

THE VASCULAR CAMBIA OF DODDER AND ITS ALLIES

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ABSTRACT

The vascular cambia of 20 species of the dodder and its allies belonging to the *Cassythaceae*, *Convolvulaceae* and *Cuscutaceae* were surveyed to assess their phenetic and phylogenetic significance. In natural condition all of them contain anomalous cambia. The *Cassythaceae* bore transitory cambium in the normal position but atypical by asymmetric activity. (The Cambium alternately retards or accentuates xylem formation on several segments and there are profuse schizogen spaces in wood. Haustoria contains both tracheids and vessels).

In stems and roots of the *Convolvulaceae* a series of widely different anomalous cambia were found which sometimes differed in stems and roots of the same species. Stems of arborescent group had bands of interxylary phloem in concentric rings, while in the primitive twiners these are arranged in radial plates. In general, a tendency was to increase the proportion of soft tissue. In *Cuscutaceae* the specified anomaly was the modified interfascicular cambium. Ray initials were absent but fusiform initials differentiated into profuse parenchyma cells and a few vessel elements.

Haustorium develops only imperforate tracheary elements. The evolutionary history of the vascular cambium in the *Convolvulaceae* was mainly one of reduction in activity and area. Thus the vesselless haustorium of *Cuscutaceae* may be regarded as a reduced form in comparison with the vessel bearing haustorium of *Cassythaceae*. It is also concluded that the primitive condition of *Cuscutaceae* is possibly derived from the general condition of *Convolvulaceae*.

INTRODUCTION

The evolution and the phylogeny of the taxa of *Cuscutaceae* are yet to be settled (Mukherjee and Bhattacharyya, 1970).

The *Cuscutaceae* and its allies bear characteristic structure in their vascular cambia. The vascular cambia in the different organs of the natural taxa produce tissues in highly specific patterns. To trace the taxonomic (phylogenetic and phenetic) relation of a taxon, along with the other criteria, the vascular cambia must have some bearings. The peculiarities of *Cuscutaceae* are in excuse of its parasitic habit. So, a comparison among the members of the analogous parasitic *Cassythaceae* and the related *Convolvulaceae* was necessary.

MATERIAL AND METHODS

The developing and mature organs of the members of the *Cassythaceae*, *Cuscutaceae* and *Convolvulaceae* (Table I) were collected from different localities. A part of these organs were fixed in FAA and the rest were preserved in the Kalyani University herbarium. Transverse and longitudinal sections, 15-50 μ m in thickness were obtained either by free hand sectioning or with the different types of microtomes. Usual process of paraffin embedding and staining with safranin-light green combination or with crystal violet iodine and a picric acid or orange G counter stain were made. About 10,000 individual sections were studied to acquaint with the anomalies described herein. The prepared slides are preserved in the Kalyani University slide collection.

RESULTS AND DISCUSSIONS

Almost all the members of the Cuscutaceae, Cassythaceae and Convolvulaceae are lianeous. Very feeble to vigorous anomalous means of secondary thickenings were widely dispersed among them. The structure of the roots are more stable than that of the stems. Roots changed less due to environment. The haustoria of the Cassythaceae and the Cuscutaceae contained modified cambia. Secondary phloem was wanting in these organs. Vessel elements occurred in the haustoria of the Cassythaceae. But, in the Cuscutaceae vessels were replaced by tracheids and sclerotic parenchyma cells (Bhattacharyya, 1975). The interesting variations of the vascular cambia are described below.

A. Cassythaceae : Cambium in the normal position, but atypical by asymmetric activity.

The Cassythaceae had a complete ring of normal cambium from the beginning of secondary thickening. It consisted of a limited circumferential stems and the cambium is active for a limited period of time. The growth is retarded over several opposite arcs of cambium and accentuated elsewhere to result a lobed stem with a star-shaped cross section. At the retarded arcs cylindrical bundles of bast fibre differentiate for an additional mechanical support. The accentuated arcs of cambium in turn are retarded at their centers to differentiate narrow bundles of bast fibre (Fig. 1). There are schizogenous spaces in wood. These lacunae also help their torsion movements.

Greatly modified lateral meristem (cambium) occurs in haustorium. Haustoria keep pace with the secondary increase of the host stem by regular cambium like divisions. The inner derivatives of the haustorial cambia differentiate into both tracheids and vessels.

Table : The locality and the name of the specimens studied

Number	Taxa	Locality
1	<i>Cassytha filiformis</i> L.	Contai, Durgapur & Madras
2	<i>Cuscuta australis</i> R. Br.	Burdwan
3	<i>Cuscuta chinensis</i> Lamk.	Calcutta
4	<i>Cuscuta hyalina</i> Roth	Udaipur
5	<i>Cuscuta obtusiflora</i> ssp. <i>latiloba</i> (Engel.) Bhatta. et Mukh.	Kalyani
6	<i>Cuscuta reflexa</i> Roxb.	Calcutta
7	<i>Cuscuta sharmanum</i> Mukh. et. Bhatta.	Burdwan & Nandigram
8	<i>Evolvulus nummularius</i> (L.) L.	Kalyani
9	<i>Ipomoea aquatica</i> Forsk.	Kalyani
10	<i>Ipomoea arborens</i> (Willd.) Sweet	Indian Botanical Garden, Shibpur
11	<i>Ipomoea campanulata</i> L.	Krishnanagore
12	<i>Ipomoea carnea</i> Jacq.	Calcutta
13	<i>Ipomoea fistulosa</i> Mart. ex Choisy	Calcutta
14	<i>Ipomoea obscura</i> (L.) Kar-Gawl.	Kalyani
15	<i>Ipomoea pes-caprae</i> (L.) Sweet	Digha, Durgapur, & Madras
16	<i>Hewittia bicolor</i> Wight	Kalyani
17	<i>Merremia gangetica</i> (L.) Cuf.	Kalyani
18	<i>Merremia hederacea</i> (Burm. f.) Hallier f.	Krishnanagore
19	<i>Operculina tarpethum</i> (L.) S. Manso.	Kalyani
20	<i>Porana paniculata</i> Roxb.	Kalyani

B. The Cuscutaceae : Cambium in the normal position but atypical for the modified interfascicular cambium.

Functional vascular cambia (Fig. 2, 3) are absent from the primitive (according to the doctrine of sequence, Yuncckedr, 1932) members of Cuscutaceae e.g. *Cuscuta australis*, *C. chinensis*, *C. hyalina* and *C. obtusiflora*. However, it is distinct in the advanced tropical members like *C. reflexa* and *C. sharmanum* (Fig. 7). The medullary rays are prominent in them. As the primary bundles increase in size by means of the fascicular cambium the rays are also extended by additional thin-walled tissue. Well-defined interfascicular cambium rarely occurs in them. Secondary xylem consists of a large number of parenchyma cells and a few vessel elements.

Haustrum of the primitive taxa is parenchymatous but in the climax members haustrum is always associated with the imperforate tracheary elements. However vessel elements are totally absent from it.

C. The Convolvulaceae : Anomalous cambia

The vascular cambia in the root and shoot of the same species always differ in structure and function. The anomalies in roots and stems are not identical. Normal secondary growth is few and far between the perennial members of Convolvulaceae. A series of widely different cambia occur in the stems and roots of the members of Convolvulaceae. For convenience these are classified below :

1. Cambium in normal position but atypical

(a) Asymmetric activity

Secondary growth at unequal rate takes place in the stems of *Ipomoea pes-caprae*, *Ipomoea aquatica* (Figs. 4, 8), *Ipomoea campanulata* (Figs. 17) and *Merremia gangetica* (Figs. 6, 10). The stele becomes two, three or more winged with alternate furrows. Tips of the phloem ray cells swell enough to keep pace with this asymmetric growth ; yet there are discrete air spaces between the endodermis and the phloem. Pericyclic cells profusely proliferate at the furrowed regions and helps in the development of the adventitious roots. The normal vascular Cambium breaks into small strips at the mature stem of *Merremia gangetica* (Sukkawala and Shah, 1960). The asymmetric growth of some fascicular Cambia finds its space in the hollow pith of the stem of *Ipomoea aquatica*. Hence no ridge is manifested on the external surface of the stem.

(b) Cessation of xylem formation

In the root (Fig. 11) and shoot (Figs. 5, 9) of *Evolvulus nummularius* the activity on the Cambium becomes modified at maturity. The xylem formation ceases over the short arcs of Cambium. The cylinders of xylem and Cambium become weavy. The furrows between the arms of the xylem are filled with secondary phloem.

(c) Modifications of the Cambium

At the stems and roots of *Ipomoea obscura* (Figs. 18, 23, 19, 20, 24) and *Hewittia bicolor* (Figs. 15, 21, 30, 31) at the root of *Porana paniculata* (Fig. 26) and at the stems of *Operculina turpethum* (Fig. 14) and *Merremia hederacea* (Fig. 16) modifications to the activity of the Cambia have been observed. The vascular Cambia initially forms a cylinder of secondary xylem but at later stage of development two or three arcs of the Cambium become modified. Modified arcs of these Cambium usually produce parenchymatous cells. Sometimes a part of these modified arcs may resume their normal activity to produce secondary wood. The initial cylinder of secondary xylem is ruptured at maturity and the parenchymatous derivatives of these modified Cambia become connected with the pith. These radial bands of storage parenchyma are as it were the broad medullary rays.

(d) Included Phloem

In the stem of *Ipomoea arborescens* and *Porana paniculata* a complete ring of normal cambium develops from the beginning of secondary thickenings and it remains active throughout the life of the plant. At maturity an anastomosing system of combretum type included phloem appears in them. In the self supporting erect plant (*I. arborescens*) alternating bands of secondary xylem and included phloem appear in concentric rings but in the primitive liane (*P. paniculata*) the xylem and phloem bands occur in radial plates.

2. Cambia in unusual positions

(a) Medullary Cambia

There are three types of medullary Cambia in the stems and roots.

(i) Normal medullary Cambia :

In the stem of *Ipomoea obscura* (Figs. 19, 20) and *Hewittia bicolor* (Figs. 21) a few arcs

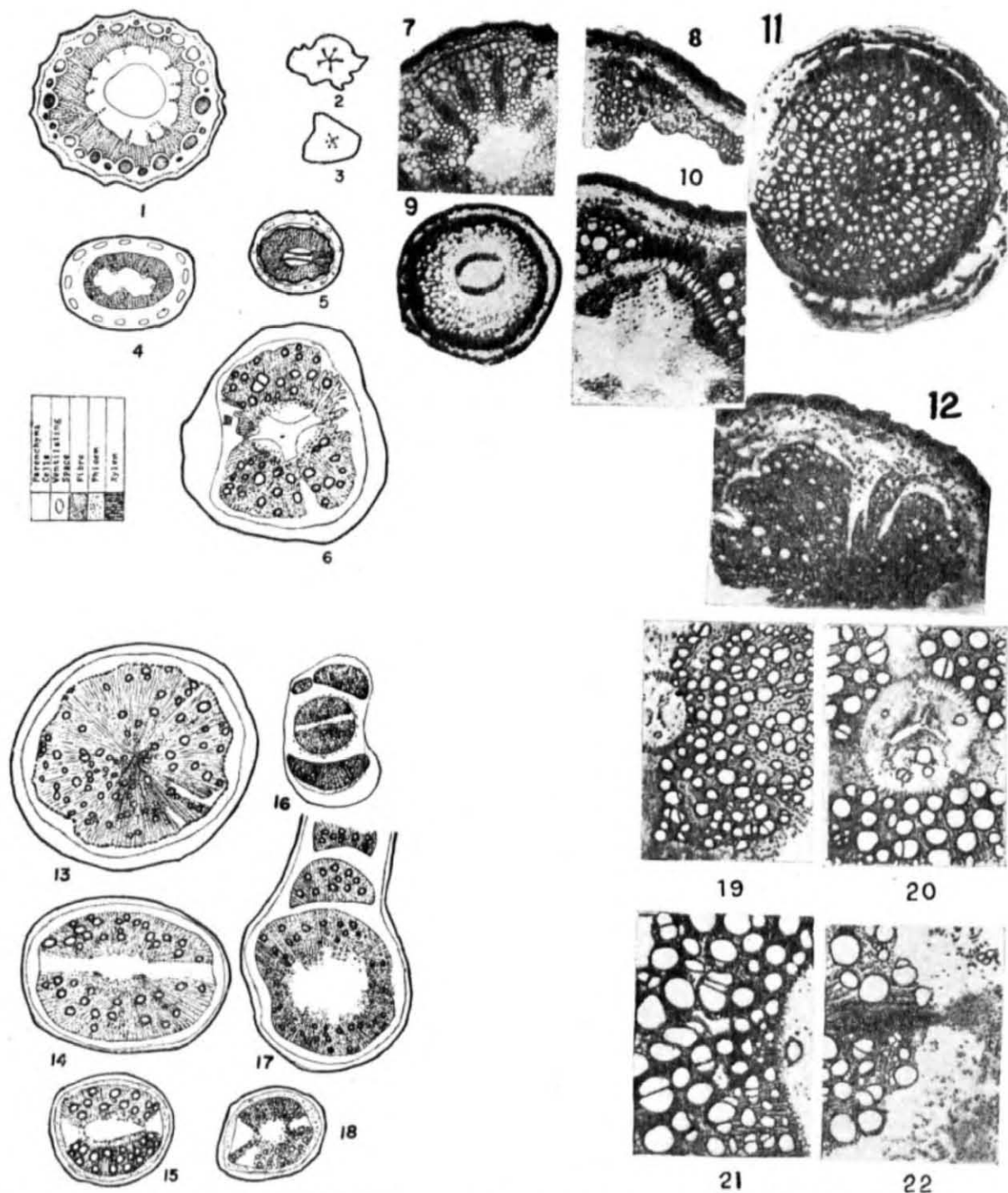


Plate I : Figs. 1-6. T. S. stem ($\times 12$) : 1. *Cassytha filiformis*. 2 & 3. *Cuscuta obtusiflora* ssp. *latiloba*. 4. *Ipomoea aquatica*. 5. *Evolvulus nummularius*. 6. *Merremia gangetica*.

Plate II : Figs. 7-10. T. S. stem ($\times 9$) : 7. *Cuscuta sharmanum* ($\times 9$). 8. *Ipomoea aquatica* ($\times 9$). 9. *Evolvulus nummularius* ($\times 9$). 10. *Merremia gangetica* ($\times 17$).

Plate III : Figs. 11-12. T. S. root : 11. *E. nummularius* ($\times 16$). 12. *M. gangetica* ($\times 27$).

Plate IV : Figs. 13-18. T. S. stem ($\times 12$) : 13. *Operculina turpethum*. 14. *Hewittia bicolor*. 15. *Merremia hederacea*. 16. *Ipomoea campanulata*. 17. *Ipomoea obscura*.

Plate V : Figs. 19-20. T. S. stem. *I. obscura* ($\times 10$) : 19. Medullary region showing the intact "initial cylinder" of secondary xylem. 20. Mature medullary region showing the torn "initial cylinder" of secondary xylem and the inverted medullary bundles. Fig. 21. T. S. stem of *Hewittia bicolor* showing a medullary bundle with single vessel element ($\times 10$). Fig. 22. T. S. root of *I. obscura* showing a cortical vascular bundle and an arc of multiplied modified cambium ($\times 10$).

of medullary Cambia produce inverted bundles with large vessels. Strong activity of these Cambia find no room in the limited pith and break the initial cylinder of secondary xylem. Such medullary Cambia in the stem of *Operculina turpethum* rarely differentiate lignified tracheal elements.

(ii) *Modified medullary Cambia in the stem :*

Two arcs of modified medullary Cambia appear in the pith of *Evolvulus nummularius*. One of the arc remains on the abaxial side and the other occurs in adaxial area (Figs. 5, 9). Instead of producing inverted bundles it produces only secondary phloem elements.

(iii) *Modified medullary cambia in the root :*

With characteristic tangential divisions some arcs of xylary procambium are modified into medullary Cambia in the roots of *Ipomoea aquatica* (Figs. 28, 29), *Hewittia bicolor* (Figs. 30, 31) and *Ipomoea obscura*. There is a modified activity in these Cambia to produce parenchymatous tissues. This modified activity at the centre of the roots displaces the exarch primary xylem elements and occasionally ruptures the initial secondary xylem ring along the wide vascular rays. In these roots large central metaxylem may be displaced and thus the radial bands of storage parenchyma may fuse at centre.

(b) *Cortical Cambia*

Different types of cortical Cambia appear in the stems and roots of the Convolvulaceae and these are classified below.

(i) *Concentric arcs of cortical Cambia :*

In the stems and roots of *Ipomoea fistulosa* (Figs. 32), *Ipomoea carnea* and in the roots of *Ipomoea arborescens*. Concentric arcs of additional Cambia arise from the pericyclic tissues. These are arranged in a ring. Each cambium functions for a short time and the succession of Cambia replaces one another. In the stem of *I. carnea*, vessels are arranged in a radial rows but in *I. fistulosa*, vessels are scattered within the secondary xylem (Bhattacharyya, 1976). Just

reverse situation has been observed in their roots. In the root of *I. fistulosa*, vessels are arranged in radial rows (Fig. 32) but in *I. carnea*, vessels are scattered within the secondary xylem.

In the root of *Ipomoea arborescens* wide vascular rays become inconspicuous. The derivatives of the first layer of the additional Cambia remain separated permanently.

(ii) *Asymmetric patches of cortical Cambia :*

In the stems and roots of *Ipomoea campanulata* (Fig. 17), *Ipomoea obscura* (Figs. 24, 22), *Operculina turpethum* and *Merremia hederacea* (Figs. 16, 25), asymmetric patches of cortical Cambia differentiate just against the bands of the secondary xylem. No Cambia has been observed against the atypical region of the first Cambium. In all cases first layer of additional Cambia arises from the pericyclic tissues. Each of the Cambium functions for a short time and succession of Cambia replace one another in the stem of *I. campanulata* (Fig. 17).

Usually four arcs of Cambia are differentiated in the roots. As a result, the external surface of the roots become quadrangular. A ring of Perivascular fibre is present in the root of *I. campanulata*. Normal vascular rays are prominent in the root of *Operculina turpethum* but these are inconspicuous in the root of *M. hederacea*.

(c) *Circular Cambia*

In the stem of *Hewittia*, a complete ring of normal cambium develops at the beginning of secondary thickenings but it is active for a limited period of time. Afterwards a ring of circular Cambia is differentiated in the pericyclic region. Each of the Cambia possesses its own means of secondary thickening and produces wide rays and tetra-arch secondary xylem.

(d) *Multiplication of modified Cambia*

Hayward (1938) observed the anomalous secondary Cambia in the storage root of *Ipomoea batatas* (L.) Lam.

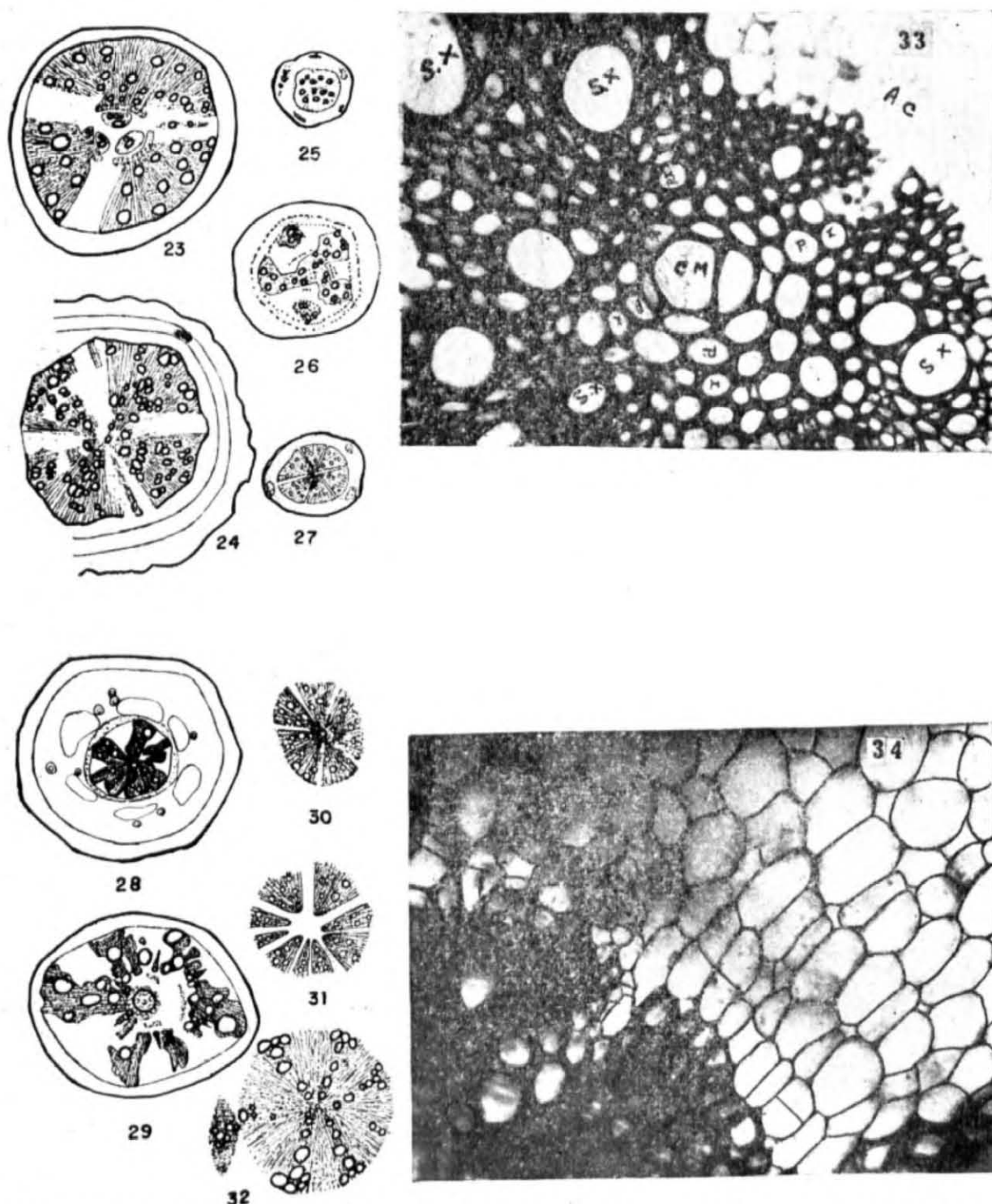


Plate VI : Fig. 23. T. S. stem of *I. obscura* showing three modified arcs of cambia and three medullary cambia ($\times 16$). Figs. 24-27. T. S. root ($\times 16$) : 24. *I. obscura* showing cortical cambium and the arcs of multiplied modified cambia. 25. *Merremia hederacea* showing cortical fibre and cortical cambium. 26. *Porana paniculata* showing multiplication of modified cambia. 27. *Ipomoea campanulata* showing the activities of the normal cambium and three cortical cambia.

Plate VII : Figs. 28-32. T. S. root ($\times 16$) : 28. *Ipomoea aquatica* showing cortical fibre, ventilating space and modified arcs of normal cambium. 29. *I. aquatica* showing three arcs of modified medullary cambia. 30-31. *Hewittia bicolor* showing the activities of the multiplied modified cambia. 32. *Ipomoea fistulosa* showing the activities of the normal cambium and the cortical cambium.

Plate VIII : Fig. 33. T. S. root : *Porana paniculata* ; portion showing the central primary xylem (C. M.), normal secondary xylem (S. x) and an arc of the multiplied and modified accessory cambium (A. C.) ($\times 70$)

Plate IX : Fig. 34. T. S. root : *Porana paniculata* ; enlarged portion showing primary xylem, secondary xylem and the initiation of accessory cambium ($\times 150$).

In the roots of *Porana paniculata* (Figs. 26, 33, 34), *Ipomoea obscura* and *Hewittia bicolor* (Figs. 30, 31), multiplication of modified Cambia has been observed. Within the derivatives of the modified Cambia, some additional Cambia are again differentiated with characteristic tangential divisions. These may be organised in tangential or in radial rows. Usual derivatives of this Cambium are parenchymatous in nature or rarely it may produce secondary phloem. Strong activity of these Cambia may disturb the original stele or may displace some arcs of the secondary xylem.

CONCLUSIONS

The nature of the vascular cambia in the roots and stems of the same species may differ. Lignified and non-lignified tissues appear either in concentric ring for an erect self-supporting plant or in radial plates for a liane. Evidently therefore this arborescent member of convolvulaceae is the "facultative liane". Multiplication of the additional cambium is the feature of the storage roots but it occurs in the normal roots of some Convolvulaceae. This behaviour is indicating thereby that such roots possess the potentiality of the storage organ.

In appearance and in function the members of Cuscutaceae resemble their analogous member of Cassythaceae but the later has a most primitive type of anomalous cambium. Therefore parasitism has no bearing on the structure and function of the cambium. Evidently in the process of evolution they independently acquire their characteristic cambia.

In cross section, the stem of the Convolvulaceae shows a single ring of bicollateral vascular bundles separated by narrow medullary rays. There are multiplication of modified cambia and other anomalous activities in the secondary body of the Convolvulaceae. Thus these anomalous activities lead to an

increase in the proportion of soft tissue. The evolutionary history of the vascular cambia in the members of the Convolvulaceae is mainly one of reduction in activity and area. This trend is again augmented in the members of the Cuscutaceae and it is normal for their fascicular and interfascicular sectors to be paranchymatous rather than woody. The area and activity of the cambium are so reduced that there are no functional cambium in the stem and haustorium of the primitive members of Cuscutaceae. But their presence in the stem and haustorium of the climax members may recall the doctrine of recapitulation. As the primitive condition of Cuscutaceae is the general condition of Convolvulaceae we may conclude that the Cuscutaceae is possibly derived from the lianous members of Convolvulaceae.

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