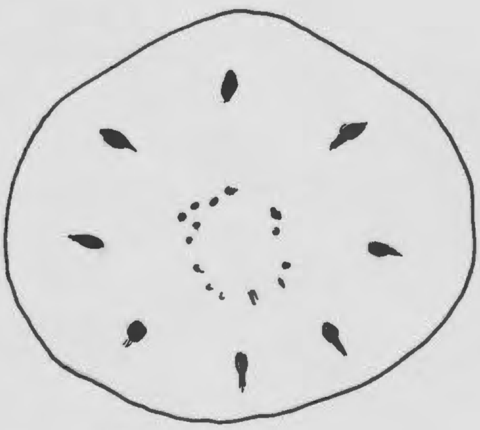
Fig. 65-69 (X 115)



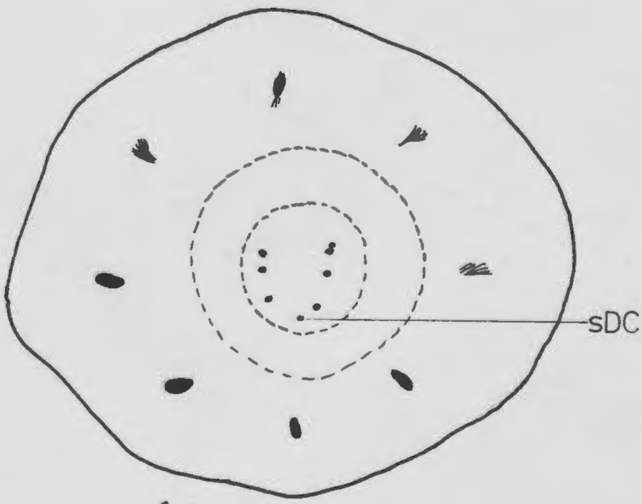
64. (X 48)



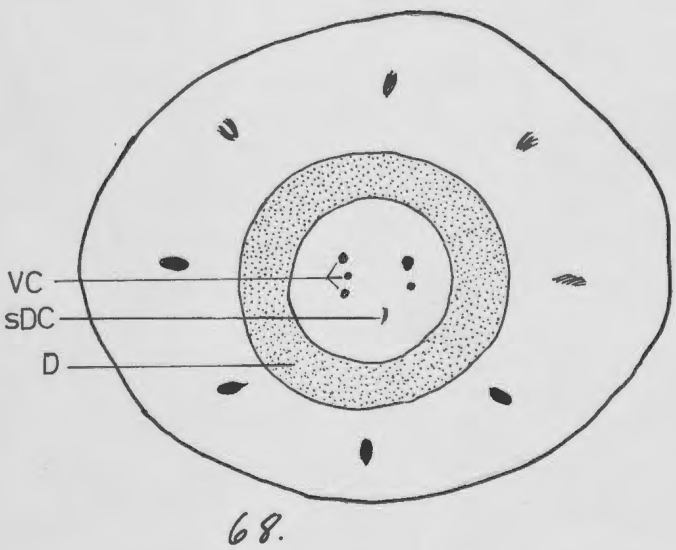
65.



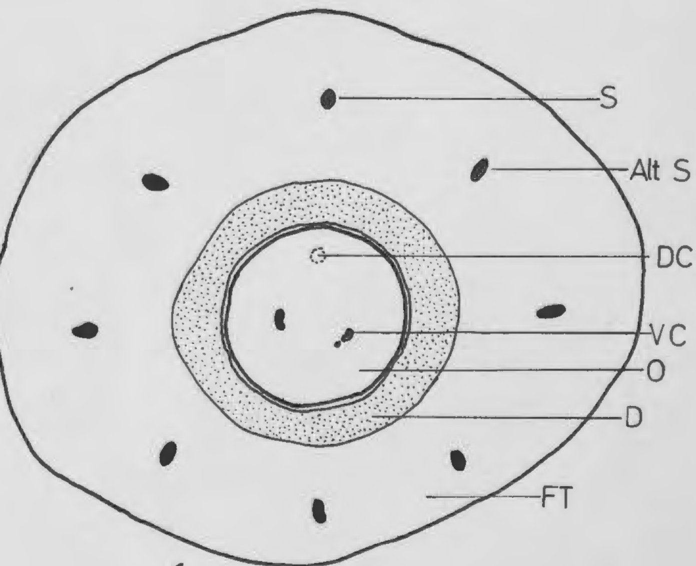
66.



67.



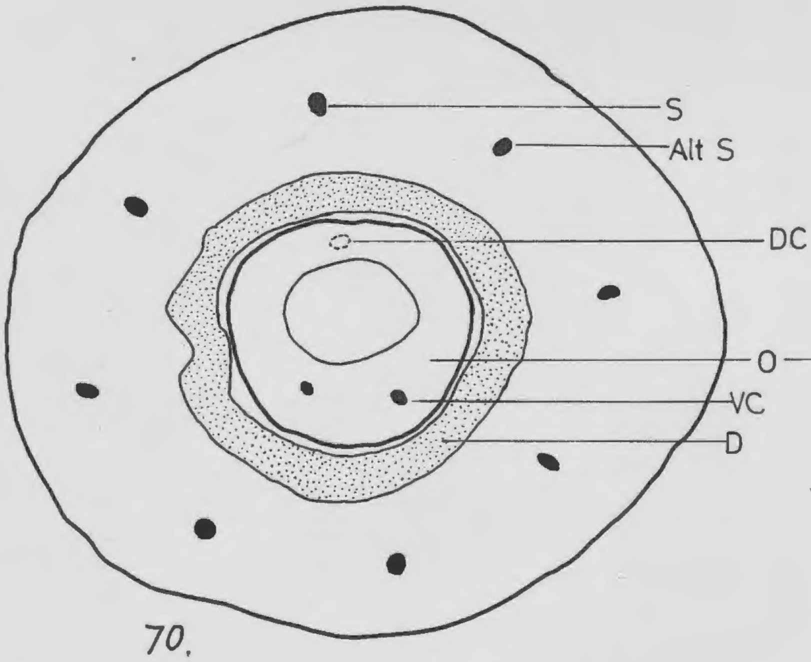
68.



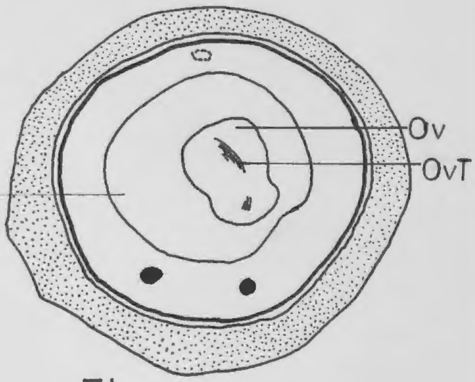
69.

Struthiola martiana

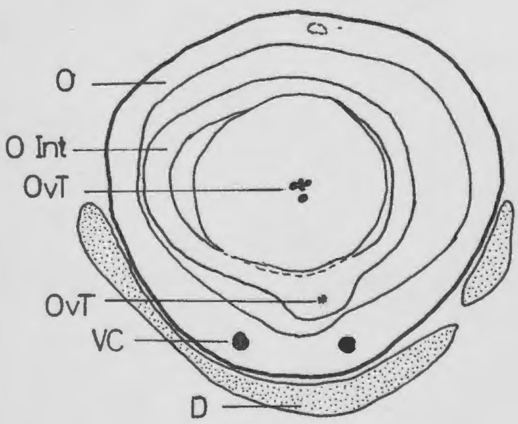
Fig. 70 - 74 (X 115)



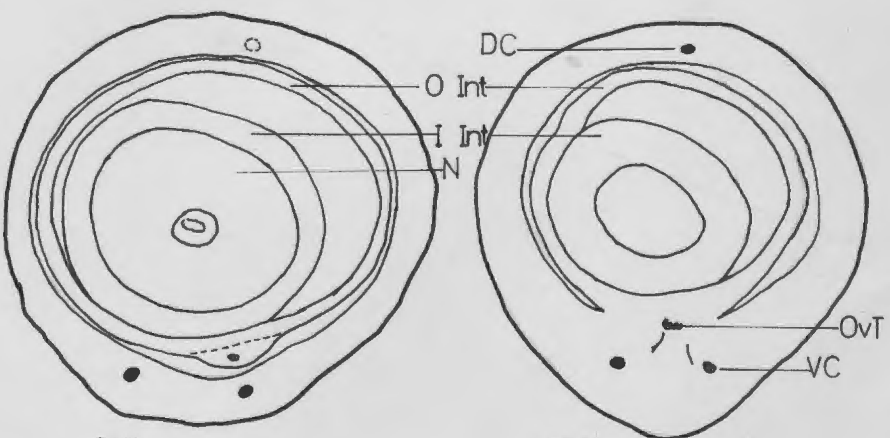
70.



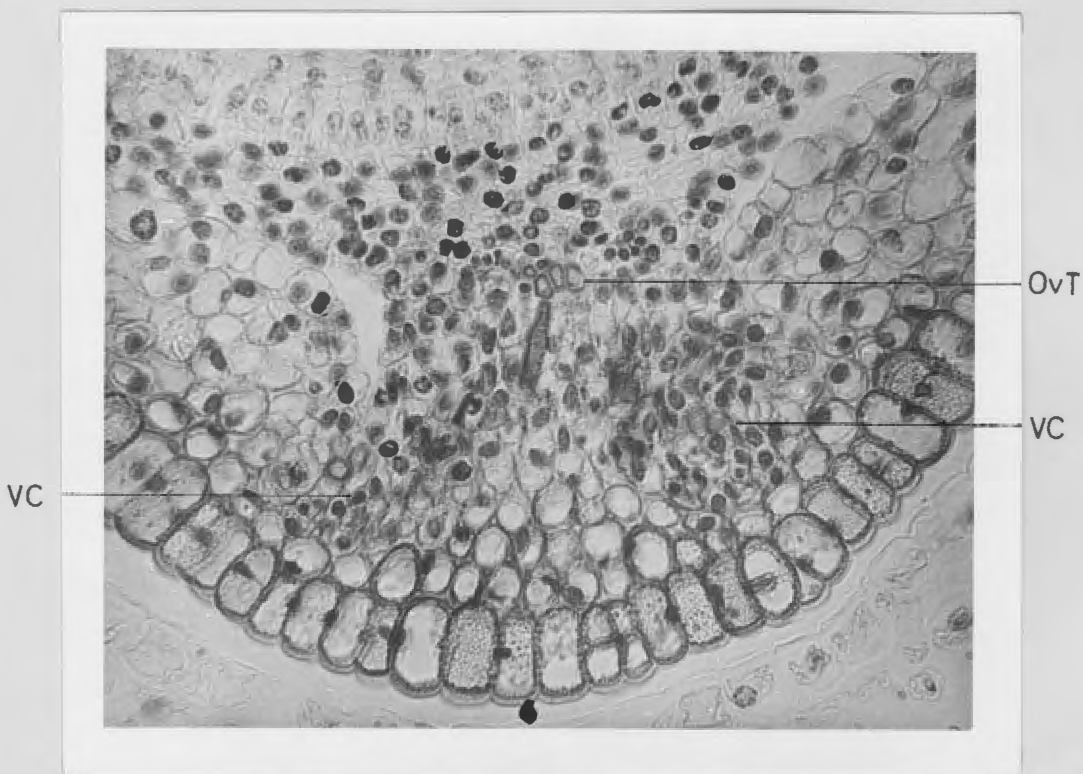
71.



72.



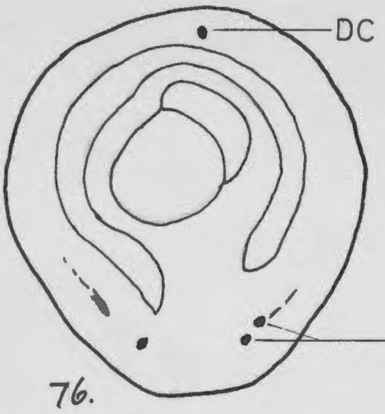
73. 74.



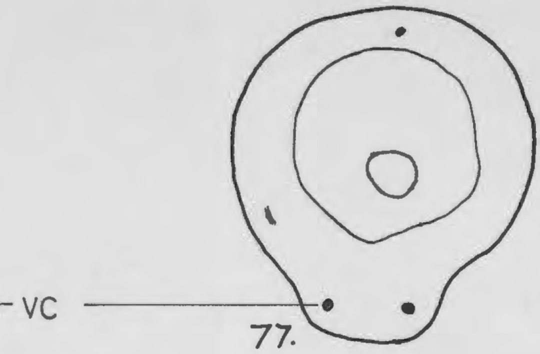
75. (X 490)

Struthiola martiana

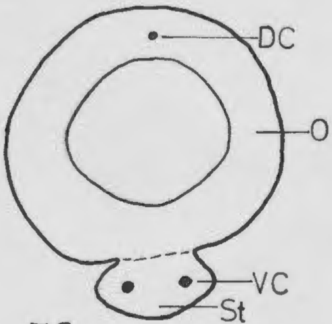
Fig. 76 - 82 (X 115)



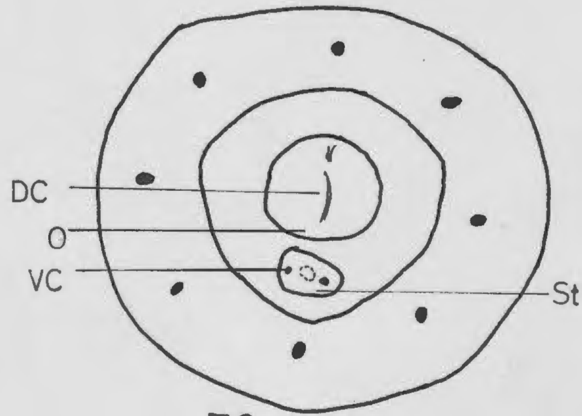
76.



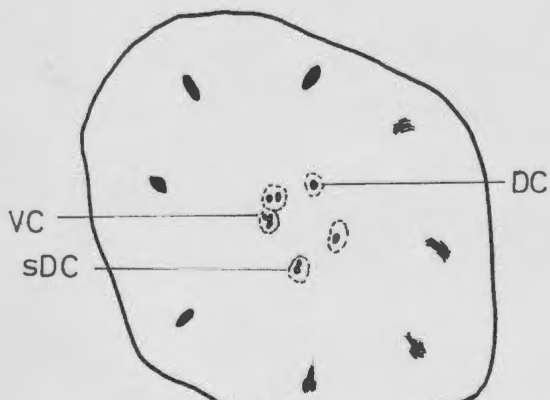
77.



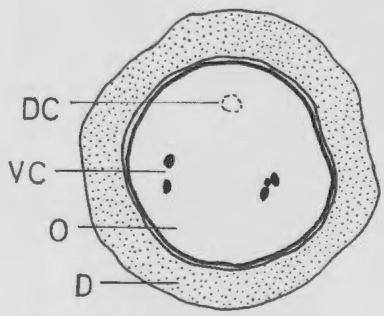
78.



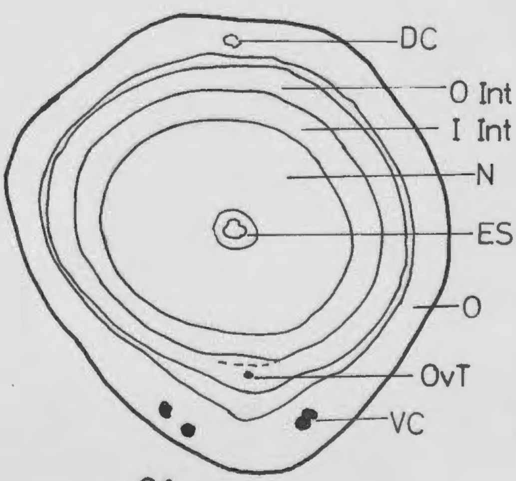
79.



80.



81.



82.

Struthiola martiana. (Fig 83-96, pp. 47 - 49).

Fig. 83 - 96. Serial T/S through the upper part of the floral tube.

Fig. 83-85. Tangential and radial divisions of the alternisepalous bundle. Vasculation and separation of the stamens.

Fig. 86-87. Repeated branching of the vascular bundles near the mouth of the floral tube.

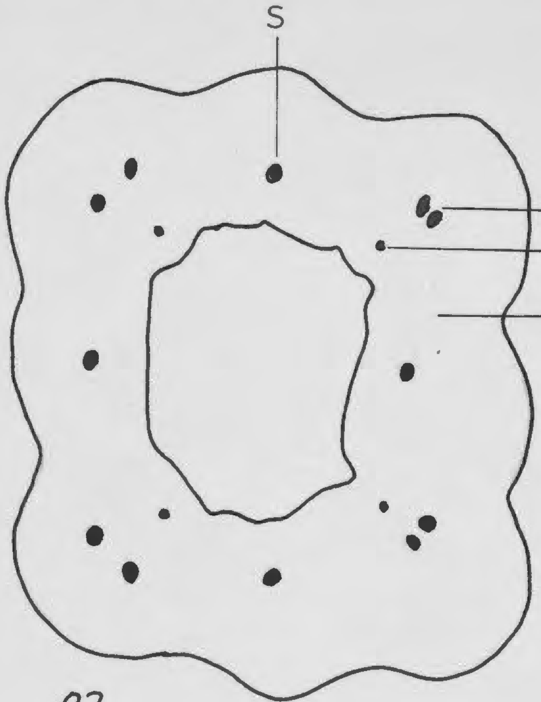
Fig. 88-93. Anastomoses of vascular bundles near the base of the petaloid scales. (The bases of the scales can be seen as bulges in the inner wall of the floral tube). Branches from adjacent antisepalous and alternisepalous bundles approach each other, anastomose and send vascular strands to supply the petaloid scales and the sepal lobes. (Note: In the diagrams it is indicated whether the vascular bundles originate from antisepalous bundles (S), alternisepalous bundles (Alt S), or from anastomosis of both (Anst).

Fig. 94. Separation of the petaloid scales and sepal lobes from the floral tube.

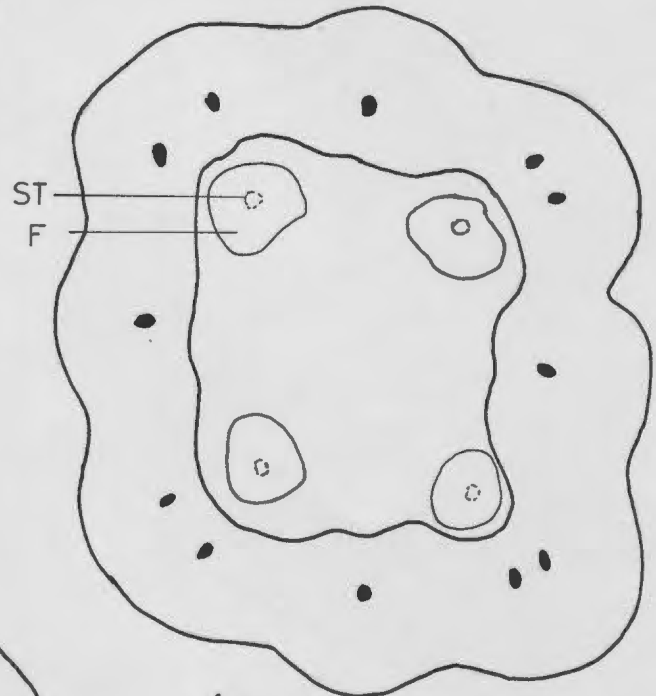
Fig. 95-96. T/S above the mouth of the tube showing the vascular tissue in the sepal lobes and petaloid scales.

Struthiola martiana

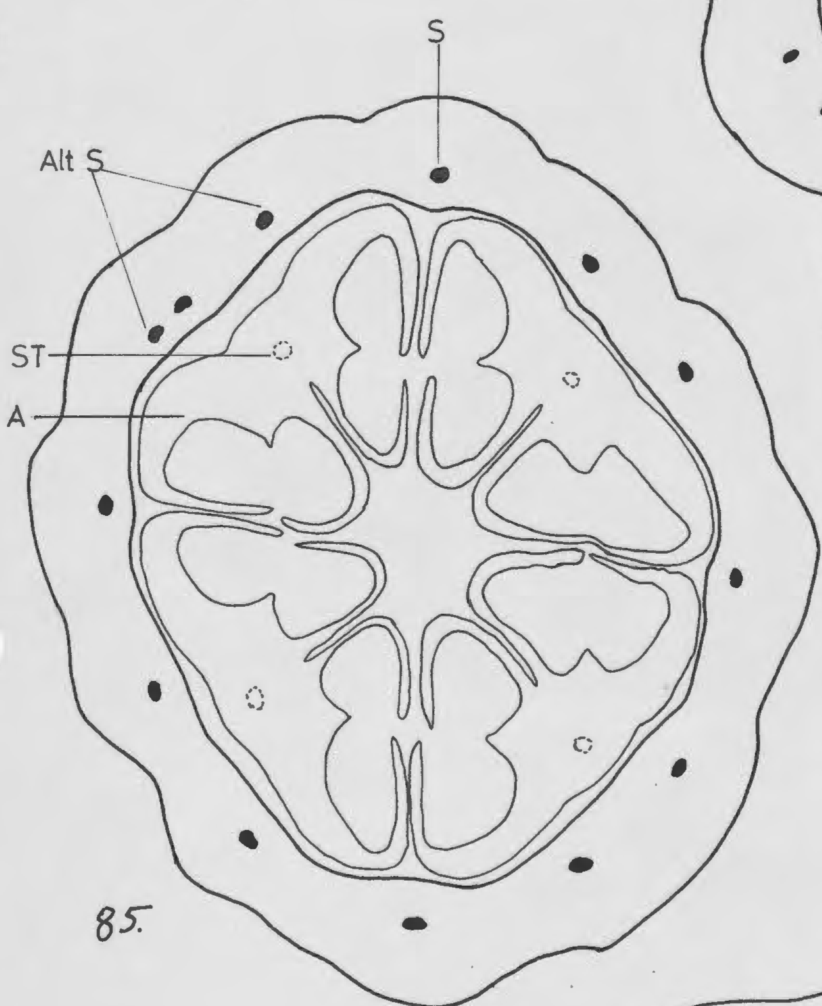
Fig. 83 - 86 (X 78)



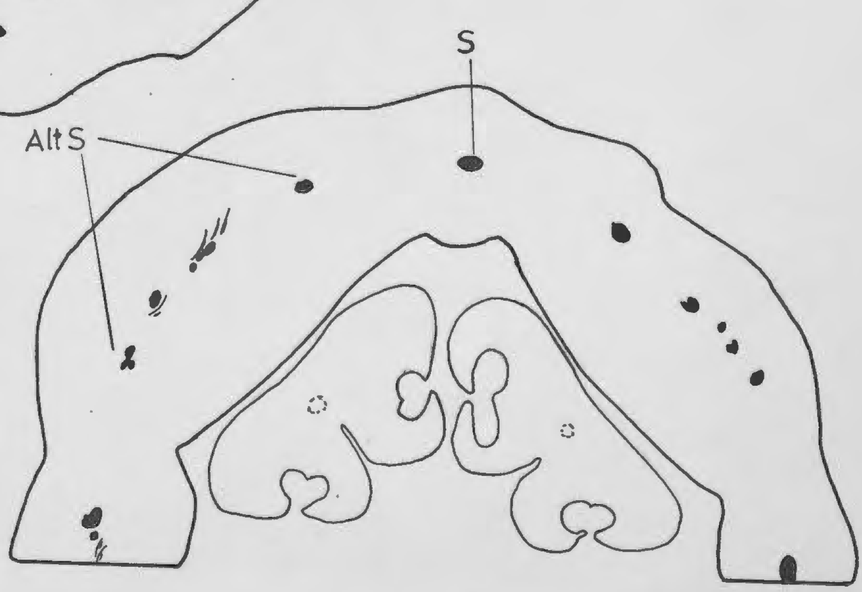
83.



84.

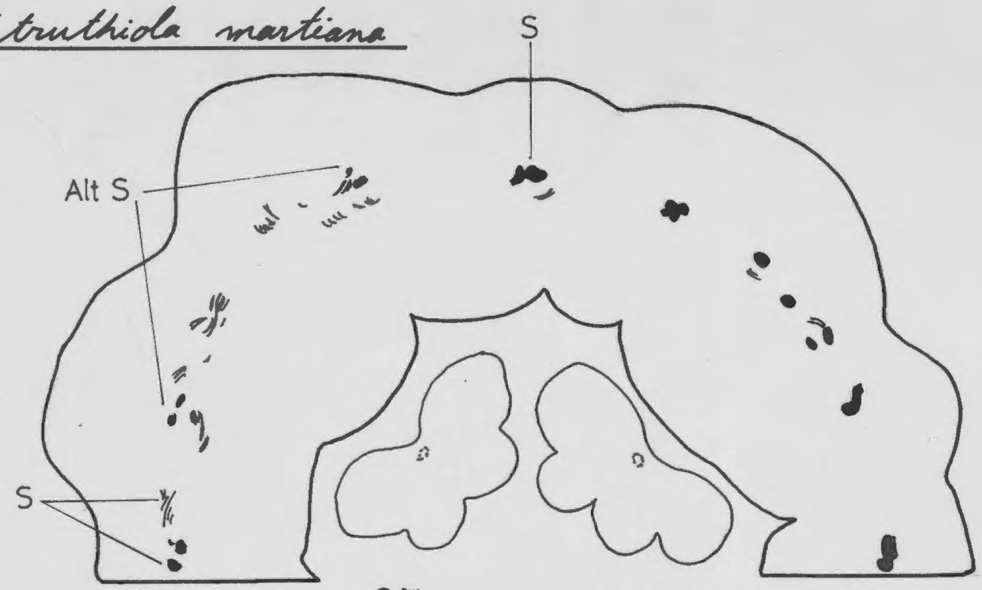


85.

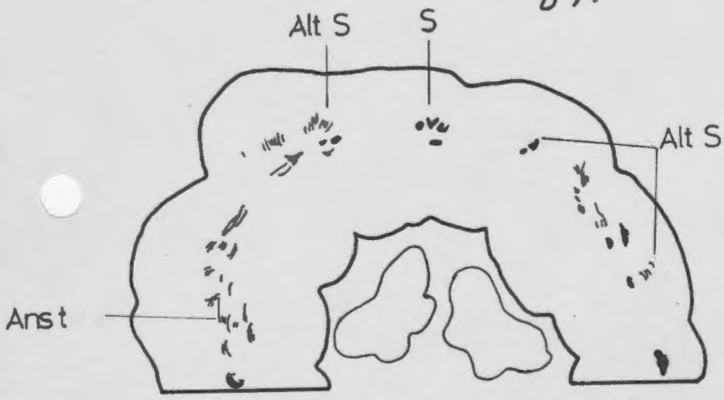


86.

Struthiola martiana

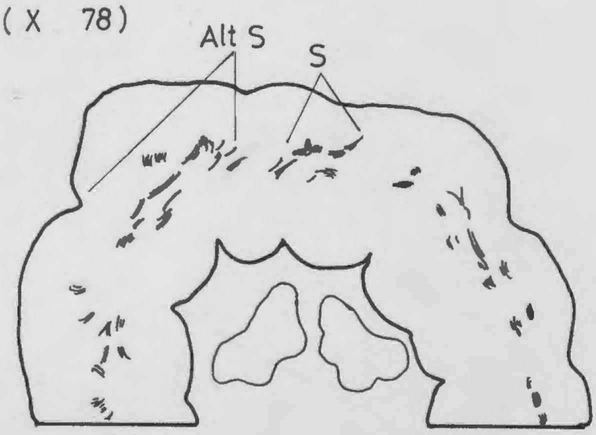


87. (X 78)



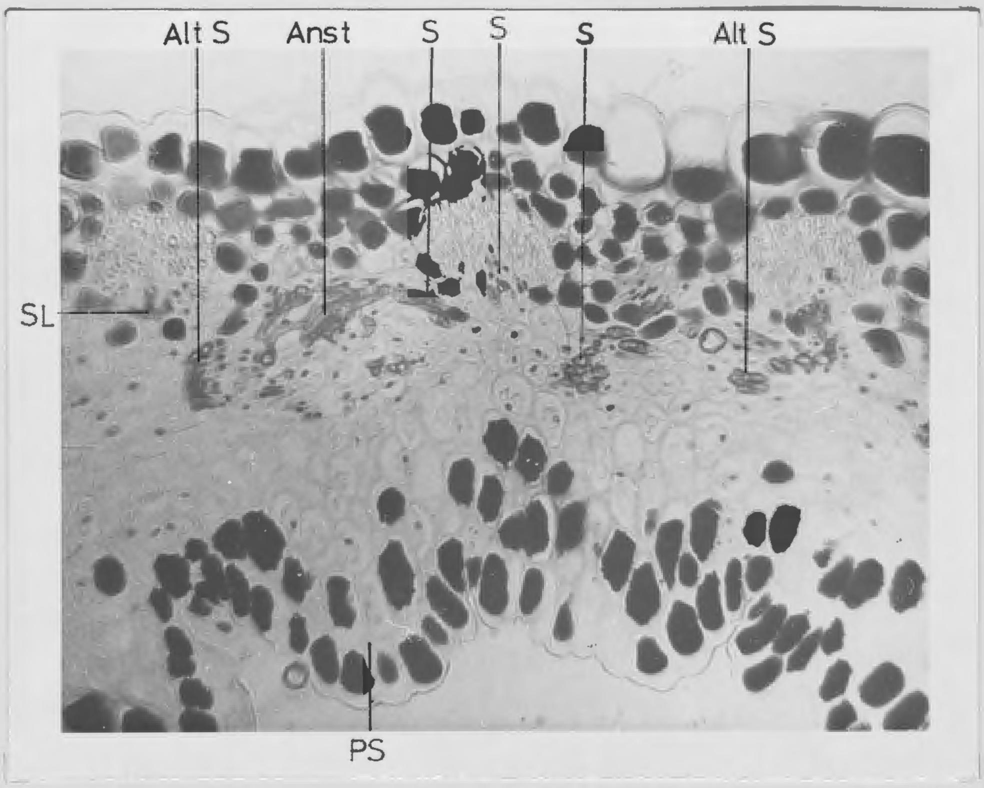
(X 47)

88.



89. (X 47)

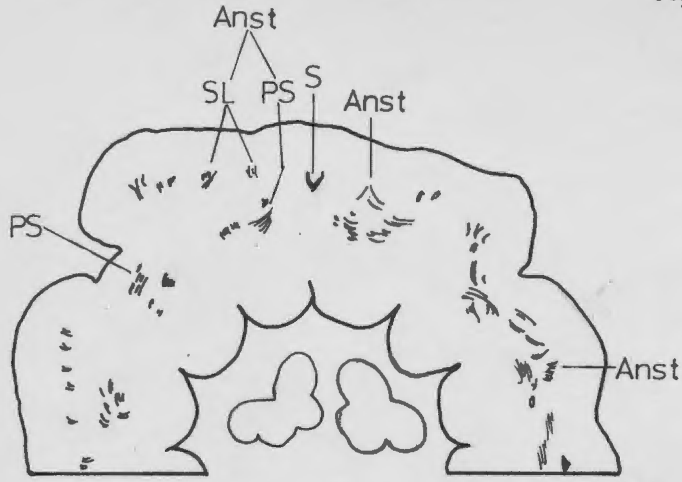
90. (X 47)



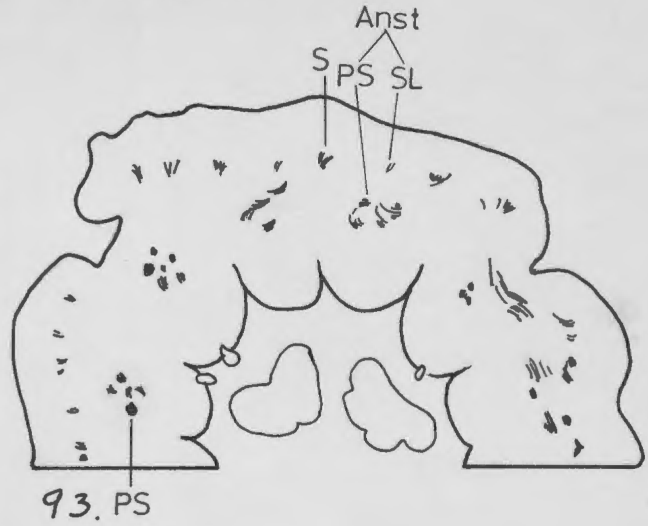
91. (X 150)

Struthiola martiana

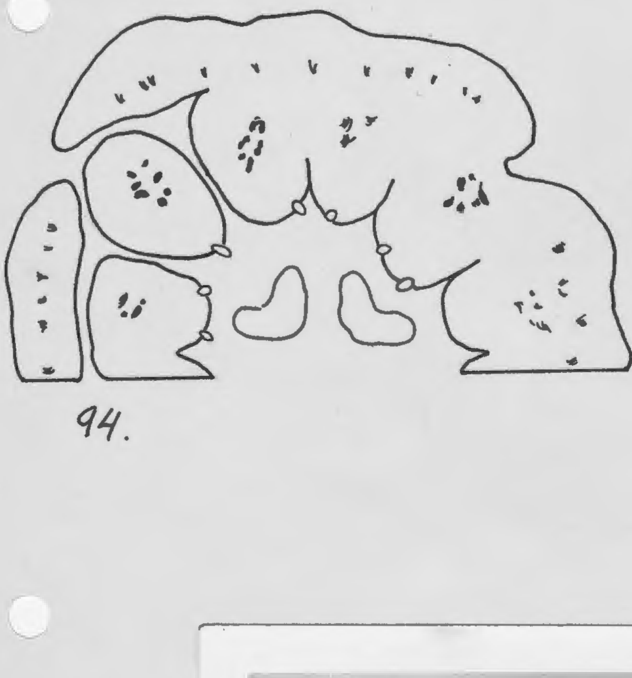
Fig. 92 - 95 (X 47)



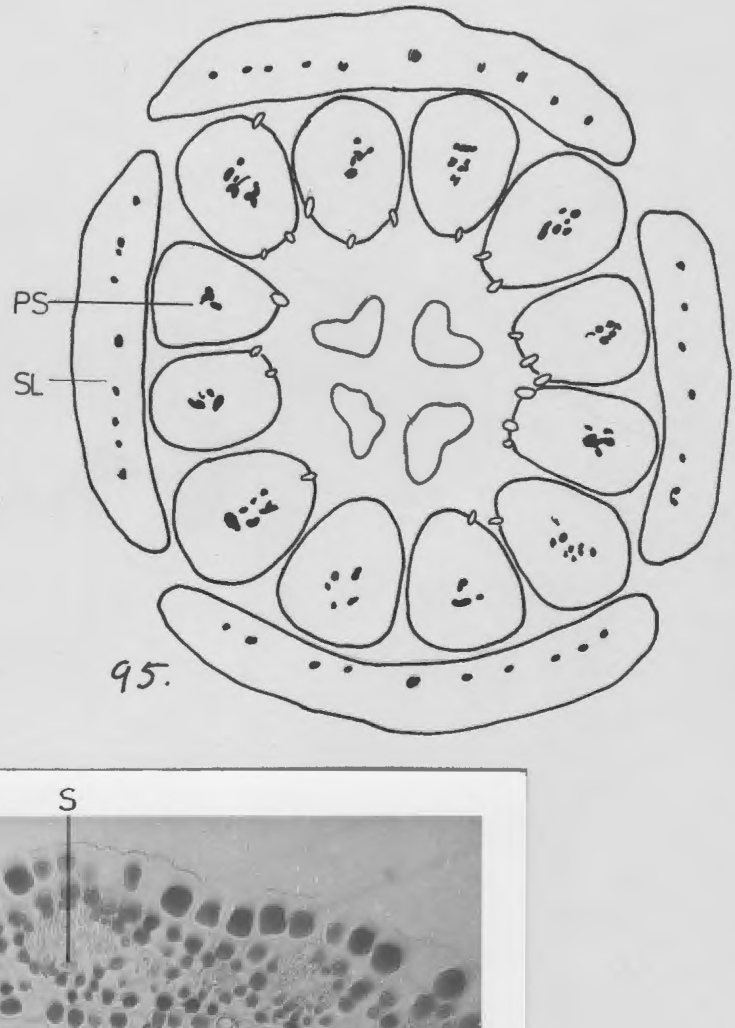
92.



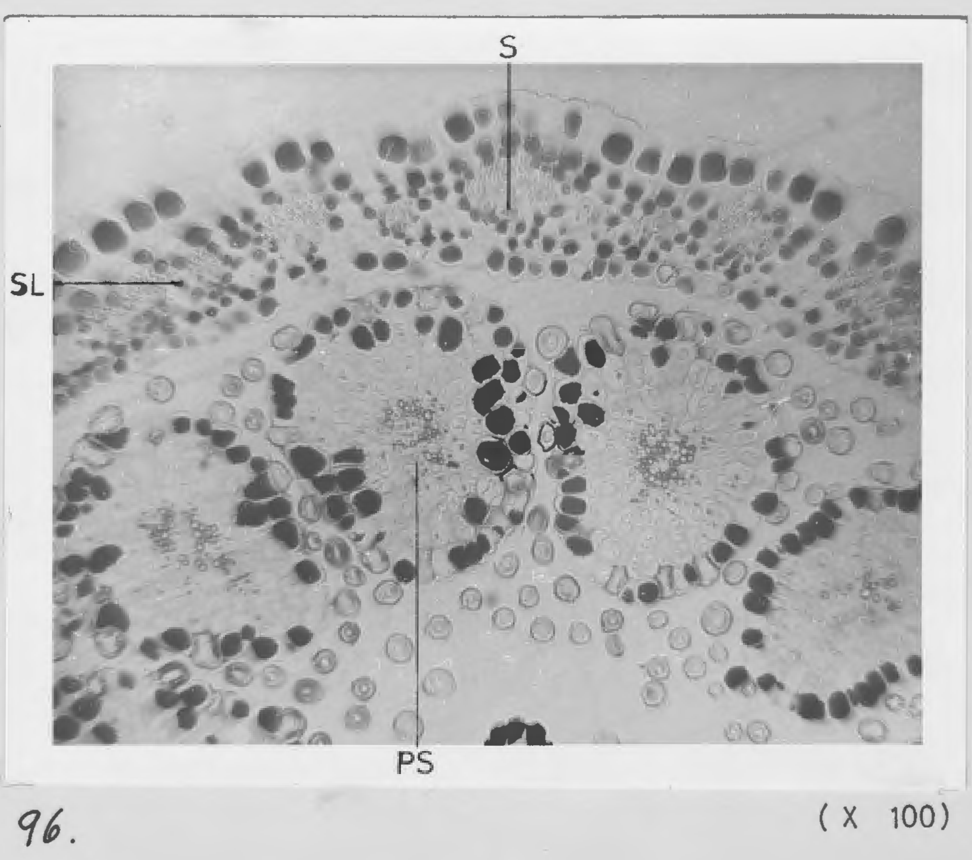
93.



94.



95.



96.

(X 100)

3. Struthiola dodecandra. (Fig. 97-121, pp. 53-59).

The peduncle and lower part of the flower. (fig. 100-107)

The divergence of traces to the bract and bracteoles follows the same pattern as described previously. Minute abortive axillary buds were observed in the axils of the bracteoles (fig. 100-101). The vascular supply of the ovary is similar to the upper part of the ovary in S. martiana: it consists of a dorsal bundle which is well differentiated only in the upper part of the ovary, and two ventral bundles near the ventral side that send branch to supply the ovule (OvT, fig. 104). The ventral carpellary bundles bifurcate at the top of the ovary. (fig. 105). The 2 branches that are closer to the centre enter the style (fig. 106), the other branches move towards the dorsal side and terminate. The dorsal carpellary bundle forms an arch over the top of the ovary and terminates (fig. 107).

The course of the vascular bundles near the mouth of the floral tube (fig. 108-111).

The floral tube consists, as in the previous cases, of 8 vascular bundles. Below the point of insertion of the stamens, the alternisepalous bundles divide tangentially (fig. 108). The inner branch, which is the stamen trace, contains no observable xylem elements. It enters the short filament (fig. 109) and runs along the connective (fig 110).

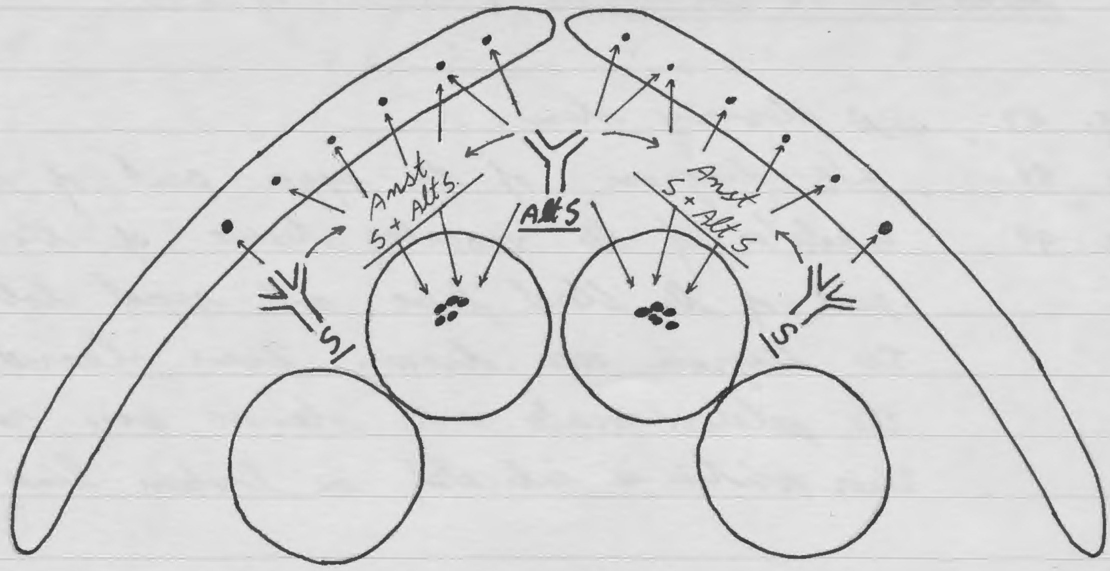
The bifurcation of the alternisepalous bundles into 2 major branches takes place at a higher level than in the previously described species, close to the top of the anthers (fig 111, fig 99).

The vascular supply of the petaloid scales and sepal lobes

At a higher level each of the 2 major branches of an alternisepalous bundle may send small strands to supply the margins of the sepal lobes behind it. Each of the antisepalous bundles divides, usually into 3 major branches. (fig. 114-116). The central one continues into the sepal lobe as a midrib (S, fig 117-118). The lateral branches approach adjacent major branches of alternisepalous bundles and form anastomoses with them near the base of the petaloid scales. (Anst. fig. 114-118). From the anastomoses traces diverge outwards to the sepal lobes. These constitute the lateral veins of the sepal lobes. The rest of the vascular tissue from the anastomoses constitutes the vascular supply of the petaloid scales. (fig. 117-119).

The vascular supply of the sepal lobe is therefore derived from three sources: 1. The midrib is derived directly from an antisepalous bundle. 2. The lateral veins are derived from anastomosing branches of antisepalous and alternisepalous bundles. 3. The extreme margins are supplied from alternisepalous bundles. The vascular supply of the petaloid scales is also derived from the anastomoses and from alternisepalous bundles, and is therefore equivalent to the lateral veins of the sepals. (The pattern of vasculation can be followed by observing carefully the successive transverse sections fig. 111-119 and from the skeleton of vascular tissue of the upper part of the tube and sepal lobes (fig. 99).

A simplified diagramatic representation of the origin of vascular supply of the sepal lobes and petaloid scales:



At the level of separation of the sepal lobes from the mouth of the tube, the petaloid scales are united in pairs to each of the sepal lobes. (fig. 118-120). This gives the impression that the petaloid scales are opposite to the sepal lobes rather than alternating with them. A comparison of the diagram to the diagrams for S. striata and S. martiana (p. 15 and p. 36 respectively) shows that the pattern of vasculation is similar in the 3 cases. A single petaloid scale in S. striata, or 3 scales in S. martiana are equivalent to a pair of scales in S. dodecandra. In the latter species it is more clear that the vascular supply of the petaloid scales and the vascular supply of the margins of the sepals is derived from the same origin, and that the vasculation of one scale is equivalent to that of half sepal lobe. This suggests that the petaloid scales form part of the sepal lobes, perhaps inner lobes or appendages of the sepal lobes. This is also supported by the fact that the scales are fused in their bases to the sepal lobes after their separation from the floral tube (fig. 119).

As in the other species, the vascular tissue extends only to the lower part of the petaloid scales.

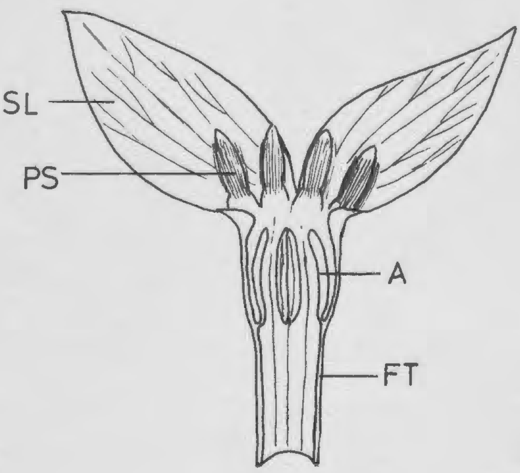
Struthiola dodecandra. (Fig 97 - 107 P.P. 54-55).

Fig. 97. . A flowering stem.
Fig. 98. L/S diagram of the upper part of the flower.
Fig. 99. Skeleton of the vascular tissue of the upper part of the floral tube and sepal lobes. The diagram was drawn from cleared material. The petaloid scales and stamens were removed. Their position is indicated in broken lines.

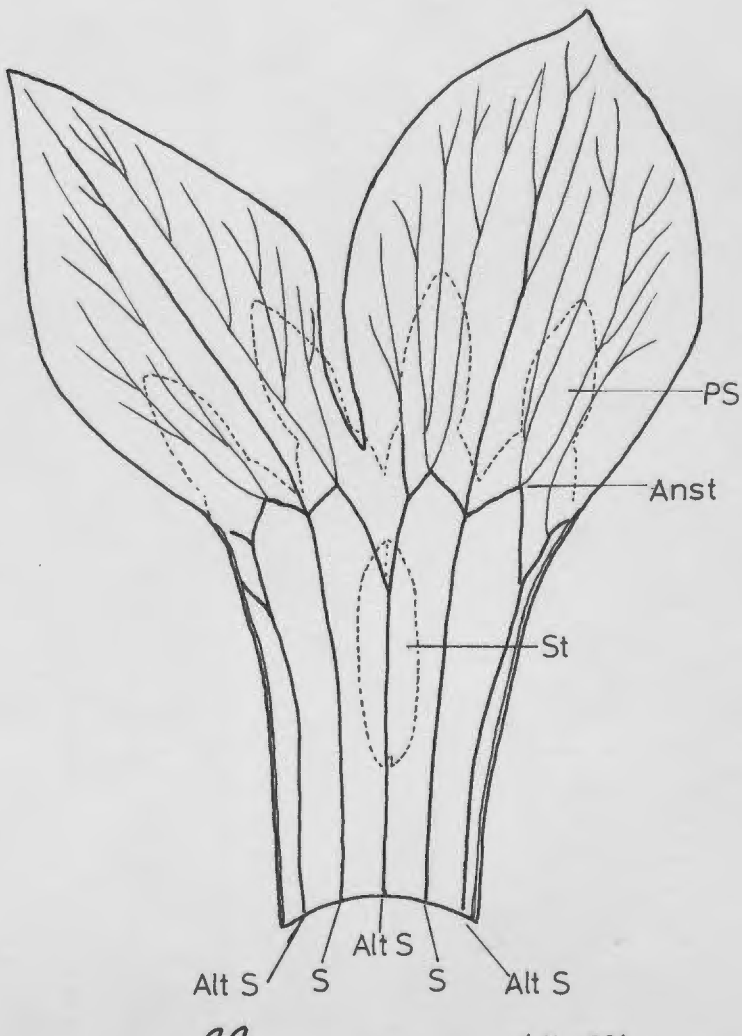
Fig 100-107. Serial T/S through the lower part of the flower.
Fig. 100-101. Divergence of traces to the bracteoles.
Fig. 102. . The floral tube, the hypogynous disc and the base of the ovary showing the carpellary bundles.
Fig. 103. The ovule trace at the chalazal region.
Fig. 104. The ovary at the placental region. A branch from one of the ventral bundles is seen diverging towards the ovule.
Fig 105. Bifurcation of the ventral carpellary bundles above the placental region. The branches of the bundles diverge dorsally and disappear.
Fig. 106 T/S of the top of the ovary at the point of attachment of the style. The ventral carpellary bundles enter the style.
Fig. 107. T/S of the floral tube, the top of the ovary and the style. The dorsal carpellary bundle arches over the top of the ovary and terminates.

Struthiola dodecandra.

97. A flowering stem. (X 25)

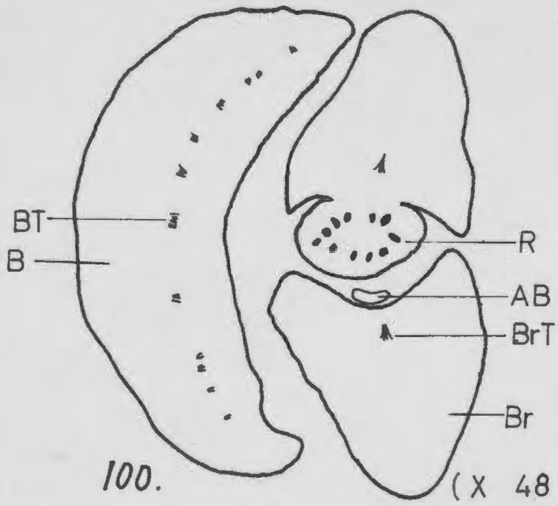


98. L/S diagram
The upper part
of the flower. (X 10)

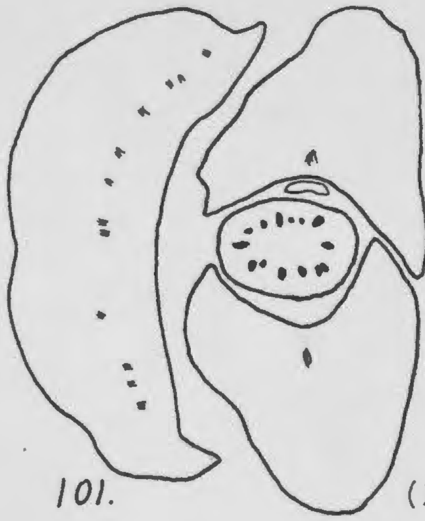


99. (X 20)

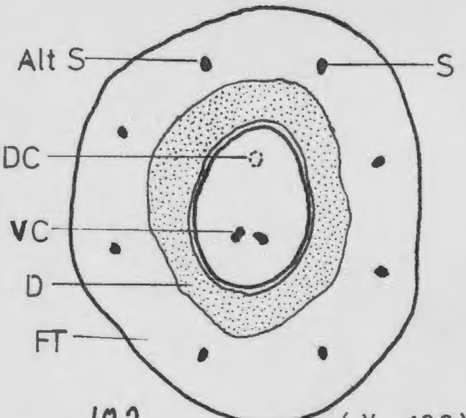
Struthiola dodecandra.



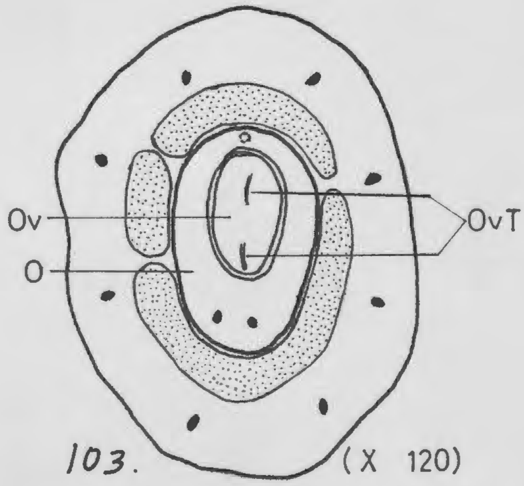
100. (X 48)



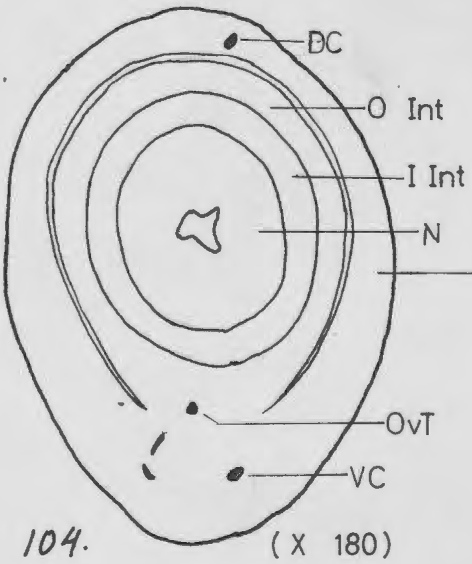
101. (X 48)



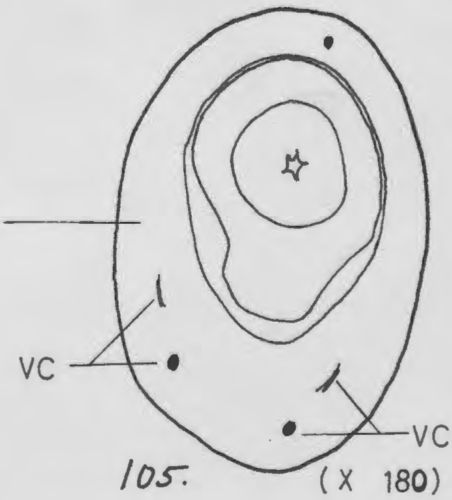
102. (X 120)



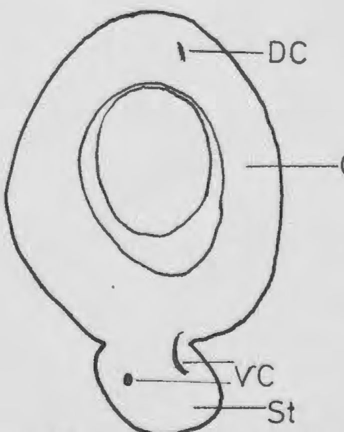
103. (X 120)



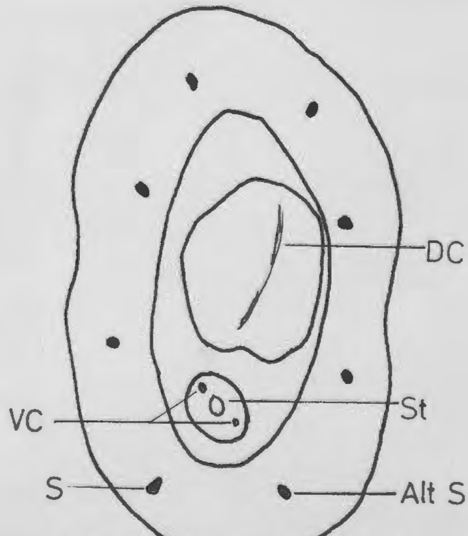
104. (X 180)



105. (X 180)



106. (X 180)



107. (X 120)

Struthiola dodecandra. (Fig. 108 - 121, pp. 57 - 59).

Fig. 108-121. Serial T/S through the upper part of the flower.

Fig. 108. The alternisepalous bundles divide tangentially giving rise to the stamen traces.

Fig. 109-110. Separation of the stamens from the floral tube.

Fig. 111. Bifurcation of the alternisepalous bundles into 2 major branches.

Fig. 112-113. Branching of the bundles near the mouth of the floral tube.

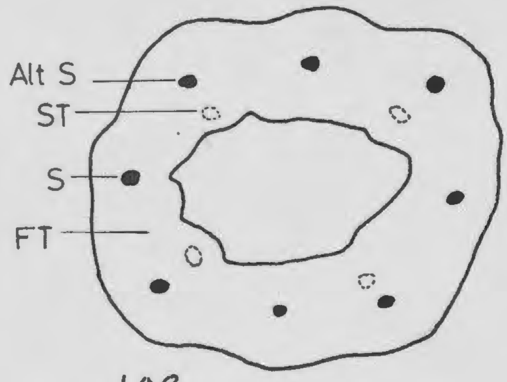
Fig. 114-119. Central strands of antisepalous bundles continue into the sepal lobes as midribs. Branches from alternisepalous bundles supply the margins of the sepals. Adjacent branches of antisepalous and alternisepalous bundles anastomose and supply the lateral portions of the sepal lobes and the petaloid scales.

Fig. 120. T/S through the sepal lobes and petaloid scales above the mouth of the floral tube.

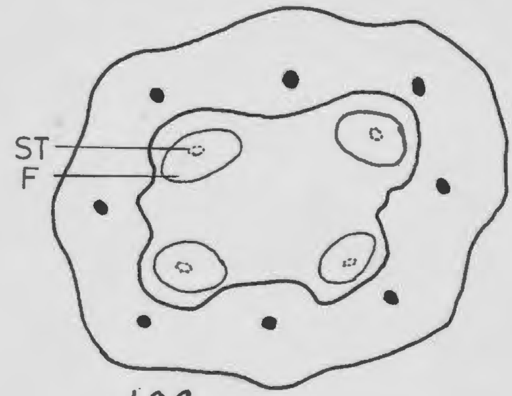
Fig 121. The vascular tissue of a petaloid scale.

Struthiola dodecandra.

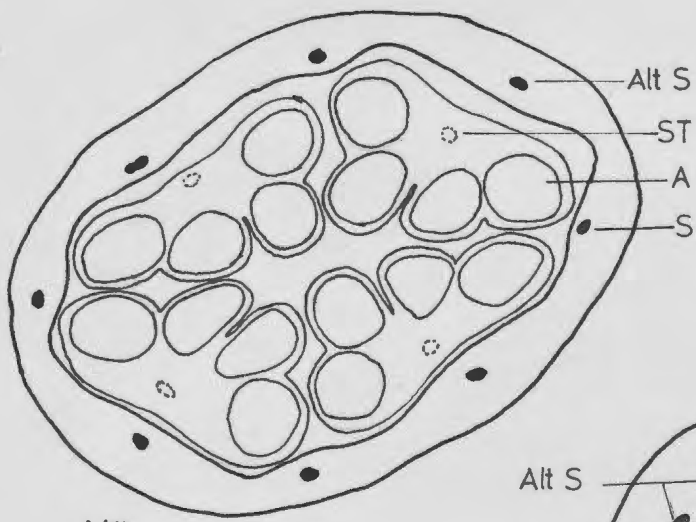
Fig. 108-113 (X 78)



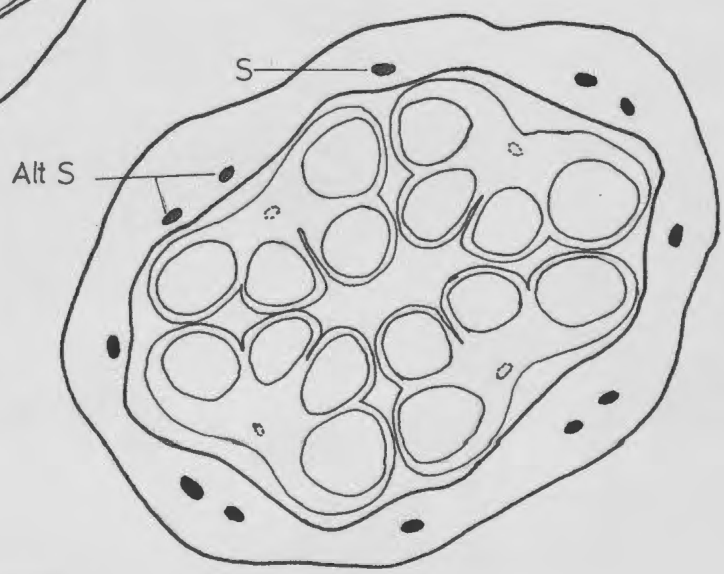
108.



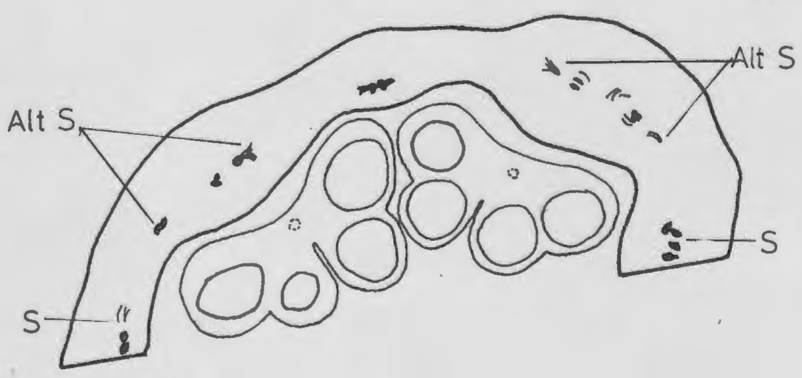
109.



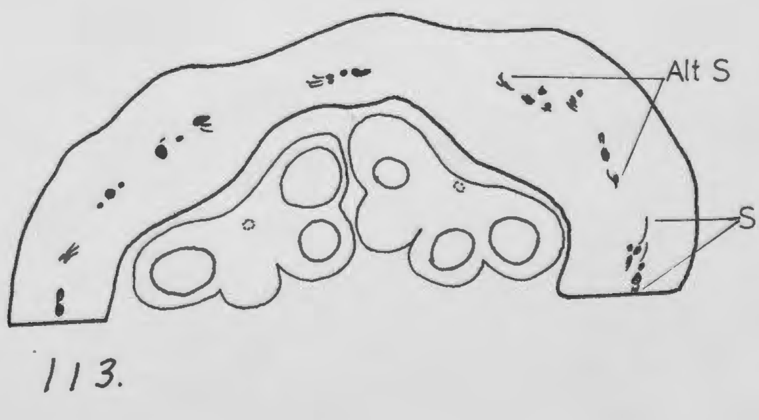
110.



111.



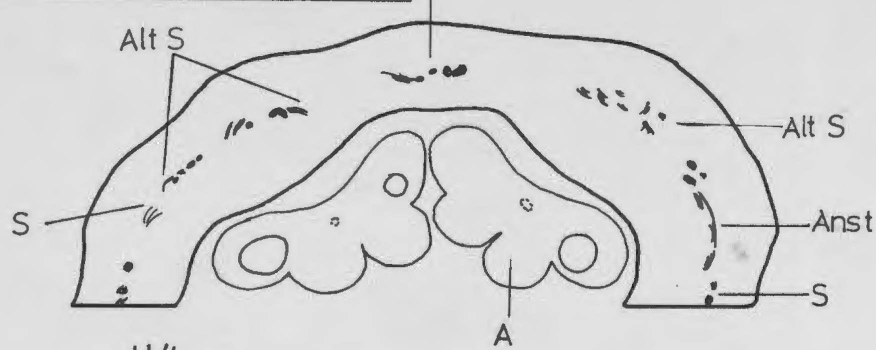
112.



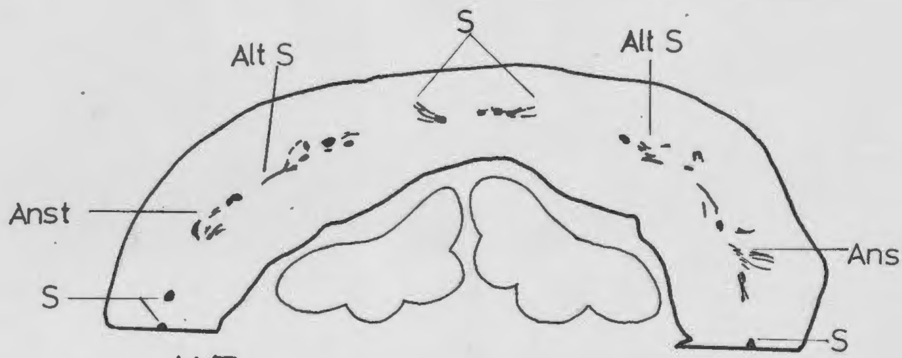
113.

Struthiola dodecandra

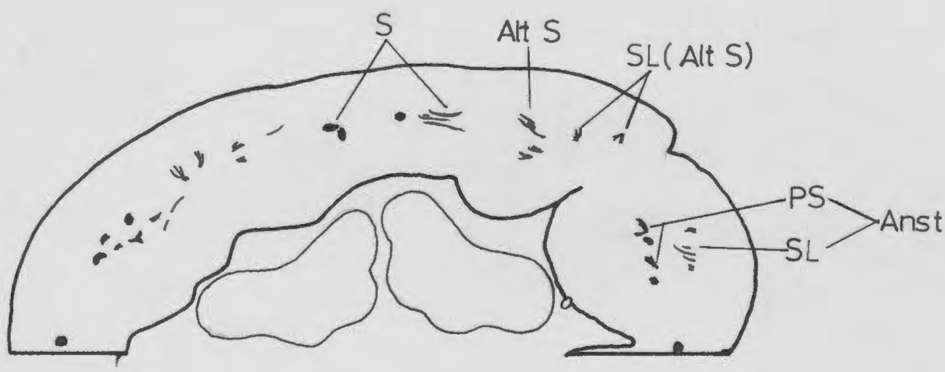
Fig. 114 - 118 (X 78)



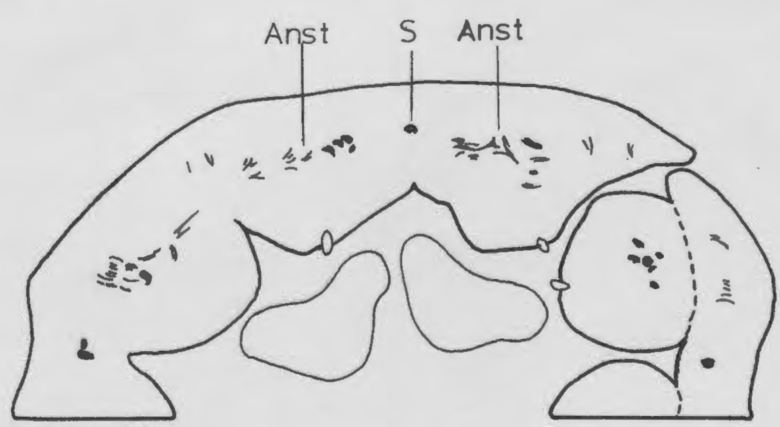
114.



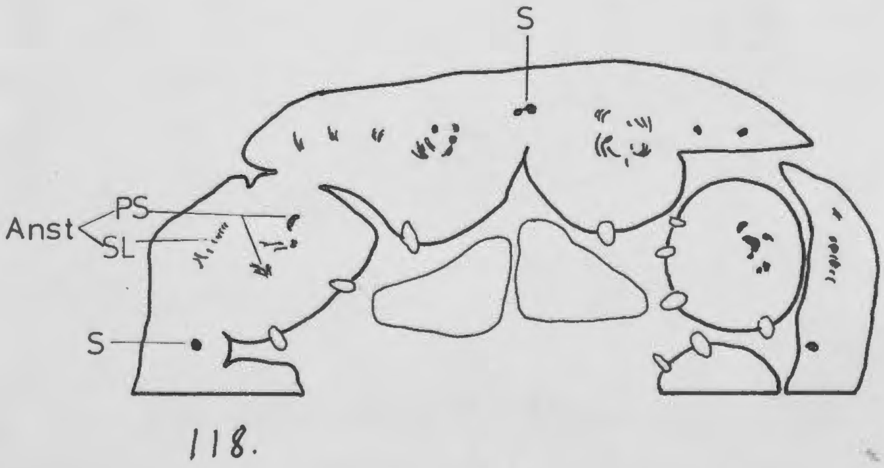
115.



116.

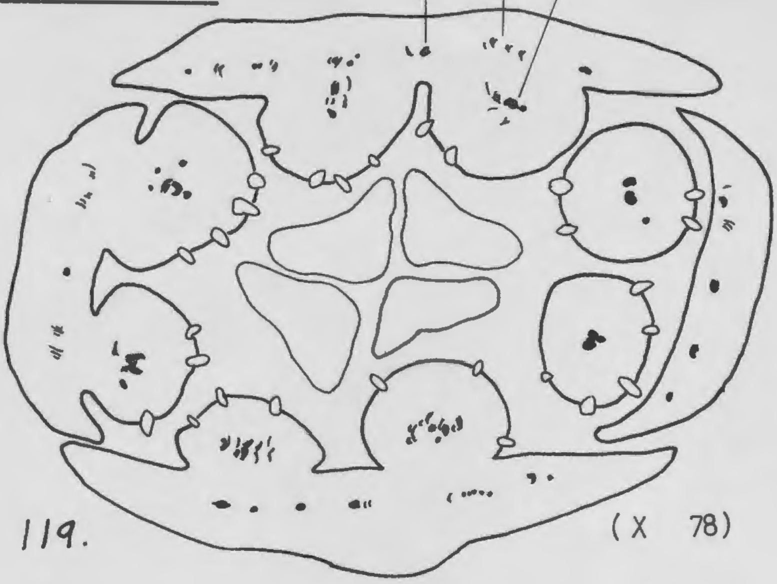


117.



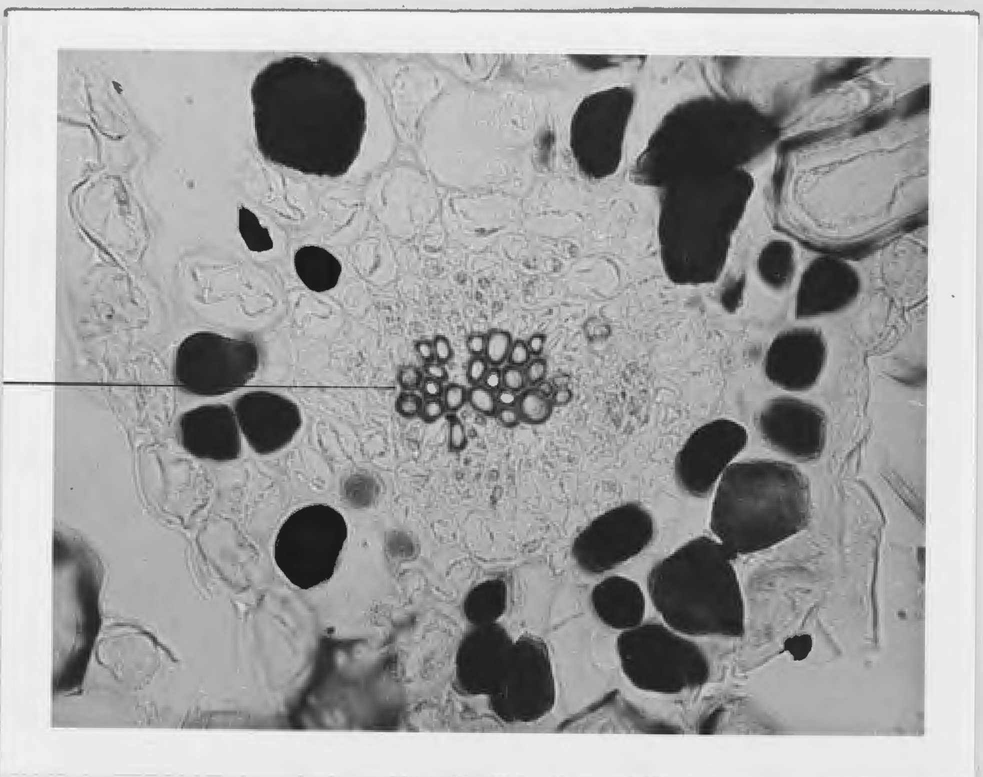
118.

Struthiola dodecandra



119. (X 78)

120.
(X 135)



121.
(X 470)

4. Struthiola ciliata. (Fig. 122 - 136, pp. 62 - 65).

The gynoecium.

In S. ciliata variations in the pattern of vasculation of the ovary and style were found in 3 specimens sectioned (will be designated here as specimens 1, 2 and 3. T/S diagrams of specimens 1 and 3 will be found on p. 64 and 65 respectively).

The divergence of bundles to the bract and bracteoles is similar to the previous cases. (fig. 129-130). Above the level of divergence of the 8 traces to the floral tube, only few bundles remain in the receptacular cylinder. The bundles are not differentiated and disappear completely (fig. 131). They reappear at a higher level, at the base of the ovary (fig 122, 132) ~~at the ba~~ As in S. striata there are 4 bundles at the base of the ovary: a dorsal carpellary bundle (DC) at the dorsal side, 2 ventral carpellaries (VC) and a single bundle at the ventral side, which represents the dosal bundle of ~~th~~ a sterile carpel (sDC). In specimen 1 this bundle extends up to the placental region where it disappears, so that in the larger part of the ovary the vascular supply consists of 4 bundles. (fig. 122 - 126). In specimen 2 the sterile dorsal carpellary bundle (sDC) disappears at the middle level of the ovary. In specimen 3 this bundle disappears at the base of the ovary (fig. 132 - 133), so that the vascular supply of the ovary consists of 3 bundles, as in S. martiana.

The ovule trace is probably derived from the ventral carpellaries, which are very close to the ventral side at the placental region. However, a direct connection between the bundles and the ovule trace could not be observed with certainty.

Another difference between the specimens examined was found in the vasculation of the style. In specimen 3 (as in S. martiana and S. dodecandra) the dorsal carpellary bundle forms an arc over the top of the ovary and terminates. The 2 ventral carpellaries diverge ventrally, enter the style and run along it on either side of the stylar canal. (fig. 135 – 136). In specimen 1 the dorsal carpellary bundle (DC) forms an arc over the top of the ovary from the dorsal to the ventral side, and enters the style together with the 2 ventral carpellaries (fig. 127–128). In that case the style contains 3 vascular bundles instead of 2, which is the case in all the other specimens described.

The structure and pattern of vasculation in the upper part of the flower is basically similar to that described for S. dodecandra.

Struthiola ciliata. (Fig 122 - 136, pp. 64-65).

Fig. 122 - 128. Serial T/S through the lower part of the flower. (Specimen no. 1).

Fig 122. T/S through the base of the flower showing the 8 tube bundles, the hypogynous disc and the base of the ovary with the carpellary bundles.

Fig. 123 - 124. T/S of the ovary and ovule showing the lowest point of the ovule trace and its termination at the chalazal region.

Fig 125. T/S of the flower at middle level of the ovary. Note the 4 carpellary bundles.

Fig. 126. T/S of the ovary at the placental region.

Fig. 127. T/S through the top of the ovary. The ventral carpellary bundles are seen in the style, which is attached laterally at the top of the ovary. The dorsal bundle (Dc) arches over the top of the ovary before it enters the style.

Fig. 128. T/S of the floral tube above the ovary showing the style with 3 bundles.

Fig. 129 - 136. Serial T/S through the lower part of the flower (specimen no. 3).

Fig 129-130. The separation of bracteoles from the peduncle. Note the abortive axillary buds in axils of the bracteoles.

Fig. 131. The receptacle above the divergence of the 8 tube traces. The carpellary traces are not differentiated at this level.

Fig. 132. The carpellary bundles at the base of the ovary, the hypogynous disc and floral tube.

Fig. 133. The ovule trace at the chalazal region of the ovule. The dorsal bundle of the sterile

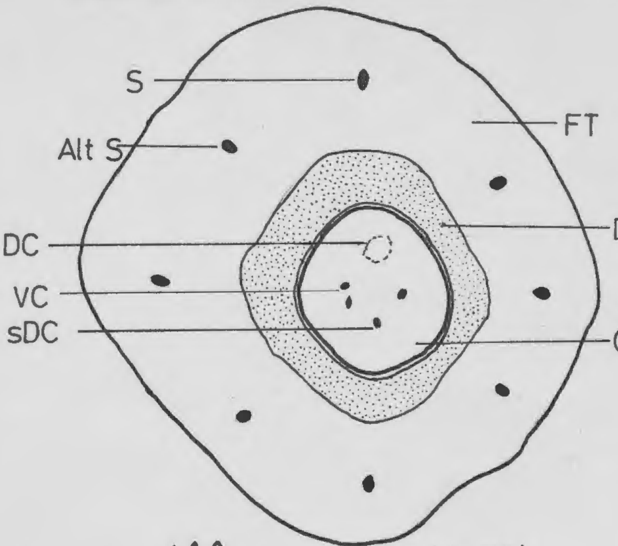
~~ca~~ carpel has disappeared. (s D c)

Fig. 134. T/S of the ovary at the placental region.

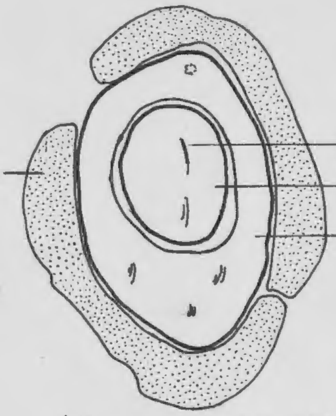
Fig. 135. T/S of the upper part of the ovary. The ventral carpellary bundles enter the style.

Fig. 136. T/S of the floral tube and top of the ovary. The dorsal carpellary bundle arches over the top of the ovary and terminates. The 2 ventral bundles are seen in the style.

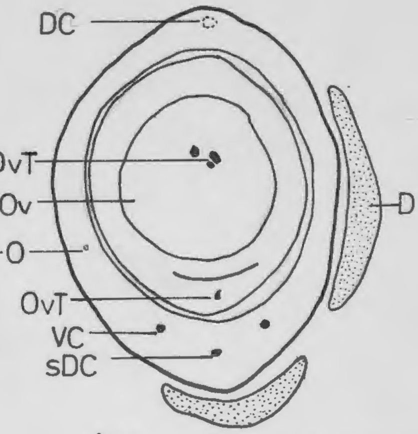
Struthiola ciliata. (Specimen no. 1.)



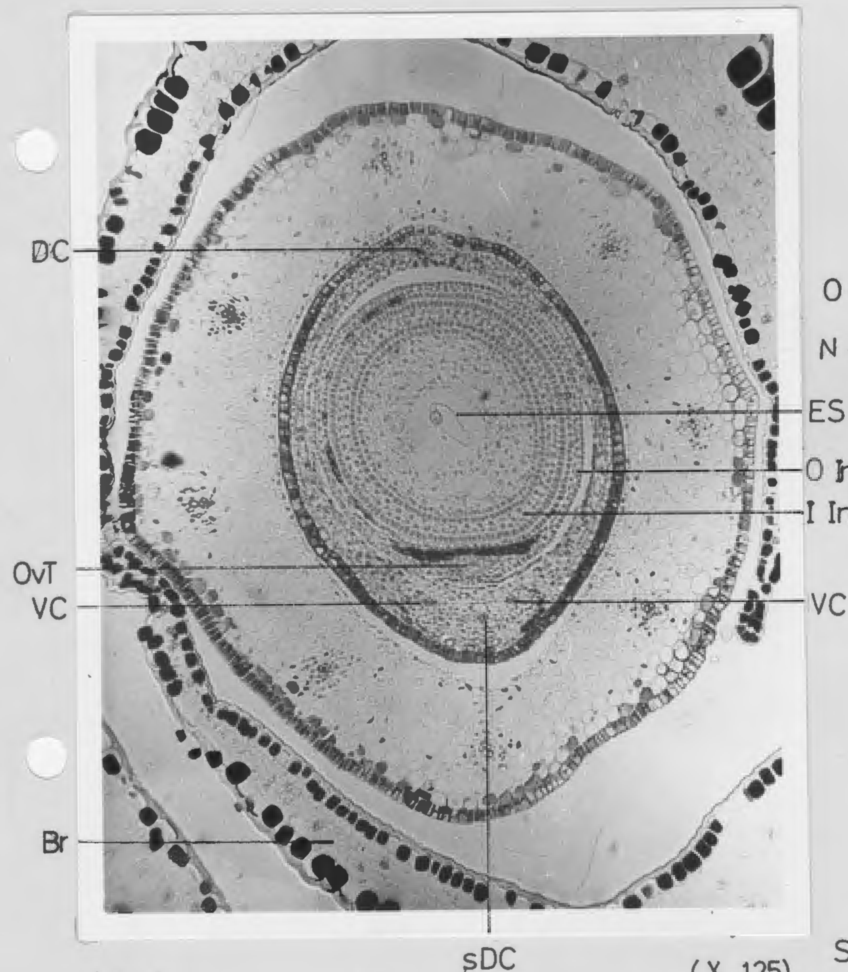
122. (X 115)



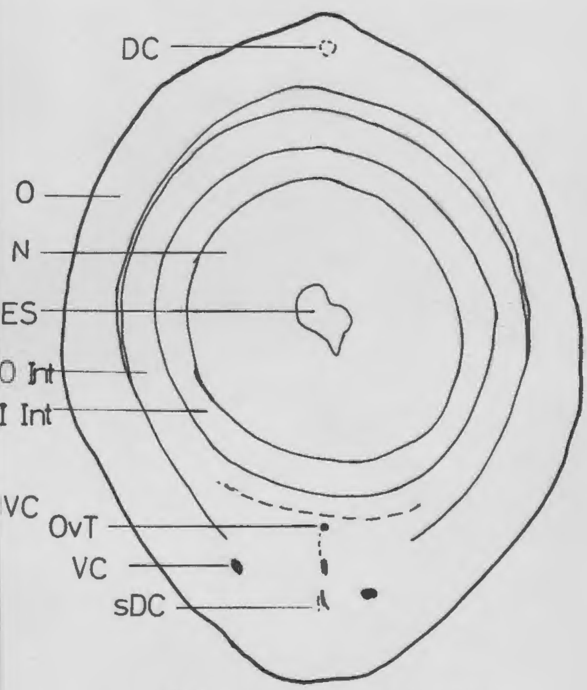
123. (X 115)



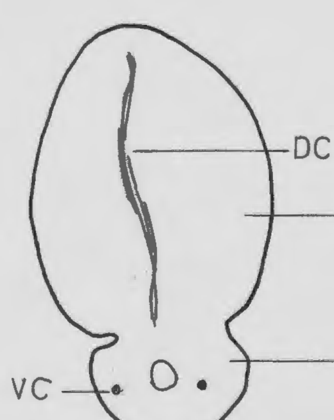
124. (X 115)



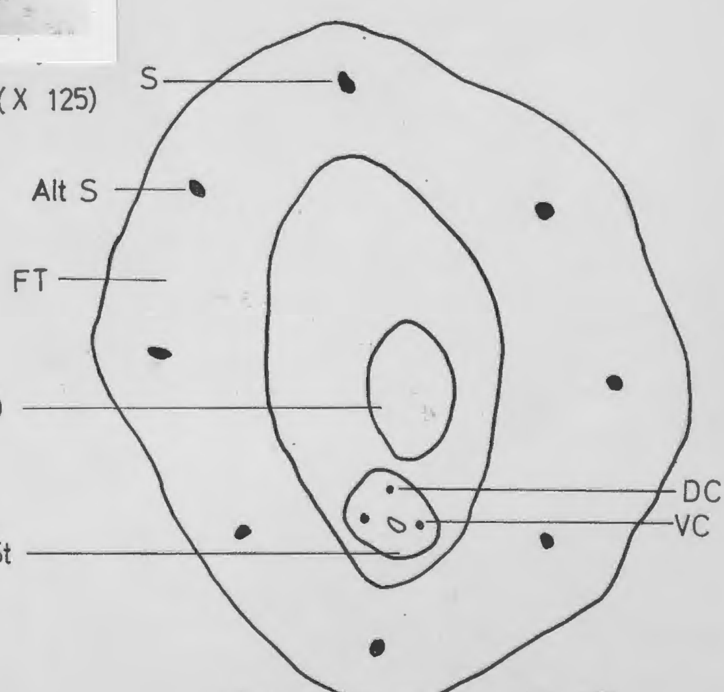
125 (X 125)



126. (X 180)

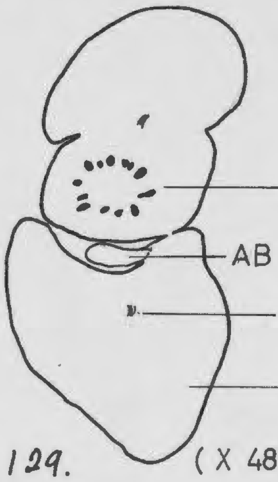


127. (X 180)

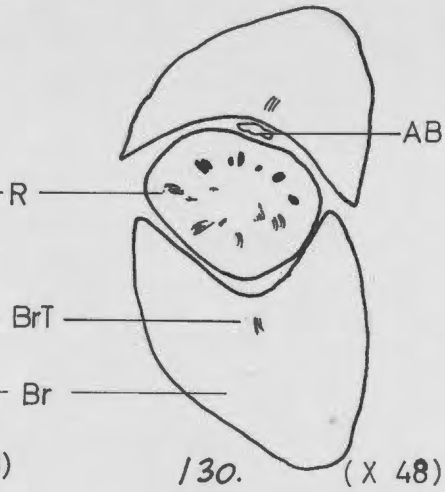


128. (X 115)

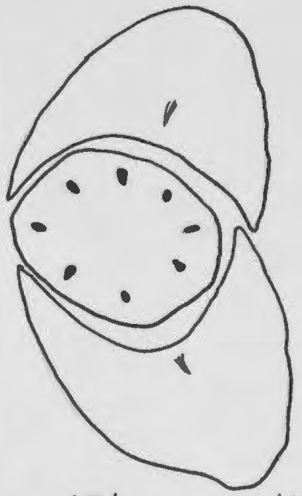
Struthiola ciliata. (Specimen no. 3)



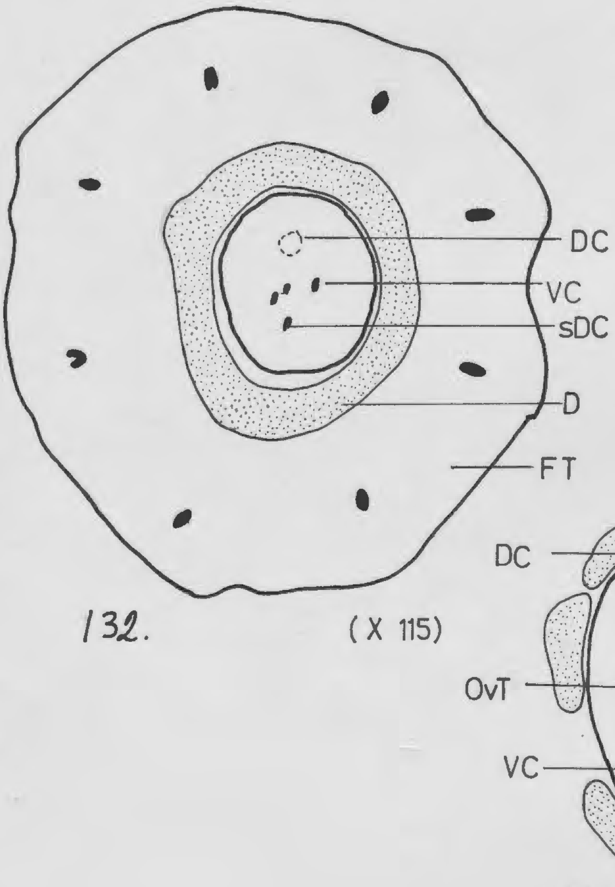
129. (X 48)



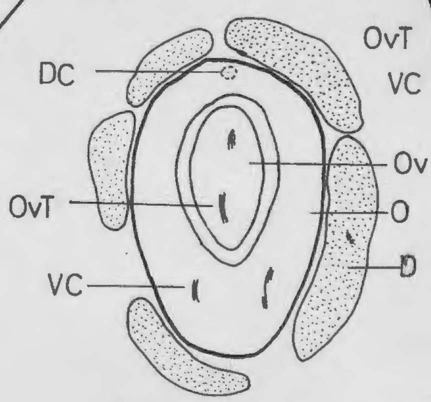
130. (X 48)



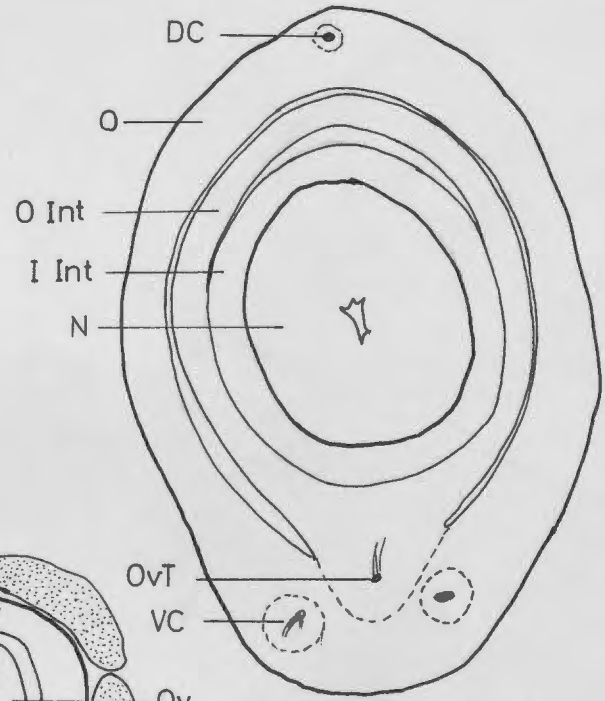
131. (X 48)



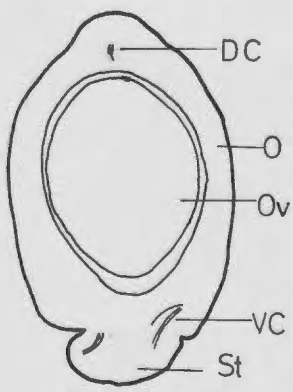
132. (X 115)



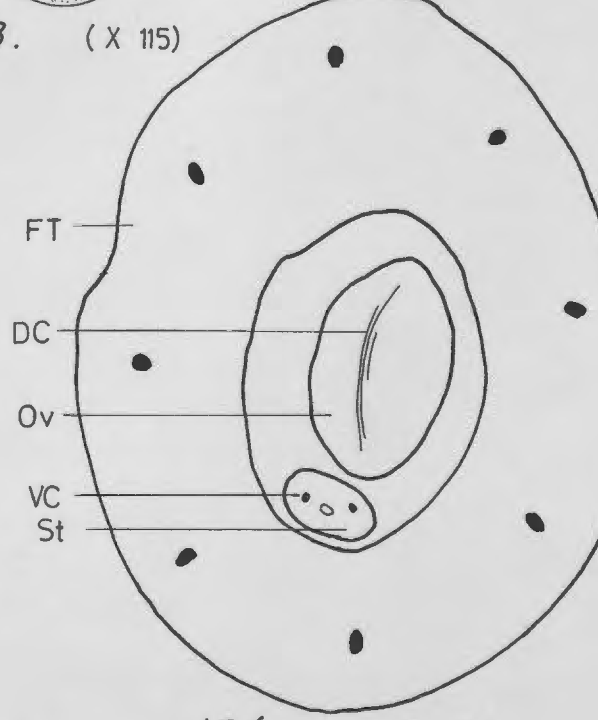
133. (X 115)



134. (X 180)



135. (X 115)



136. (X 115)

Discussion.

The nodal structure.

The nodal structure and divergence of traces to the peduncle, bract and bracteoles was found to be exceptional as compared to the usual nodal structure in Dicotyledons. The usual case is that at the nodal region traces diverge from the vascular cylinder of the primary axis to the bract (or leaf) leaving a leaf gap (or gaps). The traces to the secondary axis, which is subtended by the leaf, diverge at a higher level, so that the leaf traces and branch traces arise independently from the primary axis, and the branch gap is found above the leaf gap. (Eames and MacDaniels, 1951). In all the cases in the present work it was found that the vascular cylinder of the secondary axis is derived from the cylinder of the primary axis leaving a single gap, and the traces to the subtending bract arise from the secondary axis. (see p. 41, fig. 53-58). Thus it appears as if the bract is borne upon its axillary shoot, which in real fact is subtended by it.

In order to investigate the nodal structure, serial transverse sections were cut in the vegetative stem of Struthiola dodecandra at a point of insertion of a secondary branch subtended by a leaf. (See p. 76, fig. 137-138). It was found again that the vascular cylinder of the branch arises from the primary axis, and at a higher level gives off traces to the subtending leaf. For comparison the nodal structure of various members of the Solanaceae was investigated, where extra-axillary position of flowers or bracts may result from congenital union of organs. (Eichler, in Rendle, 1963). A similar structure was found in Datura stramonium, where the leaf is inserted upon its axillary shoot far above the node. T/S of the axillary shoot of Datura below the insertion of the subtending leaf revealed a single vascular cylinder with no sign of union of the leaf traces. This means a complete union of the vascular tissue of the leaf and the shoot up to the point where the leaf is inserted. Thus it is possible to say that in Struthiola leaf or bract traces arise congenitally with the axillary shoot. The congenital union, however, is along a very short distance and does not show any external sign, the leaves being sessile. This explains the unusual way in which the bract and bracteoles diverge.

The inflorescence.

The inflorescence of Struthiola is generally described as spike-like, with sessile flowers borne singly (or occasionally paired) in axils of bracts. (Levyns, 1950). The nature of the two lateral bracteoles has been enigmatic. The anatomical evidence brought above showed a minute abortive axillary structure consisting

ic of embryon(al) cells in the axils of the bracteoles. In some cases it appeared to be distinctly 3-lobed (fig. 62-63, 22, 130). The 3-lobed structure in the axil of a bracteole suggests a repetition of the pattern found in the inflorescence of Struthiola, i.e. a flower and two bracteoles, all in axil of a bract. It is suggested that the unit of inflorescence is a dichasial cyme in which reduction and condensation took place resulting in abortion of the lateral axes and flowers and condensation of internodes, while the bracteoles were retained. According to the present interpretation the floral bract is the bract subtending the peduncle of the dichasium, the single flower is the surviving median flower of the dichasium, and the axillary buds in the axils of the bracteoles each representing a reduced lateral branch, which in turn bears a terminal flower and two lateral bracteoles (the 3-lobes observed). (See T/S and L/S diagrams, fig. 139, 140, p. 77).

The gynoecium.

Eckardt (1937) has shown that the ovary in the Thymelaeoideae, which is unilocular and apparently unicarpellary, consists of two carpels, one of which is sterile and reduced. The fertile, functional carpel is represented by 3 main traces: a dorsal trace at the dorsal side of the ovary and 2 ventral traces oriented laterally near the ventral side. The sterile "solid" carpel is reduced to a single vestigial trace which as a result of reduction of the second carpel appears at the ventral side of the ovary close to the ventral carpellary bundles. This condition was termed by Eckardt "pseudomonomeric gynaecium". (Described by Eckardt, 1937, in 37 families of Monocotyledons and Dicotyledons). In some cases a further reduction took place in the sterile carpel, resulting in complete elimination of its traces. The ovary then contains 3 traces. 4-trace ovaries were described in Daphne mezereum (Eckardt, 1937) Dirca palustris and Lasiosiphon splendens (Heinig, 1951). 3-trace ovaries were reported in Passerina annua (Eckardt, 1937), Gnidia subulata (Heinig, 1951) and Struthiola striata (Leandri, 1930). Leandri regarded the ovary as unicarpellary.

The interpretation of the gynoecium as being pseudomonomeric and bicarpellary is also supported by the fact that in the subfamily Aquilarioideae 4 carpellary ovary occurs in Octolepis and bicarpellary ovaries occur in Aquilaria and Gyrinopsis. (Heinig, 1951).

In the species of Struthiola studied in the present work, both 4 and 3 trace ovaries were observed, in some cases within the same species. 4 carpellary traces were observed in S. striata and in S. ciliata (Dc, 2 Vc, sDC). 3 carpellary traces (DC, 2 Vc) were observed in one case in S. striata and in S. dodecandra. In S. martiana and in one case in S. ciliata 4 traces were observed at the base of the ovary, but the trace representing the sterile carpel (sDC) disappeared at the lower part of the ovary. In another case of S. ciliata this trace disappeared at middle level of the ovary. These presents intermediate positions in the reduction of the non functional carpel.

The ventral bundles that usually supply the ovule are regarded by Heinig (1951) as representing ventral carpellary bundles of the 2 carpels, the fertile and the sterile one, that arise commissurally and are therefore termed "commisural carpellary bundles". The bifurcation of these bundles, which may take place at the top of the ovary, is regarded by her as separation of the commissural bundles into their components. Although this is possible, there is another possibility, that the ventral carpellary bundles of the sterile carpel have disappeared completely, a tendency which is sometimes expressed also by the dorsal bundle. Since it is not possible to prove which of the 2 possibilities is the correct one, it was found better to designate these bundles simply as ventral carpellary bundles.

The vasculation of the style varies between species and even within the species. The more usual case is that the ventral carpellary bundles bifurcate at the top of the ovary and the branches that face the ventral side enter the style, while the other branches diverge towards the dorsal side and disappear. In one case in S. striata, the dorsal bundle of the sterile carpel vascularized the style with one of the ventral bundles. In another case in S. ciliata the dorsal bundle of the fertile carpel arched over the top of the ovary and entered the style with the ventral bundles, so that the style contained 3 bundles. A similar case was reported by Heinig (1951) in Dirca occidentalis. Variations in the vasculation of the style were reported in various members of the family by Eckardt (1937) and Heinig (1951).

The androecium

The androecium is episepalous, adnate(d) to the floral tube. The adnation includes the vascular tissue. The fused bundles are indistinguishable from their common point of origin in the receptacular stele and along the tube up to the point of tangential division that separates off the stamen trace. No remnants of the missing antisepalous bundles could be observed. This is in accord with Heinig's observation (1951) and contrary to

Leandri's observation in Struthiola.

The floral tube.

The structure of the floral tube is uniform from its base, where the 8 tube bundles depart from the floral receptacle, up to a short distance below the insertion of the stamens. The slight constriction in the tube near the top of the ovary is due to an abscission zone (fig. 48) and involves no fundamental difference in the vascular tissue.

The anatomical evidence shows that the antisepalous bundle represent sepal midribs. The alternisepalous bundles are compound. Their compound nature becomes evident in the upper part of the tube, where each of them divides first tangentially to separate the stamen trace, and then radially to form two major branches. It will be recalled that each of these branches anastomoses with branches derived from the sepal midrib and supplies the lateral part of half a sepal lobe and one or more petaloid scales opposite to it. The fact that the lateral portions of the sepal mid lobes are vascularized by the branches of alternisepalous bundles indicates that the latter are the sepal lateral bundles that are fused along the floral tube. Thus each of the alternisepalous bundles is a triple bundle, as can be seen in T/S just above the insertion of the stamens (p. 27 fig. 29). It consists of fused lateral veins of two adjacent sepals and a stamen trace. (See diagram fig. 141, p. 77). The floral tube, therefore consists of fused bases of sepals and adnated stamens.

This interpretation, suggested by Heinig (1951) is in agreement with the anatomical evidence presented in this work and is therefore adopted.

It has been pointed out by Leandri (1930) Domke (1934) and Heinig (1951) that the floral tube is appendicular in origin. The anatomical evidence supports this view. The floral receptacle is very short. The stele does not extend into the floral tube but terminates at the point where the 8 bundles that correspond to the floral appendages (sepals and stamens) diverge radially outwards and enter the tube. The carpellary bundles arise from the remainder of the stele above the point of departure of the tube bundles. This leaves no doubt that the floral tube is not of receptacular but appendicular in origin and constitutes a true hypanthium* which is formed by fused bases of perianth segments and stamens.

The petaloid scales.

The interpretation of the petaloid scales as an inner whorl of petals is related to the interpretation of the floral tube as an extended part of the receptacle. The free sepal lobes and petaloid scales were claimed to be two distinct whorls inserted at the apex of the tube-like receptacle. Since it was shown that the floral tube is not receptacular in origin, this interpretation cannot be supported.

The anatomical evidence shows that the vascular supply of the petaloid scales is derived from the same sources as the vascular supply of the sepal margins, namely from the branches of alternisepalous

---

* See definition in the introduction.

bundles (i.e. sepal laterals, according to the present interpretation) and from anastomoses of these bundles with branches of the sepal midrib. (cf. diagrams p. 15 p. 36 and p. 52). This indicates that the petaloid scales are morphologically part of the sepal whorl and not a different inner whorl. They can be regarded as appendages or corona of the sepals. These appendages are variously united or lobed, or may be absent in some forms.

The nature of the petaloid scales has been subject to dispute among the authors who have worked on the morphology and anatomy of the Thymelaeaceae.

Saunders (1939) regards the petaloid scales as petals, the vascular supply of which has been lost and used up in supplying the sepal margins. The anatomical evidence is against this view. Heinty suggested that the petaloid scales are stipules. This was refuted by Leandri (1930) on the grounds that foliage leaves in the Thymelaeaceae are exstipulate, and therefore it would be very strange to find stipules in the sepals. Leandri's view is that the petaloid scales are free tips of petals which are fused in their bases to the bases of the sepals and are represented by the alternisepalous bundles. He considers the anastomoses and exchange of bundles at the mouth of the tube to be of no importance. It is difficult to reconcile this view with the anatomical evidence, since the greater part of the vascular tissue of the sepal margins is derived from the alternisepalous bundles. Leandri's interpretation would imply that the bundles of the petals constitute the main supply of the sepal lobes.

Heinig points out that the interpretation of the petaloid scales as stipules cannot be discredited by the fact that leaves are exstipulate, since this could be a result of progressive reduction from a more primitive form.

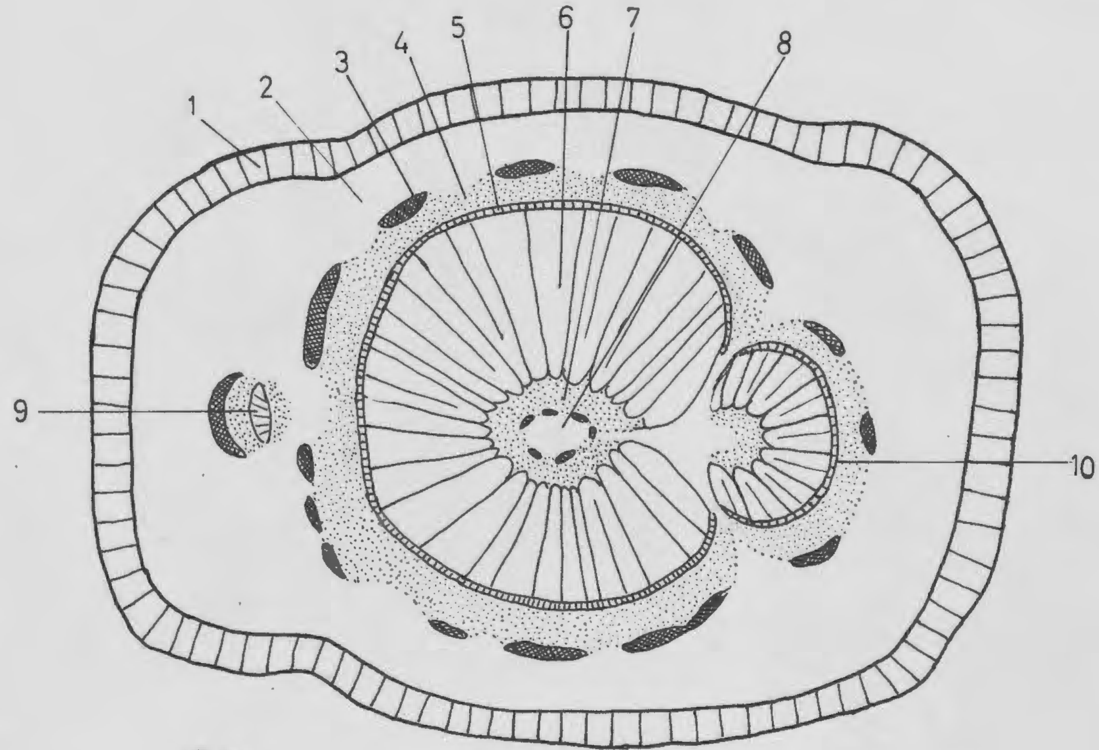
It will be noted that although the stipulate condition is sometimes regarded as being more primitive than the exstipulate one (Eames, 1961), there is no evidence to show such a reduction series in the Thymelaeaceae. Therefore it may not be ~~justify~~ justifiable to term the petaloid scales as stipules and claim that they represent relics from a primitive stipulate condition in the family. However, the analogy between the petaloid scales and stipules is not without meaning. The vascular supply to stipules is usually derived from the lateral traces of the leaf. (Eames and MacDaniels, 1951). Since the vascular supply of the petaloid scales is ultimately derived from the sepal lateral bundles, it is possible to say that morphologically they are equivalent to stipules. This does not imply phylogenetic homology between these organs. It simply implies that in the same way as stipules are regarded as part of the leaf, so the petaloid scales must be regarded as part of the sepal whorl.

Serial T/S of a vegetative stem of S. dodecandra at a nodal region (fig. 137 – 138).

1 - Epidermis.
2 - cortex
3 - Fibers
4 - External phloem.
5 - Cambial region.
6 - Secondary Xylem.
7 - Internal phloem.
8 - pith parenchyma.
9 - Congenitally fused traces to leaf and axillary bud.
10 - Congenitally fused Leaf and branch traces depart arise (congenitally) from the vascular cylinder of the stem.
11 - Leaf base.
12 - Leaf traces.
13 - Axillary bud.
14 - Branch trace.
15 - Leaf gap.

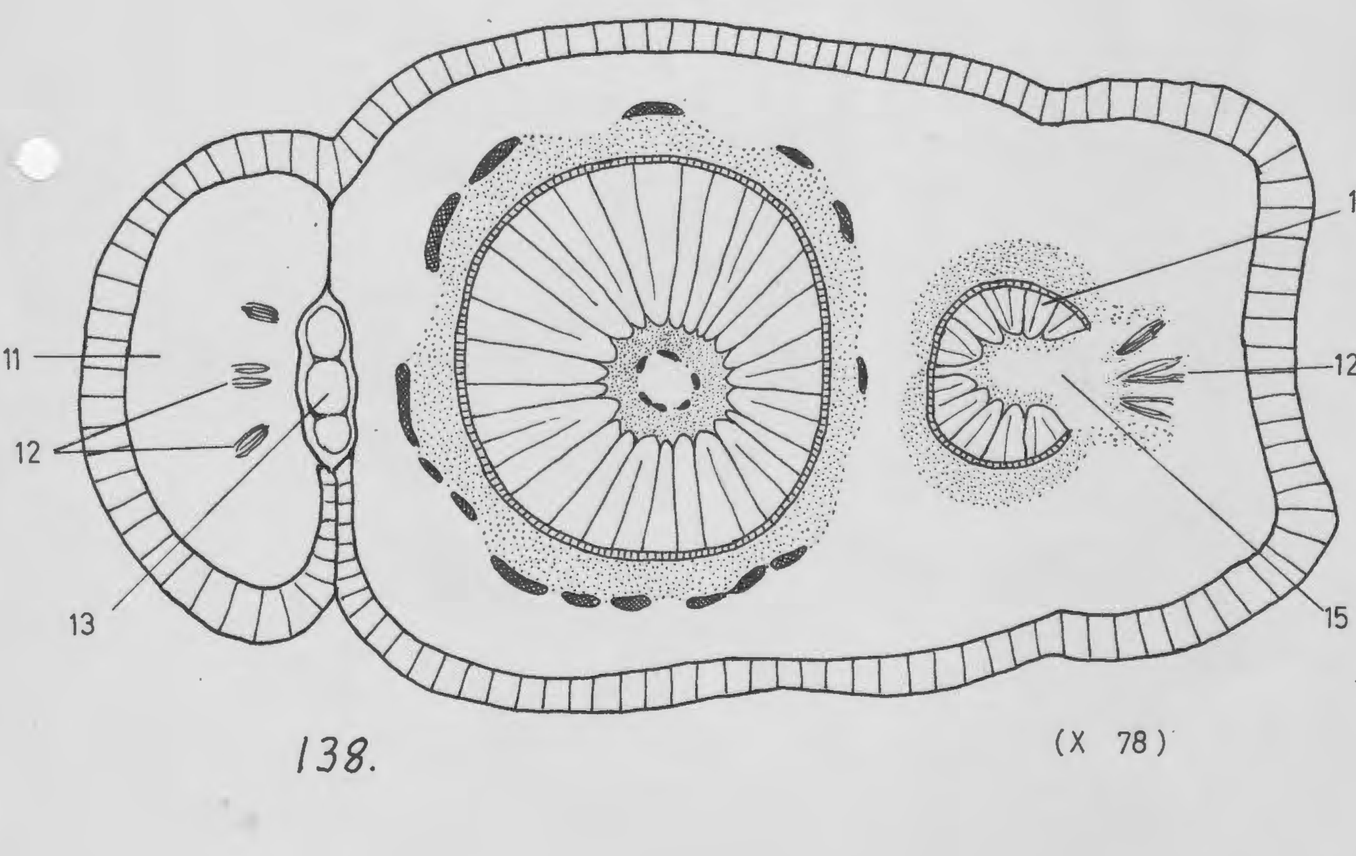
Struthiola dodecandra.

T/S of the nodal region of a vegetative stem.



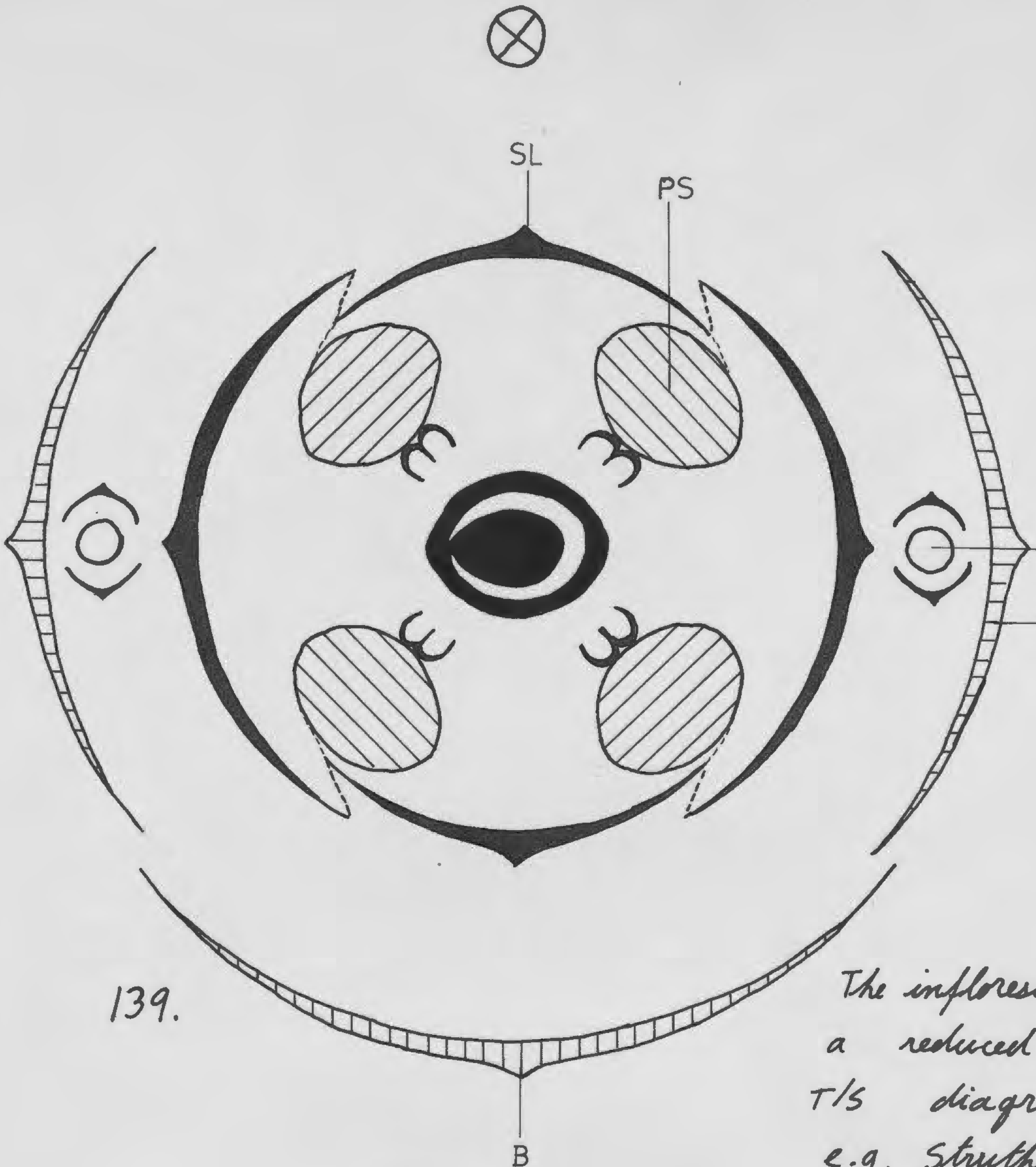
137.

(X 78)



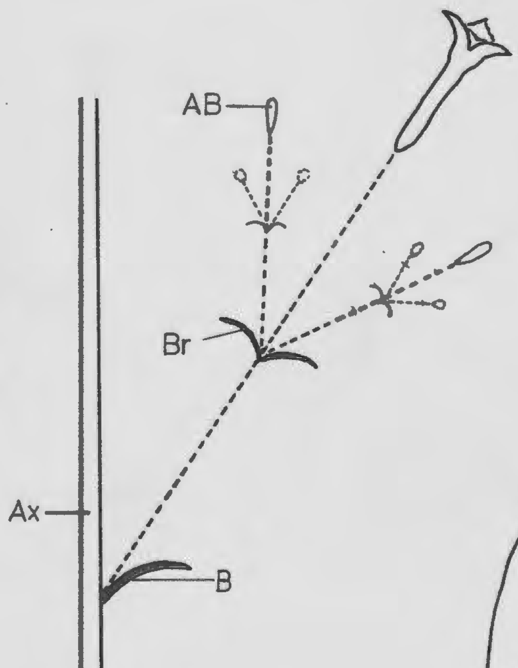
138.

(X 78)



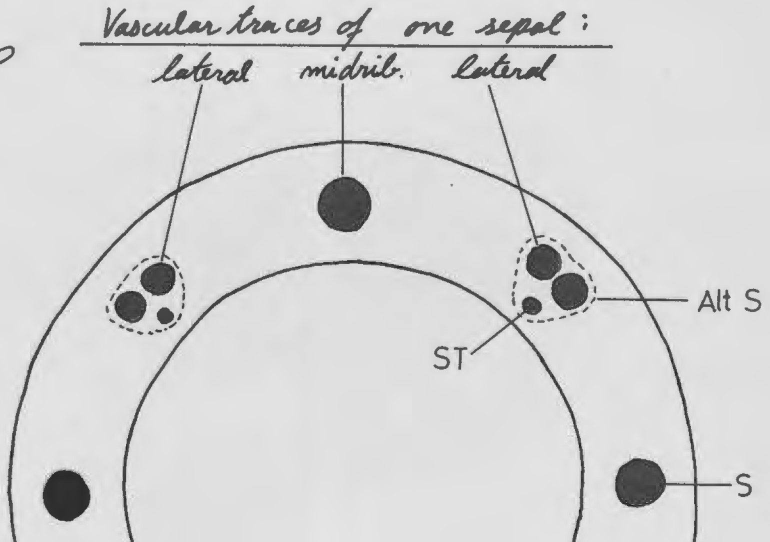
139.

The inflorescence as a reduced dichasium. T/S diagram e.g. <u>Struthiola striata</u>



140.

Interpretation of the inflorescence as a reduced dichasial cyme. Condensed axes and reduced organs are drawn in broken lines.



141. Interpretation of the bundles of the floral tube.

Conclusions

Because of the limited amount of material examined, the following conclusions are regarded as tentative and apply only to the species of Struthiola investigated.

1. The inflorescence is derived from a dichasial cyme in which the lateral axes and flowers are reduced and condensed. The inflorescence in Struthiola spp. is a compound one, a spike of dichasial cymes.
2. The bract traces arise congenitally with the traces of the axis which it subtends.
3. The floral tube is not an extension of the receptacle but a true hypanthium composed of the fused bases of sepals and stamens.
4. The petaloid scales do not represent a separate inner whorl, but form part of the sepal whorl. They can be regarded as appendages or corona of the petaloid calyx.
5. The gynoecium is syncarpous, bicarpellary, in which one of the carpels is non functional and reduced. It is represented by a single trace, or may be completely reduced.
6. The pattern of vasculation of the gynoecium is not uniform. Variations occur between species and even within a given species, representing intermediate degrees of reduction of the non functional carpel.

Literature cited

Baillon, H. (1880). The natural history of plants. 6. London.

Bentham, G. and Hooker, J. D. (1880). Genera Plantarum. 3. 1, L. Reeve, London. 1258 pp.

Bessey, C. E. (1897). Phylogeny and taxonomy of the Angiosperms. Bot. Gaz. 24: 145-178.

Domke, W. (1934)*. Untersuchungen über die systematische und geographische Gliederung der Thymelaeaceen nebst einer Neubeschreibung ihrer Gattungen. Bibliotheca Bot. 111: 1-151.

Eames, A. J. (1961). Morphology of the Angiosperms. McGraw-Hill, N. Y. 518 pp.

Eames, A. J. and MacDaniels, L. H. (1951). An introduction to plant anatomy. 2-nd ed. McGraw-Hill, N.Y. London. 427 pp.

Eckardt, T. (1937) Untersuchungen über Morphologie, Entwicklungsgeschichte und systematische Bedeutung des pseudomonomeren Gynoeceums. Nova Acta Leopoldina, N. F. 5: 1-112.

Esau, K. (1960). Plant anatomy. John Wiley. N.Y. London, 735 pp.

Gilg, E. (1895). Thymelaeaceae. In Engler, A and Prantl, K, Die natürlichen Pflanzenfamilien. 3: 6a, 216-245. Leipzig.

Heinig, Katherine, H (1946). Some aspects of the floral morphology of the Thymelaeaceae. (Abstract). Amer. Jour. Bot. 33: 821.

——— (1951). Studies in the floral morphology of the Thymelaeaceae. Amer. Jour. Bot. 38: 113-132.

Heintz, A. (1925)* Phylogenie der Cormophyten. Lund. p. 75.

Hutchinson, J. (1959) The families of flowering plants. 2-nd ed. Oxford. 1 570 pp.

Jackson, G. (1926). Crystal violet and erythrosin in plant anatomy. Stain Tech. 1: 33-34.

* The original work was not consulted.

Johansen, D.A. (1940). Plant microtechnique. McGraw-Hill. N.Y.

Lawrence, H.M. (1951). Taxonomy of vascular plants. Macmillian Co. N.Y. 823 pp.

Leandri, J. (1930). Recherches anatomiques sur les Thyméléacées. Ann. Sci Nat. Bot. 12 : 125 - 237.

Levyns, M.R. (1950). Thymelaeaceae. In Adamson, R.S. and Salter, T.M., Flora of the Cape Peninsula. Juta Co. C.T. Johannesburg. 594 - 603.

Meisner, C.F. (1856). In De Candolle Prodromus systematis naturalis regni vegetabilis. 14. Paris.

Melchior, H. (1964). Engler's Syllabus der Pflanzenfamilien. 12 Aufl. Berlin, Borntraeger, II 666 pp.

Metcalfe, C.R. and Chalk, L (1950). Anatomy of the Dicotyledons. Oxford. 2.

Payer, J. (1857)*. Traité d'organogénie comparée de la fleur. Paris. p. 481.

Rendle, A.B. (1963). The classification of flowering plants. 2. Dicotyledons. Cambridge. 640 pp.

Saunders, Edith, R. (1939). Floral morphology. W. Heffer, Cambridge 2 : 133 - 609.

Wettstein, R. (1935). Handbuch der Systematischen Botanik. Leipzig und Vienna.