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A MORPHOLOGICAL, ANATOMICAL, AND DEVELOPMENTAL

INVESTIGATION OF THE TENDRILS OF SMILAX TAMNOIDES VAR. HISPIDA

presented by

James Frank Russo

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Gary R. Hooper
Major professor

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A MORPHOLOGICAL, ANATOMICAL, AND DEVELOPMENTAL INVESTIGATION OF THE TENDRILS OF SMILAX TAMNOIDES VAR. HISPIDA

By

James Frank Russo

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ABSTRACT

A MORPHOLOGICAL, ANATOMICAL, AND DEVELOPMENTAL INVESTIGATION OF THE TENDRILS OF SMILAX TAMNOIDES VAR. HISPIDA

By

James Frank Russo

Smilax tamnoides var. *hispida* (Muhl.) Fern. is a monocotyledonous vine with paired leaf tendrils. The homology of these tendrils has been extensively debated, but most frequently the tendrils are considered homologous with stipules. The morphology, anatomy, and development of these tendrils were investigated in order to arrive at a conclusion concerning their homology.

It is concluded, on the basis of light microscope and scanning electron microscope observations, that the tendrils are elaborations of the leaf base, and are not homologous with stipules. The tendril of *Smilax* is concluded to be as fundamental a structure as the stipule of dicotyledonous taxa, because the tendril can only be interpreted in terms of the leaf base from which it developes. It is proposed that monocotyledons be interpreted in terms of their own morphology, not in terms of the morphology of dicotyledons.

To the memory of my grandfather,
Henry T. Burnell

ACKNOWLEDGMENTS

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On a personal level, Dr. Stan Flegler and Dr. Karen Baker offered the support of their friendship and experience, which helped to make this program a pleasant and rewarding one.

I could not say enough for Janice, my wife, who has heard this thesis a thousand times, but who chooses to love me still.

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INTRODUCTION

Smilax is a genus of monocotyledonous climbing vines. Many of the species of this genus climb by means of paired tendrils which respond to light and entwine nearby objects (Darwin 1875). Although this viny habit is common in the plant kingdom, the growth form of *Smilax* is unique. The tendrils are paired and are associated with the leaf base in a manner which is suggestive of many dicotyledonous structures (Fig. 1), such as stipules or leaflets. *Smilax* is a monocotyledon, however, and this pairing of the tendrils may not be indicative of a relationship with dicotyledons.

The term "tendril" has descriptive value, but the tendril is not morphologically equivalent in all taxa (Table 1). Comparison of the tendrils in Vitaceae, Cucurbitaceae, and Passifloraceae for instance, in which the tendril emerges from the node, suggests that different structures are involved in the development of the tendril. In both dicotyledons and monocotyledons, the morphological diversity of tendrils seems to indicate that the tendril has arisen independently many times in the course of evolution and morphological and functional similarities in different families and classes are examples of convergent evolution.

Recognizing this flexibility in the ontogeny of tendrils, investigators have attempted to discover from which structure or structures the tendrils of *Smilax* may have evolved. That is,

Table 1.--A proposed homology of tendrils in selected families and genera of monocotyledons and dicotyledons.

Taxa (Cronquist 1968)	Interpretation and Citation
Liliatae	
Gloriosa spp. (Liliaceae)	The tendril is an extension of the leaf tip (Arber 1920).
Smilax spp. (Smilacaceae)	The homology of the tendrils is in dispute.
Magnoliatae	
Clematis spp. (Ranunculaceae)	The petiole serves as the climbing organ (personal observation).
Passifloraceae	The terminal flower of a monochasium is thought to have been modified into the tendril (Lawrence 1951).
Cucurbitaceae	The tendril is homologous to a branch and a foliage leaf (Lawrence 1951).
Pisum spp. (Leguminosae)	The tendril is homologous to a leaflet (Bailey 1949).
Vitaceae	The tendril is homologous to the shoot apex. The axillary bud becomes the new apex (Lawrence 1951).
Tropaeolum spp. (Tropaeolaceae)	The tendrils are homologuous with petioles (arber 1920).

investigators have attempted to establish a homology between the tendrils of _Smilax_ and various structures found often associated with the leaf in other plant families. The suggested homologous structures include leaflets (Arber 1920), highly developed trichomes (Arber 1920), stipules (Arber 1920, Darwin 1875, Eames 1961, French and Fisher 1977, Sinnott and Bailey 1914, and Tyler 1907), and petioles (Hutchinson 1959).

The term "homology" has been frequently used, but it does not seem to have been well defined in any of these studies cited above. Sometimes the word was hardly mentioned, and instead phrases such as "the nature of the tendrils" or "represents" (Arber 1920) were used to imply homology. The lack of clarity which resulted from the misuse or non-use of the term "homology" has only contributed to the difficulties in arriving at a satisfactory resolution of the problem of the interpretation of the tendrils of _Smilax_.

According to Stebbins (1974) a structure may be regarded as homologous to another structure if both are descended from the same structure in a common ancestor, regardless of whether the modern structures perform the same or different functions. This definition of homology is used in this study.

In order to decide if two structures are homologous, three criteria can be used; (1) similarity in position of origin, (2) similarity in anatomical and histological characteristics, and (3) similarity in developmental pattern (Stebbins 1974). Each of these criteria have been used by investigators to determine the homology of the tendrils of _Smilax_. Unfortunately, these criteria are not absolutely reliable and their use can lead to mistaken interpretation of homology (Stebbins 1974).

Similarity in position is subject to question because, contrary to animal organs, plant organs can perform the same function in any of a number of locations (Stebbins 1974). For example the tendril terminates the leaf in *Gloriosa*, emerges from the node in *Vitis*, and is associated with the leaf base in *Smilax*. In each of these plants the tendril performs the same function though it occurs in different places.

Similarity in anatomical and histological characteristics is also subject to question. Botanists such as Arber (1925) and Eames (1961) frequently used comparative vascular anatomy to prove or disprove homology, but Carlquist (1969) has reviewed these criteria and found them to be misleading in many cases. He points out; (1) that venation relates to contemporary functions; (2) that the vascular system does not lag behind external form; and (3) that vascular bundles are not retained as in an historical archive. He also notes that venation is not a valid line of evidence to show that petals are derived from stamens or other organs. This would seem to be relevant to non-floral organs as well. Accordingly, the tendrils of *Smilax* cannot be said to be homologous with other structures such as stipules strictly on the basis of vasculature.

Similarity in developmental patterns can also be an unreliable criteria for determining homology. Patterns of development of individual organs are much simpler in plants than in animals. As a result parallel and similar but independent evolutionary modifications of structures as adaptations to similarly changed functions are much more common in plants than in animals (Stebbins 1974). In

Smilax, if the development of the tendrils were similar to the development of stipules or leaflets in some other plant, then it would still be premature to conclude that these structures were homologous.

Similarity in position of origin, similarity in anatomical and histological characteristics, and similarity in developmental pattern are not always reliable criteria for determining homology, yet they do suggest homology and I do not mean to discontinue their use. Attention should be first drawn to phylogeny, and it should be shown that the two putatively homologous structures could have been derived from a structure possessed by a common ancestor of the two forms. After this phylogenetic relationship has been shown to be at least likely, then the above criteria may be employed to establish homology.

The tendrils of *Vitis* are homologous with the shoot apex (Lawrence 1951), and in *Robinia* the axillary thorns are homologous with stipules (Gleason and Cronquist 1963). In both of these cases, however, the two homologized structures occur in species which are in the same genus. Shoot apices and tendrils both occur in the genus *Vitis*, and thorns and stipules both occur in the genus *Robinia*. In *Smilax*, however, structures such as ternately compound leaves and stipules are not found in the genus. This means that in the case of *Vitis* or *Robinia*, it is reasonable to postulate a common ancester from which the two modern forms could have developed. In *Smilax*, however, the possibility of a stipulate ancestor is remote.

At the time in which most of the theories of the homology of the tendrils of *Smilax* were being proposed, it was thought that the monocotyledons were evolved from extant dicotyledons. If this had been the case, then some structures in monocotyledons could possibly be said to be homologous to some structures in dicotyledons such as the *Smilax* tendrils being homologous with stipules in dicotyledons. It is now understood, however, that no such relationship exists among extant forms (Stebbins 1974), and that the development of monocotyledons was from a line leading to the dicotyledons or else from primitive dicotyledons (Doyle 1973, Doyle and Hickey 1976), which are now extinct.

If the phylogenetic split between dicotyledons and monocotyledons is very ancient, then any similarities in structures possessed by the two groups are likely to be the result of convergent evolution. In the case of the *Smilax* tendrils and their supposed homology with stipules, if the mechanism which brought about the similarities was convergent evolution, then I would expect only some characters of the two structures to correspond.

The purpose of this study is to examine the morphology, anatomy, and development of the leaf-tendril complex in *Smilax tamnoides* var. *hispida*, in order to arrive at a more satisfactory interpretation of the tendrils.

MATERIALS AND METHODS

Light Microscopy

Smilax tamnoides var. hispida (Muhl.) Fern. was selected for this study. Apices and internodes were collected from Red Cedar Natural Area and Baker woodlot on the Michigan State University campus. Two rhizomes were dug up, one each December for two years, and these were kept in the greenhouse to force early shoot production.

The nodes and apices used for light microscopy were fixed in a modified Nawaschin (Craf) type 2 fixative (Berlyn 1976). The modification was the substitution of 5% gluteraldehyde for formalin. The nodes and apices were stored in the fixative until needed, then dehydrated and cleared in ethanol and xylene and embedded in "paraplast" paraffin.

The woody shoots were difficult to section, therefore, both apices and nodes were soaked in a filtered solution of "Tide" laundry detergent with the exposed tissues in the solution for 2-12 hours in order to soften them. After this treatment no difficulties in sectioning were encountered.

Transverse sections (25µ) through the node were cut on a rotary microtome. The shoot apices were cut both transversely and longitudinally at 10µ. All sections were stained in Safranin and Fast Green according to Johansen (1940).

Sections were examined with a dissecting microscope at 30X to determine patterns of vascularization. When appropriate the sections were examined and photographed at higher magnification with either a Wild or a Zeiss compound light microscope.

Scanning Electron Microscopy

The apices were fixed in either 5% gluteraldehyde or Nawaschin (Craf) type 2 fixative as described previously. The material was dehydrated in ethanol and dried in a Sorvall critical point drying apparatus with CO_2 as the transition fluid. Samples were mounted on aluminum stubs, sputter-coated with 20-25nm gold, and examined in an ISI (International Scientific Instruments)-2 or an ISI-3 scanning electron microscope.

RESULTS

Morphological Observations

Local plants of Smilax tamnoides var. hispida flourished in flood plains but were also common in mesic forest environments. Shoots produced from the rhizome varied in size according to the age of the plant. Large individual plants, covering several square meters, produced numerous shoots in the spring (Fig. 2). These shoots produced two types of trichomes, one was approximately 1cm long and relatively stiff, while the other was 0.5cm long and relatively flexible (Fig. 3). Both types of trichomes became more rigid as they aged. The trichomes covered the stem to the height of 1-2m, after which the stem was glabrous. Lateral branches did not develop until the second year of shoot growth. This may have been promoted by the death of the shoot apex which occurred in the fall of the previous year.

Prophylls occurred on the lower nodes of the shoot. Their appearance was much like that of a leaf base of a normal leaf, that is the tendrils, petiole, and blade were not present. When a shoot apex was removed experimentally, an axillary bud proximal to the shoot apex developed into a new shoot producing a prophyll at the first node (Fig. 4).

The leaf arrangement in the shoot was distichous. The petiolate leaf blade was attached to the stem by an ensheathing leaf base

(Fig. 1). Distal to the attachment of the leaf base to the stem, the leaf base was truncate and the tendrils and petiole of the blade were attached to it (Figs. 1 & 4). The petiole was the median structure at this level while the tendrils occurred on either side of it (Fig. 1).

Anatomical Observations

Approximately 27 vascular bundles occurred in the leaf base at the level of its attachment to the stem. This node could not be called multilacunar, however, since no lacunae were present in Smilax. As in most monocotyledons, the vascular tissue occurred as discrete bundles throughout the stem, not in a ring of bundles as in most woody dicotyledons (Zimmermann and Tomlinson 1972). The vascular bundles in the leaf base of Smilax at the level of the attachment of the leaf base to the stem were of different sizes. Large bundles alternated with relatively small ones (Figs. 5 & 6).

The two sizes of vascular bundles differed both with respect to the size and the number of vascular elements. The larger vascular bundles contained more numerous and larger vascular elements than the small ones (Fig. 6). Both sizes of vascular bundles were surrounded by bundle sheath parenchyma (Fig. 6).

Distal to the attachment of the leaf base to the stem, the vascular pattern was somewhat different. Vascular bundle 2r* divided into two bundles (Figs. 6, 7 & 9). The two bundles which resulted from the division of trace 2r fused distally with the adjacent vascular bundles. The bundle half closest to the midvein fused with the midvein, while the more lateral bundle of this division pair fused with trace 3r (Figs. 8 & 9). The same pattern occurred also in the

*See figure 9 for coding of vasculature.

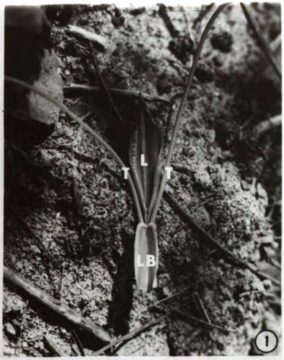
Figs. 1-4. General morphological features of Smilax tamnoides var. hispida. L, lamina. LB, leaf base. P, prophyll. T, tendril.

Fig. 1. Leaf base, tendrils, and lamina of a young leaf. Magnification: X 1.

Fig. 2. Developing shoots. Magnification: x .5.

Fig. 3. Two types of trichomes on the lower 1-2m of the shoot. Magnification: X 1.

Fig. 4. A prophyll produced by a lateral shoot. Magnification: X 1.


L
T
T
LB
①


P
②


③


P
④

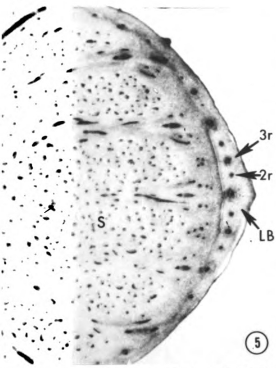
Figs. 5-8. Vascular bundles in the leaf base and stem of *Smilax tamnoides* var. *hispida*. Abaxial surface to the right. For coding of vasculature see Fig. 9. BSP, bundle sheath parenchyma. LB, leaf base. MV, midvein. P, phloem. S, stem. X, xylem.

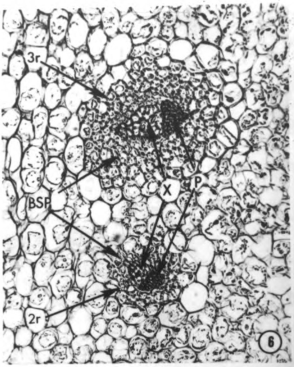
Fig. 5. Transverse section through the node. At this level the leaf base was only slightly free from the stem. Magnification: X 10.

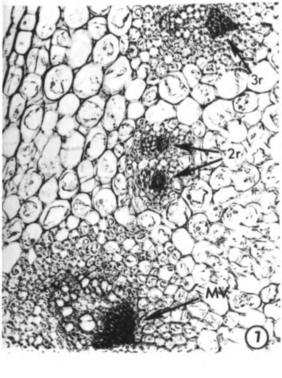
Fig. 6. Transverse section through the leaf base at the level of Fig. 5. Bundle 2r had not begun to divide. Magnification: X 100.

Fig. 7. Transverse section through the leaf base distal to Figs. 5 & 6. Bundle 2r had begun to divide. Magnification: X 100.

Fig. 8. Transverse section through the leaf base distal to Fig. 7. Both halves of bundle 2r were nearly fused with the adjacent vascular bundles. Magnification: X 100.


3r
2r
LB
S
⑤


3r
BSP
X
P
2r
⑥


3r
2r
MV
⑦

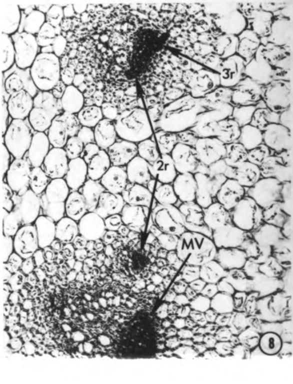

3r
2r
MV
⑧

Fig. 9. Schematic representation of the vascular organization in the right half of the leaf base of Smilax tamnoides var. hispida. Some of the lateral bundles were omitted for simplicity. The vascular pattern in the leaf base was similar on the left side. Figs. 10-15 represent transverse sections taken at the levels illustrated. The numbered bundles correspond to the numbered bundles in Figs. 10-15. This figure is not to scale. LB, leaf base. MV, midvein. P, petiole, T, tendril.

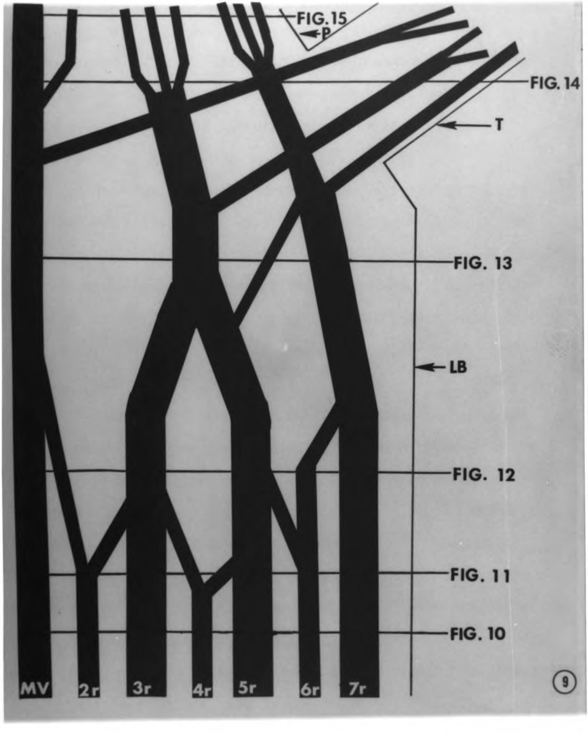


FIG. 15
P
FIG. 14
T
FIG. 13
LB
FIG. 12
FIG. 11
FIG. 10
MV
2r
3r
4r
5r
6r
7r
9

corresponding bundles on the left side of the leaf base.

The vascular bundles in the process of dividing and fusing with each other, did not remain discrete. Instead, elements in the bundles (xylem and phloem) became indistinguishable in the fusing bundles (Fig. 8). Moreover, bundle sheath parenchyma did not occur within large vascular bundles which resulted from the fusion of two. Instead combined bundles became surrounded by bundle sheath cells (Fig. 8).

A pattern of bundle division and fusion very similar to that described for trace 2r, occurred for trace 4r also (Figs. 9, 10, 11, & 12). Similarly, this pattern of bundle division and fusion occurred in trace 6r, but the pattern occurred distal to that for traces 2r and 4r (Fig. 6). The same pattern occurred on the left side of the leaf base in the corresponding vascular bundles (Figs. 10, 11, & 12).

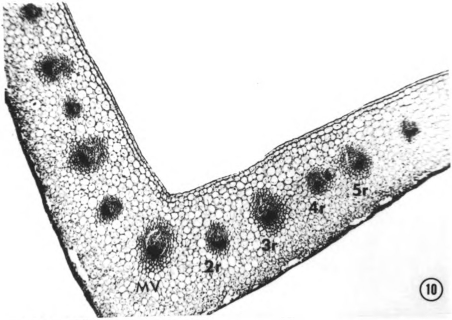
The result of this pattern of bundle division and fusion was the reduction in the number of vascular bundles at a level in the leaf base which was near the attachment of the tendrils to the leaf base. A further reduction occurred at a level just below the attachment of the tendrils to the leaf base, by a fusion of the large bundles 3r and 5r (Figs. 9, 12, & 13). At this level also a bundle split from trace 5r and fused distally with trace 6r (Figs. 9 & 13). The leaf base at the level of the attachment of the tendrils was thicker in the abaxial-adaxial plane and narrower from lateral margin to lateral margin, than at the level of its attachment to the stem (Figs. 10 & 14).

Distal to the fusion of bundles 3r & 5r, all of the bundles in

Figs. 10 & 11. Transverse sections through the proximal portion of the leaf base of Smilax tamnoides var. hispida showing the configuration of the vascular bundles. See Fig. 9 for coding of vasculature and approximate level of section. Magnification: X 55. MV, midvein.

Fig. 10. Transverse section through the leaf base. No bundle division or fusion was evident.

Fig. 11. Transverse section through the leaf base. Bundle 4r was dividing.



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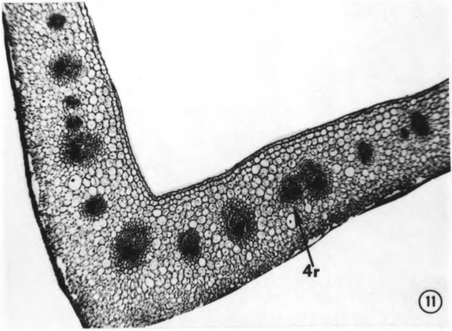
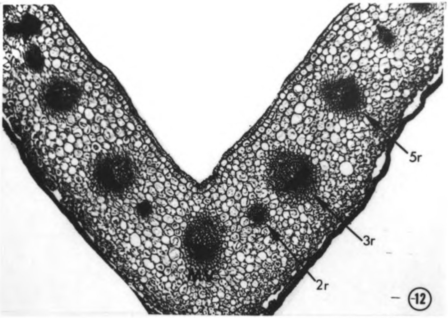


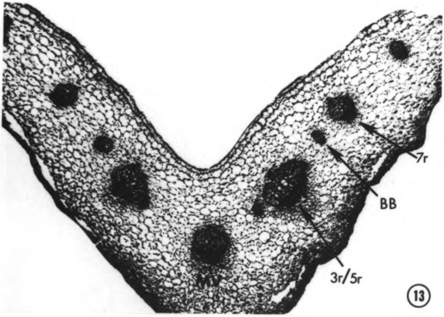
⑪

Figs. 12 & 13. Transverse sections through the median portion of the leaf base of Smilax tamnoides var. hispida showing the configuration of the vascular bundles. See Fig. 9 for coding of vasculature and approximate level of section. Magnification: X 55. BB, branch bundle. MV, midvein.

Fig. 12. Transverse section through the leaf base. Both halves of bundle 4r fused with the adjacent bundles (3r & 5r). Bundle 2r divided and the lateral half fused with bundle 3r. The midvein half of bundle 2r was not fused with the midvein at this level.

Fig. 13. Transverse section through the leaf base. Bundles 3r & 5r were fused. A branch was produced by bundle 5r proximal to this section, and it fused distally to bundle 7r.

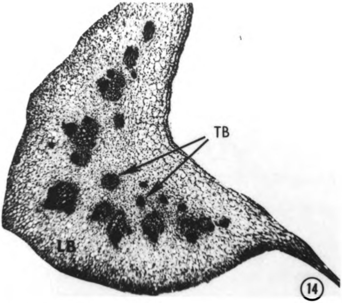

5r
3r
2r
MV
12


7r
BB
3r/5r
MV
13

Figs. 14 & 15. Transverse sections through the distal portion of the leaf base and the proximal portion of the petiole of *Smilax tamnoides* var. *hispida* showing the configuration of the vascular bundles. See Fig. 9 for coding of vasculature and approximate level of section. Magnification: X 55. LB, leaf base. P, petiole. TB, tendril branches.

Fig. 14. Transverse section through the leaf base. Tendril branches split from the main vascular bundles. These branches innervated the tendrils distally.

Fig. 15. Transverse section through the petiole.



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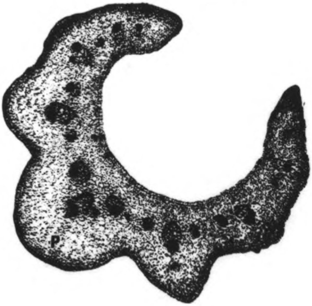


⑮

the leaf base split into unequal sized bundles (Figs. 9 & 14). Some of these bundle branches entered the tendrils, while those which did not entered the petiole (Figs. 9 & 15).

Developmental Observations

The leaf blade, tendrils, and leaf base began development as a single protuberance on the shoot apex (Fig. 16). The leaf base was initially the most differentiated structure (Fig. 17). On the distal margin of the leaf base small mounds of tissue, the blade and tendril primordia, could be seen (Figs. 17, 18, & 20). As the leaf developed, the blade primordia became more highly differentiated. At a stage in leaf development when the blade was clearly recognizable as such, the tendril primordia remained as inconspicuous mounds of tissue on the distal margin of the leaf base near the proximal portion of the leaf blade primordium (Figs. 17, 18, & 20). At a later stage in development, the blade, tendrils, and leaf base were fully differentiated (Fig. 19). The leaf blade and tendrils appeared to have developed from the leaf base.

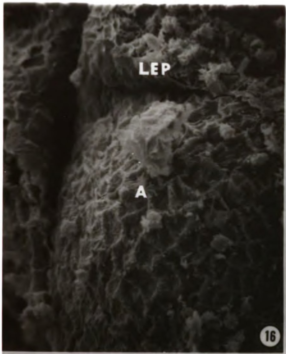
Figs. 16-19. Scanning electron micrographs of the developing leaf of *Smilax tamnoides* var. *hispida*. A, apex. LAP, lamina primordium. LB, leaf base primordium. LEP, leaf primordium. TEP, tendril primordium.

Fig. 16. The shoot apex with a developing leaf primordium. Magnification: X 630.

Fig. 17. Two leaf primordia. Blade and tendril primordia were apparent on the distal margin of the leaf base. Magnification: X 160.

Fig. 18. Two leaf primordia. The larger leaf primordium on the right shielded all but the developing lamina and some portions of the leaf base of the smaller leaf primordium on the left. One tendril of the larger leaf primordium is not visible. Magnification: X 80.

Fig. 19. Two leaf primordia. The larger leaf primordium on the left shielded the tendrils of the primordium on the right. Note that the shielded leaf primordium on the right, is the larger primordium exposed on the left in Fig. 18. One tendril of the larger leaf primordium is not visible. Magnification: X 80.



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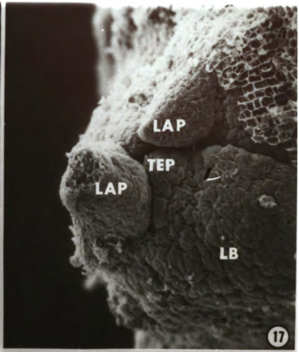

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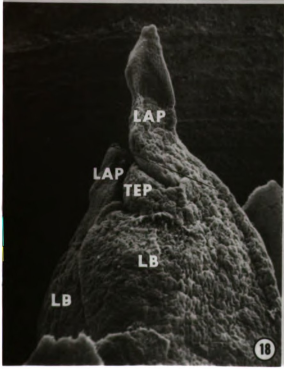

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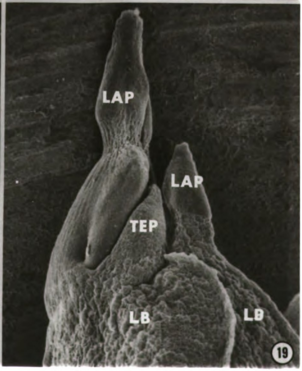

⑲

Fig. 20. Longitudinal section through the shoot apex of *Smilax tamnoides* var. *hispida*. A, apex. LAP, lamina primordium. LB, leaf base primordium. LEP, leaf primordium. TEP, tendril primordium. Magnification: X 120.


LAP
TEP
LB
LAP
LAP
TEP
TEP
LB
LB
A
LEP
20

DISCUSSION

Information on the morphology, anatomy, and development of the tendrils of Smilax can be used to evaluate the following theories of the homology of the tendrils.

1. The tendrils of Smilax are homologous with lateral members of a tripart leaf (Arber 1920).

Arber (1920) introduced but did not support, the idea that tendrils were modified members of a ternately compound leaf. The position of the tendrils is analogous to the position of lateral members of a tripart leaf, but no association exists between the bundles to the leaf blade and the bundles to the tendrils. The two bundle systems are discrete after their branching from the bundles in the leaf base (Fig. 9). In addition, developmental investigation reveals that the tendrils develop independently from the leaf blade, arising from the leaf base after the blade has begun to differentiate (Figs. 16-20).

2. The tendrils are homologous to trichomes (Arber 1920).

Arber (1920) cited Domin (1911) who maintained that the tendrils were highly developed trichomes. This theory is not supported by the morphology of the tendrils as trichomes are never found on the leaf in Smilax (Fig. 1). The tendrils are highly vascularized while the trichomes are not, and the tendrils arise from the tissues of the leaf base (Figs. 16-20), while the trichomes arise from the epidermis (personal observation).

3. The tendrils and blade have developed secondarily (Arber 1925).

Arber (1925) advocated the phyllode theory and did not attempt to homologize the tendrils with any other structure directly. The phyllode theory was that the leaf of all monocotyledons was homologous to the leaf base and petiole of dicotyledons. The blade was thought to have been lost by primitive monocotyledons. In *Smilax*, Arber (1920) believed, the phyllode had re-expanded and given rise in the process to two tendrils and a blade. The phyllode theory has been discredited by Kaplan (1973), Stebbins (1974), and Tomlinson (1970). Lacking the foundation of the phyllode theory, Arbers' (1925) interpretation of the tendrils of *Smilax* must be considered invalid.

4. The tendrils are homologous with stipules (Sinnott and Bailey 1914).

The view that the tendrils are homologous with stipules is widely held, and has been suggested by different workers for over 100 years (Darwin 1875, Eames 1961, French and Fisher 1977, Sinnott and Bailey 1914, and Tyler 1907). Before the homology of the tendrils in terms of stipules can be evaluated, both terms must be defined in terms of their morphology, anatomy, and development.

The morphology, anatomy, and development of tendrils varies widely between taxa (Table 1). Tendrils cannot be defined in terms of anatomy or development because of this variability, but can be characterized somewhat in terms of their morphology. They are elongate structures which may occur in varied locations on the plant. They may occur singly or in groups; they may branch. In general they respond to light and pressure (Darwin 1875). They are best described functionally as a portion of the stem or the leaf which is modified to serve as a holdfast organ (Gleason and Cronquist 1963).

Stipules are lateral appendages of the leaf. They are paired structures and may appear in different locations, such as the stem or the petiole (Eames 1961). Stipules may be free, or adnate to the petiole forming wings. This phenomenon has led investigators to call the hyalin margins on the leaf base of many monocotyledons stipules (Eames 1961). The use of the term stipule in this way, however, is not appropriate as will be explained.

The vascular supply of the stipules originates from that of the leaf by branching from the lateral leaf traces. A positive correlation has been established between the occurrence of a trilacunar node in dicotyledons, and the development of stipules (Sinnott and Bailey 1914). When the node is other than trilacunar, stipules are generally not found unless the leaf blade margin is toothed or lobed (Sinnott and Bailey 1914).

The leaf primordium of a stipulate dicotyledonous leaf begins as a three-lobed structure on the shoot apex, with the central lobe giving rise to the petiole and blade and the lateral lobes giving rise to the stipules (Sinnott and Bailey 1914). In addition, in dicotyledons, the stipules are precocious in their development, often equalling the blade in size for a short period of time (Sinnott and Bailey 1914). Recently Kaplan (1973) has worked with leaf development in monocotyledons and has observed that where stipules occur, they arise from the leaf base developmentally, but he does not define his use of the word "stipule".

The definition of the term "stipule" is subject to some of the same difficulties as the definition of the term "tendril". The morphology, anatomy, and development of stipules, while more precise than that of tendrils, is nonetheless varied. No single set of morphological, anatomical, and developmental criteria can characterize all stipules unless the criteria are of the broadest sort. A functional definition analogous to that used to define a tendril would be appropriate except that the functional significance of stipules is not understood, although it has been suggested they may serve in protecting the bud they subtend (Avebury 1899).

In this study, a stipule will be defined as an appendage associated with the leaf possessing a syndrome of morphological, anatomical, and developmental characteristics. In summary these characteristics include the occurence of stipules in pairs and associated with the petiole, leaf, or stem but generally near the leaf axil. The vascularization of the stipules is by means of branches from the lateral leaf traces. The node is trilacunar, or if not so, then the leaf blade has lobes or teeth. In dicotyledons, stipules develop precociously as protuberances separate from the leaf primordium on the shoot apex. In monocotyledons stipules may arise from the leaf base (Kaplan 1973). In general, however, stipules are absent from monocotyledons.

The tendrils of Smilax have some of the characteristics described above. The tendrils are located in a position on the leaf which is analogous to the occurence of stipules on many dicotyledonous plants (Fig. 1). The vascular bundles of the tendrils are branches of the bundles which innervate the blade (Fig. 9), and the tendrils arise developmentally from the tissues of the leaf base (Figs. 16-20).

Characteristics of the tendrils which are not part of the syndrome described for stipules are many. Smilax is a monocotyledon with an entire leaf margin. The node is not trilacunar (Figs. 5 & 9).

Strictly speaking, the node is not subject to the lacunar classification system, because the vascular tissue is in separate bundles and no lacunae occur. The node of Smilax could be called "multi-trace". A multi-trace node, however, is not consistent with the stipule syndrome of characteristics. In addition, developmentally the tendrils are not precocious. They arise later than the blade primordium (Figs. 16-20).

The evaluation of the evidence presented for and against the interpretation of the tendrils as homologous with stipules is very difficult, and also very subjective. The relative importance of various characters could be debated. But an understanding of the word "homology" suggests that in spite of any apparent evidence in support of the interpretation of the tendrils of Smilax as homologous with stipules, this interpretation cannot be accepted.

I discussed earlier three types of evidence which could indicate homology. These were (1) similarity in position of origin, (2) similarity in anatomical and histological characteristics, and (3) similarity in developmental patterns (Stebbins 1974). These criteria for evaluating homology are not reliable in the case of the Smilax tendrils.

In spite of certain morphological, anatomical, and developmental similarities between the tendrils of Smilax and stipules of either dicotyledons or monocotyledons, the possibility of tendrils and stipules being homologous is remote. The reason for this is that no direct phylogenetic relationship exists between Smilax and any stipulate taxon either dicotyledonous or monocotyledonous such that a common stipulate ancestor could be supposed to have existed. If no common ancestor could have existed which would have given rise to a taxon with stipules and also to Smilax with its tendrils, then stipules and tendrils cannot be homologous.

5. The tendrils of Smilax are elaboration of the leaf base.

My study indicates that the tendrils of Smilax are elaborations of the leaf base. Although this explanation may seem simplistic, it is nonetheless consistent with all available evidence.

The tendrils are attached to the leaf base (Fig. 1). When the leaf abscises in the fall, the tendrils remain attached to the leaf base and do not fall from the stem (personal observation). In addition, the vascular supply of the tendrils is derived from bundles in the leaf base and the vascular bundles to the petiole are independent of the bundles to the tendrils (Fig. 9). Finally, the tendril primordia develop from the leaf base (Figs. 16-20), not from the laminar portion of the leaf, and the leaf primordium begins its differentiation before the tendril does (Figs. 16-20). All of this evidence indicates that the tendril is associated with the leaf base, not with the leaf blade or with some other structure. In addition, this evidence is valid because there is no phylogenetic difficulty. Smilax has a leaf base, and it is logical to suppose this could have become elaborated into tendrils over time.

The interpretation that the tendrils of Smilax are elaborations of the leaf base has merit in that this hypothesis does not suggest dicotyledonous affinities as the use of the term stipule in even a very broad sense does. Tomlinson (1970) has argued that the orientation of botanists and botancial teaching toward dicotyledons has had an insidious effect on the way monocotyledons have been investigated.

He feels that monocotyledons have come to be regarded as aberrant dicotyledons and their morphology has been interpretated accordingly. I feel that the interpretation of the tendrils of *Smilax* as homologous with stipules is an example of this attempt to interpret monocotyledons according to theories and structures applicable to dicotyledons. The interpretation of the tendrils of *Smilax* as elaborations of the leaf base is an attempt to disregard this tradition of interpreting monocotyledons in terms of dicotyledons. The tendrils of *Smilax* are fundamental organs as are the stipules of dicotyledons. Just as the stipule is not homologized with any structure, but is most frequently considered to be a modification of the leaf, so the tendril of *Smilax* should not be further homologized. It is an elaboration of the leaf base, which is itself a basic structure of the plant.

It is possible to speculate on the evolutionary development of the tendril based on the adaptive needs of Smilacaceae. Tendrils are an adaptation for the climbing habit which is characteristic of Smilacaceae. The climbing habit is itself one possible adaptation to the lack of secondary growth characteristic of monocotyledons in general. Since plants evolve along the lines of least resistance and new organs are most likely to evolve from pre-existing ones (Stebbins 1974), it seems reasonable to suppose that the leaf base, which may have the greatest developmental flexibility in the leaf of *Smilax*, elongated over time and gave rise to the tendrils. Although these ideas concerning evolutionary trends in Smilacaceae are highly speculative, they are consistent with what is known to be fundamental to monocotyledons and do not invoke theories which are applicable to dicotyledons. From their ancient beginning together the two classes of flowering plants have evolved independently in response to selective pressure based upon what was fundamental to them. The time involved since the separation of the two classes is great (Doyle 1973, Doyle and Hickey 1976), and characteristics of monocotyledons should be interpreted in terms of this relatively independent evolution unprejudiced by conclusions concerning dicotyledons (Moore 1973).

As a monocotyledon, Smilax has evolved separately from any dicotyledon. The morphology, anatomy, and development of the tendrils are unlike that of any other structure in different taxa. Furthermore, the leaf base is apparently very flexible in terms of its morphology and anatomy. It may assume the form of a prophyll with no tendrils or blade, it may bear a well-developed blade and tendrils, or it may bear structures somewhat in between developmentally. The leaf base appears to have great anatomical flexability as well, because the vascular bundles can fuse and divide many times readily since the bundles do not remain discrete. Given this great flexibility in the leaf base, and the realization that the tendrils must have evolved independently, it seems likely that the tendrils have evolved from the tissues of the leaf base in response to selective pressures associated with the climbing habit.

LITERATURE CITED

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Arber, Agnes. 1920. "Tendrils of Smilax." Bot. Gaz. 69:438-443.

Arber, Agnes. 1925. Monocotyledons. (Cambridge Univ. Press, London).

Avebury, J. L. 1899. On Buds and Stipules. (K. Paul, French, Trubner & Co., ltd, London).

Bailey, L. H. 1949. Manual of Cultivated Plants. (Macmillan Pub. Co., New York).

Berlyn, G. P. and J. P. Miksche. 1976. Botanical Microtechnique and Cytochemistry. (Iowa State Univ. Press, Iowa).

Carlquist, S. 1969. "Toward acceptable evolutionary interpretations of floral anatomy." Phytomorphology. 19:332-362.

Cronquist, A. 1968. The Evolution and Classification of Flowering Plants. (Houghton Mifflin, Boston).

Darwin, Charles. 1875. The Movements and Habits of Climbing Plants. (John Murray, London).

Doyle, J.A. 1973. "The monocotyledons: their evolution and comparative biology. v. Fossil evidence on early evolution of the monocotyledons." Quart. Rev. Biol. 48:399-413.

Doyle, J.A. and L. J. Hickey. 1976. "Pollen and leaves from the mid-cretaceous potomac group and their bearing on early angiosperm evolution." 139-205. IN Beck,C.B. (ed.) Origin and Early Evolution of Angiosperms. (Columbia Univ. Press, New York).

Eames, A. J. 1961. Morphology of the Angiosperms. (McGraw Hill, New York).

French, J. C. and J. B. Fisher. 1977. "A comparison of meristems and unequal growth of internodes in viny monocotyledons and dicotyledons." Amer. J. Bot. 64:24-32.

Gleason, H. A. and A. Cronquist. 1963. Manual of Vascular Plants of Northeastern United States and Adjacent Canada. (D. Van Nostrand Co., New York).

Hutchinson, J. 1959. The Families of Flowering Plants Vol. 2. Monocotyledons. (Clarendon Press, Oxford).

Johansen, D. A. 1940. Plant Microtechnique. (McGraw-Hill, New York).

Kaplan, D. R. 1973. "The monocotyledons: their evolution and comparative biology. vii. The problem of leaf morphology and evolution in the monocotyledons." Quart. Rev. Biol. 48:437-457.

Lawrence, G. H. M. 1951. Taxonomy of Vascular Plants. (Macmillan Pub. Co., Inc., New York).

Moore, H. E. and N. W. Uhl. "The monocotyledons: their evolution and comparative biology. vi. Palms and the origin and evolution of monocotyledons." Quart. Rev. Biol. 48:414-436.

Sinnott, E. W. and I. W. Bailey. 1914. "Investigations on the phylogeny of the angiosperms. (3) Nodal anatomy and the morphology of stipules." Amer. J. Bot. 1:441-453.

Stebbins, G. L. 1974. Flowering Plants-Evolution Above the Species Level. (The Belknap Press, Mass.).

Tomlinson, P. B. 1970. "Monocotyledons- Towards an understanding of their morphology and anatomy." 207-292. IN R. D. Preston (ed.). Adv. Bot. Res. Vol. 3. (Academic Press, New York).

Tyler, A. A. 1897. "The nature and origin of stipules." Annals of the New York Academy of Sciences. 10:1-49.

Zimmermann, M. H. and P. B. Tomlinson. 1972. "The vascular system of monocotyledonous stems." Bot. Gaz. 133(2):141-155.