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ONTOGENY OF THE COTYLEDONARY REGION OF CHAMAESYCE MACULATA (EUPHORBIACEAE)[1]

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ABSTRACT

Development of the cotyledonary region in *Chamaesyce maculata* is described from germination of the seed through formation of the dense mat of branches which characterize this common weed. The cotyledonary node is trilacunar with split-lateral traces. Epicotyl development is limited to a pair of leaves ("V-leaves") inserted directly above and decussate to the cotyledons. The two V-leaves are also vascularized by three traces and insertion of these traces relative to the vasculature at the immediately subjacent cotyledonary node is asymmetrical; four of the six V-leaf traces arise on one side of the intercotyledonary plane and two arise on the opposite side. Further shoot development is limited to lateral branches that develop sequentially from cotyledonary axillary buds, and then from de novo buds which arise at bases of previously developed lateral branches. The first axillary bud to develop is located on that half of the seedling which supplies the V-leaves with four traces. Development or insertion of the third and fourth branches (first and second de novo branches) relative to the first and second (cotyledonary) branches occurs in two patterns, termed cis and trans. Subsequent de novo branches generally develop between the two most recently developed branches on that half of the seedling, gradually forming a large branch plexus at the cotyledonary region. In mature robust specimens, however, the sequence of lateral branch development may become irregular. Structure of the cotyledonary region of *C. maculata* does not readily support widely held concepts of homology between the pleiochasium of *Euphorbia* subgenus *Agaloma* and the lateral branch system of *Chamaesyce*.

STEM ONTOGENY in *Chamaesyce* S. F. Gray (or *Euphorbia* subgenus *Chamaesyce* Raf.) is unusual in that development of the epicotyl is extremely limited. Following seed germination and emergence of the cotyledons, one pair of leaves develops decussate to the cotyledons. The primary axis of the epicotyl exhibits no further extension growth; indeed, its apical meristem is commonly described as undergoing abortion (Degener and Croizat, 1938; Hurusawa, 1954; Webster, 1967; Koutnik, 1984, 1987). Growth resumes through development of lateral or secondary axes. According to Wheeler (1941), "Lateral branches arise from the apex without any particular relation to the leaves." On the other hand, Goebel (1931) and Webster (1967) describe the first pair of lateral branches to arise from axillary buds of the cotyledons. Croizat (1960: 982), however, has disputed the axillary origin of lateral branches. Disputes about their origin notwithstanding, the number and orientation of lateral branches

varies from species to species in *Chamaesyce*; some produce a small number of upright branches, whereas others, such as *C. maculata* (L.) Small (Fig. 1–4), produce a dense cluster of radiating prostrate branches.

At the anatomical level, details of the alleged abortion of the epicotyl apical meristem and intricacies of branch stem ontogeny are not well known. For example, Gaucher's (1898) anatomical monograph of *Euphorbia,* sensu lato, does not address these issues. Aside from a brief report on *Chamaesyce hirta* (L.) Millspaugh (Rosengarten and Hayden, 1983), the only previous publication on the subject is that of Veh (1928). Veh's study dealt largely with phyllotaxy of lateral branches and anatomical and embryological features of cyathia; he did, however, describe and illustrate some early ontogenetic events of the epicotyl and lateral branches. Nevertheless, Veh's descriptions do not include details of the vascular system of the seedling, nor do they document in detail the origin of successive lateral branches. Moreover, observations presented below dispute some of Veh's interpretations of these unusual developmental phenomena.

As discussed most recently by Koutnik (1984, 1987), elucidation of stem ontogeny of *Chamaesyce* bears critically on understanding its relationships with *Euphorbia* L. In concert with
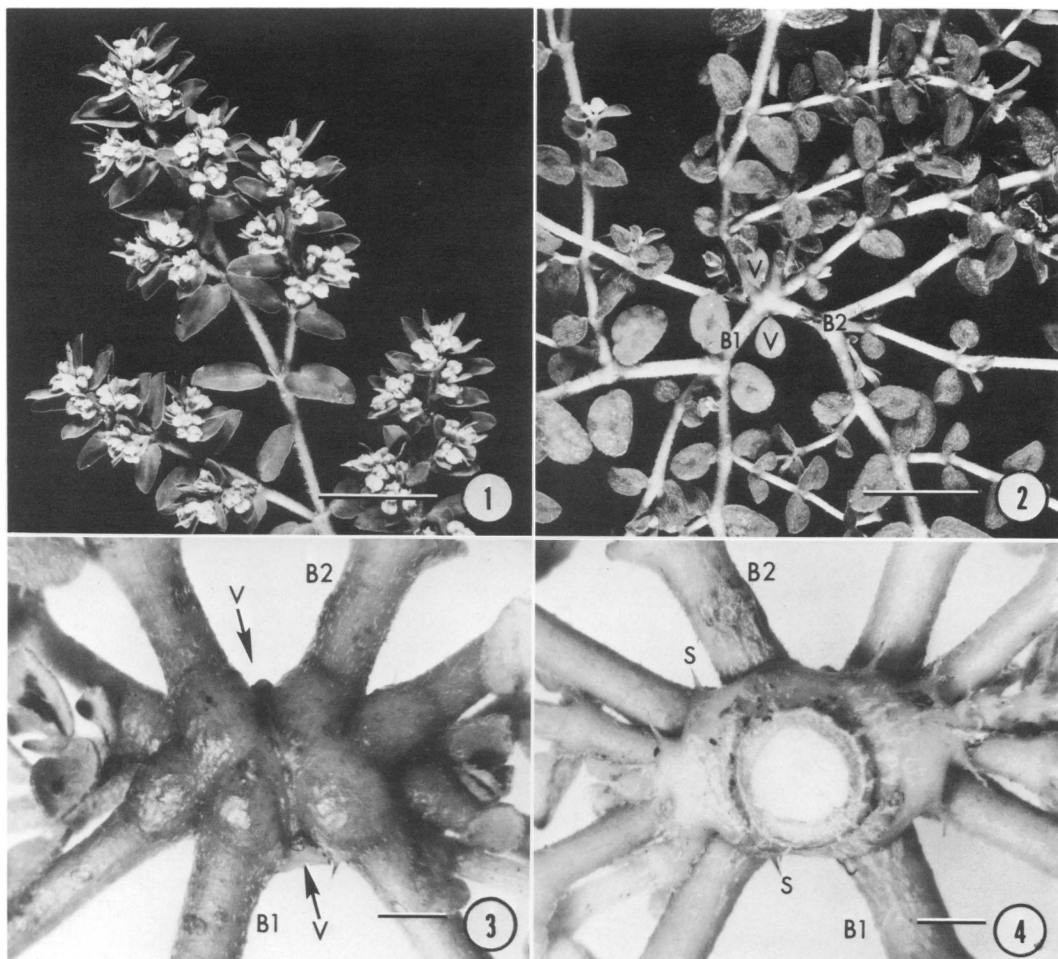
Fig. 1–4. *Chamaesyce maculata.* **1.** Branch tip bearing cyathia. Bar = 2 cm. **2.** Cotyledonary plexus of a medium-sized specimen with cis arrangement of branches. B3 and B4 project towards top of photograph. Bar = 2 cm. **3.** Cotyledonary plexus of a large specimen with trans arrangement of branches, upper surface. Bar = 1 mm. **4.** Same as Fig. 3, lower surface. Bar = 1 mm. B1, B2 = first two lateral branches; S = stipule-like flap; V = V-leaves, or V-leaf scars.

characters from leaf anatomy, photosynthetic physiology, stipules, cyathia, and seeds, stem development figures prominently in acceptance of generic versus subgeneric status for *Chamaesyce*. The present study was undertaken as part of a larger effort designed to probe the putative homologies of plant form in *Chamaesyce* and *Euphorbia*. In the communication of such comparative data, acceptance of generic status for *Chamaesyce* offers the great advantages of simplicity and clarity in referring to one taxon or the other. This essentially pragmatic taxonomic choice has been facilitated by the fact that virtually every species in the group has published names under both genera.

MATERIALS AND METHODS—Specimens of *Chamaesyce maculata* [= *Euphorbia supina*

Raf. of Wheeler (1941) and Fernald (1950); = *E. maculata* L. of Gleason and Cronquist (1963)] were collected from natural populations growing on the campuses of the University of Maryland, College Park, Maryland, and the University of Richmond, Richmond, Virginia, at various times during spring and summer of 1976 and 1982, respectively. Specimens were preserved in FAA (70 percent alcohol). Herbarium vouchers from each population sampled are deposited in URV (Department of Biology, University of Richmond). Early stages of seedling development (from emergence of the radicle through maturation of the fourth pair of leaves) were obtained from seeds sown on moist filter paper in petri dishes; after stratification for one week at 5 C (Krueger and Shaner, 1982), the seeds were exposed to an

alternating 12 hr light/12 hr dark photoperiod at ambient room temperatures. Laboratory germinated seedlings together with naturally collected plants provided a total of 67 plants that were sectioned and studied, yielding a complete developmental sequence from early stages of seed germination through large matted plants with 12 or more lateral branches visible to the naked eye. The branching patterns of large complex specimens were recorded in drawings prior to sectioning.

Standard tertiary butyl alcohol series were used to dehydrate specimens prior to embedding in paraffin and sectioning at 10 μm on a rotary microtome. Sections were affixed to slides with Bissing's adhesive (Bissing, 1974), and were stained with a combination of hematoxylin and safranin O. Photomicrographs were prepared with Kodak Technical Pan film developed with Kodak HC110 developer.

For convenience, the following terminology has been adopted for description of features of seedlings and young plants of *C. maculata*:

Cotyledonary plane—the longitudinal plane passing medially through both cotyledons (Fig. 5).

Intercotyledonary plane—the longitudinal plane situated at right angles to the cotyledonary plane and passing through the seedling axis between the cotyledons (Fig. 5).

V-leaves—the pair of leaves which develop in the intercotyledonary plane immediately above the cotyledons [so designated to distinguish vegetative leaves and cyathophylls, based on presumed homologies with certain species of *Euphorbia*; see Wheeler (1941) and Discussion].

B1, B2, B3, etc.—the successive lateral branches which develop in the cotyledonary region.

Cis—an arrangement of branches in which B3 and B4 diverge from the same side of the cotyledonary plane (Fig. 6).

Trans—an arrangement of branches in which B3 and B4 diverge from opposite sides of the cotyledonary plane (Fig. 7).

Cathodic leaf trace—a trace to the left of the median plane of the petiole as viewed from the stem axis (Howard, 1979).

Anodic leaf trace—a trace to the right of the median plane of the petiole as viewed from the stem axis (Howard, 1979).
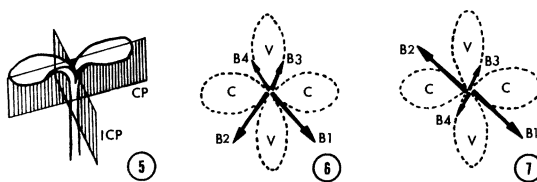

Fig. 5–7. Seedlings of *Chamaesyce maculata*. 5. Seedling upon emergence of cotyledons. 6. Cis branch pattern. 7. Trans branch pattern. B1–B4 = successive lateral branches; C = cotyledon; CP = cotyledonary plane; ICP = intercotyledonary plane; V = V-leaves.

RESULTS—*Germination*—Externally, germination first becomes evident upon emergence of the hypocotyl and radicle from the testa. The cotyledons remain within the testa for several days. During this period sections reveal the cotyledons in close proximity with cells of the endosperm which, initially, are densely packed with starch grains. Gradually, as they become depleted of starch, the cells of the endosperm lyse and appear disorganized in sections. Depletion and disruption of endosperm cells proceeds from the center of the seed, i.e., from cells nearest the cotyledons to the periphery (Fig. 8). No mature protoxylem elements have been observed in the cotyledons while they are still contained within the testa, although protoxylem may be found in the hypocotyl at this time. During early stages of germination, the epicotyl region contains neither embryonic stem nor leaf tissue (Fig. 8).

Cotyledon stage—Upon emergence from the testa, the blades of the cotyledons quickly diverge from each other, but their petioles remain tightly appressed for several days, effectively covering the epicotyl region of the seedling. During this time protoxylem maturation proceeds throughout the cotyledons and the upper part of the hypocotyl. Vasculature of the upper end of the hypocotyl consists of four collateral endarch bundles (Fig. 9) that divide into the six leaf traces of the cotyledons. The course of each median cotyledonary trace is a straightforward divergence of a hypocotyl bundle that remains consistently within the cotyledonary plane (Fig. 14, 17). The lateral cotyledonary traces arise from two bundles lying in the intercotyledonary plane; each of these bundles splits and the branches diverge sharply in opposite directions to form the lateral cotyledonary traces (Fig. 12, 13, 17, 21).

During the cotyledon stage four regions of procambium are present between the four bundles in the hypocotyl leading to the cotyledons (Fig. 9); this procambium differentiates as V-leaves and lateral branches develop (see below). Laticifers at the cotyledonary node be-
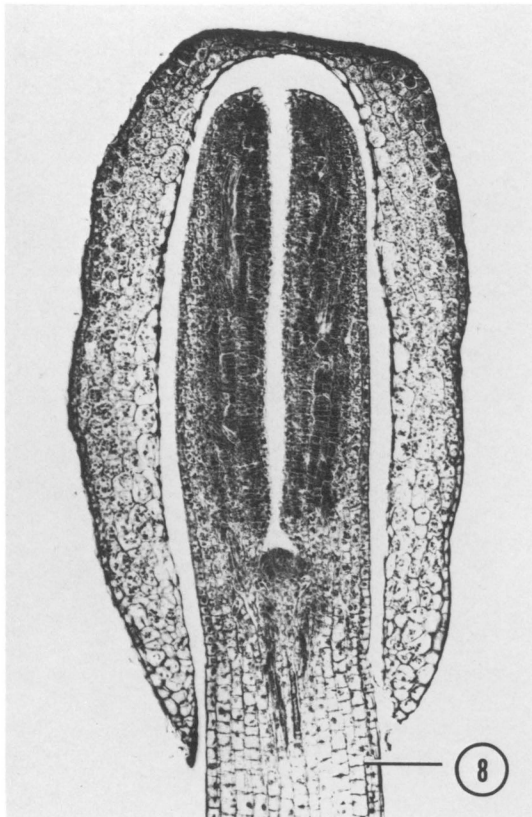
Fig. 8. Germinating seedling of *Chamaesyce maculata* with hypocotyl emergent and cotyledons enclosed by endosperm. Testa removed prior to sectioning. Bar = 100 μm.

come prominent by the time seedlings have expanded their cotyledons. As development proceeds, these laticifers progressively branch and form an intricately convoluted mass permeating the cortex of the cotyledonary region (Fig. 12, 25, 26).

V-leaf origin — While the petioles of the cotyledons are still tightly appressed, at their bases four groups of densely stained cells become evident in rapid pairwise succession (Fig. 10, 11, 13–16). The first two groups of cells to appear lie within the intercotyledonary plane and are primordia of the two V-leaves (Fig. 10, 16). Origin of V-leaf primordia is quickly followed by the appearance in the cotyledonary plane of the second two groups of cells; these are cotyledonary axillary buds which will, eventually, produce B1 and B2 (Fig. 11, 14, 15). V-leaves expand before much growth occurs in cotyledonary axillary buds. V-leaf primordia are situated at the distal end of the seedling primary axis, and basally, their adax-

ial surfaces are separated by a mere three or four cells (Fig. 10, 16). As V-leaves grow, the previously appressed petioles of the cotyledons separate and the young V-leaves become visible.

Four-leaf stage, vasculature — By the time the V-leaves are fully expanded the seedling consists of a decussate arrangement of two cotyledons and two V-leaves. The internode separating these two leaf pairs is virtually nonexistent; the lower edge of the V-leaf petioles are inserted at about the same level as the upper edge of the cotyledonary petioles (Fig. 13, 16). This close vertical juxtaposition of these leaves persists through later developmental stages.

Vasculature of the upper hypocotyl still consists of four endarch collateral bundles, as in earlier stages; however, the two bundles which bear the split lateral traces of the cotyledons become distinctly larger than the median traces to the cotyledons as a result of maturation of additional elements supplying the V-leaves. The course of each large bundle in its acropetal path from the hypocotyl is illustrated in Fig. 17 and can be decribed as follows. First, at the cotyledonary node, the common lateral bundles of the cotyledons diverge radially and then split apart tangentially in their courses towards the cotyledon petioles, leaving two bundles on either side of split trace gap (Fig. 12). These two bundles are of unequal size; the smaller one constitutes one V-leaf lateral while the larger one consists of the other lateral and the median trace to the same V-leaf. Thus, V-leaf vascular supply is asymmetrical, with two traces arising on one side of the cotyledonary split lateral gap and the other trace arising on the opposite side. Although originally off-center, the V-leaf median trace quickly attains the median position in its outward course towards the V-leaf petiole and the three traces of each V-leaf are equally spaced at the point of their entrance into the base of the petiole (Fig. 18–20). The vasculature of the V-leaves thus differs from that of the cotyledons even though these nodes are virtually contiguous and both are vascularized by three traces.

Further asymmetry in vascularization of the V-leaves is apparent when both V-leaves of a given seedling are considered together. For one V-leaf the paired median and lateral traces arise on the cathodic side of the cotyledonary split lateral gap, whereas the paired traces of the opposite leaf arise on the anodic side. In other words, if the seedling were divided at the intercotyledonary plane, one half of the seedling produces a total of four V-leaf traces (two lat-
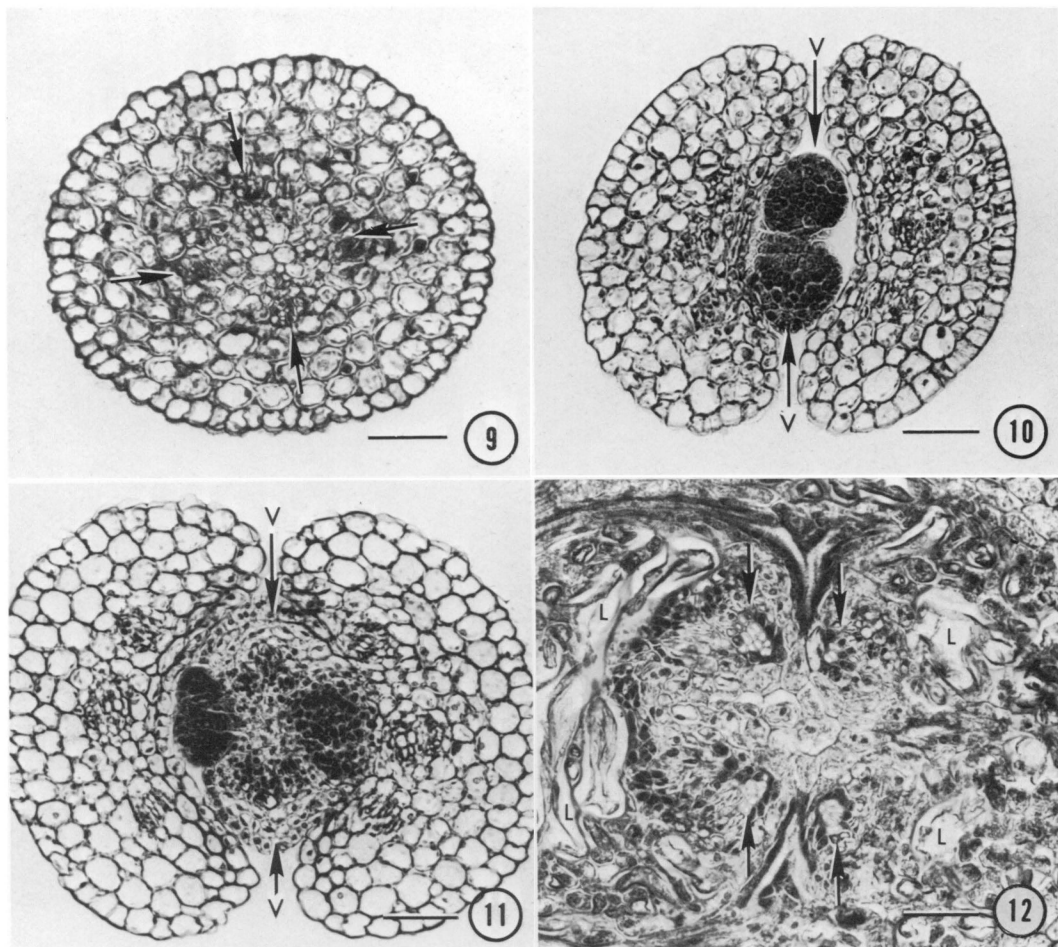
Fig. 9–12.   Transverse sections of seedlings of *Chamaesyce maculata*. **9.** Hypocotyl of seedling upon emergence of cotyledons, sectioned at 50 μm below divergence of split lateral traces of the cotyledonary node. **10.** V-leaf primordia between bases of cotyledons, same age as preceding. **11.** Slightly older seedling showing bases of still unexpanded V-leaves and buds of B1 and B2 axillary to the cotyledons. **12.** Cotyledonary node of seedling bearing fully expanded cotyledons and V-leaves. Note inequality of hypocotyl vasculature leading to the V-leaves. All bars = 50 μm. L = laticifer; V = V-leaf; arrows = hypocotyl vascular bundles.

erals and two medians), whereas the other half of the seedling produces only two traces (both laterals) (Fig. 17). In every seedling observed from this or slightly later stages, the first cotyledonary axillary bud to develop (see below) is the bud on the half of the seedling that contributes the greater number of V-leaf traces.

Four-leaf stage, branch origin—As mentioned above, the first two lateral branches become discernable during early stages of expansion of the V-leaves. The first two branches (B1 and B2) develop from axillary buds of the cotyledons (Fig. 14, 15) and, as mentioned above, one is precocious relative to the other (Fig. 18–20).

The buds that produce B1 and B2 are situated directly over the gaps formed by the departure of the cotyledonary median traces (Fig. 14). The procambium of these buds departs the stele at approximately 100 μm above the cotyledonary median gap although the procambial (and, later, the vascular) connection to one bud is initially greater because of its precocious development (Fig. 20). Basally, the shape of the procambial strand is a convex arc open towards the center of the seedling axis; this open arc quickly assumes the configuration of a closed cylinder in its acropetal course away from the seedling axis (Fig. 19, 20).

Buds which will form B3 and B4 are also visible in sections of seedlings at the four leaf
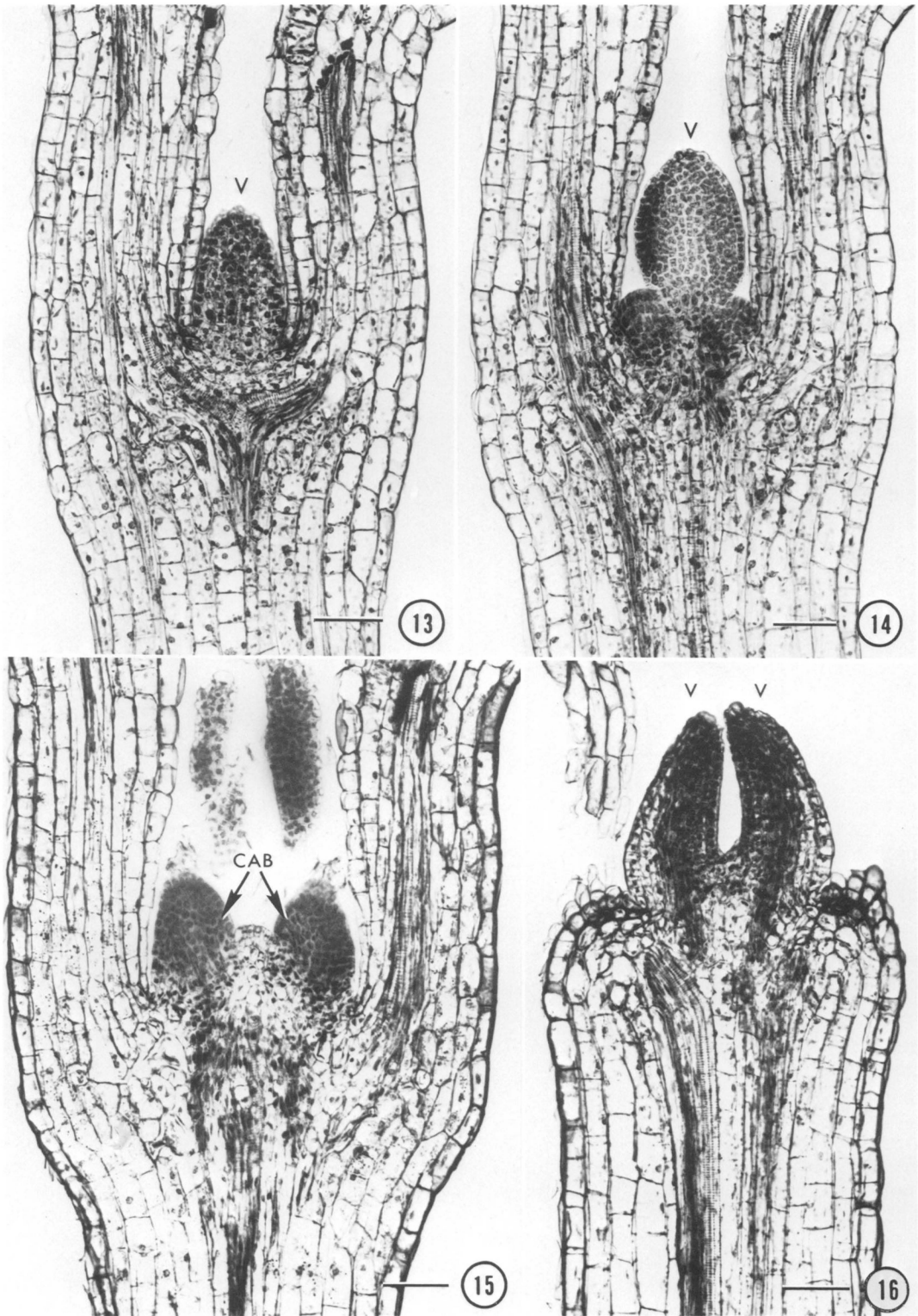
Fig. 13–16. Longitudinal sections of seedlings of *Chamaesyce maculata*. **13.** V-leaf primordium situated above the split lateral traces to the cotyledons. **14.** Oblique section showing a median trace to the cotyledon on the left, portions of both cotyledonary axillary buds, and a V-leaf primordium. **15.** Near median section through the epicotyl in the

stage, prior to the external appearance of B1 (Fig. 18, 19). The B3 bud is located lateral to the B1 bud near its base, and the B4 bud is located, similarly, near the base of B2. B3 and B4 buds are each enclosed in nonvascularized stipule-like flaps (Fig. 4, 18, 19). Buds for B3 and all subsequent branches arise de novo from tissue at the bases of older buds or branches (Fig. 25, 26). The buds for B3 and B4 may arise on either side of B1 and B2, producing young plants with either a cis or trans arrangement of branches (Fig. 6, 7). Although the spatial orientation of B1 through B4 may be altered somewhat by development of further branches, it is usually possible to determine the initial configuration (cis vs. trans) of the buds that gave rise to the first four branches even in specimens with multiple branches (Fig. 2, 3, 4, 24).

The cells located at the seedling apex, between the pair of V-leaves, are mature parenchyma bearing no signs of meristematic activity at any time during the four leaf stage or later (Fig. 15). There is no recognizable epicotylar apial meristem. Further, there is no evidence of buds axillary to the V-leaves at this or later stages.

Two-branch stage—Internally, as B1 and B2 develop, differentiation proceeds in their procambial strands, with B1 retaining its precocity (Fig. 19, 20). Although completely separate basally, some anastomosing vascular strands eventually differentiate between the vasculature of B1 and B2 near the distal end of the truncated primary axis of the seedling. As the vasculature of B3 and B4 develops, anatomy of the cotyledonary and V-leaf nodes is dominated by four arcs of vasculature supplying B1, B2, B3, and B4. These arcs quickly become typical eustelic vascular cylinders in their acropetal courses into the branches (Fig. 19). Eventually, a vascular cambium arises and the basal arcs and distal cylinders of each branch experience ordinary secondary growth (Fig. 24, 25).

Secondary growth of hypocotyl and cotyledonary node—The transition to secondary growth occurs in the hypocotyl region as lateral branches develop. By the time B2 becomes visible to the naked eye, a vascular cambium
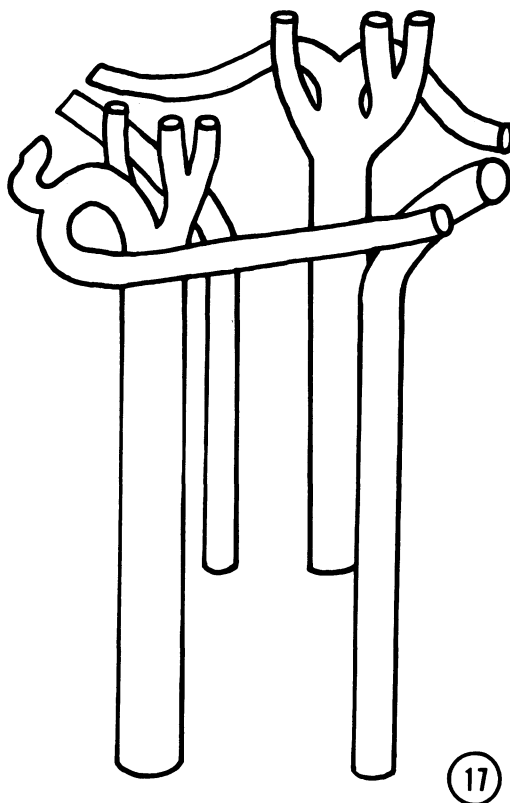

Fig. 17.   Vasculature of a seedling of *Chamaesyce maculata* at the four leaf stage, prior to the emergence of lateral branches. Traces to the cotyledons project to the right and left, traces to the V-leaves project vertically.

is present in the hypocotyl and vascular tissue of the hypocotyl assumes a cylindrical form enclosing a narrow pith (illustrated after considerable secondary growth in Fig. 22). Expansion of the vascular cylinder from secondary growth results, of course, in exertion of forces on cells of the hypocotyl cortex and epidermis. Cells of both layers become stretched tangentially, and eventually, undergo anticlinal cell divisions producing contiguous linear groups of daughter cells (Fig. 22, 23). In this fashion the cortex and epidermis keep pace with expansion of the vascular cylinder. Neither phellogen nor periderm was observed, even in very large specimens. As evidenced by tangential series of as many as eight or more cells, this process of tangential stretching and anti-

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cotyledonary plane; note cotyledonary axillary buds and nonmeristematic appearance of cells at the apex. **16.** Median section through the epicotyl region in the intercotyledonary plane showing the proximity of V-leaf primordia. All bars = 50 μm. CAB = cotyledonary axillary bud; V = V-leaf primordium.
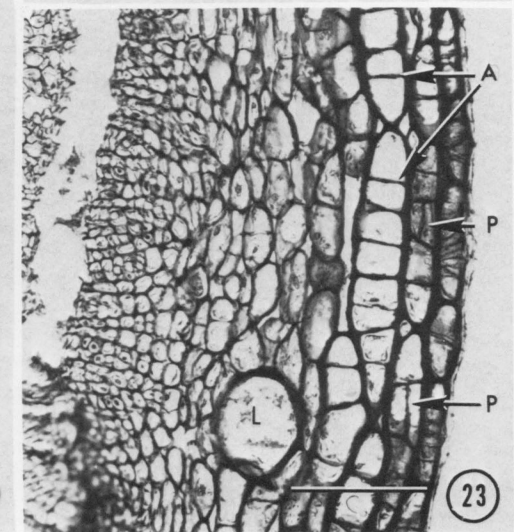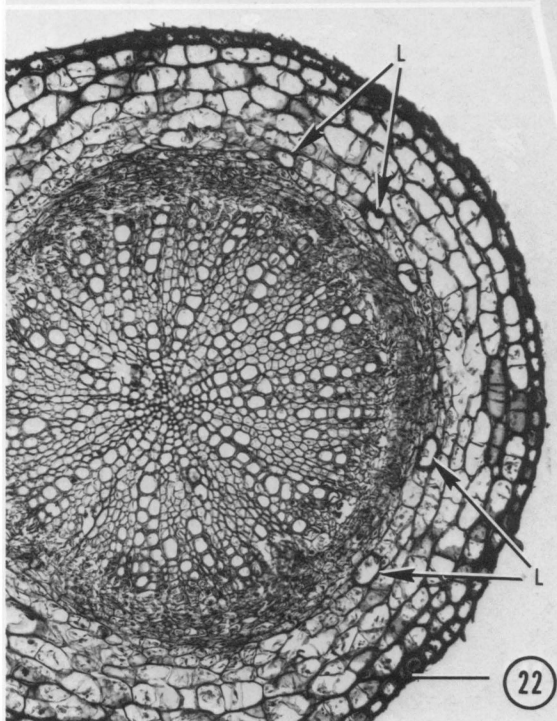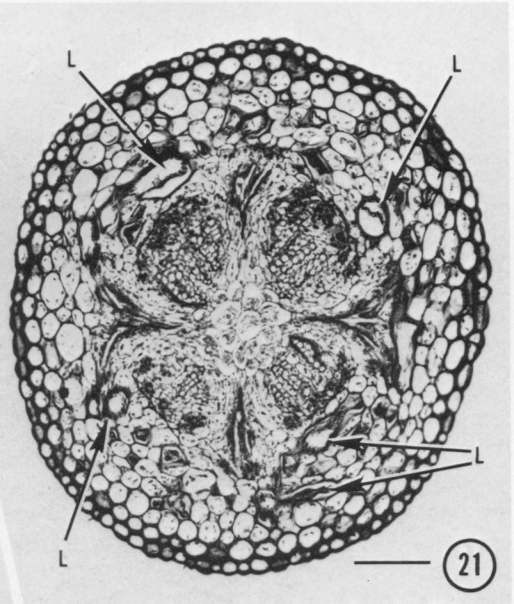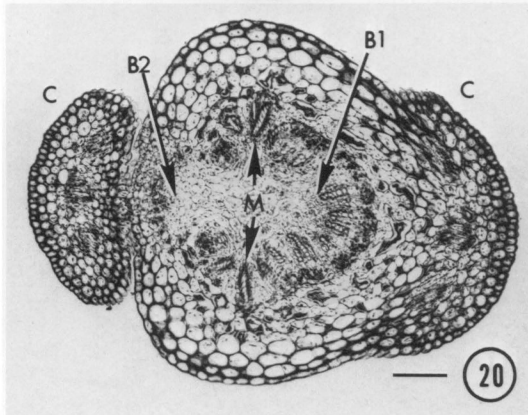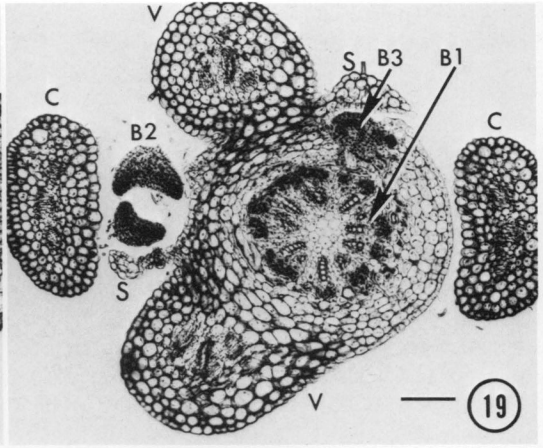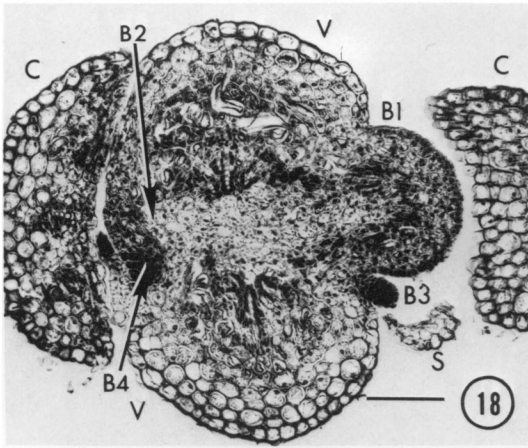
clinal division appears to continue indefinitely. In addition, a few periclinal partitions were observed in cortex cells of large specimens (Fig. 23).

As each branch commences secondary growth, its vascular cambium becomes continuous with that of the hypocotyl and, gradually, traces to the cotyledons and V-leaves in the region of the cotyledonary node become engulfed by the expanding cylinder of secondary tissues (Fig. 27). Whether or not V-leaves persist on large multiply branched specimens, their traces remain visible within the developing plexus where they provide a reliable indicator of the intercotyledonary plane (Fig. 24). Another consequence of secondary growth is that cotyledons and V-leaves, once in close proximity to each other, become separated laterally by as much as 3 or 4 mm in large specimens. Cortical parenchyma cells surrounding the cotyledonary node experience tangential stretching and anticlinal division much as in the hypocotyl.

Successive branches—At first, the sequence and sites of successive branch formation beyond B4 follows a predictable pattern. In general, successive branches develop alternately on opposite sides of the seedling, continuing the pattern established by B1 through B4. On one given side of a seedling, the position of the next branch to develop is frequently the region between the two most recently developed branches on that side of the seedling. Thus, for example, B5 arises between B1 and B3 (Fig. 24), and B6 arises between B2 and B4, etc. In large and densely branched specimens, some branches may arise in positions that do not follow the pattern described, and eventually the regularity of the pattern may break down with new branch buds arising between virtually any pair of adjacent branches.

Branches subsequent to B5 generally arise after differentiation of the vascular cambium in the cotyledonary node region. As each of these higher order branches develops, it attains

vascular connection with the rest of the plant by differentiation of cells between the developing branch and the vascular cambium. Vascular continuity for these branches is thus accomplished via secondary tissues. Lateral branches become supplied with laticifers via branching from the convoluted mass of laticifers in the cortex of the cotyledonary region (Fig. 25, 26) and intrusive growth into the developing branch.

As successive branches arise between preexisting branches, their growth and expansion exert lateral forces which push earlier formed branches away from each other. Because they develop first, B1 and B3, on one side of the plant, and B2 and B4, on the other side, experience the greatest change from their original position. For example, B1 and B2 originally project away from the seedling axis in the cotyledonary plane. In either cis or trans plants with many lateral branches, B1 and B2 may eventually project into or near the intercotyledonary plane (Fig. 2–4).

DISCUSSION—Ontogenetic events described here for *C. maculata* are completely consistent with an earlier preliminary report by Rosengarten and Hayden (1983) for *C. hirta,* at least through development of B4; later stages for *C. hirta* have not been studied. However, there are two major points of difference with other literature in the interpretation of structures and developmental events. Specifically, these differences concern the presence or absence of an epicotylar apical meristem and the sites of origin of lateral branches.

From the onset of seed germination and continuing through later developmental stages, no evidence has been found for existence of a typical apical meristem in the epicotyl of *C. maculata.* The V-leaves do arise as primordia in the epicotyl region, but their differentiation leaves virtually no meristematic residue in the epicotyl region save that of the cotyledonary axillary buds. Moreover, these V-leaves do not arise on the flanks of a well-developed apical

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Fig. 18–23.   Transverse sections through seedling and mature plants of *Chamaesyce maculata.* **18.** Seedlings at four-leaf stage showing early development of B1; note buds for B3 and B4. 19–21. Sections at various descending levels through a seedling slightly older than the preceding. **19.** Base of B1; note paired leaf primordia of B2 and de novo bud of B3. **20.** V-leaf node, with vasculature to B1 and procambium to B2. **21.** Cotyledonary node (orientation rotated 90° from Fig. 18 and 19); note greater amount of vascular tissue leading to B1 (upper half of figure) than leading to B2 (lower half); note also appearance of parenchyma cells of cortex. **22.** Hypocotyl of a moderate-sized specimen showing extensive secondary growth and partition-like anticlinal walls in tangentially stretched cells of the cortex. **23.** Portion of hypocotyl of large specimen bearing a massive branch plexus; note tangentially aligned group of eight cells in cortex. All bars = 100 μm. A = anticlinal division; B1–B3 = successive lateral branches; C = cotyledon; L = laticifer; M = median trace to V-leaf; P = periclinal division; S = stipule-like flap; V = V-leaf.
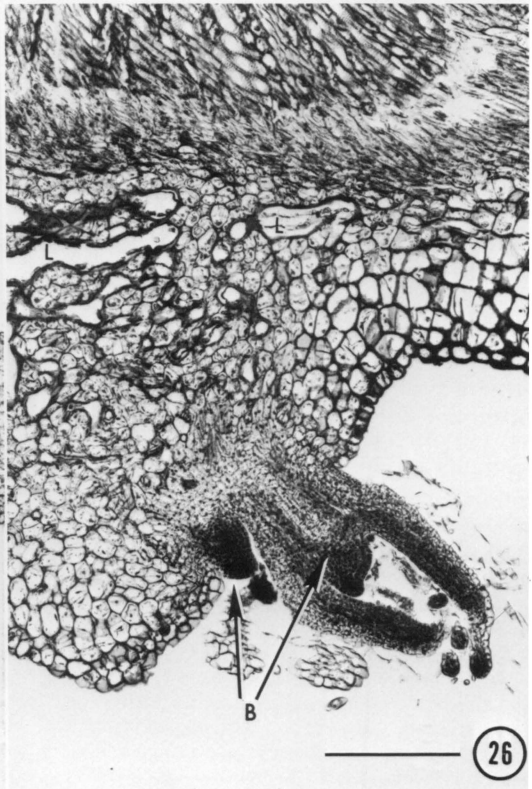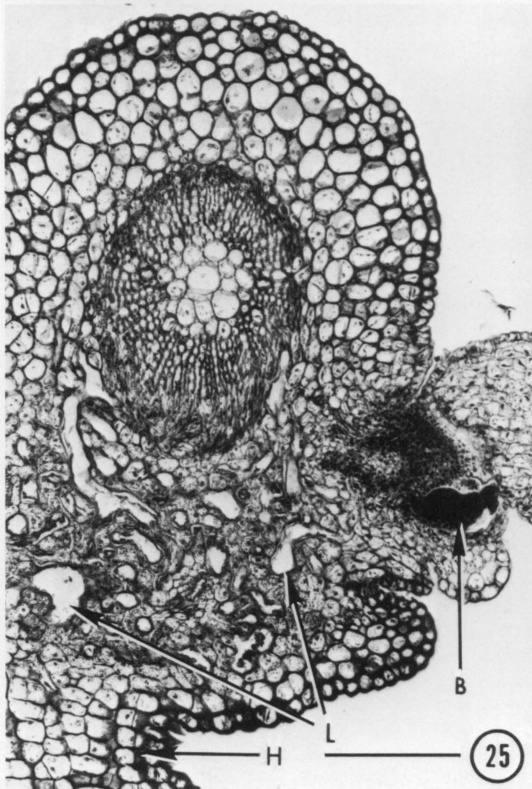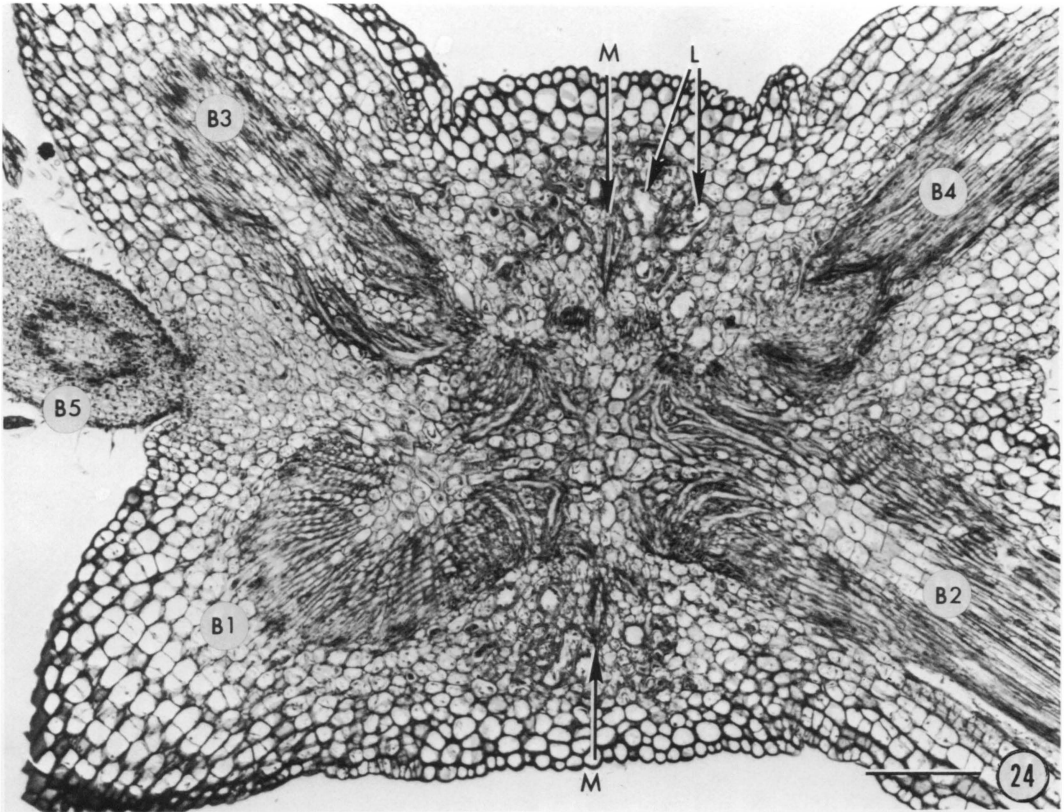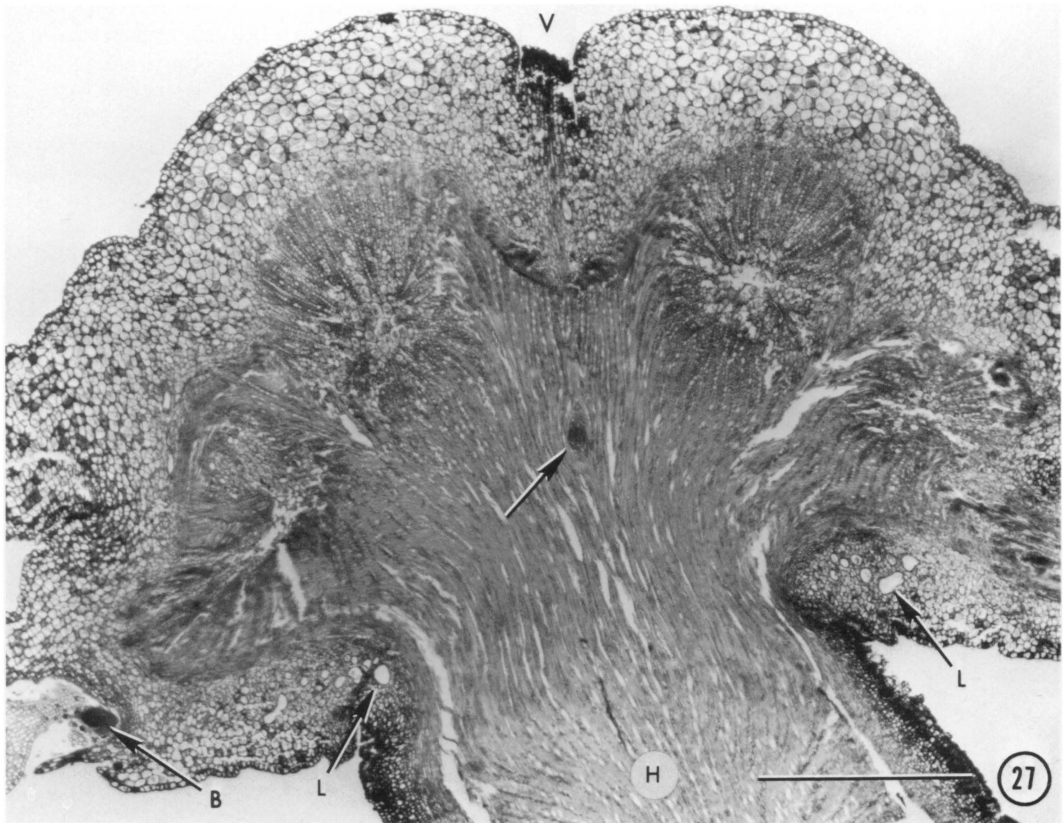
Fig. 27. Longitudinal section through a branch plexus of *Chamaesyce maculata*. Bar = 1 mm. B = de novo bud; H = hypocotyl; L = laticifer; V = V-leaf scar; arrow = common lateral trace to cotyledons, prior to splitting.

dome, rather, at their inception their adaxial surfaces are nearly contiguous and the intervening space enlarges only as a result of the growth of B1, B2, and successive branches. After development of the V-leaves, there is no meristematic dome bearing leaf primordia at the apex of the epicotyl. These observations and interpretations are in direct conflict with the often repeated statement, seldom supported by anatomical sections, that the epicotyl apical meristem of *Chamaesyce* aborts prior to initiation of lateral branches (e.g., Degener and Croizat, 1938; Hurusawa, 1954; Croizat, 1960; Webster, 1967). In *C. maculata,* the epicotyl apical meristem is simply consumed by

development of the V-leaves, leaving no remnant to "abort."

There are three instances (Veh, 1928; Degener and Croizat, 1938; and Croizat, 1960) in which published illustrations depict or at least suggest an apical meristem in the epicotyl of various *Chamaesyce* species. Veh (1928) illustrated a "Hauptvegetationspunkt" in drawings of the epicotyl region of several seedlings of a *Chamaesyce* species identified as "*Euphorbia congenera* Blume" [see Radcliffe-Smith (1980) for tentative synonymy]. In Veh's fig. 1, 11, and 12, the purported epicotyl meristems are noticeably out of alignment with the seedling's primary axis; Veh suggests that devel-

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Fig. 24–26. Sections through branch plexi of mature specimens of *Chamaesyce maculata*. **24.** Transverse section through the V-leaf node of a plant bearing a cis arrangement of branches. **25.** Longitudinal section (relative to hypocotyl) bearing a transverse section of a lateral branch; note laticifers and de novo buds. **26.** Portion of transverse section through the cotyledonary region showing two de novo buds. All bars = 200 μm. B = de novo buds; B1–B5 = successive lateral branches; H = hypocotyl; L = laticifer; M = median trace to V-leaf.

opment of cotyledonary axillary buds pushes the epicotyl apical meristem out of its original axial alignment. The positions of these supposedly displaced apical meristems, however, correspond exactly with the sites of origin of the de novo buds that give rise to B3 or B4 in *C. maculata;* it thus seems likely that Veh's "Hauptvegetationspunkt" is actually a de novo apex of a lateral branch. Veh illustrated two other supposed epicotylar apical meristems in his fig. 5, an optical section of a cleared seedling, and fig. 7, a longitudinal section. In both cases the structures labelled "Hauptvegetationspunkt" could easily be the bases of the V-leaves; the illustrations are not sufficiently detailed to demonstrate their purported meristematic nature. Significantly, Veh failed to locate epicotylar meristems in *C. thymifolia* (L.) Millsp. and *C. humifusa* Willd. In light of the evidence presented above, Veh's interpretation of an epicotylar apical meristem in "*E. congenera*" is questioned; reexamination of this species is warranted.

Croizat (in Degener and Croizat, 1938) discussed and illustrated "axial development" in a purportedly typical *Chamaesyce,* represented by *C. peplis* (L.) Prokh. (*C. maritima* S. F. Gray), and in arborescent species, represented by the Hawaiian *C. multiformis* (Hook. & Arn.) Croiz. & Deg. According to Croizat, development is essentially the same in both species, differing essentially in the number of lateral or secondary axes produced. As described and depicted, however, both differ greatly from *C. maculata* in four important respects: 1) A short (apparently several mm long) internode is depicted between the nodes bearing the cotyledons and the V-leaves (Croizat's "first true leaves"). 2) An epicotyl (or primary axis) is depicted to extend beyond the V-leaf node. 3) Lateral branches are depicted to arise from an aborted epicotylar stump situated above the V-leaf node. 4) The first two lateral branches are not depicted as axillary structures. In *C. maculata* the internode between cotyledons and V-leaves is virtually obliterated by their juxtaposition, there is no evidence of epicotyl development above the V-leaves, and the first two lateral branches definitely arise from the axils of the cotyledons. In a later exposition on the subject, Croizat (1960: 975 [illustration], 979–986 [text]) repeated his earlier description and specifically argued against axillary origin of the first two lateral branches. Except for the issue of branch position (discussed below), discrepancies between the above account and Croizat's descriptions of early development in *Chamaesyce* cannot be resolved

at present. Such important discrepancies beg for further investigation of more species.

That the first two lateral branches of *Chamaesyce* arise from axils of the cotyledons, as has been described or illustrated for various other species by Veh (1928), Goebel (1931), and Webster (1967), has been confirmed in the present study. Wheeler's (1941) statement that lateral branches in *Chamaesyce* arise without any relation to the leaves and Croizat's refusal to accept the axillary nature of B1 and B2 can be understood in light of the variability in branch position observed in *C. maculata* in the present study. The total number of branches varies with the age of the specimen, as do their angles of divergence relative to cotyledons and V-leaves. Further, branches may develop in either of two distinct patterns, cis and trans, both of which may coexist in any given population. Moreover, wild-collected specimens, through crowding, herbivory, or other physical damage, may not develop a typical expression of either branching pattern. When one considers the species to species variability in total number of branches produced, and the difficulty of analyzing branch position on pressed herbarium specimens, it is not surprising that Wheeler, Croizat, and others failed to perceive any pattern in branch development in the genus.

Although an extensive survey will be required to determine the constancy of cis and trans branching patterns in *Chamaesyce,* the diversity of expression of these two patterns in *C. maculata* may well be sufficient to explain branching patterns throughout the genus. Both cis and trans patterns were observed in *C. hirta* (Rosengarten and Hayden, 1983), and in *C. thymifolia* (Veh, 1928: fig. 24).

Plant form in certain herbaceous European legumes such as *Tetragonolobus purpureus* Moench (*Lotus tetragonolobus* L.), and *Scorpiurus muricatus* L. (including *S. subvillosus* L. and *S. sulcatus* L.), *S. vermiculatus* L., and *Securigera securidaca* (L.) Degen & Dörfler (*S. coronilla* DC.) (Dormer, 1945) appears analogous to that of *C. maculata.* In these legumes the apical meristem of the plumule is reported to be completely lacking and, moreover, these plants also produce clusters of branches from the cotyledonary node. The arrangement of these branches, as described by Dormer (1945), conforms to the trans pattern defined above.

The split lateral traces of the cotyledonary nodes of *C. maculata* and *C. hirta* (Rosengarten and Hayden, 1983) are of interest because this nodal configuration has been poorly known (Howard, 1970). Veh (1928: fig. 5) illustrated

the course of one split lateral trace, but he did not illustrate the total pattern of traces at the cotyledonary node; it seems safe to conclude, however, that the vasculature of the cotyledonary node in "*E. congenera*" is essentially similar to that described here. Apparently, the trilacunar node with common split lateral traces has not been recorded previously for Euphorbiaceae (Howard, 1970; Singh, 1972; Sehgal and Paliwal, 1974).

If anatomy of branch development described here for *C. maculata* proves typical for the genus, significant revisions in concepts of homologies of stems and leaves between *Chamaesyce* and *Euphorbia* subgenus *Agaloma* may be necessary. In *Euphorbia* subgenus *Agaloma* (Raf.) House the epicotyl produces a typical erect leafy stem (bearing numerous V-leaves); this vegetative stem is terminated by a whorl of leaves subtending a cyathium. Further cyathia develop in the forks of pleiochasial systems which arise from the axils of the whorl of leaves subtending the first cyathium. In essence, traditional interpretation (Roeper, 1824; Goebel, 1931; Degener and Croizat, 1938; Wheeler, 1941; Prokhanov, 1949; Croizat, 1960; Webster, 1967) holds the cluster of leafy lateral branches of *Chamaesyce* to be homologous with the terminal whorl of bracteate cyathium-bearing stems of *Euphorbia* subgenus *Agaloma*. Thus, *Chamaesyce* is thought to have arisen by reduction or virtual elimination of the vegetative phase, bringing the cyathium-bearing whorl to near ground level. Since the first two lateral branches in *C. maculata* arise in the axils of the cotyledons, and since subsequent branches develop de novo from the bases of preexisting branches, resemblance between the radiating branches of this *Chamaesyce* with the pleiochasial whorl of *Euphorbia* seems largely superficial. Further comparative anatomical studies are currently underway to examine the purported homologies of form in these plants.

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