Developmental Studies in Smilax.

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The Louisiana State University and Agricultural and Mechanical College
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Developmental Studies in Smilax

A Dissertation

Submitted to the Graduate School of the
Louisiana State University
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The Department of Botany

by

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ABSTRACT

The ontogeny of the shoot and the tendril-bearing leaf was studied in three species of Smilax which differ considerably in growth habit. Growth is indeterminate in S. bona-nox and S. smallii and determinate in S. pumila.

Shoot apical organization in all three species is consistent with the tunica-corpus concept. The number of tunica layers varies from two in S. bona-nox and S. pumila to three (two - four) in S. smallii. A primary thickening meristem is present only in S. smallii.

Leaves are initiated in a distichous phyllotactic arrangement by periclinal divisions in the second tunica layer of the shoot apical meristem. The leaf primordium increases in height through the activity of apical and subapical initials as well as by intercalary extension. An adaxial meristem is present near the base of leaf primordium when it reaches an approximate height of 250 μm. It is responsible for increase in thickness of the leaf base as well as delimitation of the petiolar region of the leaf.

Lamina development involves the activity of marginal meristems. The marginal initials extend the protoderm, while the submarginal initials give rise to the internal layers of the lamina. Further extension of the lamina is accomplished through the activity of a plate meristem extending from the midrib to the margin.

Tendrils are initiated by numerous periclinal divisions on both flanks of the leaf base after blade formation begins. The tendril
meristem is a wedge-shaped mass of tissue which is uniformly meristematic in early stages of development. Cessation of meristematic activity in the tendril meristem occurs relatively early in the tendril of Smilax with further elongation achieved through subterminal or intercalary cell division and enlargement. Older tendrils are indurate and coiled. The presence of structures resembling water pores and the vasculature of the tendril suggest that the tip may be hydathodal.

Shoot tip abortion in Smilax pumila involves a cessation of vegetative growth resembling that found in many woody plants. Various internal changes are associated with this phenomenon. The shoot apex becomes stratified and lacks a distinct corpus, and the surface layers of the meristem differentiate. Pith differentiation encroaches to within 50 μm of the summit of the meristem and cells throughout have more inclusions and a greater affinity for stains than the active shoot apex.

Even though there are distinct differences in growth habit, vigor, and anatomy, the three species share many developmental similarities. Hence, subtle changes in ontogeny may result in marked differences in mature structure.
INTRODUCTION

A study of the ontogeny of the *Smilax* shoot and, in particular, the tendril-bearing leaf, was undertaken to investigate some unusual features of *Smilax*. These features include its woody, climbing habit, reticulate-veined leaves, and stipular tendrils (Yates and Duncan, 1970). *Smilax* is the only genus of the Liliaceae which includes woody vines. Leaf morphology of *Smilax* is an unusual type among monocotyledons and, prior to this study, has not been subjected to a detailed ontogenetic investigation. As pointed out by Tomlinson (1970) and Kaplan (1973), extensive literature has been devoted to the comparative morphology of monocotyledonous leaves, but much less attention has been given to their comparative development. The current study compares development of three diverse species of *Smilax* to establish which ontogenetic features they hold in common, and which are species specific.

Tendrils are defined as modified leaves, portions of leaves, or as modified shoots, as in the case of the Vitaceae. Tendrils have been of interest to plant scientists for a number of years as evidenced by the work of Clos (1857), Darwin (1884), MacDougal (1892, 1896), and Goebel (1900). A number of detailed studies of tendril ontogeny in dicotyledonous plants have been made (Moens, 1956; Millington, 1966; Tucker and Hoefert, 1968; Shah and Dave, 1970 a, b; Sistrunk and Tucker, 1974). The nature of the tendrils of *Smilax* has been a matter of controversy for many years as indicated by the work of Clos...
(1857), Colomb (1887), Goebel (1900), Arber (1920), and Majumdar et al. (1947). The unbranched tendrils of Smilax are paired and born laterally at the base of the petiole. The presence of tracheary elements at the tip of the tendril and structures resembling water pores suggest that the tendril of Smilax may have a hydathodal function. Structures such as spines and adhesive discs which have been reported in tendrils of dicotyledonous genera are not found in Smilax. Due to their structural simplicity, a study of the tendrils of Smilax should be instructive in contrasting their ontogeny and differentiation with those of more complex types.

This study reveals that shoot tip abortion takes place in at least one species of Smilax. Shoot tip abortion has been studied in several dicotyledonous species (Millington, 1963; Garrison and Wetmore, 1961), but has not been described for any monocotyledons even though it is a common phenomenon. In most instances of abortion in the monocotyledons, the shoot apex converts into a terminal inflorescence, instead of undergoing cessation of growth as commonly occurs in many woody plants (Kaplan, personal communication).

A number of earlier papers have dealt with various aspects of Smilax anatomy. Arber (1920, 1925) discussed the origin and vascular anatomy of the tendrils of Smilax and interpreted the leaf using the phyllode theory of de Candolle (1827). Wilburn (1940) described seed and fruit development in Smilax pumila and Smilax bona-nox. Speese (1941) studied the distribution and duration of meristematic activity in the leaves of six species of Smilax. Coker (1944) made an extensive study of the comparative morphology of the woody species of Smilax of the United States. Caponetti and Quimby (1956) studied
both surface features and gross anatomical features of the leaves of *Smilax*. Ervin and Sikkema (1971) reported the presence of ectodesmata in the walls of the epidermal cells of *Smilax hispida*.

While no recent papers have dealt with vegetative ontogeny in *Smilax*, similar reports on other monocotyledons have appeared and are relevant (Tomlinson, 1970, 1972; Stevenson, 1973; Kaplan, 1970, 1973). It is of interest to examine the development of the dorsiventral leaf of *Smilax* in the light of Kaplan's work, particularly to elucidate the homologies of the *Smilax* tendril.
MATERIALS AND METHODS

Vegetative buds, leaves, and tendrils of *Smilax bona-nox*, *Smilax pumila*, and *Smilax smallii* were collected at various times throughout the growing season (March - August). Collections of all three species were made in St. Helena and Rapides parishes, Louisiana. In addition, collections of *Smilax bona-nox* were made in East Baton Rouge parish.

Numerous leaves and tendrils of various ages and several shoot apices were cleared and stained with safranin to show their vasculature (Arnott, 1959).

Shoot apices, leaves, and tendrils of various ages were killed and fixed under vacuum in formalin-acetic acid-alcohol, dehydrated in a tertiary butyl alcohol series, and embedded in paraffin (Johansen, 1940).

Sections were cut at 8 - 10 μm on an American Optical Model 820 rotary microtome and stained with safranin - fast green (Sass, 1951).

Sections were photographed with a Leitz Orthomat microscope camera with brightfield illumination. Standard photographic techniques were followed.

To study lamina development in *Smilax bona-nox*, leaves were collected from below the apical bud through the sixteenth node, and fixed and killed in the field using formalin-acetic acid-alcohol. This material was then washed in water mounted on a stub using Ames O.C.T. embedding medium for frozen sections. Sections were cut at
10 μm on an American Optical Model 840-C Cryo-cut microtome. Temporary slides of the frozen sections were made using glycerine jelly.

Apices of Smilax bona-nox and Smilax pumila were observed and photographed with a scanning electron microscope. The material was fixed and killed in formalin-acetic acid-alcohol. Older leaf primordia were carefully dissected away from each apex. The shoot tips were then washed in water, dehydrated in ethyl alcohol and amyl acetate, dried in a Denton critical point drying apparatus using carbon dioxide, and then mounted on specimen stubs with silver paint. The stubs holding the plant material were coated with gold on a rotary stage in a vacuum evaporator. Specimens were studied and photographed at 25kV with a Jeolco JSM-2 scanning electron microscope, using Tri-X Ortho film.

The height and width of shoot apical meristems were measured on longitudinal sections utilizing an ocular micrometer. Measurements were obtained from at least 15 apices of each species.

Growth measurements were made of S. pumila and S. smallii which represent the extremes in growth habit. Shoot growth in the field was measured every two days for a period of twenty-six days. Leaf counts were also made over the same period of time, as well as measurements of leaf length and width.

Voucher specimens were deposited in the herbarium of Louisiana State University in Baton Rouge, Louisiana.
RESULTS

MORPHOLOGICAL OBSERVATIONS:

The genus Smilax includes both woody and herbaceous plants, usually climbing or supported by a pair of tendrils on the petiole (Correll and Johnston, 1970). Smilax has a distichous leaf arrangement or 1/2 phyllotaxy. Each simple leaf is composed of a lamina, a petiole with a pair of tendrils born at the base of the petiole, and the leaf base which partially encircles the stem. The flowers of Smilax are dioecious and born in umbels on axillary peduncles. The fruit is a small red, blue-black, or black berry.

This study involves comparative developmental studies of three species which differ considerably in growth habit:

Smilax bona-nox is a common woody species and displays a climbing growth habit. This species is characterized by knotty, tuberous rhizomes 2 - 6 cm thick (Fig. 1) in clusters up to 20 cm across, and slender subterranean rhizomes 3 - 5 mm thick which give rise to erect shoots. Prickles were not observed on the swollen portions of the rhizome although Coker (1944) describes their presence as unique for the species. The subterranean rhizomes have prickles and bear roots and scales (reduced leaves) at the nodes. The erect shoots of this species are glabrous and vary in vigor (Fig. 2, 3). The terminal buds of vigorous shoots are large,

1The term woody as used here refers to the large amount of lignified, fibrous tissue in the stem and does not infer the presence of cambial activity.
ranging from 4 - 8 mm in width as compared to a width of 0.5 - 2.0 mm in less vigorous shoots. Vigorous shoots have 7 - 10 leaf primordia in the terminal bud while less vigorous shoots have 5 - 7 primordia. Prickles are absent in the uppermost nodes and internodes of vigorous shoots (Fig. 2), but are present in this region of the less vigorous shoots (Fig. 3). The most active period of growth in this species is March through June, although healthy shoot tips were collected throughout the year from plants in locations which afforded them protection from the conditions of winter. Leaves (Fig. 3, 4) vary in shape from cordate - ovate to shallowly panduriform (Duncan, 1967). The margins are usually entire, but may be spinulose (Fig. 3). The apex of the leaf is mucronate. Flowering takes place from April to June in the collection area.

*Smilax smallii* also becomes quite woody. It is a high-climbing species (up to 25 dm) with erect shoots arising from massive, knotty, tuberous rhizomes (Fig. 5, 6) approximately 7 - 10 cm thick. Numerous shoots arise from the extensive rhizome systems which are approximately 0.5 - 1.0 m across (Fig. 5). An extensive root system originates from the nodal and internodal regions of the tubers (Fig. 5, 6). Erect shoots of this species are glabrous and extremely vigorous with an average rate of shoot growth of 7 cm per day. Most vigorous growth is observed from April to June. During this period, as much as 22 cm growth in height was recorded over a 48-hour period. Terminal buds of this species are massive,

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2This figure, as well as subsequent figures reflecting growth rates, represents an average of measurements taken on five plants over a 26-day period.
ranging from 0.7 - 1.3 cm in width (Fig. 7). As young shoots emerge from the soil, the first leaves are reduced to scales (S in Fig. 6). Approximately the first five nodes above the soil level bear these scales. At approximately nodes 6 - 9, leaves with tendrils are present, but lamina development is rudimentary (La in Fig. 7). Between nodes 9 and 12, the typical, fully expanded, tendril-bearing foliage leaves are found. These usually evergreen leaves (Fig. 8) are lanceolate to elliptic-lanceolate with entire margins and acute or shortly acuminate apices (Correll and Johnston, 1970). Prickles are found only on the lower 3 - 4 m of the stem in S. smallii. Flowering usually occurs in June or July in the collection area.

*Smilax pumila* is perhaps the most easily distinguished species among the woody members of the genus. It differs from the other two species investigated in its dwarf stature, pubescence, and absence of prickles. The rhizome system consists of several small woody knots approximately 6 mm thick (Fig. 9) from which arise numerous slender rhizomes 2 - 3 mm in diameter and approximately 0.3 - 0.8 m long (Fig. 10). These rhizomes bear scales, root at the nodes (Fig. 10), and give rise to numerous aerial shoots in March and April, the most active period of growth. The aerial shoots are trailing, sub-erect, or low-climbing (Fig. 11, 12) and attain a height of 0.5 - 1.0 m. Aerial shoots measured in March and April had an average rate of growth of 0.5 cm per day. New shoots reach a point at which growth in height ceases, usually in late April or early May, and then assume a trailing habit unless they come in contact with some type of...
support to which the tendrils can become attached by coiling around the structure (at arrow in Fig. 13). Terminal buds of this species are quite small, ranging from 2.0 - 3.5 mm in width, and appear woolly due to the densely pubescent young leaves. The mature leaves are nearly glabrous on their adaxial surface and have a soft whitish pubescence on the abaxial surface. The leaves of this species are evergreen, ovate to ovate-lanceolate (Fig. 11) in shape, with an acute apex. The margin of the leaf is entire. Flowering takes place in July and August in the collection area.

ANATOMICAL OBSERVATIONS:

A. The Shoot Apex:

The shoot apical meristem of all three species studied is small and convex. *Smilax bona-nox* will be the species illustrated primarily, except where features differ somewhat in the other species. The apex is minimal in diameter after leaf initiation (Fig. 14, 15) and maximal in diameter (Fig. 16, 17) just before a new leaf is initiated. The young leaf primordia tend to obscure the apex as seen in scanning electron microscope (SEM) views (Fig. 14-17). Median longitudinal sections of the shoot tip cut in the plane of distichy reveal 5 - 10 leaf primordia in the terminal bud of the various species (Fig. 18-21). The number of primordia present varies even within each species (Fig. 18, 19).

Apical organization in all three species is best described in terms of the tunica-corpus concept (Schmidt, 1924). The shoot apex is defined here as that part of the shoot above the youngest leaf primordium or initiatory site. Shoot apices of *Smilax pumila*
and *S. bona-nox* have a biserial tunica overlying a homogeneous
corpus (Fig. 22-24). Cells of the outer tunica layer divide only
anticlinally; those of the second tunica layer (*T₂*), divide pre-
dominantly anticlinally. Rarely, however, periclinal divisions may
be seen near the summit in the second tunica layer. In *S. smallii*
the shoot apex is more highly stratified, with up to three well-defined
tunica layers. Some apices have only two tunica layers (Fig. 25)
while others have three layers in which anticlinal divisions pre-
dominate (Fig. 26). Another variation found in this species and
not in the others is the presence of a primary thickening meristem
(Fig. 21) visible as files of cells radiating outward below the apical
meristem. This is not uncommon in other monocotyledons such as
*Musa* spp. (Skutch, 1932), *Yucca*, *Dracaena*, and *Sansevieria* (Cheadle,
1937), and *Phoenix*, *Washingtonia*, and *Trachycarpus* (Ball, 1941).

The apical meristem is composed of small, densely staining,
nearly isodiametric cells. There are no apparent differences in
size, affinity for stains, or shape of cells between the summit and
the base of the apical meristem (Fig. 27, 28).

Shoot apices of *S. bona-nox* and *S. pumila* are approximately
the same size. The mean width of the shoot apex of *S. bona-nox* was
121.3 \( \mu \text{m} \) as compared to 123.9 \( \mu \text{m} \) in *S. pumila*, while the mean height
of the apex for these species was 51.2 \( \mu \text{m} \) and 46.6 \( \mu \text{m} \), respectively.
The shoot apex of *S. smallii* is considerably wider than that of the
other two species having a mean width of 170.8 \( \mu \text{m} \). Height of the
apex is comparable to the other species with the mean height of the
apex being 46.1 \( \mu \text{m} \).
The shoot apex is *Smilax* undergoes plastochronic changes in size. These changes involve primarily a reduction in width of the apex at minimal phase (Fig. 14, 15, 24). Maximal phase stages are shown in Fig. 16, 17, and 22. Height of the apex does not undergo any appreciable change between maximal and minimal phases. At minimal phase, the center of the apex is displaced and tilted slightly toward the side of the axis opposite the initiatory site (Fig. 24).

B. Leaf Development:

1. **Initiation and early ontogeny**:

Leaves are initiated in a distichous phyllotactic arrangement (Fig. 14, 15, 27). The first evidence of leaf initiation is seen as a periclinal division in the second tunica layer on the flanks of the shoot apical meristem (Fig. 22, 23). Additional divisions spread laterally around the apex, then spread vertically to enlarge the leaf primordium. At this stage the leaf primordium appears as a projecting collar (as seen in SEM view in Fig. 14, 15) which partially encircles the apex, extending approximately 2/3 of the way around the axis. A median longitudinal section through a shoot apex with a primordium in a comparable stage of development is seen in Fig. 24.

The surface layer of the primordium (protoderm) is continuous with the surface layer (T₁) of the shoot apical meristem (Fig. 24). Continuity between the subsurface layer of the primordium is also commonly observed (Fig. 25).

Following initiation from the apical meristem, the primordium increases in height through the activity of apical and subapical

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Initials as well as by intercalary extension. Cells in the position of apical and subapical initials are first seen in leaf primordia approximately 30 µm high (AI and SAI in Fig. 24). Delimitation of these cells in early stages of development is often difficult due to the fact that the entire primordium is meristematic. Apical and subapical initials are readily discernible, however, in older primordia approximately 100 µm in height (AI and SAI in Fig. 29, 30). Elongation of cells at the abaxial base of the primordium (arrow in Fig. 29) causes the young primordia to overarch the shoot apex in early stages of development.\(^3\) Apical growth by initials persists until the primordium is approximately 1,000 µm in height.

The first indication of activity of an adaxial meristem is in leaf primordia approximately 250 µm in height. Periclinal divisions are observed in the subsurface layer on the adaxial side of the primordium in median section and approximately 90 µm above the base (AM in Fig. 31). Cells resulting from these divisions increase the radial thickness of the primordium locally in this median region (at arrows in Fig. 32). The adaxial meristem is responsible for increase in thickness of the leaf base as well as, in later stages, delimitation of the petiolar region of the leaf; it is unrelated to tendril development.

\(^3\)The height of these leaf primordia was measured from the adaxial base of the primordium. The first measurement extended from the adaxial base at an angle of approximately 45 degrees to the center of the primordium. Subsequent measurements were made from this point to the tip of the primordium along an imaginary line running through the primordium equidistant from and parallel to the adaxial and abaxial surfaces.
Development of the unifacial (radially symmetrical) tip of the leaf precedes lamina development and tendril initiation, and is first evident in primordia approximately 200 \( \mu \)m high. The radial symmetry of this region is shown clearly in transverse sections (Fig. 33, 34, 37). Cellular differentiation in this region begins with vacuolation evident at the tip of leaf primordia approximately 1,000 \( \mu \)m high (Fig. 34). A primordium approximately 1,500 \( \mu \)m high has numerous cells containing raphide crystals near the apex of the young leaf (Fig. 35). Subsequent cell elongation and differentiation in this region gives rise to the attenuate tip seen in older leaves (Fig. 36). Differentiated tracheary tissue is also present in the tip (Fig. 37). Increase in diameter of the tip is accomplished through cell enlargement; no marginal growth is involved.

2. Lamina development:

The lamina originates from the median region of the meristem-encircling portion of the primordium, beginning when the primordium is approximately 500 \( \mu \)m in height. Lamina formation proceeds acropetally through the activity of marginal meristems. Young leaf primordia are roughly crescent-shaped and meristematic throughout (at top of photograph in Fig. 38). The marginal meristem is continuous from the leaf base to the unifacial tip of the young leaf primordium. The most intense region of marginal activity is the region which will become the dorsiventral blade in the mature leaf. At the margin of the developing lamina are marginal and submarginal initials (MI, SMI in Fig. 39-42). The marginal initials extend the protoderm, while the submarginal initials give rise to the internal layers.
of the lamina. These initials as well as their most recent derivatives are clearly shown in Fig. 39. Numerous mitotic figures are seen near the margin of the developing lamina (at arrows in Fig. 40), indicating that cell division occurs sporadically away from the margin. The supposition that the marginal meristem consists of only marginal and submarginal initials rather than a group of meristematic cells at any one level is strengthened by the fact that one frequently finds crystals differentiating in the most recent derivative of the submarginal initial (Fig. 41, 42). The implication here is that a continuation of marginal growth could result only from prolonged meristematic activity of the few cells separating these crystal-containing cells from the margin.

The abaxial region of the developing lamina becomes increasingly vacuolate with larger cells as development proceeds (Fig. 42). This causes the lamina to inroll in a complicate fashion as it enlarges (Fig. 43).

Transverse sections taken through various levels of the leaf show that marginal activity occurs throughout the developing leaf with the exception of the unifacial tip (Fig. 43, A-J). Most marginal activity occurs in the lamina and the leaf base (Fig. 43, D, J), but marginal activity also produces wing-like extensions of the petiole (Fig. 43, G). Differences in the degree of marginal activity are also seen within the blade (Fig. 43, B, F).

Further extension of the lamina is accomplished through the activity of a plate meristem consisting of 6 or 7 basic cell layers characterized by a preponderance of anticlinal divisions (Fig. 44).
This meristem extends from the midrib to the margins of the leaf. The continuity of the cell layers, however, is interrupted in subsequent development by formation of procambial strands and veins (Fig. 44, 45). A rapid enlargement and onset of differentiation of cells (Fig. 45) is followed by formation of intercellular spaces (Fig. 46) giving rise to the mesophyll tissue with its rather simple structure (Fig. 47).

3. Procambial development:

Procambium is first present approximately 70 μm below a primordium just beginning to form a protuberance on the flank of the shoot apical meristem (Fig. 48). This will form the median procambial strand which is visible at the base of the leaf primordium when it is approximately 100 μm high (Fig. 29). Procambium differentiates continuously and acropetally into the leaf primordium.

The base of a leaf primordium 210 μm high (lower side of the photograph in Fig. 49) has only the median procambial strand present. In a longitudinal view of a comparable primordium 216 μm in height, the median procambial strand extends to within 78 μm of the tip of the primordium (Fig. 48). Three separate procambial strands are present basally in leaf primordia approximately 600 μm in height (upper leaf X.S. in Fig. 49). All three procambial strands differentiate continuously and acropetally. Differentiation of the median strand precedes that of the two lateral strands. In a leaf primordium approximately 600 μm high, the median strand extends to within approximately 350 μm of the tip while the two lateral strands are present to a level approximately 450 μm below the tip. As the
primordia increase in size, additional procambial bundles differentiate from the axis into the leaf base.

Three separate procambial strands, one median and two laterals, differentiate in the developing lamina (at arrows in Fig. 50). Differentiation of these three strands is followed by differentiation of two more smaller lateral strands, one near each margin of the developing lamina. These five procambial strands give rise to the major vascular system of the lamina which consists of a midvein and two pairs of laterals. Each of these strands branches repeatedly to form the anastomosing network characteristic of the mature lamina. Differentiation of the reticulate minor venation system is discussed in the work of Pray (1963).

Following establishment of the morphological regions of the leaf (i.e., leaf base, petiole, tendrils, and blade), numerous vascular bundles are visible in an arcuate arrangement in the leaf base (at arrows in Fig. 51). Bundles in the petiole (at arrows in Fig. 52) and base of the lamina (at arrows in Fig. 53) have a circular arrangement which is related to the nearly radial symmetry found in these regions due to previous adaxial meristem activity (still visible as AM in Fig. 51).

Procambial bundles in the axis (at arrows in Fig. 54) have the scattered arrangement characteristic of monocotyledonous stems. The stem vasculature and relations between leaf traces were not investigated in this study.

4. Differentiation of vascular tissue:

Phloem differentiation precedes that of xylem in all vascular bundles in the shoot of Smilax. Differentiation of phloem is acropetal.
and continuous with pre-existing phloem below. Protophloem elements are first seen at the base of leaf primordia when they are approximately 550 μm high.

The first mature protoxylem elements are observed at the base of a leaf primordium approximately 1,000 μm high, unconnected with xylem in the stem. Differentiation of xylem in the base of the leaf primordium is initially discontinuous; it later becomes continuous through bi-directional differentiation within the intervening procambial areas.

Vascular differentiation in the lesser bundles and veinlets was not investigated.

Differentiation of xylem and phloem in the lamina takes place first in the median procambial strand and, subsequently, is observed in the laterals. This median procambial strand, together with two smaller strands which differentiate later in development, form the midvein of the leaf. These bundles have an arcuate arrangement (Fig. 55, 56). Differentiation of xylem and phloem is first seen in the larger central bundle (Fig. 55, 56). Mature protoxylem elements, metaxylem elements in the process of differentiation, and sieve tube elements are visible at a level approximately 2,500 μm below the tip of a leaf approximately 7,500 μm high (Px, Mx, SE in Fig. 55). The smaller bundles on either side of the large bundle still consist mostly of procambial cells at this level (Fig. 55). At approximately 3,200 μm below the tip of the same leaf, mature metaxylem elements are observed along with numerous sieve tube elements (Mx, SE in Fig. 56) in the central bundle. The smaller bundles remain largely
procambial at this level (Fig. 56). The midvein of the mature leaf consists of a central core of xylem with three strands of phloem (X, Ph in Fig. 57) aggregated into a single vein and enclosed by the fibrous bundle sheath (BS in Fig. 57).

The unifacial tip of the lamina is peculiar in that only tracheary elements are seen in this region (at arrow in Fig. 37). Cleared preparations reveal how this unusual vasculature at the tip is formed. In a leaf approximately 3,500 μm high, three protoxylem strands are visible: one median strand and two lateral strands. At approximately 400 μm below the tip of the leaf, these strands fuse and the resulting tracheary elements extend to within 100 μm of the tip of the leaf.

5. Differentiation of epidermis:

The epidermis of the leaf differentiates from the protoderm, the meristematic surface layer of cells in which anticlinal divisions predominate. Configuration of the anticlinal walls is described as undulate in the abaxial epidermis of leaves of _S. smallii_ and _S. bona-nox_ (Yates and Duncan, 1970). This is also true in the case of _S. pumila_. Configuration of the anticlinal walls in _S. smallii_ is described as straight (Yates and Duncan, 1970) in the adaxial leaf surface, while that of _S. pumila_ and _S. bona-nox_ is undulate. The outer epidermal walls are covered with a waxy cuticle. The surface of the cuticle in all species is smooth on the adaxial side and irregularly ridged on the abaxial side of the leaf (Yates and Duncan, 1970).
Guard cells and trichomes are the only two types of specialized epidermal cells present in *Smilax*. Of the three species investigated, trichomes are found only in *S. pumila*.

Guard cells are present on all above-ground vegetative structures of *Smilax*. Guard cells are paired, specialized epidermal cells which surround a pore, or stoma, in the epidermis. In all three species studied, guard cells are restricted to the abaxial epidermis of the leaf, although they have been reported to occur on both surfaces in certain other species (Yates and Duncan, 1970). Yates and Duncan (1970) describe the stomatal-subsidiary cell relationship of all species they investigated as paracytic, using the terminology of Metcalfe and Chalk (1950) for dicotyledonous plants. This term does not seem to be applicable. For example, in the case of *S. bona-nox*, two, three, or four cells are often seen in association with the guard cells (Fig. 58, 59). Figure 59 shows a stomatal complex of *S. bona-nox* having four subsidiary cells: two larger cells with their long axes parallel to the long axes of the guard cells and two smaller cells with their long axes perpendicular to the long axes of the guard cells.

Guard cells originate by anticlinal divisions of initial cells spaced among the epidermal cells. The intercellular substance between the two immature guard cells (Fig. 60) breaks down to form the pore. During initiation of stomata, a substomatal chamber develops below the guard cell pair in the mesophyll (Fig. 60). This intercellular space increases in size during maturation of the stoma (Fig. 61). Ledges of wall material are present on both the
upper and lower sides of the guard cells adjoining the stoma (Fig. 61) in the mature stomata. Chloroplasts are found in guard cells, but not in other epidermal cells.

The trichomes of *S. pumila* are described by Coker (1944) as being about 0.5 - 0.9 mm long and never straight, but curled and contorted to form a woolly blanket in mass. Using Foster's (1949) morphological categories of trichomes, these structures are best referred to as multicellular hairs. In my material, each hair consists of only three cells, although Coker (1944) reported four cells in each. Each hair consists of a foot cell within the epidermis and a 2-celled body projecting above the surface (terminology from Esau, 1967).

The hair is first recognizable as an elongated protodermal cell which, subsequently, undergoes a periclinal division. The lower cell becomes the foot, while the upper cell divides again to produce the 2-celled body. The distal derivative of this second division elongates rapidly, forming the major portion of the mature hair. The discrepancy in number of cells probably is due to the difficulty in resolving cell number in the contorted or angled base of the hair.

C. Tendril Development:

1. Initiation and early ontogeny:

Tendrils are initiated by numerous divisions on both flanks of the leaf base (Fig. 62). In all three species studied, tendril initiation occurs in the leaf primordium approximately 600 μm in height. The tendrils are initiated approximately 350 μm above the base of the primordium, just below the base of the developing lamina on either side of the median plane. Initial stages are difficult to recognize because of their orientation on the leaf primordium.
The tendril meristem is a wedge-shaped structure which is uniformly meristematic in early stages of development (Fig. 63-65). Positional relationships of the leaf base, tendrils, and developing lamina in early stages are best seen in SEM view (Fig. 66).

The tendril increases in height and becomes more massive (Fig. 67). At this stage the tip of the tendril consists of protoderm overlying a homogeneous block meristem (Fig. 67). A rib meristem is evident below the tip as well as cells which are apparently procambial (Fig. 67). The tendril remains radially organized and usually is unbranched. At a height of approximately 250 μm, the tendril tip becomes more acute (Fig. 68, 69).

2. Later development:

Cessation of the terminal meristem of the tendril occurs relatively early in Smilax. Cells begin to vacuolate at the tendril tip when it is approximately 300 μm high (Fig. 70). Further increase in height of the tendril is achieved through subterminal or intercalary cell division and enlargement (Fig. 71, 72). As the tendril continues to increase in height, the tip becomes increasingly attenuate as shown for all three species (S. bona-nox, Fig. 73, 74; S. pumila, Fig. 75; S. smallii, Fig. 76). Cells at the tip of the mature tendril are elongate with large vacuoles (Fig. 77) and, with the exception of cells containing raphide crystals, have few evident inclusions.

Following maturation of the tendril tip, the tendril continues to elongate through subterminal activity and may reach a length of 10 to 15 cm with the internal structure of the tip remaining relatively
unchanged (Fig. 78, 79). The tip of older tendrils is often curved to form a beak-like structure (SEM view in Fig. 80). Older tendrils become very hard after they undergo coiling. This is probably attributable to lignification, although these older tendrils were not sectioned.

3. Vasculature of the tendril:

The vascular supply to the tendril is formed by branching of the three large procambial bundles which enter the primordium initially, as well as from smaller bundles differentiating acropetally from the axis into the leaf base. The tendril displays radial symmetry and its bundles have a circular arrangement. In the mature tendril there are 5-6 larger bundles in a centric arrangement with numerous smaller bundles on each side of the ring formed by the larger bundles.

Vasculature of the tendril tip strongly resembles that of the unifacial tip of the leaf with only tracheary elements seen near the tip. In a cleared preparation of a tendril approximately 2,000 μm high, five protoxylem strands are seen extending from the base of the tendril. These strands fuse at approximately 400 μm below the tip, and the strand thus formed extends to within 225 μm of the tip.

4. Epidermal features:

The epidermal cells of the tendril are elongate parallel to the long axis of the tendril (Fig. 81). The anticlinal walls of the epidermal cells are straight to slightly curved (Fig. 81) in contrast to the undulate walls in the epidermis of the lamina. Stomata are present over the entire tendril in all three species investigated. Trichomes are present only on the tendrils of _S. pumila_ (Fig. 82, 83).
The trichomes are identical in structure and development to those described previously for the lamina. Structures resembling water pores are also found in the epidermis of the tendril. The presence of these structures, as well as the presence of only tracheary elements at the tendril tip, suggests a hydathodal function for the tendril. 

D. Axillary Bud Development:

Vegetative axillary buds are initiated at the second or third node below the shoot apical meristem (Fig. 84) and are present in the axils of leaves at all lower nodes. Initiation involves anticlinal divisions in \( T_1 \), \( T_2 \), and underlying layers forming a narrow, arcuate "shell zone" of columnar dividing cells in the axil of the leaf primordium (SZ in Fig. 85). Additional anticlinal divisions increase the size of the shell zone as seen at lower nodes in later stages of development (SZ in Fig. 86). Periclinal divisions in the shell zone (Fig. 85) and the area below it on the flank produce a small protuberance in the axil of the leaf at approximately node 5 (Fig. 87). Even at this early stage, the divisions in the outer two layers continue to be predominantly anticlinal. At approximately node 6, the meristems of the axillary buds show a cellular arrangement similar to that of the shoot apical meristem with a high-convex shape and a well-defined \( T_1 \) and \( T_2 \) (Fig. 88). The meristem shown in this figure is 150 \( \mu m \) wide and 80 \( \mu m \) high and lacks a prophyll.

The axillary bud of \textit{Smilax} has a single prophyll. Prophyll initiation takes place at approximately node 7 below the shoot apical meristem. The prophyll is initiated on the adaxial side of the axillary meristem and in later stages, the developing prophyll
completely encircles the meristem of the axillary bud (Fig. 89). The fully developed prophyll is conical and sheathing (Fig. 90) and forms a protective covering for the axillary meristem and embryonic leaves (Fig. 91). There is no median vascular bundle in the prophyll. Two lateral bundles are present on the adaxial side with each bundle approximately midway between the adaxial center and the margins of the prophyll.

The shoot apex of the axillary bud resembles that of the main axis in shape. The axillary meristem may occasionally be almost zonate in appearance with a group of smaller, dark-staining cells in the center of the apex, just below the summit (at arrow in Fig. 92). This is in contrast to that of the main axis which, in all apices observed, has a homogeneous corpus and biseriate tunica (Fig. 24). Formation of leaf primordia on the lateral axis is identical to that described for the main axis. The timing of procambial differentiation (PC in Fig. 92) in developing leaf primordia is also comparable to that observed in primordia of the terminal meristem.

E. Laticifers and Idioblasts:

1. Laticifers:

Laticifers are cells or series of fused cells containing a fluid called latex and forming systems that permeate various tissues of the plant body (Esau, 1967). Articulated nonanastomosing laticifers (terminology from Esau, 1967) are present in all aerial vegetative organs of the species investigated. The laticifers of Smilax are frequently associated with phloem, but are also seen within the parenchymatous tissue of the stem, leaf, and tendril.
Cells arranged in longitudinal rows, strongly resembling laticifers, are present in the stem, leaf, and tendril, although they are found in greater numbers in the tendril. These cells contain raphide crystals and at maturity are devoid of protoplasts. Raphide crystals are frequently seen forming in the protoplasts of these cells, however, and this may support the widely accepted interpretation of the role of laticifers in excretion. Esau (1967) points out that laticifers accumulate many substances commonly recognized as excretory and that such substances are more abundant than food material in the latex.

2. **Idioblasts:**

Idioblasts are cells which differ markedly from other constituents of the same tissue in form, structure, or contents (Esau, 1967). Two types of idioblasts are present in Smilax. These are the crystal-containing cells and tanniniferous cells.

Cells containing raphides are often arranged in longitudinal rows, but also occur sporadically throughout the ground parenchyma of the stem, leaf, and tendril. These cells may be distinguished from the surrounding parenchyma cells quite early (Fig. 41, 42). The crystals form in the cytoplasm, but at maturity, the crystal-containing cell is devoid of cytoplasm (Fig. 84).

Tanniniferous cells are also present in the stem, leaf, and tendril, although their distribution varies in each organ. In the stem, they have a scattered arrangement in the subepidermal layers. In the leaf, the subepidermal layer of the adaxial surface often consists of a continuous layer of tanniniferous cells (Fig. 47);
they are scattered in the subepidermal layers of the abaxial surface. Tanniniferous cells often form a continuous subepidermal layer in the tendril.

F. Shoot Tip Abortion in Smilax pumila:

Observations on *S. pumila* indicate that shoot growth in this species is determinate, with the shoot tip undergoing abortion. As a new shoot reaches its maximum erect height, the terminal bud becomes greatly reduced in size with a width of approximately 0.75 - 1.0 mm and a height of approximately 1 - 3 mm.

Various internal changes are associated with this phenomenon. Tendrils are absent on leaf primordia and young leaves within the terminal bud (Fig. 93). The shoot apical meristem becomes low-convex to flat (Fig. 93, 94). The normal tunica-corpus configuration of the meristem (Fig. 23) seen in healthy apices is altered with the shoot apex becoming stratified and lacking a distinct corpus (Fig. 94). The meristem diminishes in size due to an acceleration of cell differentiation near the apical meristem. The meristem shows differentiation in the surface layers, and pith differentiation encroaches to within 50 μm of the summit of the meristem (Fig. 94). Cells show more inclusions and more affinity for stains than in earlier stages of rapid growth of the shoot. Raphide crystals found universally in active growth stages are absent in the shoot tip under undergoing cessation.

The axillary buds below the abortive tip are also unusual in appearance (Fig. 95, 96). The shape of the axillary meristem is roughly conical (Fig. 95) rather than convex as in axillary...
meristems of shoots in active growth stages (Fig. 92). Cells of the
tunica are enlarged and vacuolate (Fig. 96). Prophyll differentiation
occurs precociously (Fig. 95, 96).

These changes become evident in erect shoots of S. pumila
just prior to their assuming a trailing habit. At the time these
changes are observed, floral buds are developing at the lower nodes
of the shoot (Fig. 97, 98). The relationship between abortion and
flowering will be considered in the discussion.

In later stages, an abscission layer forms (Fig. 99) and there
is a breakdown in cellular structure of the tip above this level
(Fig. 100). The abscission layer forms in the internodal region
approximately 5 - 6 nodes below the shoot apical meristem.
DISCUSSION

Shoot Apical Organization. In recent years, the shoot apex of seed plants has been the subject of numerous investigations. Gifford and Corson (1971) provide an extensive recent review of work on the shoot apex, including that of monocotyledons.

The apical configuration of the Gramineae with its periclinal divisions in the surface layer, is often used as representative of all monocotyledons (Clowes, 1961; Wardlaw, 1956). Numerous grass apices have been studied (Sharman, 1945; Abbe and Stein, 1954; Ledin, 1954; Brown et al., 1957; Thielke, 1962). A search of the literature, however, shows that many monocotyledons have apices with a true tunica in which leaf initiation is restricted to internal layers of the apex.

The number of tunica layers in the shoot apex of monocotyledonous plants is variable. The shoot apex of Smilax has a two- or three-layered tunica. Stant (1952) reported a uniseriate tunica for Elodea (Hydrocharitaceae), Convallaria (Liliaceae), and Carex (Cyperaceae); a two- or three-layered tunica in Luzula (Juncaceae); and usually three or four tunica layers in Narcissus (Amaryllidaceae). Ledin (1954) reported the presence of a single tunica layer in the shoot apex of Zea mays (Gramineae). Thielke (1954) found that, in the members of the Commelinaceae she studied, the tunica varied from one to two layers, both between genera and between species of the same genus. In the orchid, Neottia, Cutter (1955) regards the tunica as uniseriate. Brown, Heimsch, and Emery (1957) studied shoot apical
structure in 63 species in 21 tribes of the three major groups of the Gramineae and reported the presence of both one- and two-layered tunicas. Rohweder (1963) reported the presence of two tunica layers in each of the 15 taxa of the Commelinaceae he studied. Staff (1968) found two tunica layers in the shoot apex of Xanthorrhoea media (Liliaceae). The shoot apex of Echinodorus tenellus (Alismataceae) has two well-defined tunica layers (Charlton, 1968). Kaplan (1970) reported the presence of a three- to four-layered tunica in Acorus (Araceae). Thielke in 1962 reported that the shoot apex of Saccharum (Gramineae) is devoid of a tunica, but her later studies with this taxon indicate that the number of tunica layers present varies in different species.

The presence of three tunica layers in the shoot apex of Smilax smallii is problematical in that delimitation of the T3 (innermost tunica layer) from the corpus is difficult. The rare occurrence of periclinal divisions in the second tunica layers of the shoot apex of S. bona-nox and S. pumila as well as in the second and third tunica layers of S. smallii require a loose interpretation of the term tunica. As Esau (1967) points out however, the number of parallel periclinal layers in the shoot apex may vary during ontogeny of the plant (Gifford and Tepper, 1962; Franck, 1975) as well as during seasonal growth fluctuations (Hara, 1962). Sussex (1955) reports periodic changes in stratification in relation to the initiation of leaves. Some workers treat such changes as variations in thickness of the tunica and others interpret them as reflections of variations in stratification of the corpus. Cutter (1955), for example regards
the tunica as uniseriate in Neottia though she reports that two or three stratified layers are generally present in vegetative apices. The massive shoot apex of Xanthorrhoea media (Staff, 1968) has an unusually large number (10 - 18) of peripheral layers. Staff (1968) groups these layers into a two-layered tunica and a transitional zone of 8 - 16 layers of cells, because of the marked heterogeneity in cell size and arrangement in these regions.

The corpus in the Smilax shoot apex is a homogeneous mass of meristematic cells in which distinct cytologic zonation was not observed. Zonation has been reported for other monocotyledons: Sinocalamus (Hsu, 1944); Agropyron (Sharman, 1945); Elodea, Convallaria, Carex, Luzula, and Narcissus (Stant, 1952); Neottia (Cutter, 1955); Xanthorrhoea (Staff, 1968); Acorus (Kaplan, 1970). According to Esau (1967), the degree of distinctness of zonation varies in angiosperms and is usually better expressed in larger apices.

Size of the shoot apex. The width of the shoot apex in the three species of Smilax studied ranges from approximately 120 μm to 170 μm. Widths of other monocotyledonous apices are given for comparison: Acorus, 95 - 125 μm (Kaplan, 1970); Nuphar, 500 μm (Clowes, 1961); Phoenix, 528 μm (Ball, 1941); Washingtonia and Trachycarpus, 288 μm (Ball, 1941); Xanthorrhoea, 580 - 1283 μm (Staff, 1968); Zea, 130 μm (Clowes, 1961).

Primary thickening meristem. The presence of a primary thickening meristem below the shoot apex of S. smallii can be correlated with the large stem diameter observed in this species. In monocotyledons having thick axial organs, rapid thickening takes place below the apical meristem through the activity of the primary
thickening meristem. The presence of this meristem in monocotyledons has been noted in various monocotyledonous taxa: *Musa* (Skutch, 1932); *Phoenix, Washingtonia*, and *Trachycarpus* (Ball, 1941); *Aloe, Sansevieria, Yucca, Agave*, and *Dracaena* (Cheadle, 1937); and in certain members of the Commelinaceae (Rohweder, 1963).

**Leaf initiation.** The meristematic layers from which leaf primordia arise appear to be quite variable within the monocotyledons. In *Smilax*, leaves are initiated by periclinal divisions in the second tunica layer of the shoot apex. In the Gramineae, leaf primordia arise through periclinal divisions in the first two layers of the apex, regardless of whether one or two tunica layers are present (Kaufman, 1959; Sharman, 1945). Staff (1968) reports that periclinal divisions associated with leaf initiation are first evident in the second or third layer of the shoot apex of *Xanthorrhoea*. Leaf initiation in *Acorus* (Kaplan, 1970) occurs by periclinal divisions in the second through fourth layers of the meristem. In *Sansevieria* (Stevenson, 1973), leaf initiation begins with periclinal divisions in the third layer of the shoot apex.

**Procambialization.** Procambial differentiation is one of the first indications of specialization within an organ. Procambium is first evident in leaf primordia of *Smilax* when they are approximately 100 μm in height. This is comparable to *Acorus* (Kaplan, 1970) with procambium present in primordia 130 – 140 μm in height and *Sansevieria* (Stevenson, 1973) which has procambium present in primordia 90 – 120 μm high. More commonly, the dorsal median bundle is the first to develop but in *Acorus*, Kaplan (1970) found that this
bundle does not differentiate until after the first two pairs of lateral bundles. The situation in *Smilax* resembles that of *Sansevieria* (Stevenson, 1973) with the median strand differentiating first followed by lateral strands in paired succession, one on each side of the median strand.

**Leaf Morphology.** The leaf of *Smilax* is of particular interest in light of Kaplan's (1973) recent paper dealing with leaf morphology and evolution in the monocotyledons. A full review of monocotyledonous leaf morphology is beyond the scope of this study, but the reader is referred to the Kaplan paper (1973) for an extensive review and bibliography on the subject. As pointed out in Kaplan's paper, several interpretations of dorsiventral monocotyledonous leaves have been suggested, with one of the better known being the pseudolamina concept of Henslow (1911) and Arber (1918). Arber (1920) maintained that the blade of *Smilax* is not equivalent to the lamina of a dicotyledon. She interpreted this structure as a "pseudolamina" representing an expansion of the upper region of the petiole. In Kaplan's (1973) view, a more plausible interpretation is that of Knoll (1948) who made a comprehensive survey of the morphology of dorsiventral monocotyledonous leaves. Knoll (1948) implies that the major morphological regions in the dorsiventral monocotyledonous leaf (i.e., lamina, petiole, and sheath) have a different ontogenetic origin from leaves of dicotyledons. As pointed out by Kaplan (1973), lamina and petiole in the dorsiventral leaf would be derived from the lower leaf zone or "Unterblatt" (terminology of Eichler, 1861), while in dicotyledons, they would be derived from the "Oberblatt," or upper leaf zone. The "Oberblatt" in the dorsiventral
monocotyledonous leaf remains rudimentary (Kaplan, 1973), often reduced to a small radial apex or apical appendage atop the lamina (termed the precursor tip of "Vorlauferspitze" by Knoll, 1948). This suggests that different regions of the leaf primordium are capable of producing structurally similar but analogous subunits (Kaplan, 1973).

Kaplan (1973) suggests that the basic construction of monocotyledonous leaves consists of two regions, a distal unifacial upper sector and a proximal bifacial sheath, and furthermore that variations in leaf morphology in a range of monocotyledonous taxa are due to reciprocal elaboration, or suppression of these two sectors, or both.

Kaplan (1973) investigated several monocotyledonous species in an effort to test Knoll's leaf-base concept. In doing so, he made four developmental predictions which could be evaluated by comparative morphogenetic studies. The results of his investigation lend support to the leaf base theory.

With minor variations, foliar histogenesis in Smilax follows the developmental predictions of Kaplan (1973) and in so doing tends to lend further support to the leaf base theory. According to Kaplan's (1973) first prediction, the "Vorlauferspitze" should be the first region of the leaf to initiate from the shoot apex; the subjacent lamina, petiole, and leaf base should be differentiated from the meristem-encircling basal part of the primordium or the lower leaf zone. These is a minor variation of this theme in Smilax. The precursor tip, or "Vorlauferspitze" is not the first region of the
leaf to initiate from the shoot apex. In *Smilax*, the shape of the young primordium closely resembles that described for *Zea* by Ledin (1954), i.e., forming a projecting collar partially encircling the axis. The precursor tip, however, is the first sector of the leaf to initiate from the meristem-encircling primordium of *Smilax*. This is followed by differentiation of the lamina, tendrils, petiole, and leaf base from the lower leaf zone. The second prediction (Kaplan, 1973) is that the "Vorlauferspitze" should become differentiated from the bifacial base by the occurrence of adaxial thickening in this region in contrast to marginal activity in the base. In *Smilax*, the "Vorlauferspitze" arises in the median plane of the young leaf primordium as a radially symmetrical structure. Adaxial thickening was not observed in this region. Subsequent vacuolation and cell enlargement are responsible for increase in diameter of this region. This is comparable to the condition described in *Zantedeschia* (Kaplan, 1973). Kaplan's (1973) third prediction is that the "Vorlauferspitze," depending on the proportion of the mature leaf represented by it, should show a relatively late cessation of elongation in those species where it comprises a large proportion of the total leaf length, and the inverse relationship should hold where it is much shorter. This is true in *Smilax* where the length of the tip comprises only a minute portion of the total leaf length. Cells in this region begin to vacuolate and idioblasts in the form of crystal-containing cells differentiate below the tip when the leaf is 1,000 µm - 1,500 µm high. Elongation ceases in leaves approximately 7,500 µm in height with the tips of these leaves being attenuate.
The fourth prediction of Kaplan (1973) is that the more markedly the lower leaf zone is differentiated into lamina and petiole, the earlier in development should this differentiation take place. This prediction is also fulfilled in Smilax which has a very distinct lamina and petiole. Adaxial meristematic activity associated with delimitation of the morphological regions of the leaf occurs very early in development, becoming evident in primordia approximately 250 μm in height.

The reason for the characteristic striate venation pattern exhibited by the leaves of monocotyledons is not necessarily solved by any single theory of monocotyledonous leaf morphology according to Kaplan (1973). He points out that Knoll's leaf-base model does not explain why the lateral veins in monocotyledons are differentiated with a strictly longitudinal orientation, whereas those of many dicotyledons exhibit a horizontal or even diagonal course of inception. Leaf primordia of both dicotyledons and monocotyledons have similar patterns of meristematic activity, indicating that the study of foliar histogenesis alone will not necessarily provide any more profound insight regarding the reasons for these major differences in vein differentiation (Kaplan, 1973). He suggests that comparative studies of morphogenesis in leaves of dicotyledons possessing similar venation may be useful in attempting to elucidate the relationship of venation pattern to modes of leaf growth. It seems that a detailed study of morphogenesis in the reticulate-veined leaves of Smilax might also be useful to study this question. Pray (1963) describes the minor venation system of Smilax as remarkably similar in pattern to that of Liriodendron (Pray, 1954, 1955) and many other dicotyledons.
Interpretation of the tendril of Smilax. The occurrence of tendrils is rare in monocotyledons and this study represents the first ontogenetic investigation of a tendril-bearing taxon within this group. The tendrils of Smilax are simple, unbranched structures with relatively little cellular diversity. Numerous detailed studies of tendril ontogeny in dicotyledonous taxa have been made. Most of these studies have dealt with tendrils arising as axillary shoot apical meristems [Parthenocissus (Millington, 1966); Vitis (Tucker and Hoefert, 1968); Passiflora (Shah and Dave, 1970b); Ampelopsis (Moens, 1956)]. A notable exception is found in Doxantha (Sistrunk and Tucker, 1974) where the second pair of lateral appendages of the compound leaf primordium differentiate as thorn tendrils. The tendrils of Smilax differ in origin from all of these previously described. In Smilax, the tendrils are paired and initiate on the flanks of the leaf base rather than in an axillary position.

Apical organization of the tendril apices of dicotyledonous species often resembles that of the parent shoot (Millington, 1966; Shah and Dave, 1970b). Tucker and Hoefert (1968) report that the tendril apex of Vitis vinifera is initially similar to that of the parent shoot (i.e., having tunica-corpus organization) but becomes zonate as the tendril increases in height. Sistrunk and Tucker (1974) reported the presence of apical and subapical initials in the tendril primordia of Doxantha with these initials and their derivatives dividing predominantly anticlinally. Concomitant cellular enlargement was found to accompany elongation of the tendril in Doxantha. As in Doxantha (Sistrunk and Tucker, 1974), apical organization of the
tendril of *Smilax* does not resemble that of the parent shoot and is quite simple in structure, consisting of a protodermal layer overlying a block meristem at the tip. Cessation of meristematic activity occurs very early in the tendril of *Smilax* with vacuolatlon evident in cells at the tip of tendrils approximately 300 μm high. Onset of differentiation in *Smilax* tendrils is much earlier than in those of *Vitis* (Tucker and Hoefert, 1968) where differentiation of the tendril tip begins when the tendril is 7 - 10 mm long. In *Smilax*, as in *Vitis* and *Ampelopsis* (Tucker, 1968) apical degeneration results from accelerated acropetal differentiation within the apex and a depressed rate of cell division. Further growth in height of the tendril of *Smilax* is accomplished through intercalary extension. The tendril tips of dicotyledonous genera have been reported to differentiate into a variety of structures: hydathodes in *Vitis* (Tucker and Hoefert, 1968); thorns in *Doxantha* (Sistrunk and Tucker, 1974); and adhesive discs in *Ampelopsis* (Moens, 1956). The tendril tip in *Smilax* does not differentiate into any such structure. There are several features of the tendril of *Smilax* however which might indicate a hydathodal function. Although relatively unspecialized in structure, the tendril has an abundant vascular supply with 5 or 6 major bundles and numerous minor bundles. In young tendrils, 5 - 6 protoxylem strands extend continuously from the base to the tip of the tendril where they fuse. Phloem is not present in these vascular strands near the tip. The absence of phloem is a common feature of hydathodes (Tucker and Hoefert, 1968). The tracheary elements at the tendril tip are somewhat comparable to those in *Vitis* (Tucker and Hoefert, 1968)
although epithem, the spongy tissue normally associated with hydathodes, is not present. Paradermal sections of the tendril tip show numerous guard cell pairs in the epidermis which are open, suggesting perhaps that these may actually be water-pores, another characteristic of a hydathode.

The nature of the tendrils of *Smilax* has been a matter of controversy for many years. Clos (1857) interprets the tendrils of *Smilax* as "un double prolongement lateral des éléments cellulo-vasculaires du petiole." Colomb (1887) reviews the previous work on *Smilax* tendrils. He pointed out that the tendrils of *Smilax* had been interpreted by some as lateral leaflets of a compound leaf and by others as metamorphosed stipules. Colomb (1887) interpreted the tendrils as a bipartite ligule with each tendril being a demi-ligule. Arber (1920) also reviewed previous interpretations and pointed out that the tendrils had been regarded by some as metamorphosed trichomes or emergences. Arber (1920) interpreted the tendrils of *Smilax* in light of the phyllode theory as "equivalent in morphological value to the petiole, and as having originated through a dedoublement or chorisis of that organ." Majumdar et al. (1947) studied the tendrils of *Smilax macrophylla* and arrived at the same conclusions as Arber (1920). All of these interpretations are based on observations of external morphology or on transverse sections taken at various levels through the leaf of *Smilax*. Prior to this study, ontogeny of the tendril has been completely neglected, which has led to interpretive errors. For example, Arber (1920) and Majumdar et al. (1947) propose that the tendrils arise by a chorisis
or splitting of the petiole, yet tendril initiation takes place prior to delimitation of the morphological regions of the leaf of Smilax.

The similarity in vasculature of the tendril tip and the tip of the lamina could perhaps be interpreted as indicating homology between the tendrils and the lamina. Sistrunk and Tucker (1974) based their interpretation of the thorn-tendrils of Doxantha as modified leaflets of a compound leaf on similarities in structure of the tip of both structures. If the tendrils and the lamina are indeed homologous in Smilax, the tendrils could be interpreted as lateral leaflets of a compound leaf. In compound leaves, leaflets are initiated in acropetal sequence along the compound leaf primordium (Foster, 1935; Sistrunk and Tucker, 1974). The leaflets originate in this case from the "Oberblatt," or upper leaf zone. The tendrils of Smilax originate from the lower leaf zone. Comparisons are difficult due to the shape of the respective primordia. In Doxantha (Sistrunk and Tucker, 1974), the compound leaf primordium is radially symmetrical and leaflets are initiated on the adaxial surface of the primordium. The primordium in Smilax encircles the meristem and the initiatory sites of the tendrils are physically separated from the median plane of the primordium where the lamina and petiole differentiate. In compound leaves, one normally thinks of a common axis, or rachis to which the leaflets are attached. If this were the case in Smilax, the bifacial, sheathing portion of the leaf would have to be regarded as the rachis since the tendrils as well as the lamina and petiole attach at this point.
The most logical interpretation of the tendrils of *Smilax* based on ontogenetic evidence is that they are metamorphosed stipules. Their origin on the flanks of the primordium resembles that described for the stipules of *Rosa centifolia* by Mitra (1948). It is ironic that, historically, the first two interpretations which were made of the tendrils of *Smilax* seem now to fit best with the ontogenetic data. The interpretation of tendrils as lateral leaflets of a compound leaf and as metamorphosed stipules were consistently denied in all subsequent papers dealing with the tendrils of *Smilax*.

**Shoot tip abortion.** Shoot tip abortion has not been described for any monocotyledons even though it is a common phenomenon. Shoot tip abortion in *S. pumila* involves a cessation of vegetative growth resembling that found in many woody plants. The sequence of events involved with shoot tip abortion in *S. pumila* follows closely that described for *Ulmus americana* (Millington, 1963). The presence of flower buds on shoots with aborting tips, or in early stages of abortion, suggests that flowering may be related to the phenomenon of abortion or that both are controlled by a common factor. Photo-period has been shown to exert some influence on abortion in woody plants as pointed out by Romberger (1963). In *Robinia* (Wareing, 1954; Wareing and Roberts, 1956) and *Catalpa* (Downs and Borthwick, 1956; Downs, 1958) abortion can be hastened by short photoperiods and delayed by long photoperiods. Removal or destruction of lateral buds from shoots has been found to delay apical abortion (Garrison and Wetmore, 1961). In *Ulmus*, Millington (1963) found no indication of a stimulus to shoot abortion related to flowering or fruit drop.
Nitrogen deficiency accelerates shoot tip abortion in *Ulmus* (Millington, 1963). A number of factors, external and internal, may be involved in the timing of shoot tip abortion (Millington, 1963). Garrison and Wetmore (1961) found a correlation between shoot abortion and decline in auxin levels, but they point out that no causal relation was established nor did they obtain evidence for an auxin inhibitor. Considering the acropetal progression of necrosis in the aborting tip, Millington (1963) suggests the possibilities of senescence factors moving acropetally in the shoot.

Shoot tip abortion in *S. pumila* is a system which would lend itself to further experimental study to see whether abortion could be accelerated, delayed, or averted by hormonal manipulation.

**Stomatal–subsidiary cell relationships.** The stomatal–subsidiary cell relationship in *Smilax* is quite variable with the stomatal complex having 2, 3, or 4 subsidiary cells. Stebbins and Khush (1961) classified the stomatal complex of monocotyledonous leaves into four types. They reported that many species of the Lilliales belong to the type in which guard cells are not associated with any subsidiary cells. This generalization does not apply in the case of *Smilax* where definite subsidiary cells are present.

Recent studies have dealt with ontogeny of the stomatal complex (Fryns-Claessens and Van Cotthem, 1973; Tomlinson, 1974). Fryns-Claessens and Van Cotthem (1973) divided the developmental pathways of perigenous stomata into six types. Paliwal (1969) reported aperigenous development in the Liliaceae. This aperigenous type however does not fit *Smilax* since in this type, the adult stomata are
devoid of subsidiary cells. Tomlinson (1974) deals only with development of the stomatal complex in monocotyledons. He recognizes two major categories based on the presence or absence of oblique divisions in neighboring cells. He points out that *Smilax* does not conform to any of his proposed arrangements for development of the stomatal complex.

The variability found in the arrangement of subsidiary cells in *Smilax* renders this feature of little taxonomic value at the species level. This variability, however, would lend itself to further research. It would be interesting to discover if each type of stomatal complex in *Smilax* has a different ontogenetic sequence, or if all types originate by modifications of one basic scheme of development.

Developmental comparisons. The large shoot apex with the deep tunica in *S. smallii* can be correlated with the extremely vigorous growth of this species. In contrast, the shoot apices of *S. pumila* and *S. bona-nox* are smaller and consistently show only a two-layered tunica—features which can be related to less vigorous growth than that observed in *S. smallii*. The massive stems of *S. smallii* can be attributed to the activity of the primary thickening meristem below the shoot apex in this species. Stems of *S. bona-nox* and *S. pumila*, on the other hand, are smaller and derived primarily by the activity of the shoot apex.

Tendrils of *S. bona-nox* and *S. smallii* are generally larger than those of *S. pumila*. This probably represents an adaptation to the climbing habit characteristic of *S. bona-nox* and *S. smallii*. In addition, the production of tendrils with a reduced blade observed
at lower nodes in the shoots of *S. smallii* is probably another adaptation to climbing in this species.

The size of the rhizome of all three species studied can be correlated with size and vigor of the aerial stems. The most massive rhizome system is found in *S. smallii*, the most vigorous species, while the smallest rhizome system is that of *S. pumila* which represents the other extreme of growth.

Older stems of all three species become quite woody due to deposition of lignin in the stem tissues. Older stems of *S. smallii* were not studied to determine if they display secondary growth, although secondary growth in monocotyledons is often associated with the presence of a primary thickening meristem (Esau, 1967). There may be a developmental continuity between the two meristems (i.e., the primary thickening meristem and the meristem giving rise to the secondary tissues) when both are present in a given plant (Esau, 1967). Ball (1941) discussed secondary growth in the stems of certain palms and mentions "the young cambia of certain woody members of the Liliaceae."

Even though there are definite differences in growth habit, vigor, etc., the close relationship of these species is supported by a number of developmental similarities. Leaf initiation, for example, is first evident as a periclinal division in the $T_2$ regardless of whether two or three tunica layers are present. The sequence of events in leaf ontogeny is identical in all three species studied although the differences in duration and timing of events, which are responsible for differences in lamina form are subtle and difficult to study. The development of procambium as well as the differentiation of vascular
tissues in all three species is comparable. The origin and development of the tendrils is also identical in all three species studied. It seems then, that subtle changes in ontogeny can result in marked differences in mature structure.
LITERATURE CITED


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Wilburn, H. I. 1940. Seed and fruit development in *Smilax*. M.S. Thesis, University of North Carolina, Chapel Hill.

PLATE LEGENDS

Fig. 1. Rhizome system of S. bona-nox. Tu, tuber; R, rhizome; Rt, root. X 0.4.

Fig. 2. Vigorous shoot tip of S. bona-nox. La, lamina; T, tendril; P, petiole; TB, terminal bud. X 2.

Fig. 3. Dwarf shoot tip of S. bona-nox. TB, terminal bud; Pk, prickles. X 1.

Fig. 4. Mature foliage leaves of S. bona-nox. X 0.4.
Fig. 5. Rhizome system of *S. smallii*. Paler distal portions represent new growth. X 0.2.

Fig. 6. One tuber of *S. smallii* and lowermost nodes of aerial shoot. Tu, tuber; Rt, root; S, scale leaves. X 0.5.

Fig. 7. Shoot tip of *S. smallii*. La, lamina; T, tendril; LB, leaf base; TB, terminal bud. X 1.

Fig. 8. Mature foliage leaves of *S. smallii*. X 0.6.
Fig. 9. Rhizome system of *S. pumila*. Tu, tuber; R, rhizome. X 1.

Fig. 10. Rhizome of *S. pumila* bearing scale leaves and roots. S, scale leaf; Rt, root. X 1.

Fig. 11. Trailing growth habit of *S. pumila*. X 0.1.

Fig. 12. Climbing growth habit of *S. pumila*. X 0.2.

Fig. 13. Tendrils of *S. pumila* coiled around stem. X 0.2.
Fig. 14. Shoot apex of *S. pumila* in minimal phase with tip of leaf 2 removed to show the apical dome. Scanning electron microscope (SEM) photograph. SA, shoot apex; L, leaf. X 350.

Fig. 15. Shoot apex of *S. pumila* with two youngest leaf primordia intact and partially obscuring the shoot apex. SEM photograph. L, leaf. X 300.

Fig. 16. Shoot apex of *S. bona-nox* in maximal phase in view from above. Tip of leaf 2 has been removed. SEM photograph. L, leaf. X 235.

Fig. 17. Shoot apex of *S. bona-nox* in maximal phase in lateral view, with tip of leaf 2 removed. SEM photograph. L, leaf. X 230.
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Fig. 21. Shoot tip of S. smallii in longitudinal median section with 10 leaf primordia. Note primary thickening meristem (PTM) below the shoot apex. X 41.
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Fig. 23. Shoot apical meristem of S. bona-nox in longitudinal median section with a new leaf forming a protuberance on the right flank (at arrow). X 340.

Fig. 24. Shoot apical meristem of S. pumila at minimal stage showing tunica-corpus configuration. Apical and subapical initials (AI, SAI) are shown in the youngest leaf primordium 30 $\mu$m in height on right side of apex. Longitudinal median section. X 330.

Fig. 25. Shoot apical meristem of S. smallii in longitudinal median section showing two tunica layers ($T_1$, $T_2$) and corpus (C). X 500.

Fig. 26. Shoot apical meristem of S. smallii in longitudinal median section showing three tunica layers overlying corpus. X 200.
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Fig. 28. Base of same apical meristem (SA) along with young leaf primordia of *S. bona-nox* in transverse section. X 400.

Fig. 29. Leaf primordium of *S. smallii* 100 μm in height showing apical and subapical initials (AI, SAI) at the tip and procambium (Pc) at the base. Vacuolation at the abaxial base of the primordium is indicated by the arrow. X 250.

Fig. 30. Leaf primordium of *S. pumila* 100 μm in height showing apical and subapical initials (AI, SAI) in longitudinal median section. X 250.
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Fig. 32. Adaxial meristem (AM) activity in leaf primordium of *S. bona-nox* 300 µm high in longitudinal median section. X 560.
Fig. 33. Unifacial tip of leaf (at arrow) of *S. bona-nox* 570 µm in height showing cells at the tip are still meristematic. Transverse section. X 440.

Fig. 34. Unifacial tip of leaf (at arrow) of *S. bona-nox* 1,000 µm high showing vacuolation of cells at the tip. Transverse section. X 395.

Fig. 35. Unifacial tip of leaf of *S. smallii* 1,500 µm high showing crystal containing cells (CC) near the tip. In longitudinal median section. X 480.

Fig. 36. Unifacial tip of older leaf of *S. smallii* showing attenuate tip. Longitudinal median section. X 135.

Fig. 37. Unifacial tip of older leaf of *S. bona-nox* in transverse section. Xylem tracheary elements visible (at arrow) in the center. X 375.
Fig. 38. Young, crescent shaped leaf primordia of *S. bona-nox* in transverse section. Leaf at top in figure is 370 μm high; leaf at bottom is 700 μm high. X 215.

Fig. 39. Marginal and submarginal initials (MI, SMI) and their derivatives shown in transverse section through lamina of young leaf of *S. bona-nox*. X 1,765.

Fig. 40. Marginal and submarginal initials (MI, SMI) in developing lamina of *S. bona-nox*. Mitotic figures are indicated by arrows. Transverse section. X 560.

Fig. 41. Marginal and submarginal initials (MI, SMI) in developing lamina of *S. bona-nox*. Crystal containing cells (CC) are present below the submarginal initial. Transverse section. X 870.

Fig. 42. Vacuolation in abaxial region of developing lamina (at arrow) of *S. bona-nox*. Crystal containing cells (CC) differentiating below margin. Transverse section. AD, adaxial surface; AB, abaxial surface. X 630.
Fig. 43. Outline drawings made at various levels below the tip of a leaf of *S. bona-nox* approximately 7,500 μm high.

A. 370 μm below the tip
B. 700 μm below the tip
C. 1,100 μm below the tip
D. 2,040 μm below the tip
E. 3,100 μm below the tip
F. 3,250 μm below the tip
G. 3,450 μm below the tip
H. 3,600 μm below the tip
I. 3,800 μm below the tip
J. 5,000 μm below the tip
Fig. 44. Plate meristem (PM) activity in developing lamina of S. bona-nox in transverse section. AB, abaxial surface; AD, adaxial surface. X 370.

Fig. 45. Enlargement and onset of differentiation of cells in the developing lamina of S. bona-nox seen in transverse section. AB, abaxial surface; AD, adaxial surface. X 435.

Fig. 46. Formation of intercellular spaces in the developing lamina of S. bona-nox in transverse section. AB, abaxial surface; AD, adaxial surface. X 325.

Fig. 47. Leaf of S. bona-nox with differentiated mesophyll. A hypodermal layer of tanniniferous cells is present on the adaxial side of the lamina. Transverse section. AB, abaxial surface; AD, adaxial surface. X 350.
Fig. 48. Procambium (Pc) present 70 μm below developing primordium on right side of shoot apex of S. pumila. Procambium extends to within 78 μm of the tip of the leaf 216 μm high at the left side of the apex. Longitudinal median section. X 340.

Fig. 49. Shoot tip and leaf primordia of S. bona-nox. Base of leaf 210 μm high with only median procambial bundle present (at arrow) at top in figure. Leaf at bottom in figure is 600 μm high and has three procambial bundles (at arrows). Transverse section. X 175.

Fig. 50. Developing lamina of S. bona-nox with three procambial bundles (at arrows) in transverse section. X 260.

Fig. 51. Leaf base of S. bona-nox showing arcuate arrangement of bundles (at arrows) in transverse section. AM, adaxial meristem. X 150.
Fig. 52. Petiole of S. bona-nox showing centric arrangement of bundles in transverse section. X 140.

Fig. 53. Base of lamina of S. bona-nox with centric arrangement of bundles in transverse section. X 140.

Fig. 54. Procambial bundles (Pc) in the stem of S. bona-nox in transverse section. X 140.

Fig. 55. Early stage in formation of midvein of the leaf of S. bona-nox. Three bundles are present with the larger central bundle having differentiated protoxylem elements (Px), metaxylem elements in the process of differentiation (Mx), and sieve tube elements (SE). Transverse section 2,500 μm below the tip of a leaf 7,500 μm high. X 400.
Fig. 56. Later stage in formation of midvein with differentiated protoxylem (Px), metaxylem (Mx), and sieve tube elements (SE) in the larger bundle. Transverse section of leaf of S. bona-nox 3,200 μm below the tip of a leaf 7,500 μm high. X 380.

Fig. 57. Midvein of mature leaf of S. bona-nox with a central core of xylem (X) and three clusters of phloem (Ph) surrounded by a fibrous bundle sheath (BS) in transverse section. AB, abaxial surface; AD, adaxial surface. X 230.

Fig. 58. Arrangement of guard cells (G) and subsidiary cells (SC) in leaf of S. bona-nox. Paradermal section. X 520.

Fig. 59. Guard cell pair with four subsidiary cells (at arrows) at base of prickle of S. bona-nox. Paradermal section. X 685.

Fig. 60. Immature guard cells (G) and substomatal chamber (at arrow) in leaf of S. bona-nox. Transverse section. X 1,015.

Fig. 61. Mature guard cells with ledges of wall material present on both upper and lower surfaces. Transverse section of leaf of S. bona-nox. X 1,200.
Fig. 62. Flank of leaf base of *S. pumila* showing divisions (at arrow) involved with tendril initiation. Sagittal section. X 355.

Fig. 63. Tendril (T) of *S. pumila* 72 µm in height and uniformly meristematic in sagittal section. X 610.

Fig. 64. Tendril (T) of *S. bona-nox* 80 µm high and uniformly meristematic in sagittal section. X 575.

Fig. 65. Tendril (T) of *S. smallii* 100 µm in height and uniformly meristematic. Base of tendril at arrows. Sagittal section. X 300.

Fig. 66. Tendril (T) 120 µm high, developing lamina (La), and leaf base (LB) of *S. bona-nox*. SEM photograph. X 170.

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Fig. 67. Tendril (T) of *S. pumila* 138 μm high in sagittal section. Pd, protoderm; BM, block meristem; RM, rib meristem; La, lamina. X 465.

Fig. 68. Tendril (T) of *S. smallii* 250 μm high showing attenuate tip. Sagittal section. La, lamina. X 150.

Fig. 69. Tendril (T) of *S. bona-nox* 300 μm high showing attenuate tip. SEM photograph. La, lamina; LB, leaf base. X 170.

Fig. 70. Tip of tendril of *S. bona-nox* 350 μm high showing vacuolation of cells at the tip. Sagittal section. X 575.
Fig. 71. Tendril (T) of *S. pumila* 468 μm high in sagittal section. La, lamina. X 145.

Fig. 72. Tendril (T) of *S. smallii* 500 μm high in sagittal section. Pc, procambium. X 170.

Fig. 73. Tendril (T) of *S. bona-nox* 651 μm high with attenuate tip in sagittal section. La, lamina. X 150.

Fig. 74. Tendril (T) of *S. bona-nox* 800 μm high with attenuate tip in sagittal section. X 135.

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Fig. 75. Tip of tendril (T) of *S. pumila* 1,416 μm high in sagittal section. X 150.

Fig. 76. Tip of tendril of *S. smallii* 1,812 μm high in sagittal section. Raphide crystals in crystal containing cells (CC) near tip. X 260.

Fig. 77. Tip of tendril of *S. pumila* 2,000 μm high in longitudinal median section. X 350.

Fig. 78. Tip of tendril of *S. bona-nox* 70 mm long in longitudinal median section. X 240.

Fig. 79. Tip of tendril of *S. bona-nox* 100 mm long in longitudinal median section. X 240.
Fig. 80. Tip of older tendril of *S. bona-nox*. SEM photograph. X 220.

Fig. 81. Tip of tendril of *S. pumila* showing elongate epidermal cells. SEM photograph. X 455.

Fig. 82. Tendril tip of *S. pumila* showing mass of trichomes. SEM photograph. X 105.

Fig. 83. Epidermis of tendril of *S. pumila* showing trichomes. SEM photograph. X 360.

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Fig. 84. Early stage in axillary bud development in *S. smallii* with shell zone (SZ) beginning to form in axil of leaf 3 (L3) in longitudinal median section. X 150.

Fig. 85. Periclinal in shell zone (at arrow) in axil of leaf of *S. smallii* in longitudinal median section. X 230.

Fig. 86. Later stage in shell zone formation (SZ) in *S. smallii*. Longitudinal median section. X 180.

Fig. 87. Later stage in axillary bud development of *S. smallii* with small protuberance (at arrow) forming in axil of leaf at node 5 below the shoot apex. Longitudinal median section. X 180.

Fig. 88. Axillary bud meristem at node 6 below the shoot apex of *S. smallii* prior to prophyll initiation. Longitudinal median section. T₁, T₂, tunica layers; C, corpus. X 250.
Fig. 89. Prophyll (Pr) development of *S. bona-nox*. The axillary meristem is also visible. SEM photograph. X 270.

Fig. 90. Fully developed prophyll of *S. bona-nox* in SEM photograph. X 90.

Fig. 91. Axillary bud of *S. pumila* with prophyll (Pr) and young leaf primordium ($L_1$) on left side of apex in longitudinal median section. X 170.

Fig. 92. Axillary bud of *S. pumila* with prophyll (Pr) and young leaf primordium ($L_1$). Meristem is zonate in appearance. Procambium (Pc) visible below leaf primordium at left of apex. Longitudinal median section. X 530.
Fig. 93. Shoot tip of *S. pumila* undergoing abortion. Longitudinal median section perpendicular to the plane of distichy. X 45.

Fig. 94. Shoot apical meristem of *S. pumila* showing various changes associated with abortion. Longitudinal median section perpendicular to the plane of distichy. X 350.

Fig. 95. Axillary bud below tip of shoot undergoing abortion. Longitudinal median section. Pr, prophyll; SA, shoot apex. X 160.

Fig. 96. Meristem of axillary bud below tip of shoot undergoing abortion. Vacuolation in tunica at arrow. Longitudinal median section. X 375.

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Fig. 97. Young floral bud of *S. pumila* in longitudinal median section. X 245.

Fig. 98. Older floral bud which has undergone elongation of the receptacle. Longitudinal median section of *S. pumila*. X 455.

Fig. 99. Shoot tip of *S. pumila* just prior to abscission showing breakdown of cellular structure in longitudinal median section. X 265.

Fig. 100. Abscission zone in stem of *S. pumila* in longitudinal median section. X 75.

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VITA

Benjamin F. Martin, Jr. was born 7 December 1946, in Greenwood, Mississippi. He attended public schools in Sulphur, Louisiana and graduated from Sulphur High School in 1964.

In September 1964 he entered McNeese State College in Lake Charles, Louisiana and received the Bachelor of Science degree with a major in Botany in August 1968. He entered graduate school at McNeese State University in September 1968, and received the Master of Science degree in biology in May 1970. He then served in the U.S. Navy for 18 months and was honorably discharged in January 1972.

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EXAMINATION AND THESIS REPORT

Candidate:  Benjamin F. Martin, Jr.

Major Field: Botany

Title of Thesis: Developmental studies in Smilax.

Approved:

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EXAMINING COMMITTEE:

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Date of Examination:

October 16, 1975