TENDRILS OF THE CUCURBITACEAE:

THEIR MORPHOLOGICAL NATURE ON ANATOMICAL EVIDENCES

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INTRODUCTION

All but one genus, Ecballium, of the family Cucurbitaceae are characterized by the possession of a simple or variously branched extra-axillary tendril. Its morphological nature has attracted the attention of workers from the early part of the nineteenth century. Different authors working on different materials have tried to interpret the morphology of this organ but they never agreed to a common explanation, e.g., Müller (1887) interpreted it as 'axis plus leaf', Green (1905) and Majumdar (1926) as 'branch', Trinkgeld (1923) as 'leaf', Green (1905) again as 'stipule', and so on. Lately Miss Khansaheb (1947) revived interest in this organ of climbing. She studied anatomically the tendril and the node bearing it in a number of cucurbits, and found that the tendril received its vascular supply both from the leaf-trace bundles (outer ring) and the cauline bundles (inner ring) of the axis. This led her to the conclusion that the tendril is a *leaf-stem complex*.

In order to find out the true morphological nature of this climbing organ anatomical studies of the nodes and vascular supplies to this organ (tendril) of twenty-four species of the Cucurbitaceae under fourteen genera were undertaken and the results and conclusions are recorded in this short report.

MATERIALS AND METHODS

The following twenty-four species were collected from Dacca town and its suburbs:

	Species	Vernacular name	Habitat
1.	*Benincasa hispida* Cogn.	Chalkumra	Cultivated
2.	*Bryonopsis laciniosa* Naud.	Mala	Wild
3.	*Citrullus colocynthis* (Linn.) Schrad. ..	Mâkâl	Wild
4.	*Citrullus vulgaris* Schrad.	Tarmuj	Cultivated
5.	*Coccinia indica* (Naud.) Wight and Arn. ..	Telâkuchâ	Wild
6.	*Cucumis sativus* Linn.	Sashâ	Cultivated
7.	*Cucumis melo* Linn.	Futi	Cultivated
8.	*Cucumis* sp.	X	Wild
9.	*Cucurbita maxima* Dachesne	Mithâkumrâ	Cultivated
10.	*Gymnopetalum cochinchinensis* Kurz. ..	X	Wild
11.	*Lagenaria vulgaris* Seringe	Lâu	Cultivated
12.	*Luffa cylindrica* (Lour) Roem.	Dhoondol	Cultivated and Wild
13.	*Luffa acutangula* Roxb.	Jhingâ	Cultivated
14.	*Luffa graveolens* Roxb.	X	Wild

	Species	Vernacular name	Habitat
15.	*Momordica charantia* Linn.	Uchchhe	Cultivated
16.	*Momordica cochinchinensis* Spreng.	Kâkrol	Cultivated
17.	*Momordica dioica* Roxb.	Bankâkrol	Wild
18.	*Momordica* sp.	X	Wild
19.	*Mukia maderaspatana* Kurz.	X	Wild
20.	*Thladiantha calcarata* Clarke	X	Wild
21.	*Tricosanthes anguina* Linn.	Chichingâ	Cultivated
22.	*Tricosanthes cucumerina* Linn.	Banchichingâ	Wild
23.	*Tricosanthes dioica* Roxb.	Patol	Cultivated
24.	*Zanonia indica* Linn.	X	Wild

The material was fixed in F.A.A. and washed thoroughly before use. Transverse sections were made, both free-hand and with hand-microtome. For the study of nodal anatomy the following technique was adopted: 1·5% hot agar solution was smeared evenly on a slide. The slide was then placed over a warm plate with water underneath it, so that the fixing material did not solidify before the sections were placed and arranged serially. After the operation the slides were removed from the warm plate and the fixing material was allowed to cool down to fix the sections in proper positions. When the glue dried the sections were stained either differentially with safranin and fast green and made permanent, or stained only in safranin, mounted in glycerine solution and sealed with a paraffin preparation.

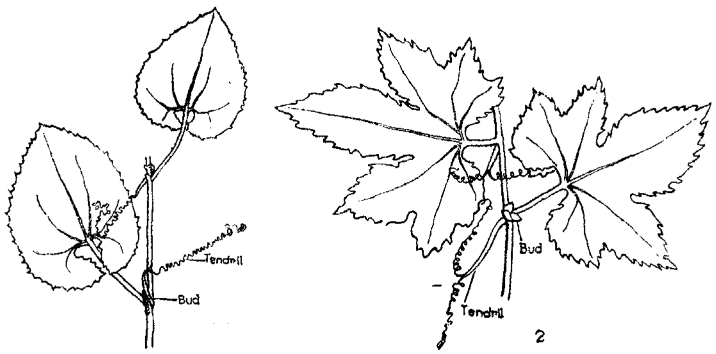
To study the vascular disposition at the node and its leaf, bud and tendril the former was cleared in the following way:—first of all the somewhat hard epidermis was peeled off with a pair of fine forceps avoiding any damage to the vasculature. Then the nodal piece was warmed with a small quantity of concentrated HCl for five to seven minutes, then 30 to 35 c.c. of 10% NaOH solution was poured slowly down the test tube and warmed for two to three minutes; all the soft tissues precipitated down leaving the vascular system intact with some soft tissues still attached. This was taken out of the test tube, rinsed thoroughly in water; stained in dilute safranin and again washed in water; the attached soft tissues were then removed with a mounted needle and a fine camel hair brush. The cleared and stained vascular system was then mounted in 40–45% glycerine and sealed. Figures were drawn with the help of a camera lucida.

Abbreviations used

The following abbreviations have been used: *L*—leaf; *L'*—1st lateral leaf-trace bundle; *L"*—2nd lateral leaf-trace bundle; *M*—median leaf-trace bundle; *T*—Tendril; T^1—1st tendril-trace bundle; T^2—2nd tendril-trace bundle; *B*—bud; *b*—bud-trace bundles; 1, 2, 3, 4, 5 refer to vascular bundles of the outer and 6, 7, 8, 9 and 10 refer to vascular bundles of the inner rings, of the axial stele. The same number has been retained for these bundles in the axial rings of different internodes; supply of the outer bundles from those of the inner is indicated by a number in brackets, the number refers to the bundle of the inner ring.

Observations

The tendrils in the Cucurbitaceae may be simple (Fig. 1) or branched (Fig. 2). Each of them is differentiated into a comparatively strong basal portion which remains erect and an upper part which is coiled.



TEXT-FIG. I

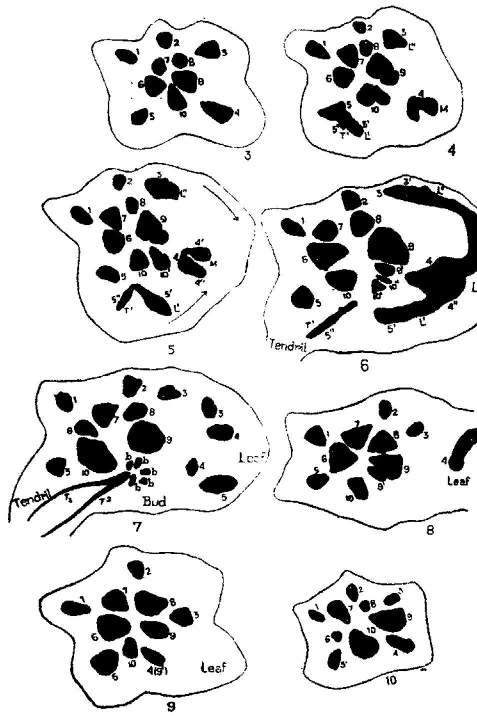
FIG. 1. Habit sketch of *Thladiantha calcarata* Clarke. ($\times \frac{1}{3}$); FIG. 2. Habit sketch of *Bryonopsis laciniosa* Naud. ($\times \frac{1}{3}$).

Anatomy of the node.—The vascular bundles of the node, like those of the internode, are unequal and dissimilar. In the internode the ten bundles are arranged in two rings; those of the outer ring (Fig. 3—1, 2, 3, 4, 5) are smaller in size and extent than those of the inner one (Fig. 3—6, 7, 8, 9, 10). But in some species the vascular bundles of the two rings in the node come so close to one another that it becomes rather difficult to assign them to their respective rings. In the present description of the nodal anatomy the bundles will, however, be referred to as if they are arranged in two rings with these assigned numbers.

A. *Vascular supply of the leaf.**—Each leaf receives three bundles (3, 4, 5) all of which come from the outer ring at the node. The bundles of the outer ring are, therefore, regarded as leaf-trace bundles. The median bundle remains simple in Bryonopsis (Figs. 11, 12), Coccinia, Lagenaria, Benincasa, but it becomes deeply cleft in the form of 'U' on its way to the base of the petiole of the leaf in Thladiantha (Figs. 4, 5) and in Citrullus, Cucumis, Cucurbita, Gymnopetalum, Luffa, Momordica, Mukia, Tricosanthes, and Zanonia. The median bundle (4), simple or lobed, goes as a whole to supply the leaf leaving a gap in the outer stelar ring. The gap, thus formed, is then occupied by a bundle branched off from one of the larger inner bundles, 9 in the case of Thladiantha and 10 in the case of Bryonopsis, which also supplies traces to the bud (Figs. 9, 15).

The first lateral bundle (L′) of a leaf is formed by the branching of bundle 5 of the outer ring flanking the median bundle (Figs. 4–6 and 11-12). The second lateral (L″) may be formed as in the case of the first lateral, from a part of bundle 3 on the other side of the median, e.g. in Benincasa, Coccinia, Luffa, Momordica, Thladiantha (Figs. 5-6), or the whole bundle 3 may go to supply the leaf as its second lateral, as in Bryonopsis (Figs. 12–15), Citrullus, Cucurbita, Cucumis, Gymnopetalum, Lagenaria, Mukia, Tricosanthes and Zanonia. When the entire bundle goes to supply the leaf as a lateral its position in the next internode is taken by a branch of bundle 9 of the inner ring, which also takes part in the vascular supply to the bud (Figs. 13–15). In this respect the second lateral and its reconstitution at the next higher internode takes place exactly in the manner of the median trace bundle.

* The course of the bundles of the outer and inner rings have been followed through two contiguous internodes and the intervening node. Figures in serial transverse sections have been given for only two representative species, *Thladiantha calcarata* Clarke, and *Bryonopsis laciniosa* Naud. In all the figures the median and the two lateral bundles are marked 4, and 3, 5 (outer ring) respectively.



TEXT-FIG. II

FIGS. 3–9. Serial transverse sections of one internode to the base of the next higher internode through a node of *Thladiantha calcarata* Clarke showing the vascular supplies to leaf bud and tendril. (×12). For explanation of Fig. 10, see Text-fig. III.

The origin and vascular supply to a Cucurbita leaf may be summarized as follows:—

(i) The stelar system (axial) consists generally of ten vascular bundles arranged alternatively in two rings.

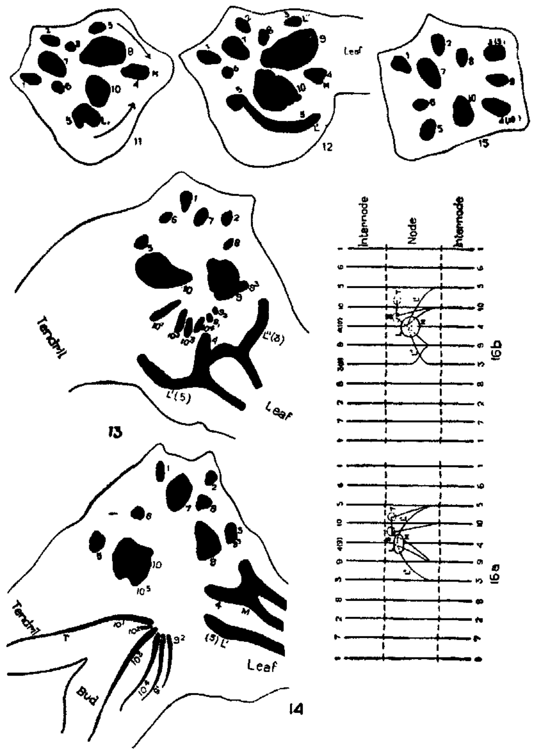
(ii) Three bundles from the outer ring contribute to the formation of the three-bundled trace of each leaf.

(iii) One entire bundle constitutes the median and goes to the leaf causing a gap in the outer ring of axial bundles, which is later filled up at the next higher internode by a branch coming from a much larger bundle of the inner ring. This larger bundle also sends a branch to the axillary bud (Figs. 4–9 and 13–15).

(iv) The first lateral is always a branch of the vascular bundle of the outer ring placed immediately lateral to the median (Figs. 4–6 and 11–13).

(v) The second lateral may be either a branch of the other proximal bundle of the outer ring as in the case of the first lateral as in Thladiantha (Figs. 5-6), or the whole bundle may go to supply the leaf, when a branch from a bundle of the inner ring comes to occupy its place in the outer ring as in Bryonopsis (Figs. 11–15). This bundle of the inner ring also sends out a branch to the bud (cf. the case of the median).

B. *Vascular supply of the bud.*—Normally the bud traces branch off from bundles 9 and 10 of the inner ring (Figs. 6, 7 and 13, 14) which also send out branches to occupy the gaps in the outer ring caused by the departure of the lateral and median traces of the axillant leaf. These bundles of the inner ring enlarge before they give out the bud traces (Figs. 6-7 and 12–14). The vascular supplies to the bud thus come exclusively from the bundles of the inner ring (described cauline) as their branches.



TEXT-FIG. III

FIGS. 10–15. Serial transverse sections of one internode to the base of the next higher internode through a node of *Bryonopsis laciniosa* Naud. showing vascular supplies to leaf, bud and tendril. (×12). FIGS. 16*a* and 16*b*. Diagrammatic representations of the course of vascular bundles from one internode to the next internode through a node of *Thladiantha calcarata* Clarke and *Bryonopsis laciniosa* Naud. respectively.

C. *Vascular supply of the tendril.*—According to the nature and mode of vascular supply from axial ring of bundles the tendrils may be grouped under two general types, namely (*a*) the *Bryonopsis* type, and (*b*) the *Thladiantha* type. In the first type the tendril supply is derived exclusively from the bud trace which in turn is formed by the branches coming from bundles 9 and 10 of the inner ring. Thus here the tendril receives all its vascular supply directly from the stelar system of the axillary bud (Figs. 13, 14). This category includes the tendrils of Bryonopsis, Benincasa, Citrullus, Coccinia, Cucumis, Cucurbita, Lagenaria, Momordica, Mukia, Tricosanthes and Zanonia.

In the 'Thladiantha' type, on the other hand, each tendril receives two bundles one of which comes from the bud trace (9′, 9″, 10′, 10″) while the other from one of the laterals (5′) of the leaf trace (Figs. 5–7). Thus the second type of tendril receives its vascular supply both from the bud stele and a lateral trace of the axillant leaf.

Discussion and Conclusion

The tendril of the Cucurbitaceae has attracted the attention of various workers from the nineteenth century, and quite a number of divergent views on its morphological nature have so far been put forward.

Müller (1887) examined anatomically a number of tendrils and came to the conclusion that in both simple and compound tendrils the non-sensitive base is a shoot axis and the upper portion a leaf-spindle, i.e. the tendrils are *axis plus leaf*. But in Cucumis he found the tendril to be entirely *foliar* in nature.

Engler (1904) who collected specimens with thorn-like appendages, one of which grew out into a tendril, regarded the tendril as a *stipule*.

Green (1905) made the following suggestions to explain the nature of the tendrils in the Cucurbitaceae: the tendril is (i) one of a pair of stipules, the other being suppressed; (ii) extra-axillary branch at the side of a leaf; (iii) if the extra-axillary bud develops into a flower, then the tendril is peduncular in origin, i.e. one of the flower stalks becomes modified and adnate to the leaf-stalk and appears as a tendril.

According to Green, Naudin holds that a branch arises in the axil of a leaf; and that in the case of a simple tendril it becomes completely merged with the petiole, or with stem and grows no further, the only sign of this branch is one leaf which it bears on one side but which is reduced to the mid-rib: *This is the tendril.* Compound tendril, according to him, is formed by the elongation of the branch which bears several leaves that are modified into tendril branches. Green also quotes Payer according to whom the tendril is formed by the splitting of the petiole.

Braun and Wydler (quoted in Rendle, 1952) regarded a simple tendril as one of the bractlets of the axillary flower, while in a compound tendril each branch was believed to be a rib of a simple leaf.

Goebel (1905), who does not accept anatomy as evidence, regards simple tendril as prophyll of axillary shoots of which only one developed, whereas branched tendrils are axes which bear leaves transformed into branches of the tendrils.

Hägerup (1930) regarded all compound tendrils to be modified shoots, and in Cucumis it is the first prophyll of the secondary axis.

Sawhney (1919-20) on the basis of vascular contribution regarded arms of branched tendrils and upper part of the simple tendrils as homologous with leaves, and the basal part with shoot axis.

Trinkgeld (1923) supports Müller in all his interpretations, namely, simple tendril of Cucumis is entirely foliar; in simple tendril of other cucurbits basal part is a transformed shoot axis, upper portion terminal leaf, and in branched tendrils basal portion is the shoot axis, and branches are metamorphosed leaves. This interpretation is based on the analogy of the arrangement of vascular bundles which is in a ring in the axis, and dorsiventral in the leaf, and also on the distribution of sclerenchyma which is in a ring in the axis, but as bundle-caps in the leaves.

Majumdar (1926) from specimens of *Cucurbita maxima* Dachesne collected by him supported the shoot nature of the branched tendril, i.e. axis plus leaves modified.

Khansaheb's (1947) interpretation is based on a study of the anatomy of nodes, and the vascular supply to the tendril. She found that tendrils in her specimens received vascular supplies from bundles of both the inner and outer rings of the axial stele (cf. Thladiantha type, Figs. 4–6), and on the basis that the vascular bundles of the outer ring are leaf-trace bundles and those of the inner ring are cauline bundles (cf. Sawhney, 1919-20) she interpreted tendril as a *leaf-stem complex*.

The results of the present studies are recorded in the foregoing pages; and according to the nature of the vascular supply from the axis the tendrils have been divided into two major types, namely, (1) the *Bryonopsis type*, and (2) the *Thladiantha type*.

In the tendrils of the first type, represented by those of *Bryonopsis laciniosa* Naud., the vascular supply comes entirely and directly from the bud trace. From the nature of the origin of vascular supply, the tendrils in these cases cannot be identified with leaf. The presence of sclerenchyma in the form of a closed ring in the cucurbits is a stem feature, therefore it cannot be the petiole or the ribs of a leaf. It cannot be regarded as a bud also, as its origin is not connected with a leaf, and its vascular supply is also different from the normal mode of supply to a bud in these species as well as in the majority of dicotyledons.

The tendril of the first category is, therefore, regarded as an *outgrowth of the bud axis*. Such outgrowths are not unusual, and Arshad Ali (1955) and Fattah (1955) have shown respectively that the tendrils of the Vitaceae and the inflorescence axes of the Solanaceae are outgrowths of the axes which bear them.

In the second category the tendrils receive vascular supply partly from the vascular system of the bud axis and partly from a branch of the lateral trace bundle destined to supply the axillant leaf. On the dictum of Sinnott and Bailey (1914), any organ at the base of the leaf getting vascular supply from the branch of a lateral leaf-trace bundle should be regarded as a stipule. This has been supported by later workers (Mitra and Majumdar, 1952). Therefore, the tendril of this category should be interpreted as *stipule-stem complex*.

Nature of the vascular bundles in the stelar rings

The axial stele consists of ten vascular bundles arranged in two rings, five in the outer and five in the inner. The bundles of the outer ring have been described as 'leaf-trace bundles' and those of the inner ring as 'cauline bundles'. My studies of the vascular system of the axis done in serial transverse sections through two consecutive internodes and the included node show that the vascular supplies to the leaf, bud and the tendril at each node are derived directly and indirectly from the bundles of the inner ring.

When a bundle of the outer ring goes to supply a leaf, a branch from one of the inner ring bundles comes to take its place in the next higher internode. But the bud receives all its vascular supply from the bundles of the inner ring. Therefore, the bundles of the inner ring not only supply the bud traces but also send out branches to supply the leaf. It is to be noted that the bundles of the inner ring never bodily shift to the outer ring. The bundles of the outer ring are, therefore, really leaf-trace bundles passing through an internode on their way to the leaves higher up in the axis. The bundles of the inner ring may be called 'cauline bundles' in the sense that they never leave the axis as a whole causing gaps in the axial cylinder; they only send out branches to the leaf and axillary bud. It will be interesting to note how these bundles end in the apical meristem of an adult shoot.

The dual nature of the internodal bundles, i.e. foliar (leaf trace) and cauline (axial), indicates the dual nature of the axis, namely, the outer mantle served by the leaf-trace bundles, and the core served by the cauline bundles. If this interpretation is correct then it supports the *mantle-core* theory of Hofmeister (1851), Saunders (1922) and revived by Mitra and Majumdar in 1952.

Summary

The morphological nature of the tendrils of the Cucurbitaceae has been studied anatomically. According to the nature of vascular supply they are described as:—(1) an 'Outgrowth of the bud axis' when its vascular supply comes only from the bud trace, and (2) 'Stipule-stem complex' when its vascular supply is derived from branches of both the bud trace and of a lateral of the trace of the axillant leaf. 20 out of 24 species studied have their tendrils supplied by bud stele alone. The bundles of the outer ring are really leaf-trace bundles and those of the inner ring cauline.

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* Literature marked with an asterisk have not been seen in original by the author.

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