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THE UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

ANATOMY OF THE SEED AND SEEDLING OF

HERRANIA NYCTERODENDRON

A DISSERTATION

SUBMITTED TO THE GRADUATE FACULTY

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degree of

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BY

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Norman, Oklahoma

1972

ANATOMY OF THE SEED AND SEEDLING OF

HERRANIA NYCTERODENDRON

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ANATOMY OF THE SEED AND SEEDLING OF
HERRANIA NYCTERODENDRON

CHAPTER I

INTRODUCTION

According to Schultes (1958) Herrania was first discovered in 1784 by Padre Eloy Valenzuela on an expedition lead by Padre Jose Celestina Mutis. Although Valenzuela considered the plants distinct from Theobroma, they were included in Theobroma until Justin Goudot (1844) described Herrania as a new genus within the Sterculiaceae. Although research and field observations seem to uphold Herrania as a distinct genus there are some who doubt its taxonomic validity (Schultes, 1958). Species of Herrania are small trees ranging from 9 to 30 feet tall and are native to the tropics of South America. Schultes (1958) discusses 17 species, noting that each has a distinct range of tolerance to altitude between sea level and 4,000 feet.

This study is primarily concerned with the seed and seedling anatomy of Herrania nycterodendron Schultes. A detailed description of the mature plant is given by Schultes (1958), describing it as a small tree attaining a height of 25 feet (Figure 14) with a simple, erect trunk bearing flowers on the lower portion and large, compound leaves on the upper portion. The species is native to the westernmost parts of the

Amazon Valley (Figure 15) where it grows on well-drained soil of dense forest at an altitude of 300 to 1,000 feet. Little morphological work has been on Herrania. A survey of the literature revealed one article by Lewelyn Williams (1936, page 323) on the wood anatomy of Theobroma mariae, later identified by Schultes (1958) as H. nitida. Other than a study of the seedling periderm (Chapman, 1968), the seedling anatomy of Herrania is unknown.

I made a brief study of the seed and seedling of Herrania cuatrecasana Garcia-Barriga for comparative purposes. Schultes (1958) describes H. cuatrecasana as a small tree attaining a height of 9 feet which is native to the upper reaches of the Putumago River in Colombia (Figure 15). This species is found on well-drained soil of dense forest between altitudes of 300 and 1,000 feet.

CHAPTER II

MATERIALS AND METHODS

Fruits of Herrania nycterodendron and Herrania cuatrecasana were collected by Dr. Alberto Taylor from cultivated plants at the Centro de Enseñanza e Investigación of the Instituto Interamericana de Ciencias Agrícolas de la Oea in Turrialba, Costa Rica. The fruits were coated with wax for preservation.

After removal of the mucilaginous and fibrous seed coats, approximately 250 seeds of H. nycterodendron and 50 seeds of H. cuatrecasana were planted in 1½ cm of vermiculite over soil. The pots were maintained in the University of Oklahoma greenhouse. Seeds and seedlings were harvested at various stages of development. After fixation in formalin-acetic acid-50% ethyl alcohol (Johansen, 1940) and paraffin infiltration, the material was embedded in Paraplast (60 C). Longitudinal and transverse sections were made at 10μ and stained in safranin (Sass, 1958) and fast green (Boke, 1952). Eight-month stem and root tissues were embedded in celloidin. Transverse sections were cut at 15μ and stained in iron alum and safranin (Wetmore, 1932). Leaf tissue was cleared in Lactic acid and stained with pararosaniline hydrochloride (Boke, 1970).

CHAPTER III

OBSERVATIONS

The fruit of Herrania nycterodendron (Figure 14 B) is ellipsoid, 10 - 12 cm long, and 4 - 5 cm in diameter. It is apically elongated, slightly constricted near the tip, and the base is indented. Stellate trichomes form a velvety covering over the thick pericarp and peduncle. The strongly ribbed fruit has five primary and five secondary ribs, which are broad and rounded; the five locules contain approximately 100 seeds. The mature fruit is gray-yellow.

The seed (Figure 1 A, B), composed chiefly of cotyledons, is triangular-ovate, approximately 10 X 8 X 6 mm, with a coat composed of a thick outer zone of gray mucilage; a middle zone of flattened, thick-walled cells; and an inner zone of thin-walled cells. Thickness of the inner zone increases from one or two cell layers over the cotyledons (Figure 24) to several layers over the indentations leading to the epicotyl at the bases of the cotyledons (Figures 20, 21). A small, distinctive group of cells at the root end of the seed is part of this inner zone of the seed coat (Figure 22).

The cotyledons are closely appressed, except at the base (Figure 26). Epidermal cells along the appressed zone are slightly elongated and parallel to the long axis of the cotyledons (Figure 25), and a small depression filled with tanniferous cells (Figures 27, 28, 30) is present

at the apex. Below the depression, cells of the hypodermis are elongated (Figure 30). Procambial tissue consisting of small, elongated cells which are often surrounded by large, elongated, tanniferous cells, is present in the cotyledons. Parenchyma cells of the cotyledons (Figure 25), which contain abundant tannin and oil (MacLean, 1952), become smaller near the abaxial epidermis (Figure 24). Mucilage cavities occur in the cotyledon bases.

The primary axis is small and contains procambial tissue and scattered tanniferous cells, commonly in groups of two or three (Figure 26). The shoot meristem has a single-layered tunica and recently divided cells are noticeable, but mitotic figures were not evident (Figure 51). One or two developing leaves lacking trichomes overtop the meristem (Figure 20), and the first four are arranged and produced in the sequence indicated by figure 12.

Developing multicellular hairs are present in the indentations at the bases of the cotyledons. Each hair is four to five cells in length and is initiated by a periclinal division in a single epidermal cell. The foot cell protrudes slightly above the epidermal surface, and a multicellular head filled with tannin later develops by anticlinal divisions of the upper cell or cells (Figures 18 A, B, 32, 41, 44).

Continued growth of the seed within the fruit results in the enlargement of the cotyledon bases by intercalary growth, indicated by files of recently divided cells, leaving the radicle in a slight depression (Figure 23). Intercalary growth then causes the primary axis to elongate and the root depression to disappear (Figures 26, 29), but no growth of the root meristem is apparent (Figures 26, 29). Mucilage cavities

develop in the pith of the epicotyl, while those in the bases of the cotyledons enlarge (Figure 26), and the outermost cells at the base of the embryo become filled with tannin (Figures 26, 29). More multicellular hairs develop in the indentations at the bases of the cotyledons, some up to eight cells in length, while a few form on the outside of the cotyledon bases and on older leaves.

Between the third to seventh day of seedling development the cotyledons undergo the greatest change. The bases enlarge by intercalary growth (Figures 2, 47), buds form (Figure 50), and the metaxylem matures. Mucilage cavities line the adaxial side of the proximal portion of the vascular tissue in the cotyledons, while tannins increase in the dermal tissue. Small stomatal mounds develop on the proximal parts of the cotyledons and hypocotyl by periclinal divisions and radial elongation of the hypodermis (Figures 31, 32, 36, 47). Two crescent-shaped guard cells develop at the apices of the mounds (Figures 31, 32, 34, 35, 36), which are formed from loosely organized, often tanniferous cells (Figures 31, 32, 36). The embryonic axis also enlarges by intercalary growth (Figure 47), and mucilage cavities increase in the pith of the epicotyl. Small unicellular hairs (Figure 32, 40) form on older leaves, hypocotyl, and cotyledon bases each by elongation of a single epidermal cell, or from two to several cells formed by anticlinal divisions of an earlier cell.

Activity of the root meristem is initiated between the seventh and thirteenth day of seedling development. As the radicle elongated (Figures 3, 48, 49), the outer tier produces the root cap, the middle tier produces the cortex, and the inner tier produces the central cylinder

(Figures 52, 53) in which the protoxylem and metaxylem soon mature. The cortex becomes wide, composed of large rounded cells with a periderm developing in the outer layers (Figure 54), and tannin appears in the root cap and endodermis but is absent from cells below the root cap initials (Figures 52, 53). Tanniferous cells extend from the endodermis of the root (Figures 10 H-K, 54) into the hypocotyl where they form a discontinuous ring around the stele (Figure 10 F, G). The first secondary roots (Figure 10 I, J) are initiated immediately below the hypocotyl and often grow slightly upward into the root or hypocotyl cortex, breaking through the surface somewhat above their point of origin.

A band of enlarged stomatal mounds (Figures 33, 49), similar in structure to those found on the cotyledons, form on the hypocotyl by periclinal division and radial elongation in the hypodermis and cells immediately beneath. Further developments at this stage of growth are initiation of periderm (Chapman, 1968), appearance of protoxylem in older leaves, and, in some cases, the development of meristematic activity at the bases of cotyledons, adaxial to the vascular tissue (Figure 55).

Cotyledons remain closely appressed through the thirteenth to nineteenth days of seedling growth. This causes the hirsute, leafy shoot to emerge at an angle from the space between the bases of the cotyledons (Figures 4, 12). The first leaves to develop lack laminae and are thus the size and shape of the stipules with which they are sometimes fused (Figure 13 A-D). Subsequent leaves develop small (less than 3 mm long), elongate to rounded blades of compact cells, short petioles, and are about the same length as the stipules (Figures 7, 13 E). Both leaf axis and stipules have a central vascular strand surrounded by a large-celled

cortex and small-celled epidermis.

Many large unicellular trichomes occur singly or in groups on the stem and leaves and are associated with longitudinally elongated mounds encasing their bases (Figures 39, 42). Multicellular hairs on the stem are short with large tanniferous heads (Figures 18 C-E, 39, 42), and the foot cell does not protrude above the epidermal surface. Rudimentary stomatal mounds (Figure 37) with tanniferous guard cells and short-necked multicellular hairs (Figure 38) occur on the lower portion of the cotyledons, above the enlarged bases.

As the shoot and root in the 19- to 30-day seedling increase in length (Figures 5, 6, 56), periderm initiation spreads upward in the hypodermis of the stem, producing one or two cell layers of phellem, while proliferations resembling lenticels develop in the hypocotyl (Chapman, 1968). Root cortex growth is terminated by development of tanniferous periderm in the pericycle, and as the root stele increases in diameter through secondary growth, the cortex splits, first in areas of secondary root development, then along the entire axis (Figures 5, 6).

During the second month of seedling development the 4th through 6th leaves mature (Figure 7); the early maturing ones have rounded blades approximately 11 mm long and later ones have larger, elongate blades (Figures 7, 59). The abaxial surface of a blade is light green with numerous hairs, whereas the adaxial surface is dark green with few hairs, and the veins protrude on both surfaces, but more so on the abaxial side (Figure 63). The petiole (Figure 62) and midvein (Figure 63) of a leaf (blade 11 X 11 mm) have an arc of vascular tissue on the abaxial side, with tanniferous cells along the periphery of the vascular tissue.

Surrounded by the vascular tissue is a pith containing a mucilage duct which is large in the petiole, smaller in the midvein. The midvein and secondary veins extend beyond the leaf margin, forming spinules (Figure 61) which consist of vascular tissue surrounded by parenchyma and epidermis and covered with large unicellular hairs. Cells of the cortex are large, becoming smaller near the epidermis. In the petiole the cortex is wider on the abaxial side than on the adaxial side.

Five types of hairs occur on the leaf: 1) large, thick-walled unicellular hairs (Figure 43), which occur singly or in groups only along veins; 2) small unicellular hairs (Figure 40), which occur singly or in groups; 3) flattened unicellular hairs (Figures 18 H, I, 64), which occur in groups of three or four only along veins of the abaxial surface; 4) short multicellular hairs similar to those found on the stem (Figures 18 C-E, 42); 5) long multicellular hairs (Figures 18 F, 45, 46). Small unicellular hairs and both types of multicellular hairs are also found along veins, but not exclusively.

The shoot has an ectophloic siphonostele surrounded by cortex with large cells to the inside and smaller cells near the epidermis. At each node a trace divides into an inner foliar strand and two outer stipular strands (Figures 11, 76, 77, 78), and the trace of each lateral bud diverges from the stele above a leaf trace (Figures 11, 78, 79). Lateral buds remain dormant as long as the apical meristem remains active, resulting in an unbranched shoot exhibiting strong apical dominance.

As root growth continues, cells of the cortex break down and the cortex partially sloughs away (Figures 57, 58). Secondary roots have a small vascular strand and a tanniferous endodermis, with a thin cortex

surrounded by a small-celled epidermis.

A sequence of leaf types is evident on the 7- to 9-month-old seedling; the oldest leaves have simple, entire blades; intermediate-aged leaves have simple, lobed blades; and the newest leaves are large and compound (Figures 7, 8, 60). Earliest compound leaves have two or three leaflets but the number increases on subsequent leaves until leaves on a fully matured plant have seven (Figure 14 A).

Mature simple leaves have a long petiole and a blade approximately $19\frac{1}{2}$ X 10 cm with well developed venation (Figure 75), abundant hairs, long spinules, and drip tips. The internal anatomies of the petiole (Figure 69) and midvein (Figure 71) are essentially identical, consisting of an ectophloic siphonostele encircling a wide pith with large mucilage cavities. External to the vascular tissue and adjacent to the phloem is a layer of sclerenchyma and external to this is a dark-staining cortical band. The most noticeable difference between the petiole and midvein is a prominent flattening of the adaxial side of the midvein and thinning of the dark-staining cortical band in this flattened region.

Prominent ridges occur on the abaxial surface of the midvein and are oriented parallel to the longitudinal axis of the vein. The prominent dark-staining cortical band of the abaxial side of the midvein extends into these ridges (Figure 71), where it seems to be associated with the bases of large unicellular hairs (Figure 43), common along the ridges.

An enlargement of the cortex occurs where the petiole joins the blade (Figure 70). There is no dark-staining cortical band in this region, which is otherwise anatomically the same as that of the midvein.

Secondary veins (Figure 73) have a slightly different anatomy than the midvein, principally in the adaxial portion. The vascular tissue is mostly arranged on the abaxial side of the secondary veins, with the adaxial side characterized by a small area of vascular tissue and prominent sclerenchyma extending from the xylem well out into the cortex. A dark-staining cortical band occurs only on the abaxial side and, as in the midvein, extends into prominent ridges on the abaxial surface; a single, large mucilage cavity occurs in the center of the secondary vein, surrounded by pith. Tertiary veins (Figure 72) have a central core of xylem with phloem and sclerenchyma adjacent on the abaxial side and no pith or mucilage cavity; otherwise they have the same anatomy as secondary veins. Minor veins (Figure 74) have a central core of vascular tissue surrounded by sclerenchyma which extends to both the upper and lower epidermal surfaces.

The petioles of a medium-sized, mature, simple leaf (blade 8 X 4 cm) and a large leaf have similar anatomy except that the cortical band is not as well developed in the adaxial portion of the medium leaf (Figures 65, 69). The midvein of the medium leaf (Figure 66) resembles the secondary vein of the large leaf (Figure 73) except that the adaxial vascular tissue is scattered and there is less sclerenchyma in the adaxial protrusion of the vein in the former. The anatomy of a secondary vein (Figure 67) of the medium leaf is similar to that of a tertiary vein of the large leaf (Figure 72). The midvein and secondary veins end in spinules (Figure 61), but venation (Figure 68) is not as well developed, and hairs are not as abundant as in the large leaf.

The blade (Figures 67, 72) is composed of an upper epidermis of

large cells, one layer of palisade chlorenchyma, two or three layers of loosely organized spongy chlorenchyma, and a lower epidermis composed of smaller cells with stomates.

Cotyledons persist on the 7- to 9-month seedling, but are withered (Figure 8). Significant secondary growth in the stem and root results in an increase in width and outward displacement of the phloem (Figures 83, 85) and partial crushing of the pericycle in the root (Figure 86). The phloem appears as elongate wedge-shaped areas containing bands of fibers (Figures 84, 86), and the rays contain abundant bands of tanniferous cells, especially near the periphery of the stem. The xylem in the center of the root remains immature and resembles pith.

As periderm increases throughout the plant the outer layers tend to split and slough off (Figures 83, 84, 85, 86). Small proliferations of the periderm resembling lenticels develop on the root (Figure 9; Chapman, 1968) but are no longer present on the hypocotyl. Abundant mucilage cavities develop throughout the plant and starch accumulates in the older xylem of both stem and root and in the pith of the stem.

Herrania cuatrecasana

The fruit of Herrania cuatrecasana differs from that of H. nycterodendron in having numerous small stinging hairs along the ribs, fewer seeds (approximately 60), a slightly larger diameter (7-8 cm). It also lacks a basal indentation. The seeds of H. cuatrecasana (Figure 17 A, B) are slightly larger (12 X 12 X 4 mm) and more flattened and triangular than those of H. nycterodendron, other characters being essentially the same.

Periderm development occurs earlier than in H. nycterodendron, its initiation beginning as the base of the embryo enlarges. This early initiation occurs a few cell layers beneath the surface of the enlarged region. The periderm quickly fills with tanniferous material, producing small inward protrusions (Figures 80, 81, 82) and cutting off the tissues, which die and crack (Figures 19, 80, 82).

As the shoot emerges from the opening at the base of the cotyledons, the 1st leaf protrudes from the opening on the side opposite the rest of the shoot. The developing leaves of H. cuatrecasana are more oblong and more reflexed than those of H. nycterodendron, but other seedling characters are the same.

Theobroma cacao

Dr. Margaret Hamilton collected fruits of Theobroma cacao L. in Hawaii, but the seeds did not germinate when planted in the University of Oklahoma greenhouse. Barton (1965) has shown that the seeds of Theobroma cacao rapidly lose their viability unless special procedures of preserving and storing the seeds are followed.

The fruits of Theobroma cacao and Herrania are similar. The tanniferous embryo of T. cacao (Figure 16 A) is 23 X 11 X 6 mm and covered by a mucilagenous outer seed coat. The cotyledons are greatly folded but can be physically separated, and the primary axis is large (Figure 16 B). Small hairs (Figure 18 G), similar to the multicellular hairs of Herrania, are present.

FIGURES

1A. Line drawing of seed (seed coats removed). B, side view of A.

(A, X4; B, X0.65)

2. Three to 7-day seedling. X4

3. Seven to 13-day seedling. X4

4. Thirteen to 19-day seedling. X4

Key to abbreviations:

c cotyledon

cb base of cotyledon

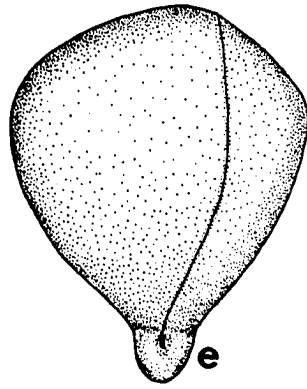
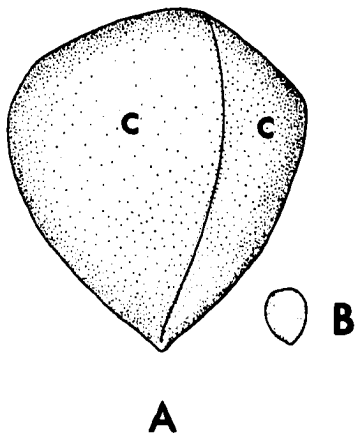
e enlarged base of embryo

es emerging shoot

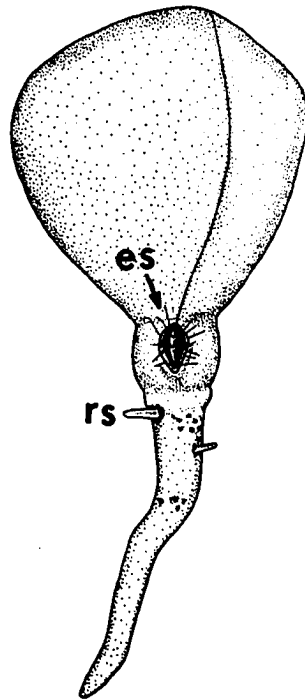
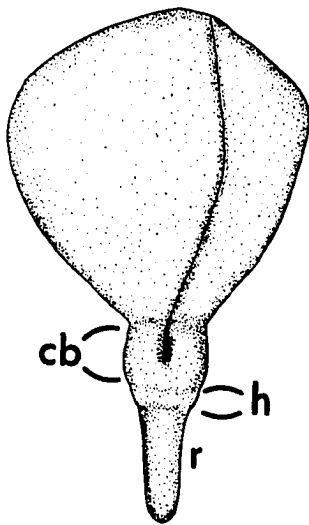
h hypocotyl

r primary root

rs secondary root



①

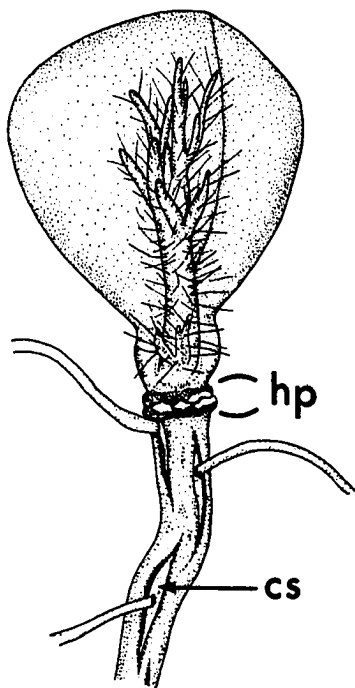


FIGURES

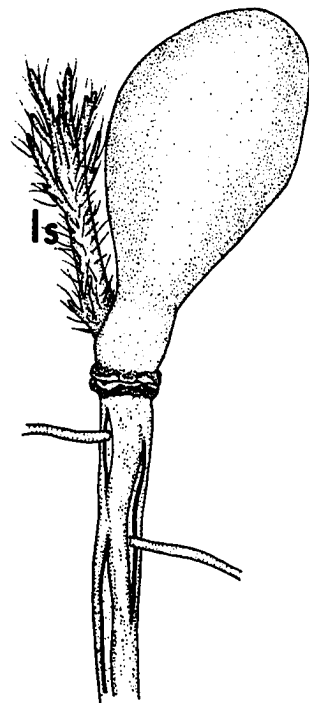
5. Nineteen to 30-day seedling. X4
6. Side view of figure 5. X4
7. One to 2-month seedling. X2
8. Seven to 9-month seedling. X0.125

Key to abbreviations:

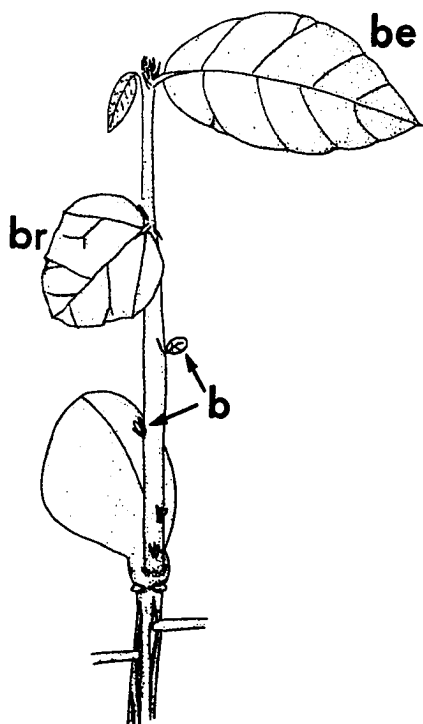
- b first leaves with blades
- bc first compound leaf
- be elongated blade
- bl lobed blade
- br rounded blade
- cs cracking and sloughing cortical tissue
- hp proliferated cells of hypocotyl
- ls leafy hirsute shoot
- w withered cotyledons



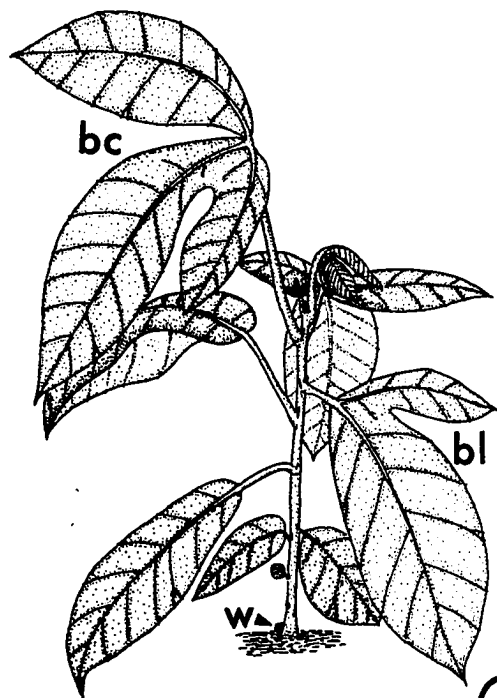
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6



7



8

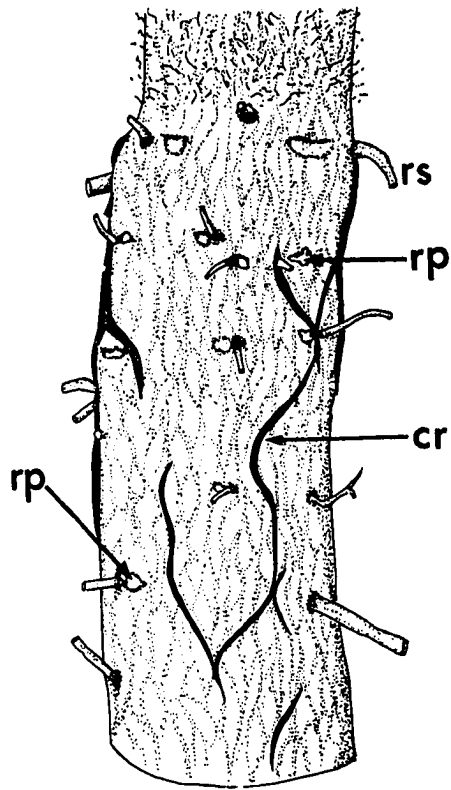
FIGURES

9. Root of 8-month seedling. X5.3.
10. Transition region of 10-day seedling. A-E, cotyledon and shoot.
F,G, hypocotyl. H-K, root.
11. Leaf gap.
12. Positions of first four leaves (1-4, successively younger).
13. Early leaves (A-E, successively younger). X7.5
- 14A. Mature plant (taken from drawing by Schultes, 1958). B, fruit.
(A, X0.002; B, X0.4)

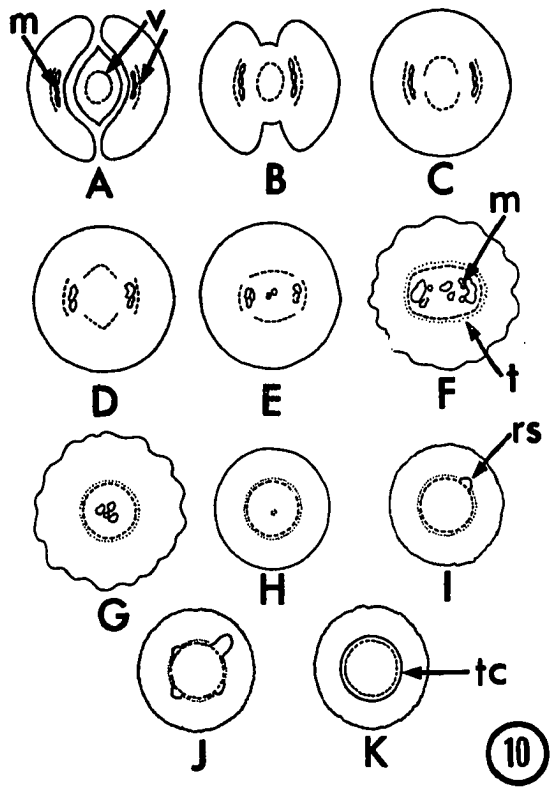
Key to abbreviations:

- a leaf axis
- al leaf axis with lamina
- c cotyledon
- cr remains of root cortex
- f fruit
- g direction of shoot growth
- m mucilage cavities
- rp root proliferated cells
- rs secondary root
- s stipule
- t ring of scattered tanniferous cells
- tc continuous ring of tanniferous cells

tf foliar trace
tb lateral bud trace
u union of axis to stipules
uo union of axis to one stipule
v vascular tissue



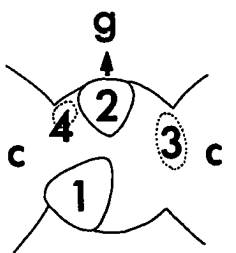
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10



11



12



A



B



C

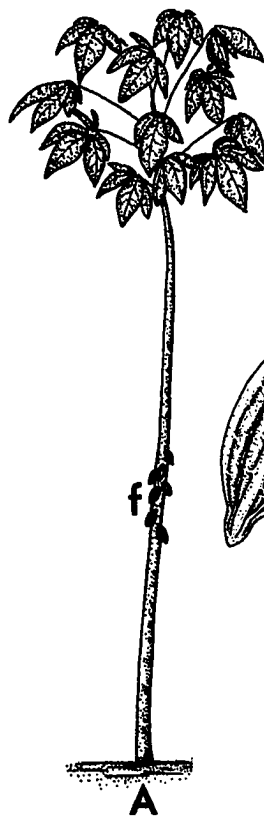


D



E

13



A

B

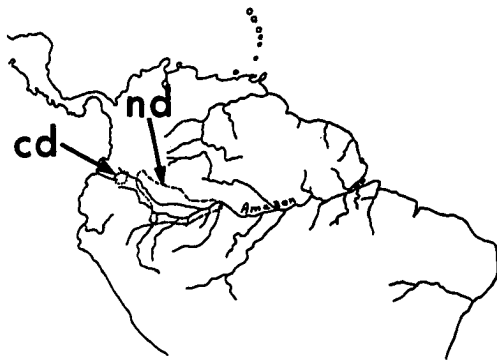
14

FIGURES

15. Map of South America, showing known distribution of H. nycterodendron and H. cuatrecasana (taken from map by Schultes, 1958).
- 16A. Seed of Theobroma cacao (seed coats removed). B, side view of A. (both, X2.2)
- 17A. Seed of H. cuatrecasana (seed coats removed). B, side view of A. (A, X3; B, X0.65)
- 18A,B. Multicellular hairs of embryo or early seedling. C-E, small multicellular hairs of stem and leaves. F, large multicellular hair of leaf. G, multicellular hair of Theobroma cacao. H, surface view of flattened unicellular hairs. I, longitudinal section of H. (A,B X135; C-E X255; F, X160; G, X135; H,I, X95)
19. Twenty day seedling, H. cuatrecasana. X7.3

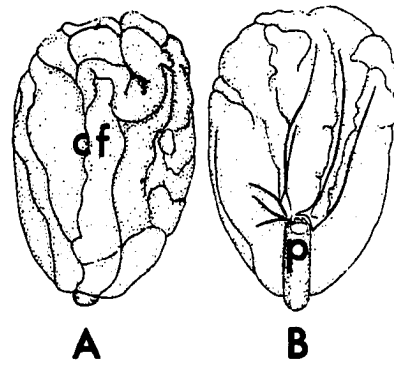
Key to abbreviations:

- c cotyledon
- cc cracked cotyledon base
- cd known distribution of H. cuatrecasana
- cf folded cotyledon
- hp proliferated cells of hypocotyl
- nd known distribution of H. nycterodendron
- p primary axis



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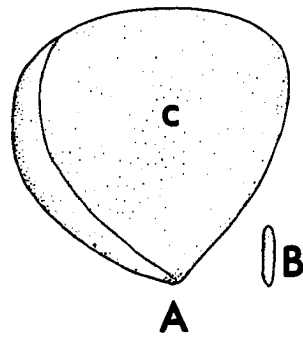
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A

B

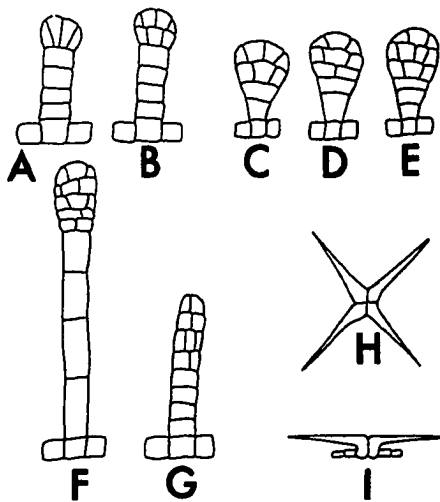
16



A

B

17



A

B

C

D

E

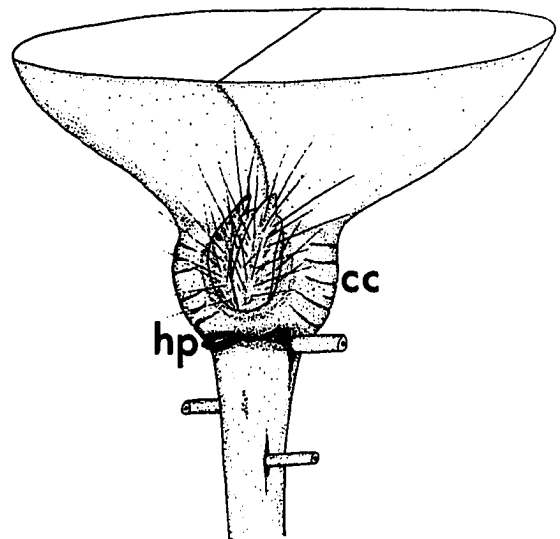
F

G

H

I

18



cc

hp

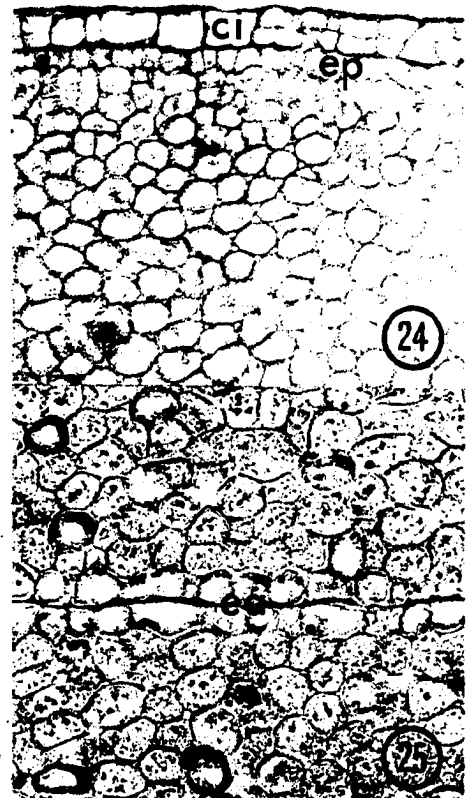
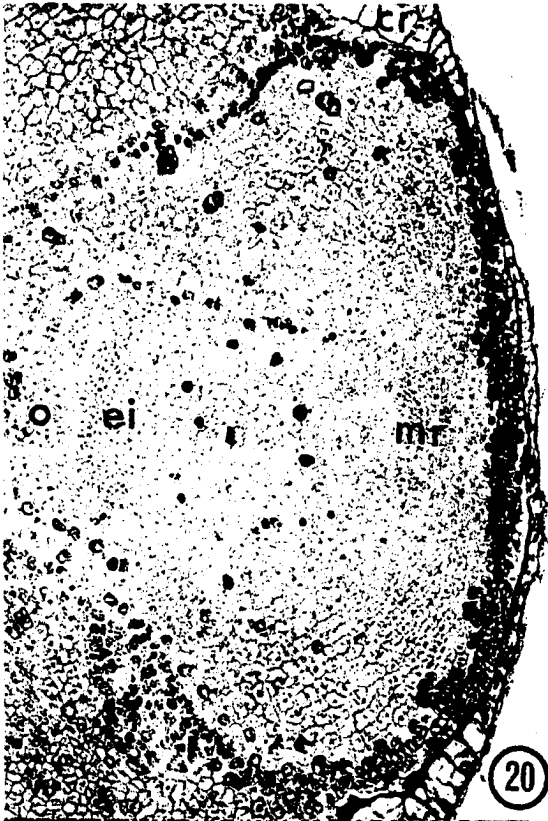
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FIGURES

- 20, 23. Longitudinal sections of embryonic axis. X120
21. Longitudinal section of inner seed coat over indentation at base of cotyledons. X160
22. Longitudinal section of group of inner seed coat cells at root end. X300
24. Transection of cotyledon and inner seed coat. X230
25. Longitudinal section of cotyledons. X260

Key to abbreviations:

- cb cotyledon base
- ci inner seed coat
- d depression at root end
- ea adaxial appressed epidermal layers
- ei epicotyl
- ep abaxial epidermis
- m mucilage cavity
- mr root meristem
- o overtopping leaves
- pt procambial tissue

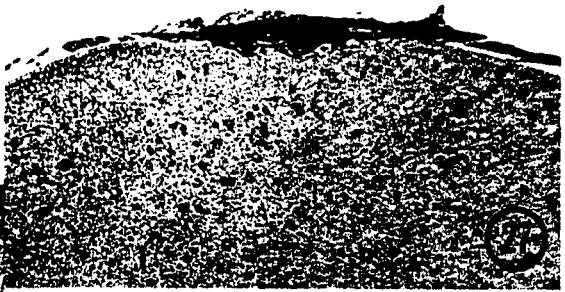


FIGURES

- 26, 29. Longitudinal section of embryonic axis. (26, X82; 29, X120)
27. Longitudinal section of depression at apex of cotyledons. X37
28. Magnification of figure 27. X140
30. Magnification of figure 28. X350

Key to abbreviations:

- ea adaxial appressed epidermal layers
- m mucilage cavity
- mr root meristem



FIGURES

- 31. Longitudinal section of small stomate mounds. X260
- 32. Longitudinal section of small stomate mound, multicellular hairs, and small unicellular hairs. X260
- 33. Longitudinal section of large stomate mound. X160
- 34, 35. Surface view of guard cells of small stomate mounds. X340
- 36. Longitudinal section of small stomate mounds. X340
- 37. Longitudinal section of rudimentary stomate mounds. X260
- 38. Longitudinal section of rudimentary multicellular hair. X260

Key to abbreviations:

sl large stomatal mound



31



32



33

33



34

34



35



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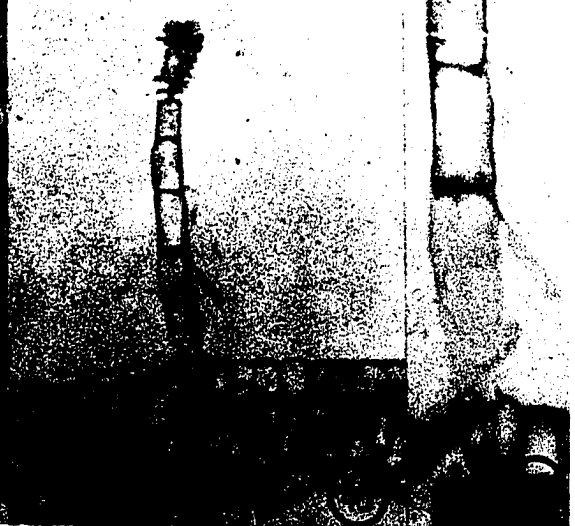
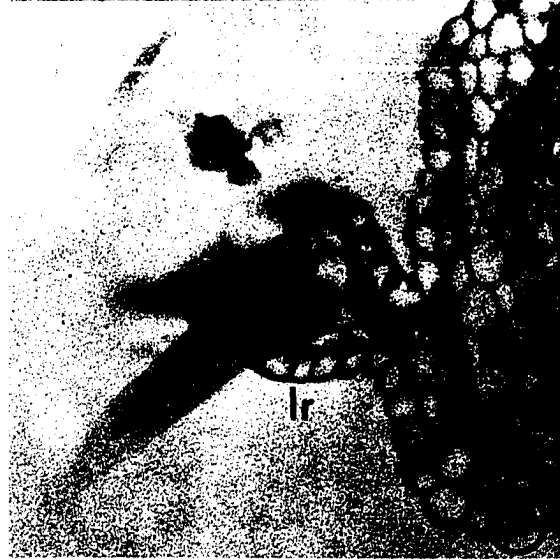
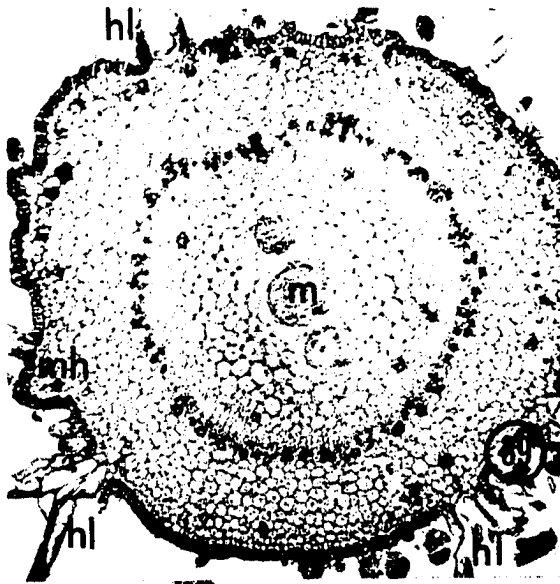
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FIGURES

39. Transection of stem of 20-day seedling, showing longitudinal sections of hairs. X95
40. Longitudinal section of small unicellular hairs of stem. X350
41. Longitudinal section of multicellular hairs in indentations at base of cotyledons. X340
42. Longitudinal section of large unicellular hair and multicellular hairs of stem. X160
43. Longitudinal section of thick-walled, large, unicellular hairs of leaf. X350
44. Transection of heads of multicellular hairs in indentations at base of cotyledons. X230
45. Longitudinal section of long multicellular hair on abaxial surface of leaf. X200
46. Magnification of figure 45. X380

Key to abbreviations:

- ba dark-staining cortical band
- hl large unicellular hair
- hm multicellular hair
- hx transection of head of multicellular hair
- lr longitudinal ridge
- m mucilage cavity
- mh mound of enlarged unicellular hair



FIGURES

47. Longitudinal section of 7-day seedling. X32
48. Longitudinal section of 13-day seedling. X32
49. Longitudinal section of 10-day seedling. X82
50. Longitudinal section of 7-day seedling, showing cotyledonary buds.
X120
51. Longitudinal section of epicotyl meristem of 10-day seedling. X340

Key to abbreviations:

bu	cotyledonary buds
c	cotyledon
e	enlarged base of embryo
ei	epicotyl
mr	root meristem
rp	primary root
sl	large stomatal mound
ss	small stomatal mounds



FIGURES

- 52. Longitudinal section of root meristem of 10-day seedling. X160
- 53. Magnification of figure 50. X310
- 54. Transection of root of 10-day seedling. X100
- 55. Longitudinal section of meristematic tissue in proximal portion of cotyledon of 13-day seedling. X160

Key to abbreviations:

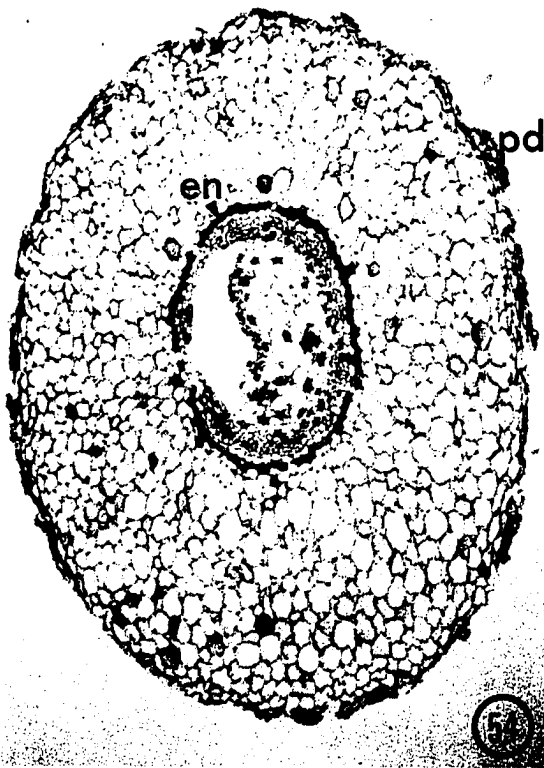
en	endodermis
mt	meristematic tissue
pd	periderm
rc	root cap
v	vascular tissue



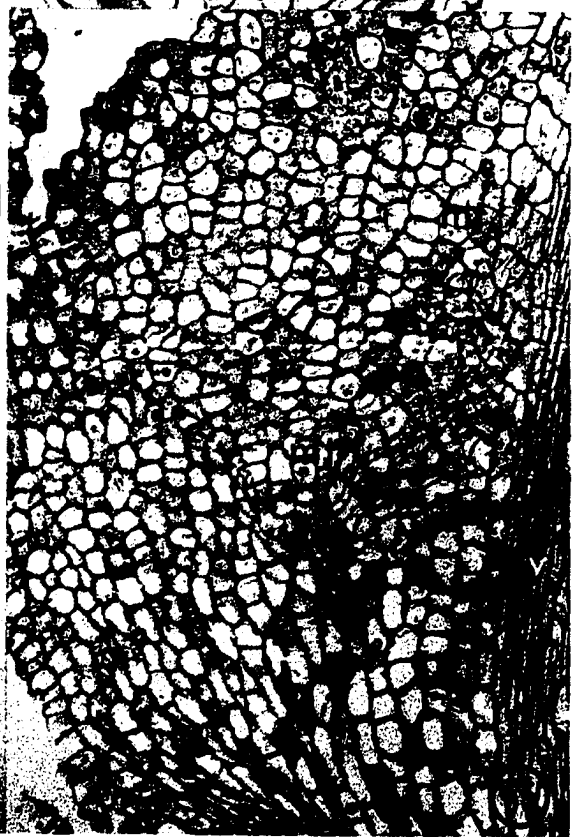
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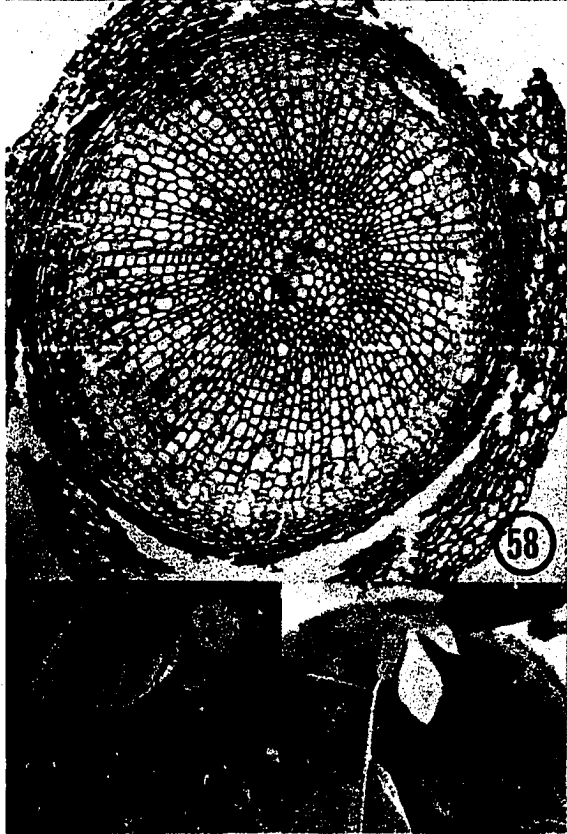


FIGURES

- 56. Longitudinal section of 1-month seedling. X33
- 57. Longitudinal section of 1 and $\frac{1}{2}$ -month seedling. X33
- 58. Transection of root of 2-month seedling. X95
- 59. Two month seedling. X0.5
- 60. Eight month seedling showing immature compound leaf. X0.125
- 61. Spinule of 8-month seedling. X42

Key to abbreviations:

- be elongated blade
- br rounded blade
- hp proliferated cells of hypocotyl
- sr sloughing cortical tissue

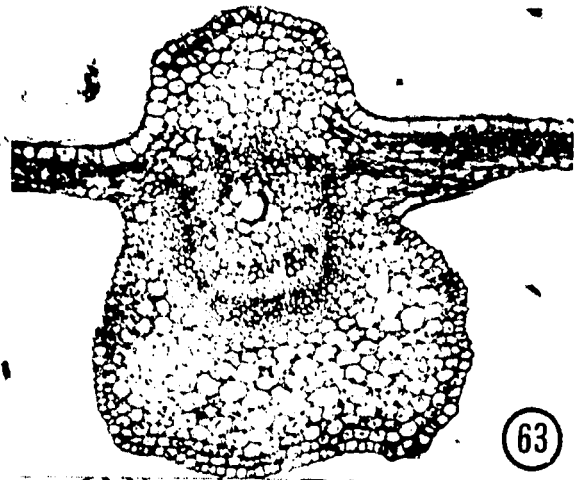
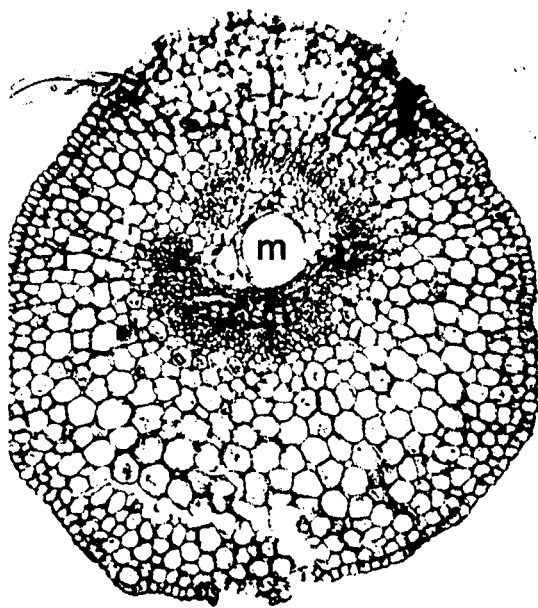


FIGURES

- 62. Transection of petiole of 2-month seedling. X160
- 63. Transection of midvein of 2-month seedling. X160
- 64. Abaxial surface view of leaf venation of 2-month seedling. X42
- 65. Transection of petiole of 8-month seedling, blade 8 X 4 cm. X110
- 66. Transection of midvein of 8-month seedling, blade 8 X 4 cm. X130
- 67. Transection of secondary vein of 8-month seedling, blade 8 X 4 cm.
X160
- 68. Abaxial surface view of leaf venation of 8-month seedling, blade 8
X 4 cm. X42

Key to abbreviations:

- ba dark-staining cortical band
- fh flattened hair
- hl large unicellular hair
- lr longitudinal ridge
- m mucilage cavity

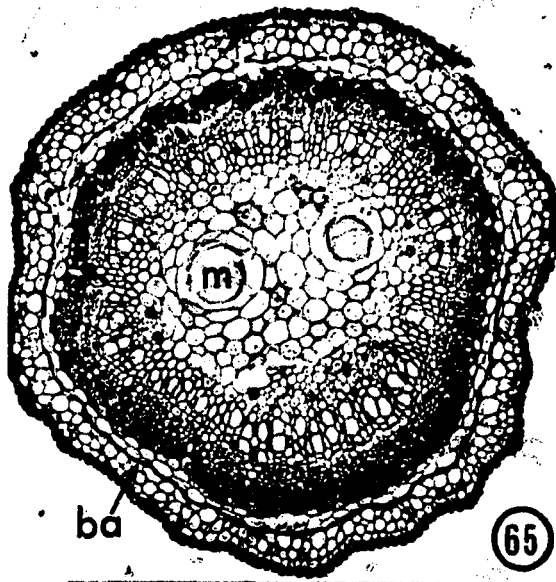


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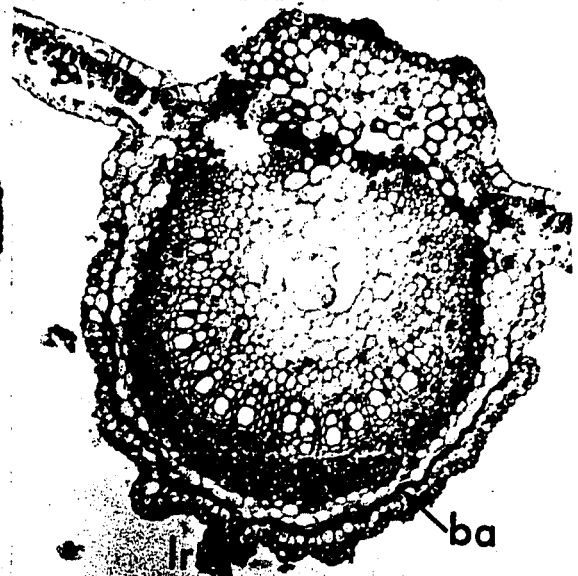
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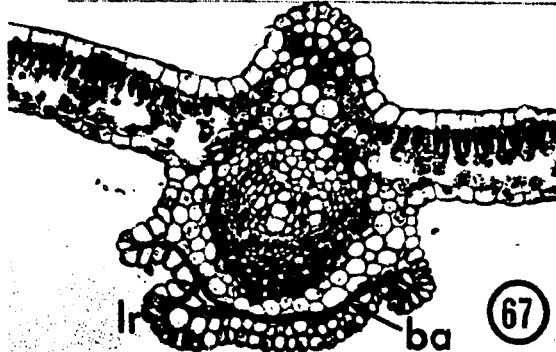
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66



67



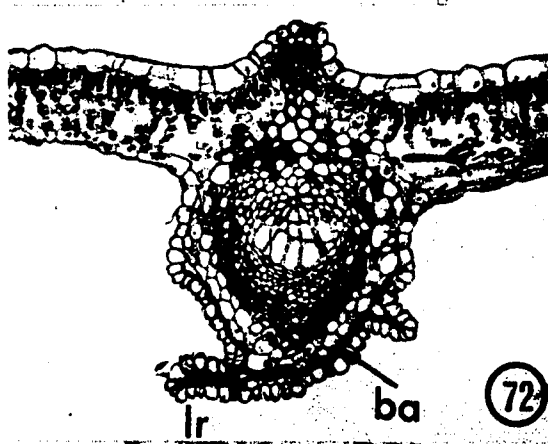
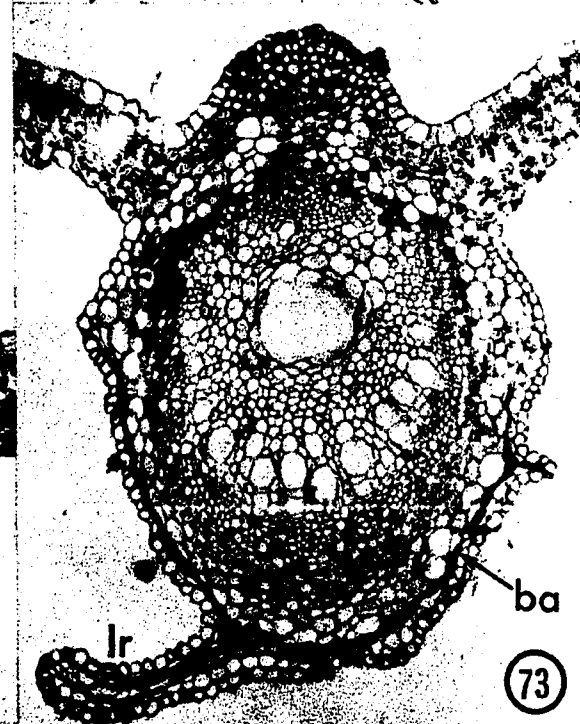
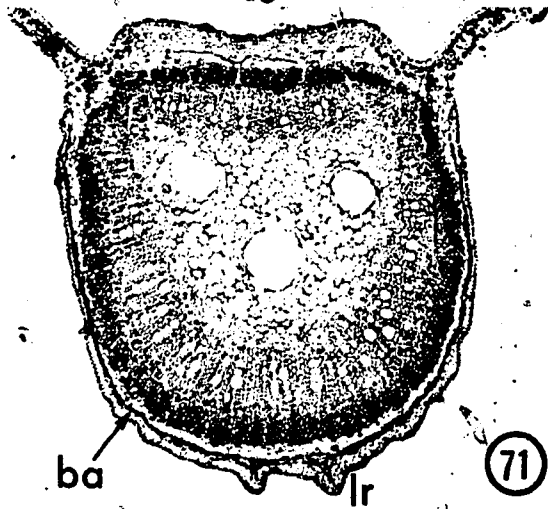
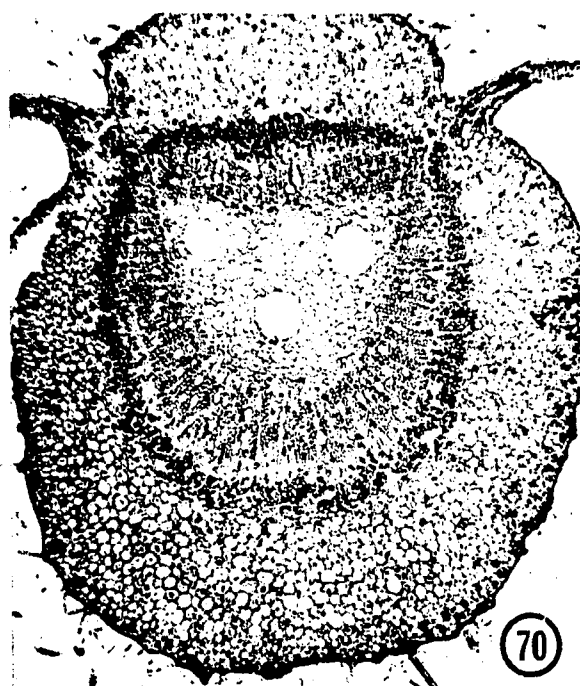
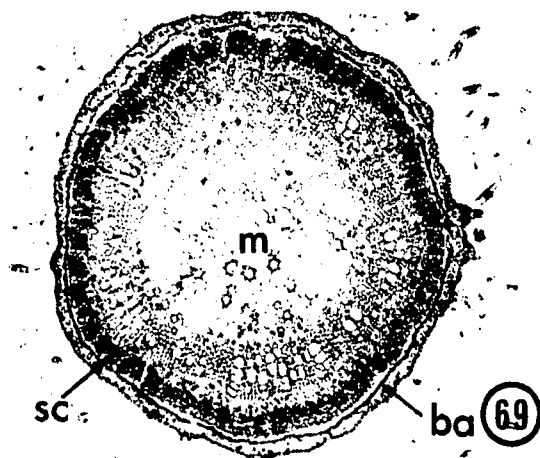
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FIGURES

69. Transection of petiole of 8-month seedling, blade $19\frac{1}{2}$ X 10 cm. X38
70. Transection of area where petiole joins blade of 8-month seedling, blade $19\frac{1}{2}$ X 10 cm. X33
71. Transection of midvein of 8-month seedling, blade $19\frac{1}{2}$ X 10 cm. X38
72. Transection of tertiary vein of 8-month seedling, blade $19\frac{1}{2}$ X 10 cm. X160
73. Transection of secondary vein of 8-month seedling, blade $19\frac{1}{2}$ X 10 cm. X130
74. Transection of minor vein of 8-month seedling, blade $19\frac{1}{2}$ X 10 cm. X380
75. Abaxial surface view of leaf venation of 8-month seedling, blade $19\frac{1}{2}$ X 10 cm. X42

Key to abbreviations:

- ae adaxial epidermis
- ba dark-staining cortical band
- lr longitudinal ridge
- m mucilage cavity
- sc sclerenchyma band

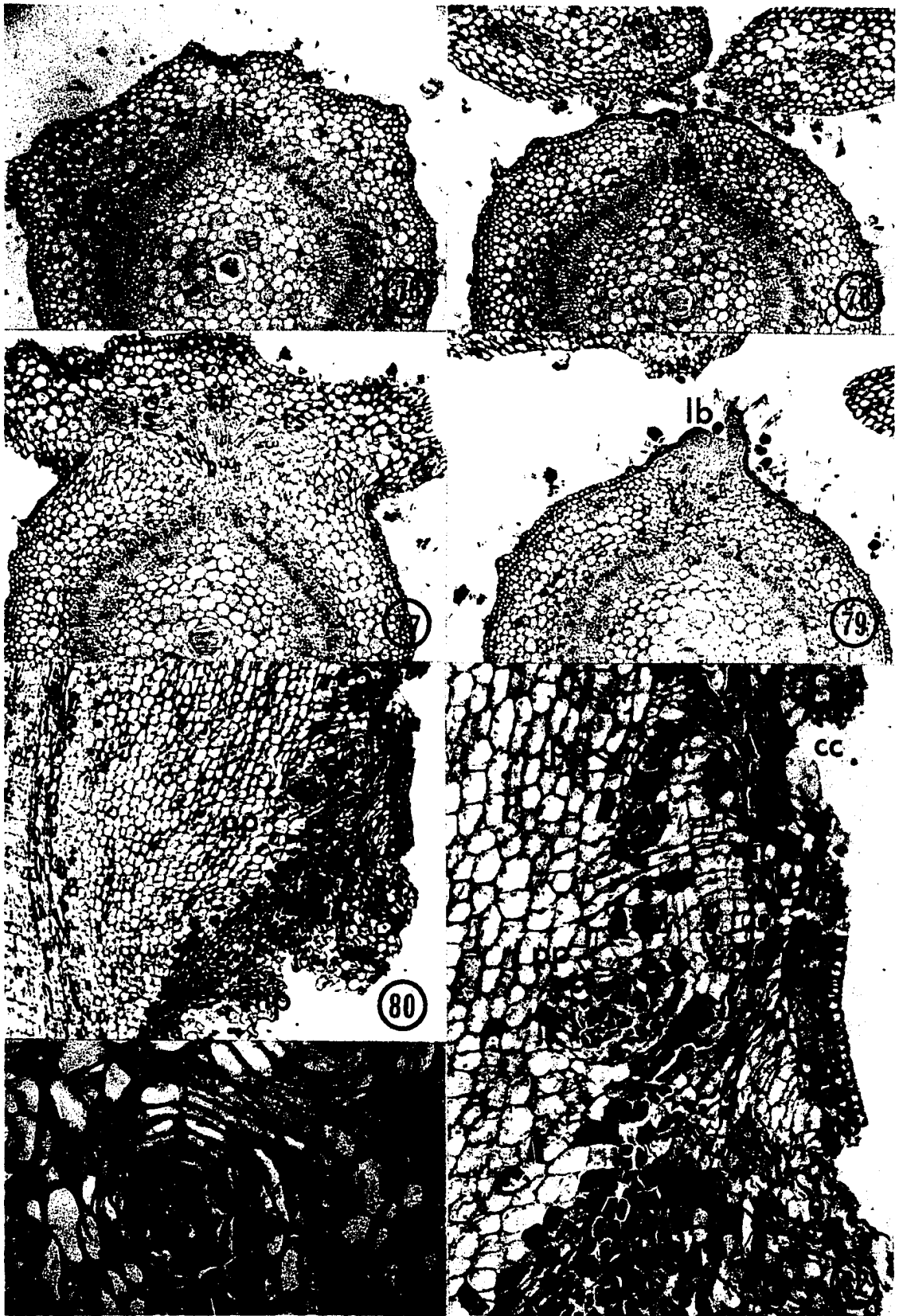


FIGURES

- 76-79. Serial transections through node of 2-month seedling. X92
80. Longitudinal section of lower enlarged region showing peridermal protrusions, H. cuatrecasana. X100
81. Transection of peridermal protrusions, H. cuatrecasana. X310
82. Longitudinal section of peridermal protrusions, H. cuatrecasana. X160

Key to abbreviations:

- a leaf axis
- cc cracked base of cotyledon
- hp hypocotyl proliferated cells
- lb lateral bud
- pd periderm
- pp inward peridermal protrusions
- s stipule
- tb lateral bud trace
- tf foliar trace
- tl leaf trace
- ts stipule trace



FIGURES

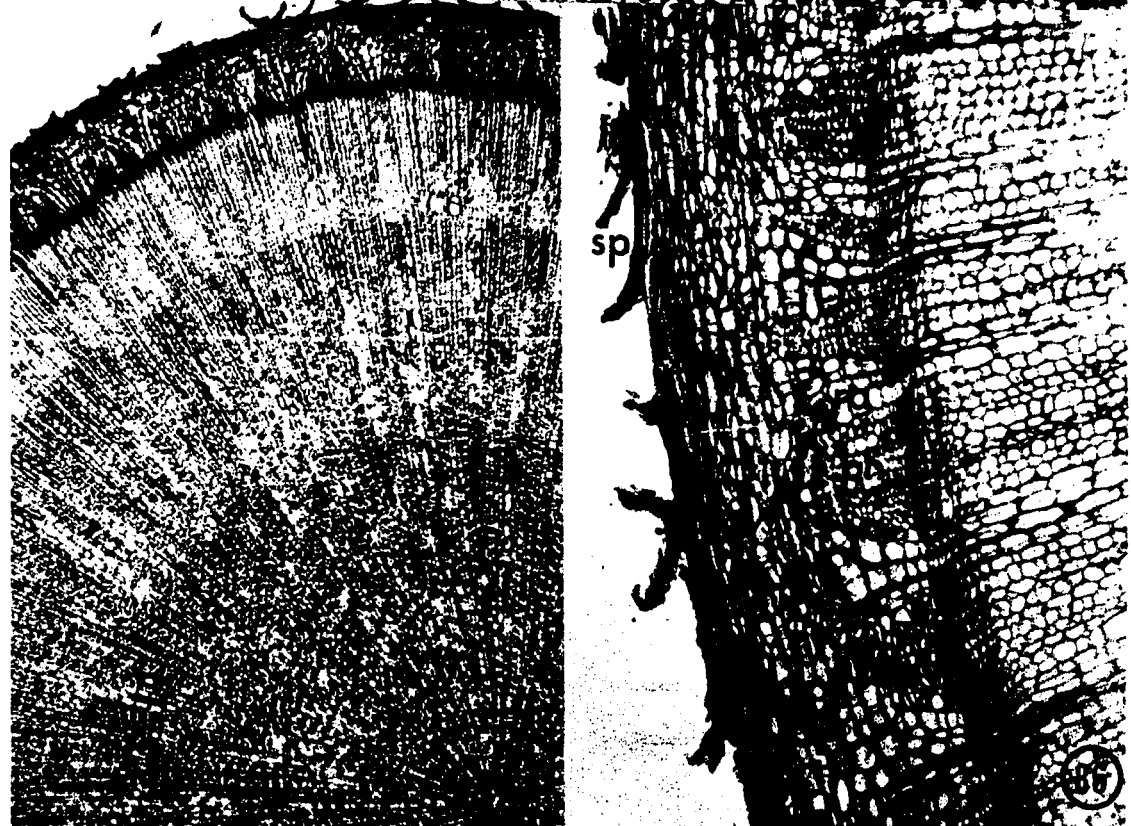
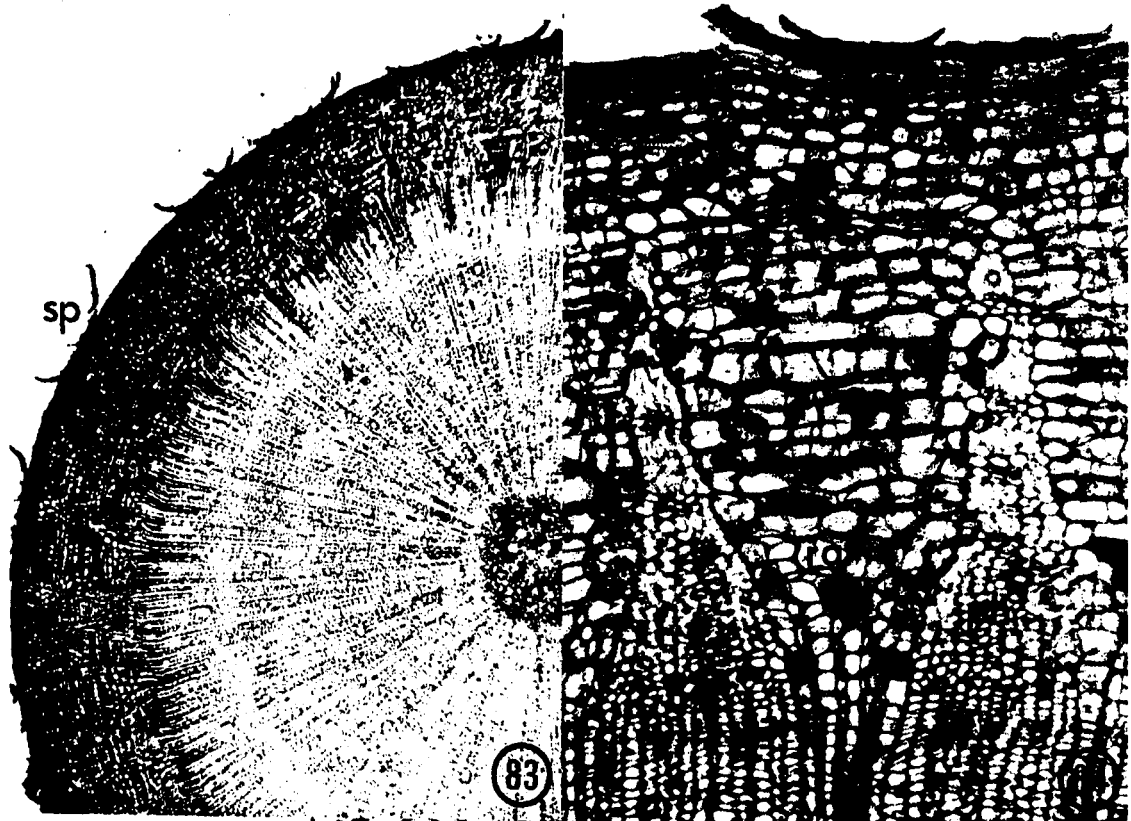
83. Transection of shoot of 8-month seedling. X33
84. Magnification of figure 83. X160
85. Transection of root of 8-month seedling. X31
86. Magnification of figure 85. X100

Key to abbreviations:

ph phloem

ra ray

sp sloughing periderm



CHAPTER V

SUMMARY AND DISCUSSION

The strongly ribbed fruit of Herrania nycterodendron is ellipsoid and contains approximately 100 seeds. The embryo is triangular-ovate and composed of two large, appressed cotyledons with a minute primary axis. Bases of the cotyledons and embryonic axis enlarge by intercalary growth, and the root meristem remains inactive until after this enlargement. Small and large stomatal mounds and lenticel-like proliferations of the periderm develop on the enlarged region; later, periderm proliferations develop on the root. The root elongates and the hirsute, leafy shoot emerges from the bases of the cotyledons. Since the cotyledons do not separate, the shoot emerges at an angle and grows beyond the cotyledons. Leaf development proceeds from leaves without laminae to simple, entire leaves, to simple, lobed leaves, and finally to compound leaves. Main veins have a dark-staining cortical band associated with longitudinal ridges and large unicellular hairs. A cylinder of vascular tissue surrounds a wide pith which contains mucilage cavities.

According to Schultes (1958), Herrania nycterodendron closely resembles H. cuatrecasana and is distinguished by its "... curious type of fruit. The fruit of Herrania nycterodendron has a dry, somewhat coarse and fibrous rind which is covered completely with a soft indument of velvety hairs; it lacks the stinging hairs which are usually present in this genus. The ribs of the fruit of Herrania nycterodendron are broad

and rounded, with deep furrows. The fruit is apically much more bluntly rounded, in most cases, than is that of related species." Schultes mentions that a mature tree of H. nycterodendron has ashy-yellow scrobiculate bark and ranges up to 25 feet tall, whereas H. cuatrecasana has whitish, maculate bark and ranges up to 9 feet tall. He also describes differences in flower structure, position, and number.

Several additional differences both in morphology and anatomy were noted between the two species. Herrania nycterodendron has a triangular-ovate seed approximately 10 X 8 X 6 mm, whereas H. cuatrecasana has a triangular, flattened seed approximately 12 X 12 X 4 mm. The unfused area at the base of the cotyledons is greater in H. cuatrecasana than in H. nycterodendron, resulting in the protrusion of the first leaf from the side opposite the rest of the shoot. The enlarged base of the embryo in H. cuatrecasana is slightly flattened, but that of H. nycterodendron is rounded. Periderm develops earlier in H. cuatrecasana and forms inward protrusions which do not occur in H. nycterodendron. Early formation of a periderm and enlargement of the base of the embryo in H. cuatrecasana results in a splitting of the outer tissue. The first leaves of H. cuatrecasana have more union of stipule and blade, and the laminated leaves are more oblong, with greater blade reflexion during development.

Morphology of the seeds of Herrania and Theobroma supports the separation of the two genera. The seed of Theobroma is large, with a well developed primary axis and greatly folded, free cotyledons, whereas H. nycterodendron has a small axis with large, nonfolded, and appressed cotyledons.

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