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# The Morphology of Hydrilla (*Hydrilla Verticillata* (L. f.) Royle)

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## ABSTRACT

Examination of the structures of hydrilla (*Hydrilla verticillata* (L.f.) Royle) using light and scanning electron microscopy provide a permanent detailed record of the important features of this plant and aid in the interpretation of its morphology. Heretofore undescribed structures that were found during this study include the presence of small dormant axillary buds that form at the base of larger dominant axillary buds, turions forming on apices of branches, asexual reproductive structures (lateral stem buds) that develop near the base of vertical stems, and the presence of abscission layers at the base of axillary turions and lateral stem buds.


*Key words:* turions, flowers, electron microscopy, abscission.

## INTRODUCTION

Hydrilla is a submersed aquatic macrophyte that belongs to the family Hydrocharitaceae. It is an economically important plant that grows in a variety of aquatic situations: in static water, in water flowing up to 1.8 ms, and in waters from a few centimeters to 15 m deep. Extensive growths can severely reduce waterflow by clogging the filters of irrigation pumps and trash racks, and interfere with boating, water skiing, swimming, fishing and navigation. Dense infestations of hydrilla can also significantly reduce the holding capacity of storage ponds.

Hydrilla is not native to the United States. Its presence was first reported on the west coast of Florida in 1958 (2). Since then, it has spread to several other states. In 1976, it was reported in Florida, Georgia, Alabama, Mississippi, Louisiana, Iowa, and Texas (6). By 1983, it had been found in North Carolina, South Carolina, Tennessee, California, Maryland, Virginia, and Washington D.C.

The presence of hydrilla can be easily overlooked because of its morphological similarity to several other aquatic plants such as egeria (*Egeria densa* Planch.), American elodea (*Elodea canadensis* Michx.) and Nuttall's elodea (*Elodea nuttallii* (Planch.) (St. John).

Ancibor (1) described the vegetative morphology of hydrilla and Mitra (10, 11, 12) both the vegetative and asexual reproductive structures. Cook and Luond (4) have given an account of the floral biology of hydrilla. The embryogeny of hydrilla seed has been reported by Lakshmanan (9). With the exception of Pendland (13) who studied the ultrastructure of hydrilla cells at high magnifications using an electron microscope, these authors relied heavily upon line drawings to convey their findings. In the present study, we present the morphology of hydrilla using light and scanning electron micrographs.

## MATERIALS AND METHODS

Cultured specimens harvested at the USDA Aquatic Weed Research Facility at Davis, California, were used fresh or preserved. Preserved specimens of axillary turions were obtained from USDA/ARS, Fort Lauderdale, Florida 33314.

*Light microscopy-paraffin sections.* Small pieces of tissue were fixed in a mixture of formalin-ethanol-acetic acid (16), dehydrated in ethanol and embedded in Paraplast.[2] Sections were stained with safranin-fast green.

*Light microscopy-plastic sections.* Horizontal stem and root tissue were fixed in glutaraldehyde, dehydrated in ethanol and embedded in JB-4 plastic[2] (3). Sections were stained with 0.25% toluidine blue.

*Light microscopy-free-hand sections.* Some tissues were free-hand sectioned with a razor blade and examined directly without further treatment. Other tissues were treated with an iron chloride-hydrochloric acid solution to detect tannin (8).

*Scanning electron microscopy.* Several tissues were fixed in glutaraldehyde, dehydrated in ethanol, and critical-point dried in carbon dioxide. They were then coated with a 50 nm layer of gold palladium in a sputter-coater and examined in a scanning electron microscope at 20 keV. Other tissues were examined directly in the fresh, wet state at 3 or 20 keV.

## OBSERVATIONS AND DISCUSSION
## PART I. MORPHOLOGY OF THE VEGETATIVE ORGANS

*Growth habit.* While hydrilla is not yet widely established in California, we examined its growth habit in numerous aquatic situations located throughout the state. In Lake Murray, near San Diego, some populations were found rooted in water 14.3 m deep. Hydrilla formed extensive canopies in water 0.7 to 2.4 m deep in Lake Ellis at Marysville, in the shallows of Lake Murray, and in outdoor cultures at Davis. Canopies developed when numerous stems grew and formed many branches (Figure 1). Long trailing stems of plants growing in canals near El Centro, California, were observed.

*Leaves.* Leaves, occurred in pairs, or whorls of 3 to 10 (Figure 2), were elongated, and varied in length (5 to 15 mm) and in width (2 to 4 mm). Each leaf had a single central vein (Figure 3). Chloroplasts were abundant in both epidermal layers. Tannin cells were scattered over the leaf surface. The leaf margins were serrate. Scanning electron and light micrographs showed that each serration

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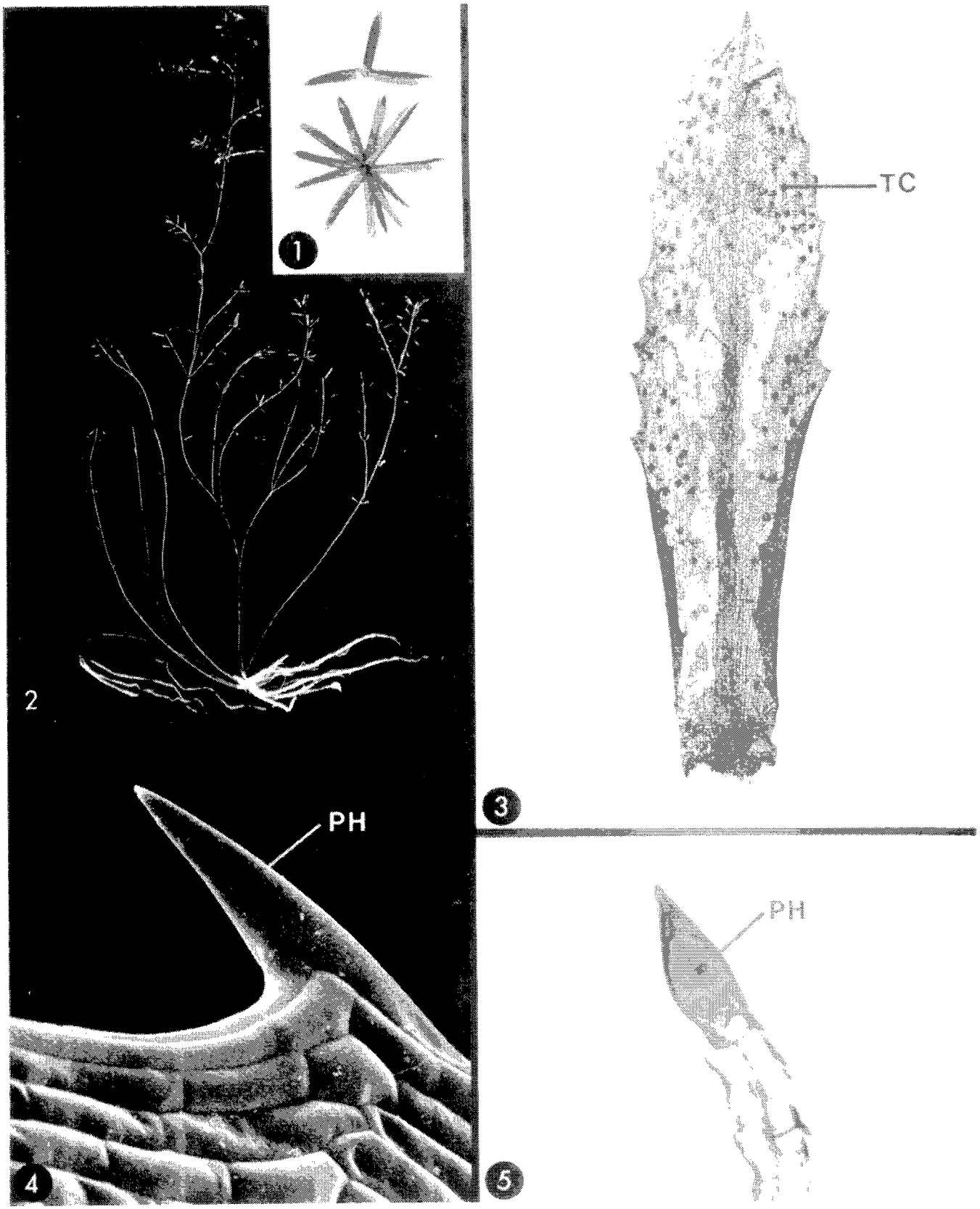


*Plate 1.* Figure 1. Growth habit of hydrilla, X 0.05. Figure 2. Whorls of 3 and 10 leaves, X 0.75. Figure 3. Upper surface of leaf with serrated margins and tannin cells, X 8. Figure 4. SEM micrograph of leaf serration with prickle-hair, X 100. Figure 5. Prickle-hair on apex of leaf vein, X 40.

terminated with a spine-like prickle-hair cell (1) (Figure 4) that had a thickened wall surrounding a large cavity (Figure 5). Several multicellular emergences were usually present on the abaxial surface of the central vein (Figure 6). The most prominent of these emergences were on mature leaves. The emergences also terminated with a prickle-hair (Figure 7).

The leaf lamina was comprised of two layers of cells, the upper and lower epidermis (Figure 8). The upper epidermal cells were approximately four times larger in cross-section than those of the lower layer (Figure 9). The vascular tissue was surrounded by several mesophyll cells. Examination of serial transverse sections of several leaves showed that the number of cells comprising a vascular bundle varied from 14 to 16 (Figure 10). Sieve tubes and companion cells were small and difficult to distinguish. Some cells were notably thick-walled.

*Stems.* The stems of hydrilla varied in length from a few centimeters to several meters and were either erect, horizontal or subterranean. Erect stems supported branches, leaves, flowers and asexual reproductive structures. They developed on a vertical axis and originated from nodal buds that occured along horizontal stems (Figure 11). Usually, several erect stems formed at a single node.

Horizontal stems originated from buds located near the bases of newly germinated asexual reproductive structures. These stems also formed on branch cuttings that were planted in hydrosoil.

Subterranean stems formed when hydrilla plants were subjected to periods of decreasing light and temperatures. Stems formed from buds at the base of erect stems grew downward into the soil (Figure 12). Their length varied from 1 to 15 cm and they terminated with an asexual reproductive structure, the subterranean turion.

The anatomy of the different stems was similar. Transverse sections through the internodal area of erect and horizontal stems showed large lacunae separated by single rows of cells (Figures 13 and 14). The epidermal cells were radially narrow and the external surface was without a conspicuous cuticle. One to two rows of collenchyma cells lay adjacent to the epidermis.

The central cylinder was surrounded by a single layer of cells, the endodermis (Figures 15 and 16). Casparian strips were clearly visible in the endodermis of some specimens (Figure 17). Sieve tubes and companion cells were distinguishable. Metaxylem was not observed near the endodermis as described by Ancibor (1). In fact, our specimens showed no tissue suggestive of xylem. At the center of the central cylinder was a large lacuna. Ancibor (1) regarded this lacuna as protoxylem; however, Haberlandt (5) referred to this structure as a central intercellular passage that evolved from an axil strand.

Longitudinal sections through a stem revealed that the cells in the nodal region surrounding the conductive tissue to the leaves were small and spherical (Figures 18 and 19). Cells immediately above were compressed—more than the cells immediately below the node. Transverse sections through the nodes showed conductive tissues radiating outward to the leaves (Figure 20). Diaphragm cells were between and above and below these conductive tissues. The walls of diaphragm cells were thick and stained dark (Figure 21). These cells aid in strengthening the nodal area. The central lacuna was constricted through the nodal area. Other lacunae in the aerenchyma tissue were more sparse in the nodal area than in the internodal area. Dark tannin cells were interspersed throughout the aerenchyma tissue.

The anatomy of the horizontal stem was similar to that of erect stem (Figures 22 and 23). Consequently, the term horizontal stem was used in lieu of rhizomes, stolons, or runners as suggested by Haller (6) and Mitra (10). The aerenchyma had 3 large rows of lacunae that surrounded the central cylinder. The smallest row of these lacunae lay next to the central cylinder.

*Roots.* Roots developed at the base of each erect stem, occasionally at a branch along an erect stem, or at nodes on floating plant fragments (Figure 24). They were normally white, but older roots turned green in ambient light. The diameter of the roots varied considerably, sometimes up to 2 mm on larger plants. A long tapering root cap protected the root meristem. Examination of longitudinal sections of roots showed that the epidermal cells were greatly elongated along the root axis (Figure 25). The outermost underlying cells of the cortex were compressed and increased in length towards the center. Transverse sections showed the cortex cells were large, thin-walled, and were dispersed with numerous small lacuna. The central cylinder was made up of only a few cells (Figure 26).

*Axillary scales.* Two axillary scales (squamulae intravaginales) developed at the base of each leaf (Figure 27). They were 0.25 to 0.5 mm long, and lay tightly compressed against the stem in an upright position. The upper margin had long tubular, thick-walled secretory cells filled with tannins (Figure 28). Ancibor (1) reports their function is to secrete a protective mucilaginous substance. We found that the ovate center of the scale consisted of several cells elongated along the main axis and one cell layer thick. The axillary scales formed early in the development of hydrilla plants. Histologically prepared specimens showed they also occurred at the base of young leaves in turions and stem apices.

## PART II. MORPHOLOGY OF THE REPRODUCTIVE ORGANS

The terminology of several of the reproductive structures is confusing and an attempt was made to clarify this terminology. Hydrilla forms both sexual and asexual structures. Examination of these structures indicated that both types of reproductive organs were dependent on undifferentiated tissues in stem meristems. Stem meristems occurred as small buds in the axils of leaves or branches, herein referred to as axillary buds, or as apical buds on terminal stem nodes. They both were borne on elongated or very short stems.

The descriptions of the asexual reproductive tissues that formed are based on their site of development. Such tissues included branch segments, lateral stem buds, and axillary and subterranean turions. The terminology for axillary and subterranean turions used in this paper follows that of Mitra (10, 11). Although branches are a vegetative organ, individual plants develop from their segments. Therefore, branch formation and subsequent development of the repro-

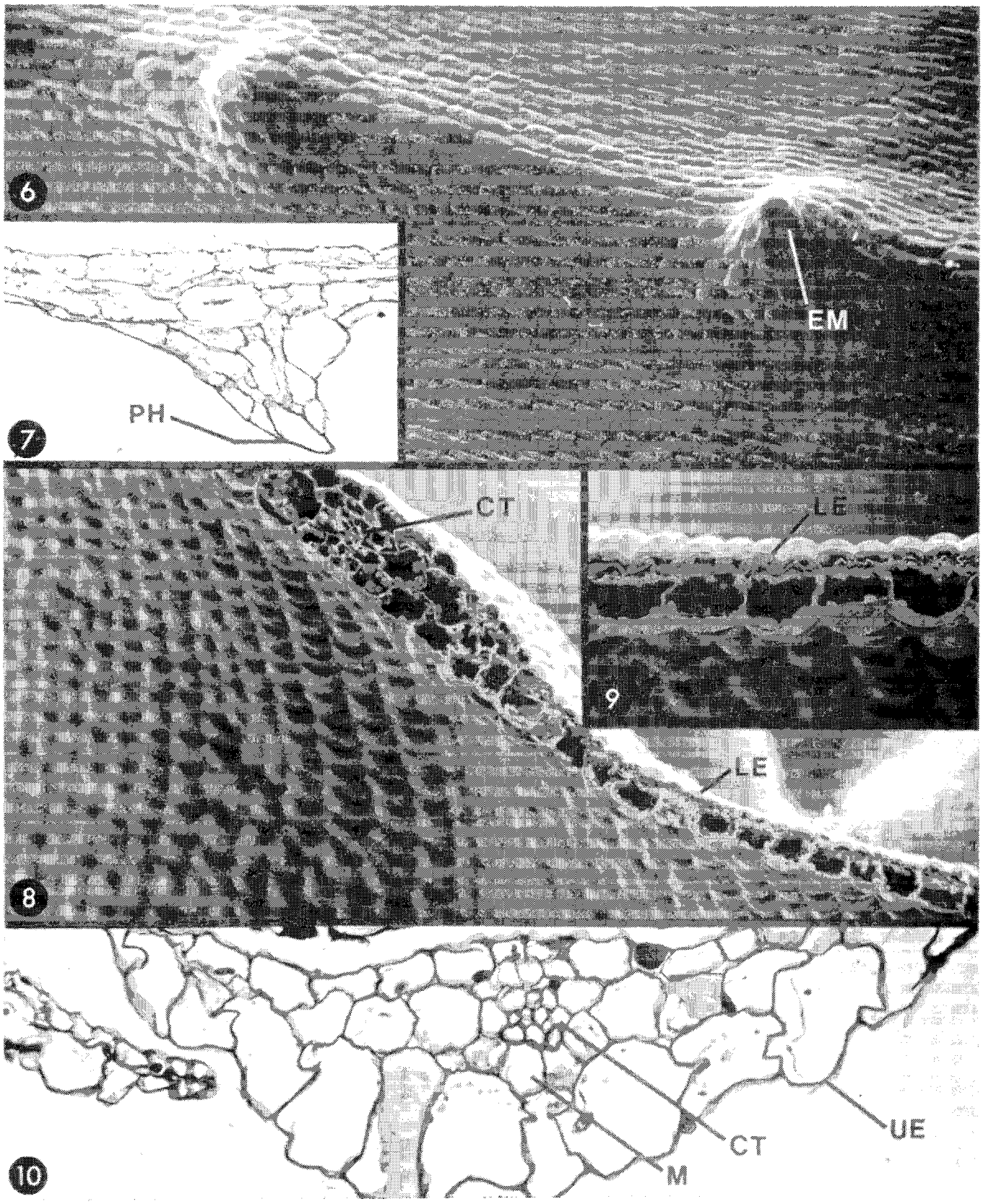


*Plate 2.* Figure 6. SEM micrograph of leaf vein on the lower surface showing mature multicellular leaf emergences, X 50. Figure 7. Histological preparation through a longitudinal section of a leaf emergence with prickle-hair, X 70 Figure 8. SEM micrograph of transverse section of leaf (inverted position), X 50. Figure 9. Enlarged area of same leaf showing large upper and small lower layers of epidermal cells, X 100. Figure 10. Light micrograph of transverse section showing conductive tissue and mesophyll, X 200.

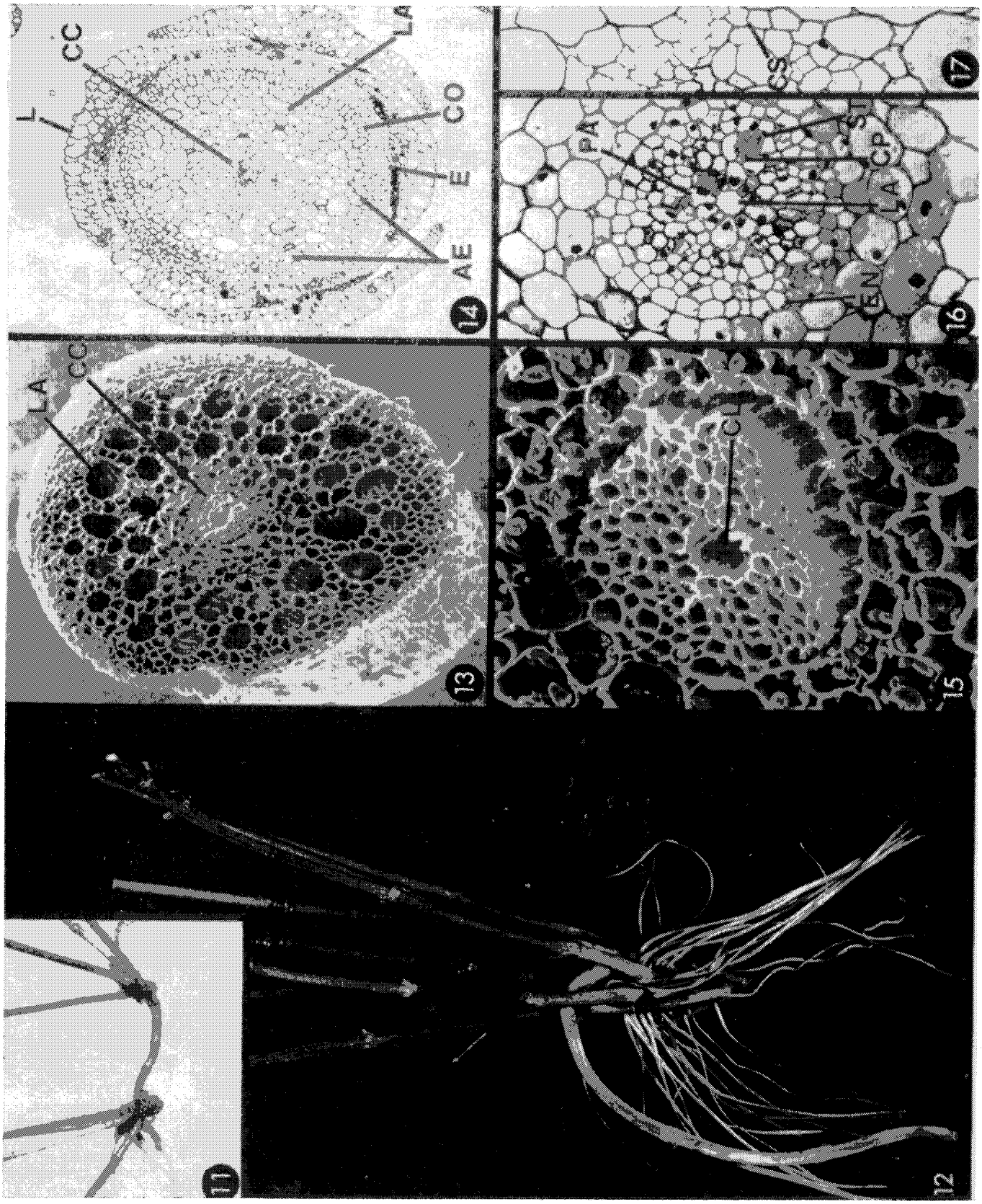


*Plate 3.* Figure 11. Horizontal stem with erect stems growing at two nodes, X 1. Figure 12. Erect stems emerging from base of mature plant, X 2. Figure 13. SEM micrograph of transverse section through stem internode, X 70. Figure 14. Histological section of area adjacent to a stem node, X 50. Figure 15. SEM micrograph showing central cylinder of stem internode (walls of endodermis are ruptured). Surrounding parenchyma cells are filled with plastids, X 300. Figure 16. Transverse section showing central cylinder in stem internode, X 190. Figure 17. Section of endodermis showing Casparian strips, X 200.

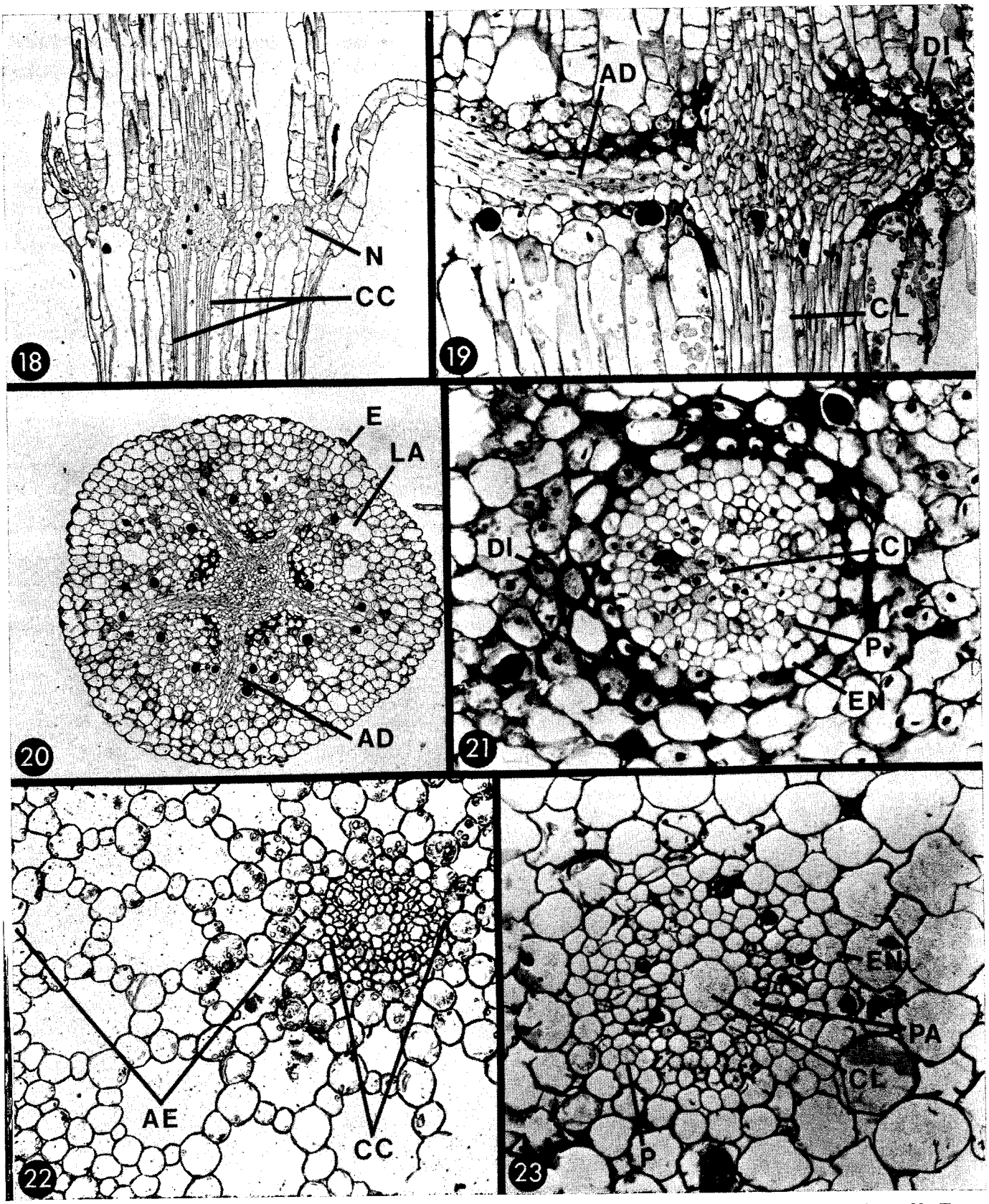


*Plate 4.* Figure 18. Longitudinal section through stem, X 100. Figure 19. Enlarged area through a stem node, X 200. Figure 20. Transverse section through a stem node showing conductive tissue radiating to leaves, X 75. Figure 21. Central cylinder through a nodal section of stem, X 250. Note dark-walled diaphragm cells. Figure 22. Transverse section through internodal area of an underground stem, X 160. Figure 23. Enlarged central cylinder in underground stem, X 300.

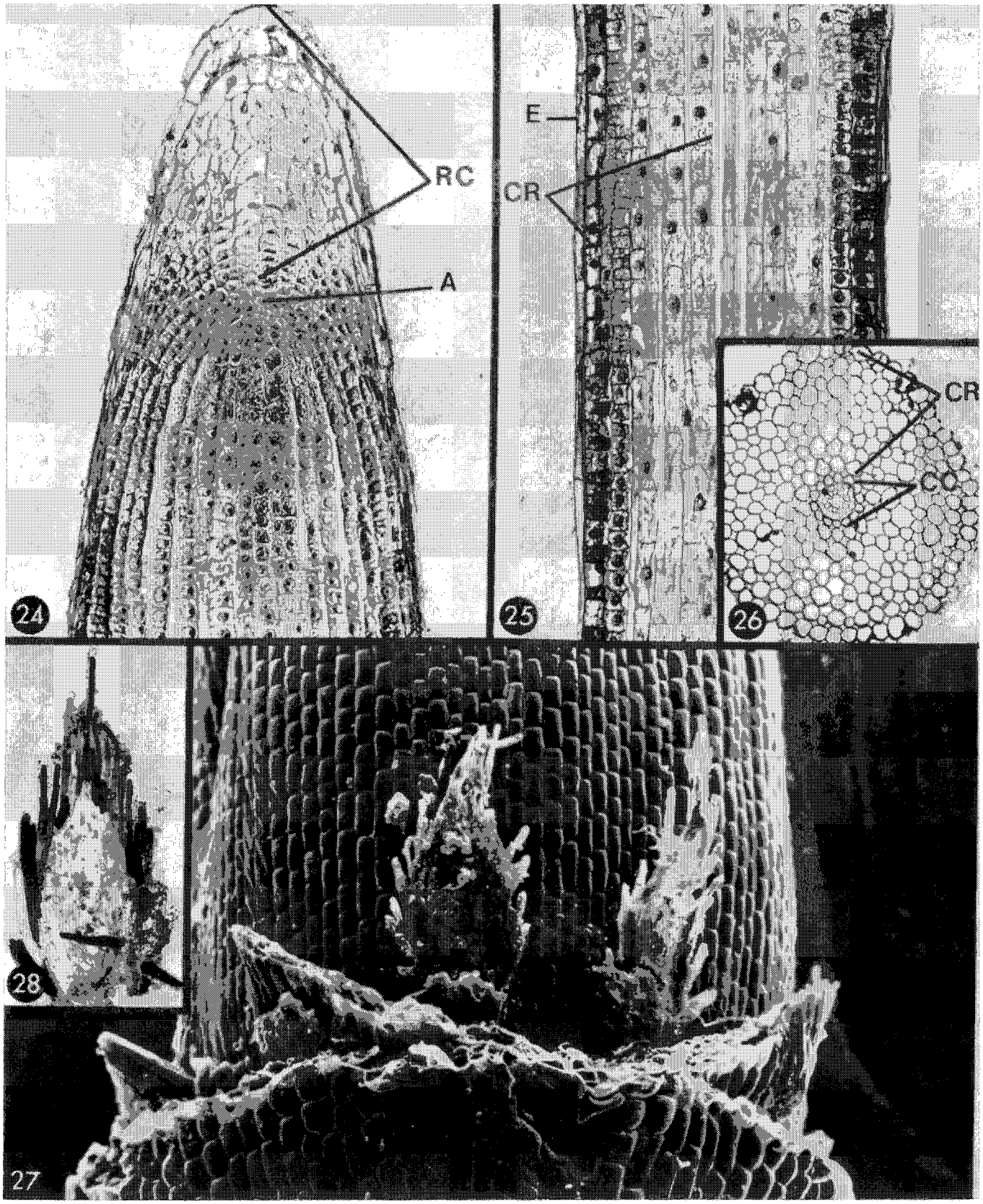


*Plate 5.* Figure 24. Longitudinal section of root apex with prominent root cap, X 130. Figure 25. Longitudinal section of root near apex, X 130. Figure 26. Transverse section through mature root, X 150. Figure 27. SEM micrograph of two axillary scales at base of leaf (leaf removed), X 100. Figure 28. Light photomicrograph of an axillary scale with tannin-filled marginal cells, X 150.

ductive parts derived from them are included in this section. The axillary buds had several thick outer leaf-like bud scales and membranous inner tissues that protected the meristems (Figure 29). Their lengths varied from 0.5 to 3.0 mm, depending on the stage of the growth. A dome-shaped apical meristem with swollen leaf primordia was exposed when the bud scales and fine inner tissues were removed (Figure 30). Axillary buds usually occurred in pairs, both located within the same group of bud scales (Figure 31). The larger bud was dominant. The smaller bud often formed an identical structure after the larger bud had grown or not developed normally (Figure 32).

*Inflorescences.* Pieterse, in his review on hydrilla (14), reported that hydrilla had been described as being both monecious and dioecious. Plants with female flowers have been found in the previously mentioned stages of the United States. Male flowers have also been found growing in Washington D.C. and in North Carolina.[3] In May 1983, seed were found by the senior author on cultured specimens grown at Davis, California. Cook and Luond (4), Mitra (10), and Reed (15) each described some aspects of flowering and Blackburn et al, (2) and Haller (7) mentioned the period for female flowers of hydrilla in Florida. In California, the flowering period occurs primarily during late September through October.

In June 1983, hydrilla plants that were growing in Washington, D.C. and nearby in Virginia and Maryland were sent to Davis, California, for culturing in small outdoor tanks. Both male and female flowers formed on these plants in September 1983 (Figure 33). Flowering ceased the first week in November. The young male flowers were sessile and solitary or in pairs in the axils of leaves, usually above the female flowers (Figure 34). These flowers were obovate and approximately 1.24 mm in diameter by 3 mm long. Leaf scales on the parent axillary but were fused together, forming a protective bract-like covering over the flower. Several protuberances were located on the top of the covering. One large protuberance in the center was cylindrical and truncate. The other protuberances were acute, terminating with a prickle hair. The male flower had 3 broad sepals (1 mm wide by 1.5 mm long) 3 narrow petals (0.6 mm wide by 1.25 mm long), and 3 4-locule stamens on short filaments (1.5 mm long). A short pedicel positioned on an abbreviated stem supported the perianth (Figure 35). These stems were approximately 0.5 mm long, but elongated to 1.0 mm shortly before the male flowers abscissed at the stem. The pedicels also elongated from 0.5 mm to about 1.0 to 2.0 mm at the same time. We found that the base of the pedicel separated from the stem inside the perianth covering. Gas bubbles from photosynthetic activity accumulated inside the covering and the resulting pressure caused the covering to split, releasing the flower. When stem apices with male flowers were placed in dishes in subdued sunlight, they usually did not separate from the stems (Figure 36). The freed flowers floated on the water surface where they opened, resulting in widely recurved sepals and petals (Figure 37). The open male flowers were approximately 4.0 to 4.5 mm long. As the perianth opened, the anthers which were tightly compressed against the sepals, sprang upward causing them to dehisce laterally and throw pollen grains into the air. The pollen was round, had bacula on the exine layer, and a slit-shaped furrow (Figure 38).

Female flowers developed from axillary buds formed near the apices of branches or the main stem of intact plants, or along the stems of floating fragments. The flower bud was cylindrical and tapered at the apex (Figure 39). The young inflorescence consisted of a perianth enclosed by a pair of fused membranous bracts (spathe) and a pistil with 3 stigmas, a short hypanthium, and an ovary (Figure 40). When the flower bud grew, the hypanthium elongated carrying the perianth, up to 10 cm, to the water surface. A gas bubble formed around the perianth (Figure 41). It protected the stigmas from the surrounding water. When the perianth reached the water surface, the sepals and petals spread. The water surface tension between the perianth parts held back the water to form a cavity (Figure 42). A second flower bud developed adjacent to the base of the mature flower. Occasionally, this bud developed a second flower (see section on axillary turions). The late development of these buds extended the span of the flowering period over a longer time. As many as 6 flowers were observed to form on a single branch. Female flowers were frequently observed to form above the male flowers late in the flowering period.

The perianths we examined consisted of 3 petals (0.5 mm wide by 2.5 mm long) and 3 sepals (1 mm wide by 3 mm long) (Figure 43). These were fused below to form a hypanthium. Both sepals and petals were membranous and white or light green with red streaks. The styles were enclosed in the hypanthium and they lengthened as the hypanthium elongated. The stigmas (Figure 44) were 1.0 to 1.5 mm long and made up of bundles of clear elongated cells aligned end-to-end. The terminal cells projected outward (thumblike) (Figure 45). The immature ovary was approximately one-fourth diameter larger than the hypanthium diameter. The young ovules were acorn-like (Figure 46). The cavity of the ovary was filled with a viscous fluid.

Pollination took place when the airborne pollen grains dropped into the cavity formed by the perianth. Also, many of the male flowers were observed sailing upright over the water surface on the tips of recurved sepals and petals. They bumped against the female flowers and some pollen grains spilled into the flower cavity and contacted the stigmas. Cook and Luond (4) noted that when the water level rose after the flowers had opened, the vulnerable stigmas were protected by an air bubble forming from the pliable sepals and petals. The perianth opened again when the water level receded.

The ovaries we examined had two variations in shape. The flowers that formed near the shoot apices late in the season had short hypanthiums, because of the shorter distance to grow to the water surface (Figure 47). The surface contour of these ovaries was irregular, due to the swollen ovules within. Female flowers that formed further down the stems early in the flowering period had long hypanthiums and uniformly swollen ovaries (Figure 48). The number of mature ovules were fewer in the ovaries that

[3]Kenneth Langland. Personal communication. September 13, 1983.

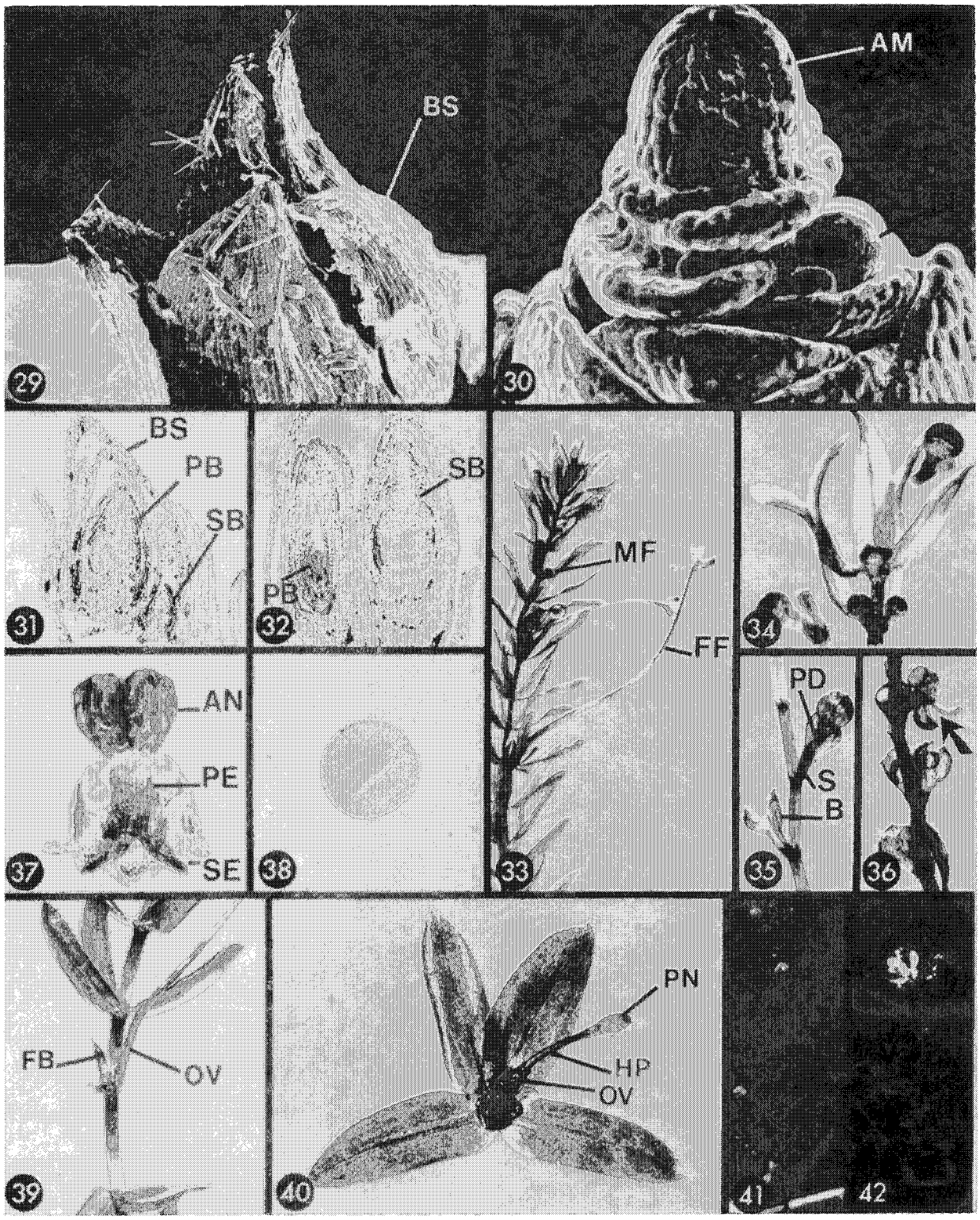


*Plate 6.* Figure 29. SEM micrograph of a fresh axillary bud, X 100. Numerous diatoms are present on the outer surface of the bud scales. Figure 30. Axillary bud with well developed branch bud (branch scales removed, cells on apical meristem are slightly damaged), X 200. Figure 31. Longitudinal section showing primary (non-dormant) and (dormant) secondary meristems in an axillary bud, X 140. Figure 32. Longitudinal section of an axillary bud showing development of secondary bud (right) after growth activity in the primary bud (left) has ceased, X 120. Figure 33. Male and female flowers on same stem, X 1. Figure 34. Male flowers situated near apex of stem, X 4.6. Figure 35. Unopened male flower (upper) on elongated pedicel and stem, X 4. Empty bracts remaining after the flower has abscissed (lower). Figure 36. Attached open male flower (arrow) and empty bracts with prominent prickle hairs, X 4. Figure 37. Mature open male flower with reflexed sepals and petals and pollen-filled anthers, X 11. Figure 38. Pollen grain with slit-like furrow, X 120. Figure 39. Female flower bud beginning to elongate (leaves removed) X 1.5. Figure 40. Perianth and hypanthium emerge from flower bud, X 4. Figure 41. Gas bubble formed around the perianth during the elongation of the hypanthium X 3. Figure 42. Vase-like receptacle formed by the perianth floating at the water surface, X 3.

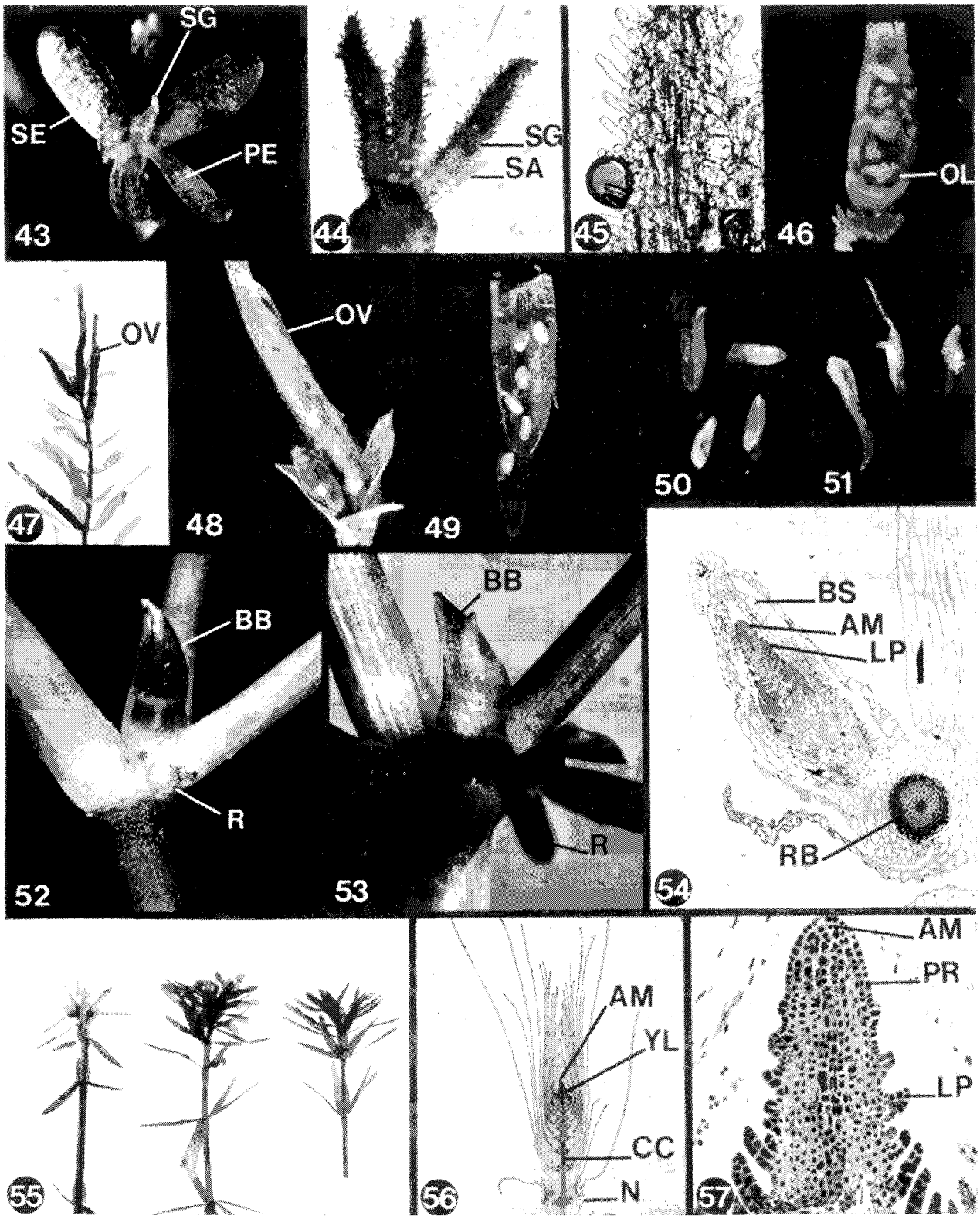


*Plate 7.* Figure 43. View of female flower showing stigmas, sepals, and narrow petals, X 5. Figure 44. Enlarged stigmas and staminodes (stained with toluidine blue 0 to enhance color), X 24. Figure 45. Outgrowths of terminal cells on the surface of stigma, X 160. Figure 46. Immature ovules in young ovary, X 8. Figure 47. Enlarged ovaries from flowers developed late in the flowering period, X 1.8. Figure 48. Ovary formed early in the flowering period, X 6. Figure 49. Longitudinally cut ovary with ovules showing parietal placentation, X 6. Figure 50. Seed-like ovules that were found to lack embryos X 9. Figure 51. Excised ovules that were growing in ovaries, X 9. Figure 52. Branch bud in axil of branch (surrounding leaves removed, X 15. Figure 53. Branch bud with elongating root, X 30. Figure 54. Longitudinal section of axillary bud showing apical meristem and leaf primordia protected by surrounding bud scales, X 60. Figure 55. Stem apices with varying arrangement of clustered leaves, X 0.8. Figure 56. Longitudinal section through dormant stem apex, X 10. Figure 57. Enlarged view of stem apex, X 80.

developed early than in those that formed late. These ovaries abscissed from the stems and floated at the surface, whereas the ovaries with mature ovules remained on the stems. Both variations of the ovaries were 8 to 11 mm long by 1.0 to 1.7 mm in diameter. The ovaries each had 1 to 7 swollen ovules that were attached to the ovary wall by a funiculus (Figure 49). Some of the swollen ovules were seedlike. They were about 0.5 mm wide and 1 to 2 mm long, compressed laterally, and the surface finely striated (Figure 50).

Numerous seedlike ovules were examined to determine if fertilization had taken place. Histological sectioning revealed that it had not. However, we observed several swollen ovules to grow inside the ovaries (Figure 51). These structures were mostly in ovaries that formed near the apices late in the flowering period. Although these structures had the appearance of young seedlings, meristem tissue was lacking.

*Branches.* Initially, a single bud formed in the axil of a leaf. As the bud matured, its base became broad and the apex beak-like (Figure 52). This bud developed into a branch. Occasionally, a smaller bud formed along the leaf line at the node. This bud formed a root (Figure 53). When the branch and root were severed from the parent plant, they formed a separate plant.

Examination of a longitudinal section through a branch bud showed several overlapping bud scales surrounding an apical meristem and a root bud at the base (Figure 54). The apical meristem had numerous primordial leaves developed along the cone-like structure. The root bud had 4 outer rows of darkly stained cells and 10 uniformly concentric rows of cells with large nuclei.

*Stem apices.* The apex of each stem had an apical meristem that remained dormant during the winter months (Figure 55). Late in the fall, elongation of internodes ceased causing the nodes near the apex to compact and form a dense cluster of leaves. The overlapped leaves at the terminal 9 to 12 nodes elongated, but remained folded over the apical meristem (Figure 56). The apical meristem was approximately 1 mm long, cylindrical and terminated with a dome (Figure 57). The external layer of cells (protoderm) covered the inner mass of cells (ground meristem). Leaf primordia were in various stages of development along the meristem. Many of the apices became separated from the parent plant, overwintered, and grew the next spring.

*Non-terminal segments.* Non-terminal segments of stems were found floating in the water throughout the growing season (Figure 58). Most segments were found in late fall when natural fragmentation of the stems took place. The segments separated next to the node (Figure 59) where the cells were compact (also see Figure 18) and apparently the weakest. Many stem segments floated until roots developed and then became attached to the soil. These segments, lacking an apical meristem, still continued to grow by forming new branches from axillary buds occurring along the stems. These viable segments developed into complete plants. The authors also observed that some stem segments lost their leaves late in the fall, and sank to the bottom, overwintered, and developed into plants the next spring.

*Lateral stem buds.* Late in the fall when water temperatures cooled and days became shorter, another asexual structure formed, the lateral stem bud. They formed at nodes on erect stems near the soil surface (Figures 60 and 61). They were 1 to 5 cm long, including a support stem that was 1 to 20 mm long. The leaves were tightly clustered, dark green, and had aristate tips. No leaf scales were observed on the structures. The leaves closest to the apical meristem overlapped, protecting it from adverse conditions. The base of the stem of a mature lateral stem bud had several rows of compressed cells, the zone of abscission (Figures 62 and 63). The zone of abscission on the main stem had only one layer of compressed cells. The structures separated in early winter and sank to the bottom where they overwintered.

*Turions.* Turions are asexual propagules that provide a method by which hydrilla can perpetuate itself from year to year. We found that their size varied from 3 to 15 mm and they were green or white depending on their site of formation. The turions formed either on erect stems growing in the water column, on floating stem fragments or on the end of stems in the hydrosoil. The external anatomy varied slightly on turions formed above and below the soil; however, the internal structure of these turions was similar. The differences in their appearance have led them to be called different names, "axillary turions" for those formed above soil and "tubers" for the structures formed in the soil. They will, herein, be referred to as axillary turions and subterranean turions, respectively. Their similarities and dissimilarities are noted in the following descriptions.

*Axillary turions.* The mature axillary turion was a green, ovate structure set on a short stem and covered with numerous overlapping pointed leaf scales (Figure 64). They usually developed from axillary buds situated in the axils of leaves or branches (Figure 65).

The outer leaves thickened, the tips became aristate, and the base gradually enlarged as food reserves accumulated. Axillary turions were occasionally observed to develop on the apices of branches (Figure 66). They also formed on the ends of geotropically positive-oriented stems that had begun to grow in soil and then were placed in light to continue to develop (Figure 67). Late in the flowering period, axillary turions were observed to form at the base of female flowers (Figure 68).

Overlapping leaf scales and leaves surrounded a dormant plant within the propagule (Figure 69). The nodes were compressed, and several well-formed branch buds were present along the main axis (Figure 70). The dormant plant had an apical meristem, enclosed by young leaves (Figure 71).

An abscission zone developed between the base of the axillary turion and the end of the supporting stem (Figure 72). The layers separated in late autumn, causing the axillary turions to abscise and sink to the hydrosoil.

When the axillary turion germinated, the internodes below the apical meristem rapidly elongated and branch buds swelled (Figures 73 and 74). Only the young leaves elongated. The leaf scales did not grow, differentiating them from the leaves. The leaf scales had axillary scales at their bases, suggesting that the leaf scales were originally leaf tissue (Figure 75).

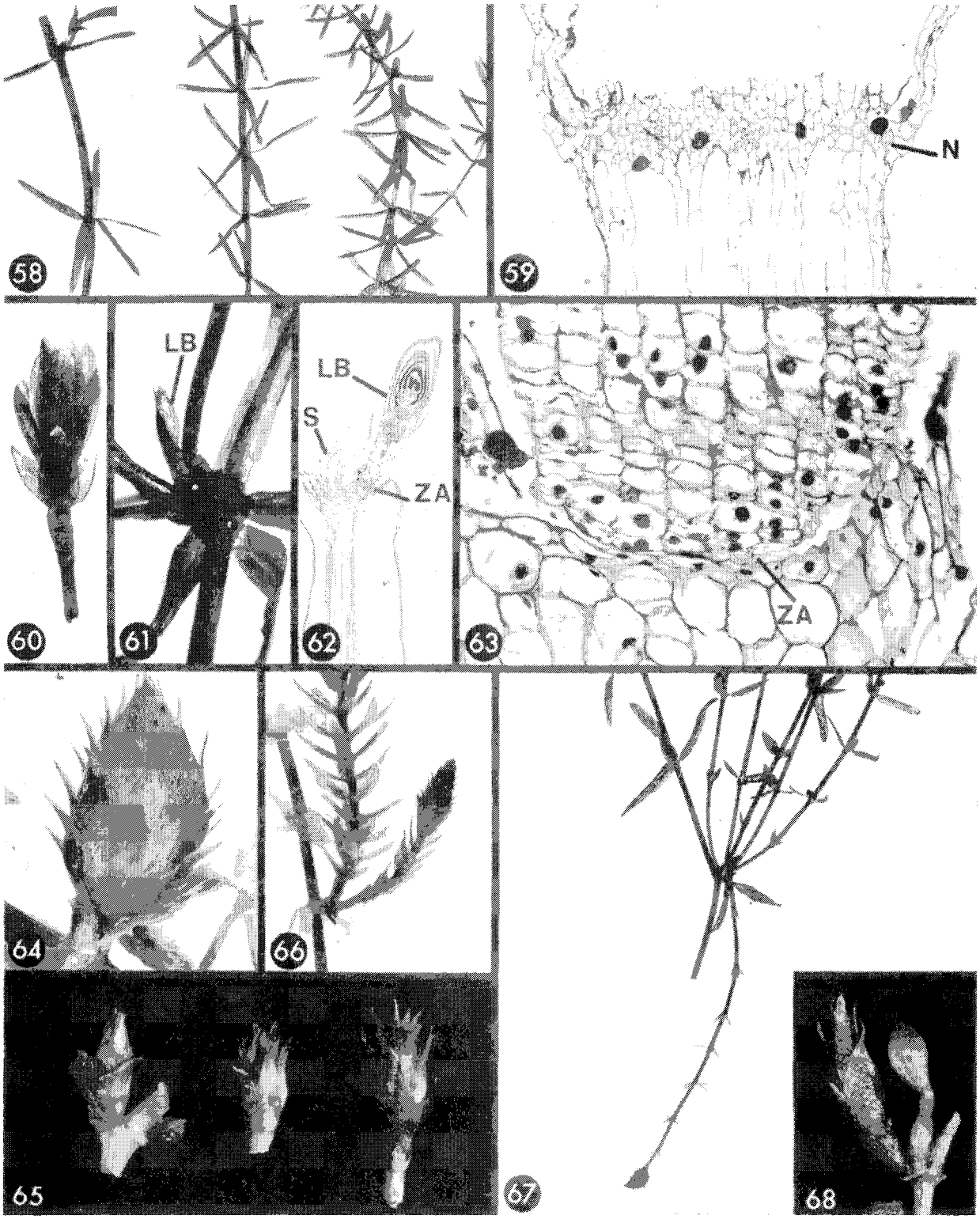


*Plate 8.* Figure 58. Stem fragments with axillary buds (arrow), X 0.8. Figure 59. Longitudinal section of stem segment showing site of fragmentation next to node, X 60. Figure 60. Clusters of compressed leaves surround and protect the apical meristem of the lateral stem bud, X 5. Figure 61. Early stage of development of lateral stem bud, X 5. Figure 62. Longitudinal section through lateral stem bud showing axillary position and structure X 3.5. Figure 63. Zone of abscission at base of lateral stem bud, X 250. Abscission layers have separated. Figure 64. Axillary turion attached to stem at node, (leaves removed) X 8. Figure 65. Three stages of turion development, X 4. Tips of several clustered leaf scales beginning to show at apex (left). Leaf scales are differentiating (center). External features are well-formed and development is nearly complete (right). Figure 66. Under stress conditions, axillary turions may form at unusual sites, such as the apex of a branch, X 1. Figure 67. Axillary turion formed from a developing subterranean turion that was removed from the hydrosoil and placed in sunlight, X 0.8. Figure 68. Axillary turion formed from bud at the base of a female flower late in the flowering period, X 4.

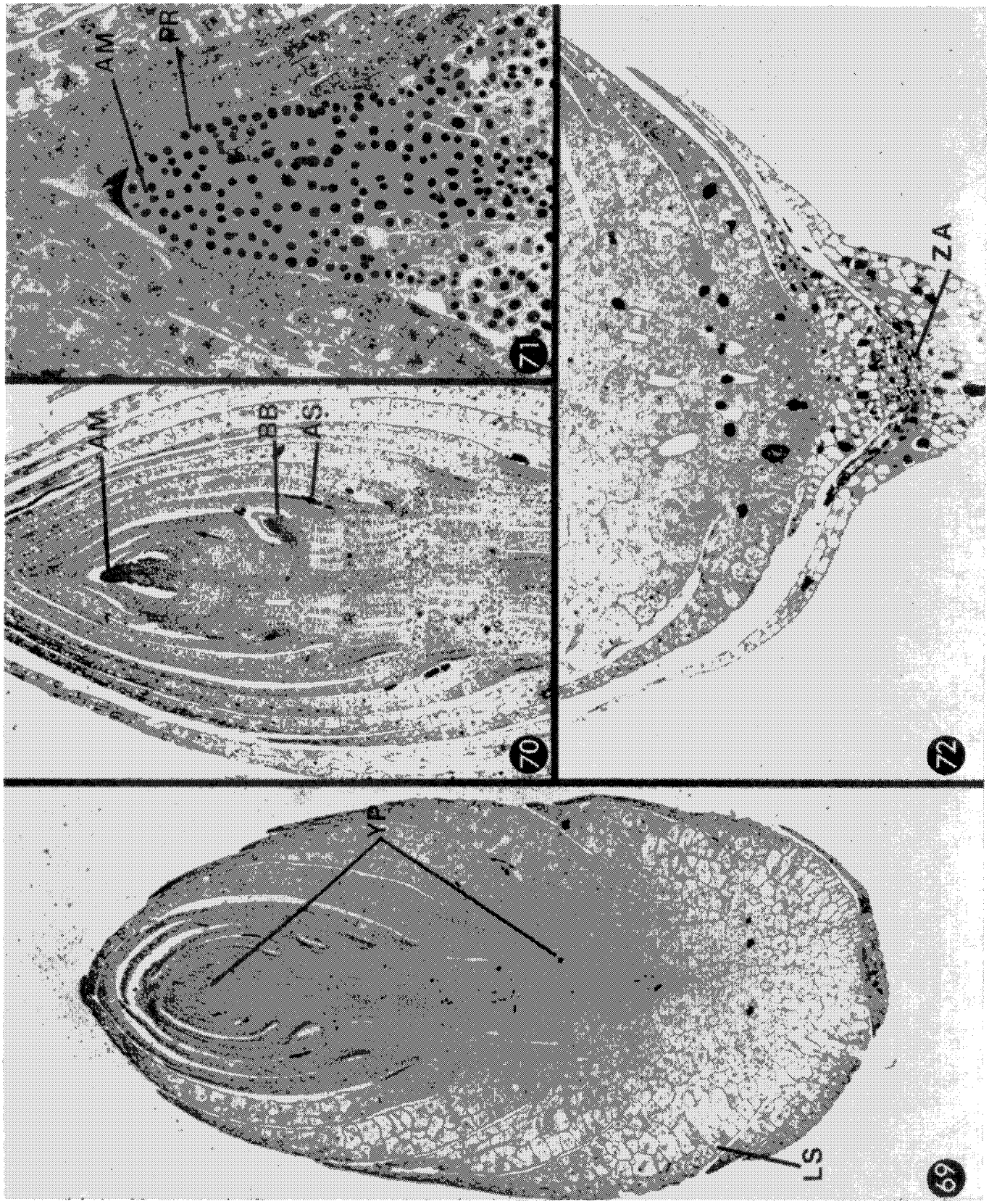


*Plate 9.* Figure 69. Longitudinal section of axillary turion with dormant young plant and thick leaf scales, X 17. Figure 70. Longitudinal view showing various structures comprising the young dormant plant within an axillary turion, X 24. Figure 71. Enlarged view of apical meristem in an axillary turia, X 100. Figure 72. Zone of abscission at base of axillary turion, X 45.

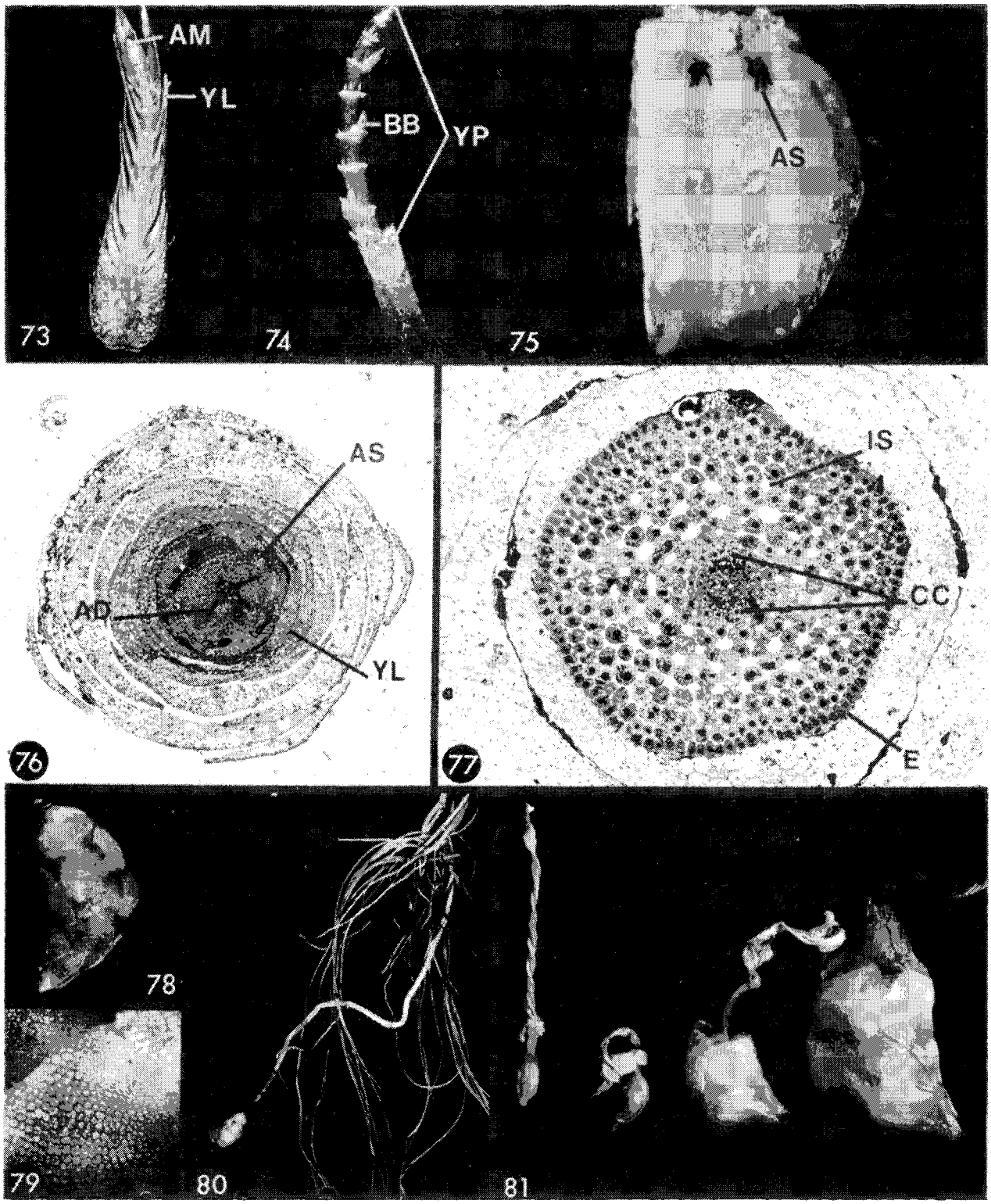


*Plate 10. Figure* 73. Germinating axillary turion cut longitudinally, X 4. Figure 74. Elongating axillary turion with leaves removed showing long internodes in mid-region, X 4. Base of turion shows central area where young plant differentiates into storage tissue. Figure 75. Inner surface of excised leaf scale with two prominent axillary scales (stained with ferric chloride), X 15. Figure 76. Transverse section through nodal area in a mature turion showing the arrangement of overlapping leaves and leaf scales, position of axillary scales, and vascular tissue to the leaves, X 16. Figure 77. Transverse section through the internodal area of a young plant within an axillary turion showing numerous intercellular air spaces and well-developed epidermis, X 40. Figure 78. Mature subterranean turion, X 4. Figure 79. Outer surface of leaf scale with hexagon cells, X 10. Figure 80. Subterranean turion formed at terminal node of an underground stem (hydrosoil removed), X 1. Figure 81. Developing subterranean turions (preserved specimens), X 5. Early stage of formation (stem twisted from drying) (left). Structure with initial swelling from accumulation of food reserves (center). Nearly mature specimen (right).

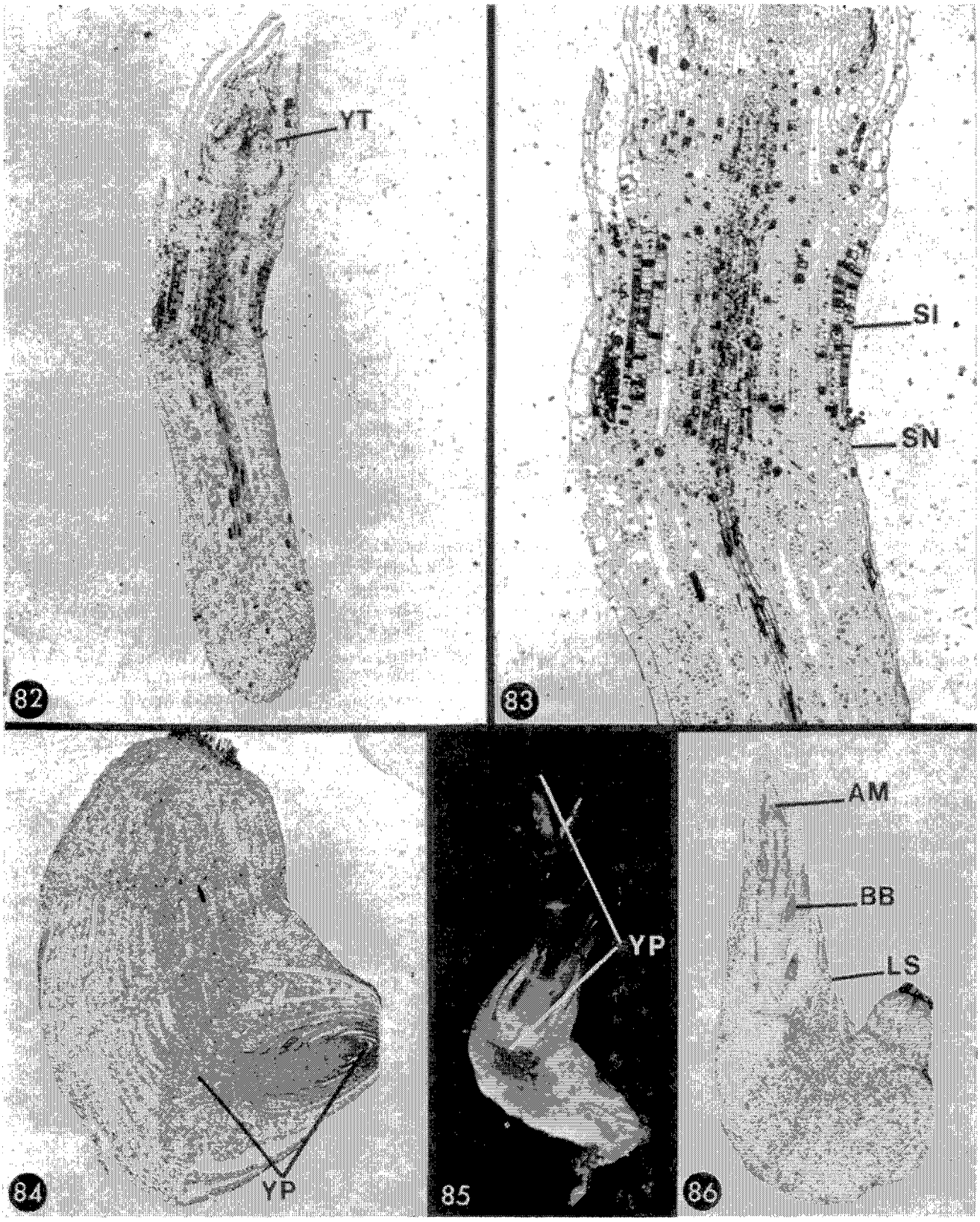


*Plate 11.* Figure 82. Longitudinal section of young subterranean turion beginning to form at end of a subterranean stem, X 24. Figure 83. Enlarged area of developing subterranean turion showing support node and internode, X 50. Figure 84. Longitudinal section through mature subterranean turion showing position of young dormant plant, X 16. Figure 85. Hand cut section through a germinating subterranean turion, X 4. Figure 86. Early stage of germination of subterranean turion with elongating leaves and internodes and swelling branch buds, X 6.5.

Transverse sections through the nodal area of axillary turions showed well-developed conductive tissues to young leaves (Figure 76). Axillary scales were also observed. Large intercellular air spaces occurred in the internodal area of the young plant (Figure 77). The cells in this region had large nuclei and dense cytoplasm. Epidermal cells were well developed, their outer walls appeared thick and continuous. The structure of the central conductive tissue in the turion was similar to that in erect stems. The overlapping leaf scales were several layers of cells thick near the base, and contained an abundance of plastids. These multiple layers may aid in protecting the inner structures from desiccation.

*Subterranean turions.* Subterranean turions were swollen structures up to 15 mm long, that developed in the hydrosoil (Figure 78). The outer covering was composed of thick overlapping leaf scales that had an external layer of hexagon-shaped cells (Figure 79). This structure was normally white, but turned green when germinated in ambient light.

Subterranean turions formed at the terminal nodes of erect stems that had exhibited positive geotropism (Figure 80). In the fall, several normally erect stems grew downward penetrating the soil 1 to 10 cm before directional growth ceased. The meristem at the terminal node continued and enlarge from the accumulation of food reserves (Figure 81). Early in the development of the turion a support node and internode formed. The turion developed from tissues terminal to the support internode. The internode cells were small and many had heavy deposits of tannins (Figure 82). Photographs taken in the early stages of development revealed that the plastids were larger in the internodal cells above the support node than in the cells of the support internode (Figure 83).

The mature subterranean turions did not abscise but became free of the parent plant when the attached stem decomposed or the support internode ruptured.

The anatomies of the axillary and subterranean turions were similar. The subterranean turion differed by having the terminal one-third of the structure bending at an angle of about 90 degrees, thus placing the apex in an approximate horizontal position (Figure 84). Longitudinal sections through a mature subterranean turion showed that the structure was composed largely of storage tissue in the basal two-thirds region.

A dormant young plant within the turion occupied most of the upper one-third (Figure 85). This young plant consisted of a series of nodes and compressed internodes. The lower region of the young plant extended radially out into the storage tissues. Young leaves formed at each node, with axillary scales present at the base of each. The apex of the young plant terminated with an apical meristem protected by a cluster of young leaves. Branch buds were also present along the nodal tissue. Germination was similar to that of axillary turions (Figure 86).

Some leaf scales of the subterranean turions were several rows of cells thick. We found that a thick cuticle covered the external cell walls of the epidermis. Examination of scanning electron micrographs through the central area of a subterranean turion showed a large number of plastids in all the cells, including those in the central cylinder.

## FIGURE ABBREVIATIONS

Key for figures: AB, axillary bud; AD, vascular tissue to leaves; AE, aerenchyma; AM, apical meristem; AN, anther; AS, axillary scale; B, bract; BB, branch bud; BS, bud scale; CC, central cylinder; CL, central lacuna; CO, collenchyma; CP, companion cell; CR, cortex; CS, Casparian strip; CT, conductive tissue; DI, diaphram cells; E, epidermis; EM, emergence; EN, endodermis; FB, flower bud; FF, female flower; HP, hypanthium; IS, intercellular air space; L, leaf, LA, lacuna; LB, lateral stem bud; LE, lower epidermis; LP, leaf primordia; LS, leaf scale; M, mesophyll; MF, male flower; N, node; OL, ovule; OV, ovary; P, phloem; PA, parenchyma; PB; primary bud; PD, pedicel; PE, petal; PH, prickle hair cell; PN, perianth; PR, protoderm; R, root; RB, root bud; RC, root cap; S, stem; SA, staminode; SB, secondary bud; SD, seed; SE, sepal; SI, support internode; SG, stigma; SM, stamens; SN, support node; ST, sieve tube; TC, tannin cell; UE, upper epidermis; YL, young leaf; YP, young plant; YT, young subterranean turion; ZA, zone of abscission.

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