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SEEDLING DEVELOPMENT IN SPECIES OF *CHAMAESYCE* (EUPHORBIACEAE) WITH ERECT GROWTH HABITS

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ABSTRACT

Seedling development is described for *Chamaesyce hirta*, *C. hypericifolia*, and *C. mesembrianthemifolia* as discerned by light microscopy and scanning electron microscopy. Although these species ultimately develop erect to ascending growth habits, epicotyl development is limited to the production of a single pair of leaves located immediately superjacent to and decussate with the cotyledons. The shoot system develops from one or more buds located in the axils of the cotyledons. In all respects, seedling ontogeny is very similar to that of previously studied prostrate species of *Chamaesyce*. Evidence from seedling ontogeny thus contradicts a hypothesis concerning homologies of plant form pertinent to the origin of *Chamaesyce* from *Euphorbia* that was first articulated by Roeper in 1824. These results support an alternative hypothesis based on proliferation of branches from the cotyledonary node in hypothetical ancestral elements within *Euphorbia* where this morphology can be found in perennial hemicryptophytes as well as certain annual species.

RESUMEN

Se describe el desarrollo de la semilla de *Chamaesyce hirta*, *C. hypericifolia*, y *C. mesembrianthemifolia* al microscopio óptico y microscopio electrónico de barrido. Aunque estas especies desarrollan finalmente hábitos de crecimiento de erectos a ascendentes, el desarrollo del epicótilo se limita únicamente a la producción de un par de hojas localizadas inmediatamente encima y decusadas con los cotiledones. El sistema de ramas se desarrolla a partir de una o más yemas localizadas en las axilas de los cotiledones. La ontogenia de la semilla es en todos los aspectos muy semejante a la de las especies de *Chamaesyce* postradas estudiadas previamente. Esta evidencia de la ontogenia de la semilla contradice la hipótesis relativa a las homologías, de la forma de la planta, relativas al origen de *Chamaesyce* a partir de *Euphorbia* emitida por Roeper en 1824. Estos resultados apoyan la hipótesis alternativa basada en la proliferación de ramas a partir del nudo de los cotiledones en los hipotéticos elementos ancestrales de *Euphorbia* donde puede encontrarse esta morfología en hemicriptófitos perennes así como en algunas especies anuales.

The genus *Chamaesyce* Gray can be distinguished from its close relatives in *Euphorbia* L. by a series of morphological, physiological, and developmental characters (Webster 1967, 1994; Koutnik 1984). The peculiar features of seedling ontogeny in *Chamaesyce* are often asserted to be characteristic for the genus (Degener & Croizat 1938; Koutnik 1987). However,

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seedlings of only a few species have been studied anatomically (Veh 1928; Mangaly et al. 1979; Rosengarten & Hayden 1983; Hayden 1988). Moreover, these few anatomical studies have generally focused on species of section *Chamaesyce*, a group characterized by radiating, prostrate branches. This paper describes seedling development in species with erect to ascending growth habits for comparison with the known structures and developmental events of prostrate species. Further, this paper critically assesses the interpretation of Mangaly et al. (1979) who described extra-axillary origin of lateral branching in seedlings of *Chamaesyce* and it is the first study to examine *Chamaesyce* seedlings with the scanning electron microscope (SEM).

We document and describe seedling development for three species representing two sections of the genus characterized by erect to ascending stems. *Chamaesyce hypericifolia* (L.) Millsp., the type species of section *Hypericifoliae* (Boiss.) Hurus., is a widely distributed weed (Holm et al. 1979) thought originally to be native to warm regions of the Americas (Webster 1967; Koutnik & Huft 1990). *Chamaesyce hirta* (L.) Millsp. is also classified in section *Hypericifoliae* and has similar present day status as a pantropical weed (Cardenas et al. 1972; Holm et al. 1979); however, it may be native to both the New and the Old World tropics (Koutnik & Huft 1990). *Chamaesyce mesembrianthemifolia* (Jacq.) Dugand is a shrubby plant classified in section *Sclerophyllae* (Boiss.) Hurusawa and found near seashores of the Caribbean and northern South America (Long & Lakela 1976; Acevedo-Rodríguez 1996). Although *C. hypericifolia* is often characterized as an herb, under favorable conditions it can produce weakly woody stems approaching a meter in height and 1 cm in basal diameter; thus, it can attain a stature comparable to that of *C. mesembrianthemifolia*. In contrast, *C. hirta* is smaller, and somewhat intermediate between the prostrate growth habit typical of section *Chamaesyce* and the erect growth habits of sections *Hypericifoliae* and *Sclerophyllae*. In *C. hirta*, each plant produces multiple stems, but seldom as many as found in species of section *Chamaesyce*, and while these stems are sometimes more or less prostrate, they more frequently ascend, but seldom to heights exceeding 15 or 20 cm.

MATERIALS AND METHODS

Specimens of *C. hirta* were collected in 1982 from weeds among nursery stock in a Richmond, VA, garden center. Plants of *C. mesembrianthemifolia* were collected at West Summerland Key, Florida, in 1983 and plants and seeds of *C. hypericifolia* were collected from Big Pine Key, Florida, in 1986. All three species have been maintained subsequently in greenhouse cultivation at the University of Richmond. Adult plants were prolific in cultivation; over several years *C. hypericifolia* produced many thousands of seedlings whereas *C. hirta* and *C. mesembrianthemifolia* each produced several hundred. Preparations of *C. hirta* and *C. hypericifolia* were derived from seedlings obtained spontaneously from containers of sterile soil placed in the vicinity of mature greenhouse-grown plants. Preparations of *C. mesembrianthemifolia* were derived largely from a dense mass of seedlings collected in the wild from the surface of a small anthill and supplemented with greenhouse materials. Herbarium vouchers at URV for materials studied include: *C. hirta—Hayden 614*; *C. mesembrianthemifolia—Hayden 709*; and *C. hypericifolia—Hayden 1433*, *3252* and *3281*. All specimens were preserved in FAA (formalin—acetic acid—70% alcohol). Numbers of seedlings studied for each species are as follows: *C. hirta*—30 for light microscopy (LM); *C. hypericifolia*—30 for LM and 42 for SEM; *C. mesembrianthemifolia*—17 for LM and 14 for SEM.

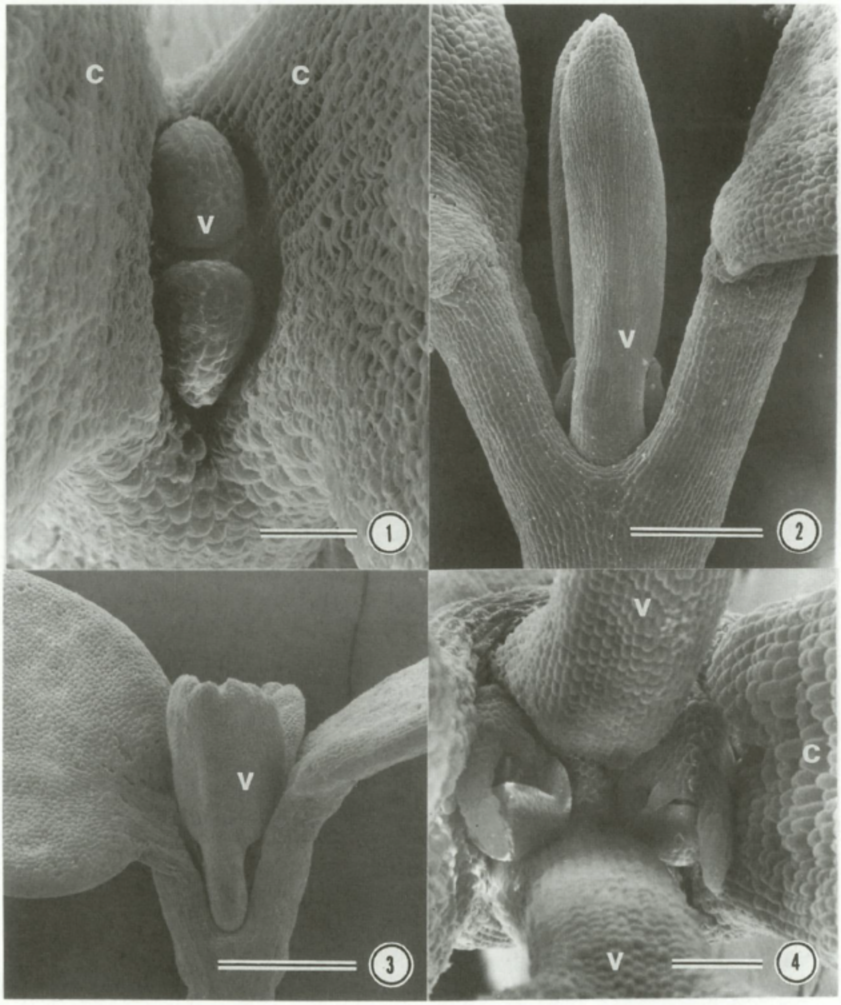
For light microscopy, fixed seedlings were trimmed to remove structures more than 5 mm below or above the cotyledonary node (if present), dehydrated in a tert-butanol series, embedded in paraffin, sectioned at 10 µm, affixed to slides with Bissing's adhesive (Bissing 1974), and stained in a combination of safranin and hematoxylin (Johansen 1940). Photomicrographs were prepared from Kodak Technical Pan film developed in Kodak HC110 developer at dilution F. For SEM, fixed seedlings were trimmed, dehydrated in ethanol, subjected to critical point-drying with CO_2 as the intermediate solvent, affixed to stubs with aluminum tape, sputter-coated with a gold-palladium mixture to a thickness of 40 nm, and observed with a Hitachi S-2300 SEM. Scanning electron micrographs were prepared from Kodak Tri-X film developed in Kodak HC110 developer at dilution B.

RESULTS

External morphology

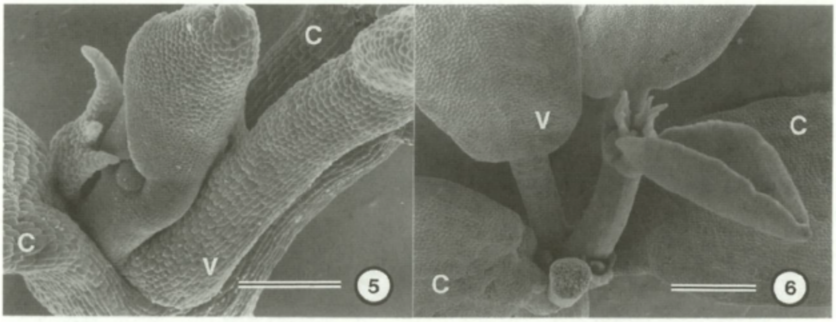
In the seed and during initial stages of germination, the cotyledons are tightly appressed. Upon germination, blades of the cotyledons diverge first, leaving their petioles in close contact. Soon, however, petioles also diverge, revealing primordia for the first pair of true leaves (Figs. 1–3). Following Hayden (1988), these first leaves are referred to as v-leaves to indicate their supposed homology with leaves on the vegetative axis of *Euphorbia* species classified in subgenus *Agaloma* (Raf.) House and subgenus *Esula* Pers. Upon their full expansion, v-leaves are inserted directly superjacent to and decussate with the cotyledons (Fig. 3). There is no residue of meristematically active cells at the epicotyl apex following v-leaf formation (Figs. 4, 9, 10, 15–17). Seedling growth continues via lateral branches that arise from buds axillary to the cotyledons (Figs. 4–8, 10–12, 15, 17, 20).

Although multiple buds routinely develop in the axils of each cotyledon (Figs. 11, 20), just a single lateral branch dominates early growth in *C. hypericifolia* and *C. mesembrianthemifolia* (Figs. 5, 6). This first, dominant branch is



FIGS. 1–4. Seedlings of *Chamaesyce*, SEM. 1. *C. hypericifolia*, *Hayden 3281*, v-leaf primordia, top view of seedling soon after divergence of cotyledonary petioles; bar = 100 µm. 2. *C. hypericifolia*, *Hayden 3690*, cotyledons and v-leaf primordia, lateral view; bar = 250 µm. 3, 4. *C. mesembrianthemifolia*, *Hayden 709*. 3. Cotyledons and v-leaf primordia, lateral view; bar = 500 µm. 4. Epicotyl apex, petioles of cotyledons and v-leaves, and cotyledonary axillary buds; bar = 100 µm. c = cotyledon; v = v-leaf.

erect or slightly inclined from vertical. Growth of additional lateral branches at the cotyledonary node as plants grow older is highly variable in these two species. Vigorous specimens with sparse or no competing nearby vegetation tend to produce one or two additional basal branches, but these remain smaller than the first branch unless the latter is removed or dam-



FIGS. 5,6. Cotyledonary node of seedlings of *Chamaesyce mesembrianthemifolia*, *Hayden 709*, each with one v-leaf removed, SEM. 5. Bud in axil of cotyledon; bar = 250 µm. 6. Young lateral branch, arising from axil of cotyledon; bar = 500 µm. c = cotyledon; v = v-leaf.

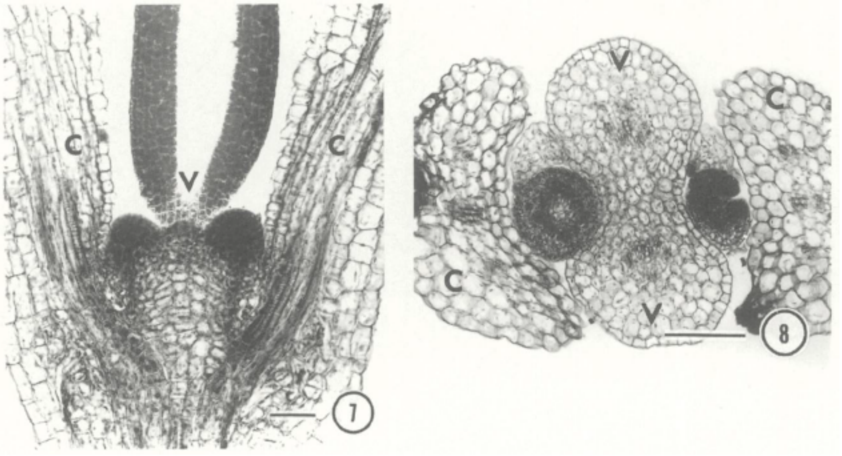
aged. It is not unusual for nearly the entire aerial system in these species to develop from the first dominant branch that arises at the cotyledonary node.

Initially, seedlings of *C. hirta* are similar to those of *C. hypericifolia* and *C. mesembrianthemifolia*. However, in *C. hirta*, multiple lateral branches develop from the cotyledonary node. The first two branches arise one each from the axils of the cotyledons and, frequently, two additional branches develop from buds located at the bases of the first two branches.

Anatomical structure

Cotyledon stage.—The hypocotyl is traversed by four vascular bundles that ascend from the radicle to the cotyledonary node. Two of these bundles, each located on opposite sides of the axis, constitute the median traces to the cotyledons; each passes directly from the hypocotyl into the petiole of its respective cotyledon. The other two bundles form four lateral traces to the cotyledons; each splits into two bundles at the cotyledonary node and the resultant pair of traces diverge towards cotyledons on opposite sides of the stem. Cotyledonary node vasculature is thus trilacunar with split laterals (Fig. 19). The system of non-articulated branched laticifers that ultimately permeates the plant body arises from initials located external to the vascular tissue at the cotyledonary node.

V-leaves.—V-leaves arise on the flanks of the epicotyl apex (Figs. 1, 9). As soon as v-leaf primordia can be detected, cells of the epicotyl apex are larger and more vacuolate than those of the v-leaf primordia (Fig. 9). Thus, the only meristematically active cells of the epicotyl apex are fully consumed in formation of the v-leaves. Each v-leaf is vascularized by three traces that differentiate from procambium near the split lateral traces to the cotyledons; of the three traces for a given v-leaf, two traces insert on one side of the cotyledonary split lateral and one trace inserts on the opposite side. General



FIGS. 7, 8. Seedlings of *Chamaesyce hirta*, *Hayden 614*, LM. 7. Cotyledons, their lateral buds, and portions of one v-leaf, longitudinal section in the cotyledonary plane; bar = 50 µm. 8. Cotyledon petioles, their lateral buds, and v-leaf petioles; bar = 100 µm. c = cotyledon; v = v-leaf.

vascular development of the seedling continues as the v-leaves develop. Once the v-leaves are fully expanded, the hypocotyl contains four well-defined vascular strands that supply the first four leaves of the seedling.

Branch development.—SEM micrographs of intact seedling apices and LM sections reveal branch primordia in the axils of the cotyledons (Figs. 4, 7, 8, 12, 15, 17, 20). Lateral branches arise from ordinary lateral buds located at the cotyledonary node. The densely-stained and meristematically active lateral buds (or the subsequent active branch apex, e.g., Fig. 13) contrast sharply with the inert epicotyl apex (Figs. 7, 8, 10, 12, 17). Each axillary bud is also associated with a non-vascularized, persistent stipule-like flap of tissue (Figs. 10, 11, 18). Whereas stipules located on subsequent nodes (i.e., nodes of the lateral branch) generally consist of a planar interpetiolar sheath, stipules at the cotyledonary node are elongate and bear a distinct curve that conforms with the curved surface of its associated bud primordium.

At their initiation, the buds that produce lateral branches are clearly not aligned with the axis defined by the hypocotyl and truncated epicotyl. In time however, the first, dominant, branch of fully erect species assumes an apparent axial position (Fig. 14), a consequence of its growth and expansion concomitant with that of the hypocotyl.

DISCUSSION

Based on previous literature (Veh 1928; Mangaly et al. 1979; Rosengarten & Hayden 1983; Hayden 1988) and the species described above, early stages of seedling development in *Chamaesyce* appear to be similar in sections *Chamaesyce*, *Hypericifoliae*, and *Sclerophyllae*. Common features include the vascular architecture of the cotyledonary node, the development of v-leaves and their vascular supply, and the origin of lateral branches from the axils of the cotyledons. The potential for multiple branches from the cotyledonary node is also uniform throughout the species for which seedling ontogeny is known. The chief differences between previously studied prostrate species and the erect or semi-erect species documented here involves the number of lateral branches that develop from the axils of the cotyledons and their orientation with respect to gravity. Thus, species of section *Chamaesyce* routinely produce multiple branches that radiate at ground level, whereas most species of sections *Hypericifoliae* and *Sclerophyllae* produce one dominant, erect branch and, sometimes, another small, subsidiary branch. *Chamaesyce hirta* appears somewhat intermediate in that it produces a limited number of semi-erect branches.

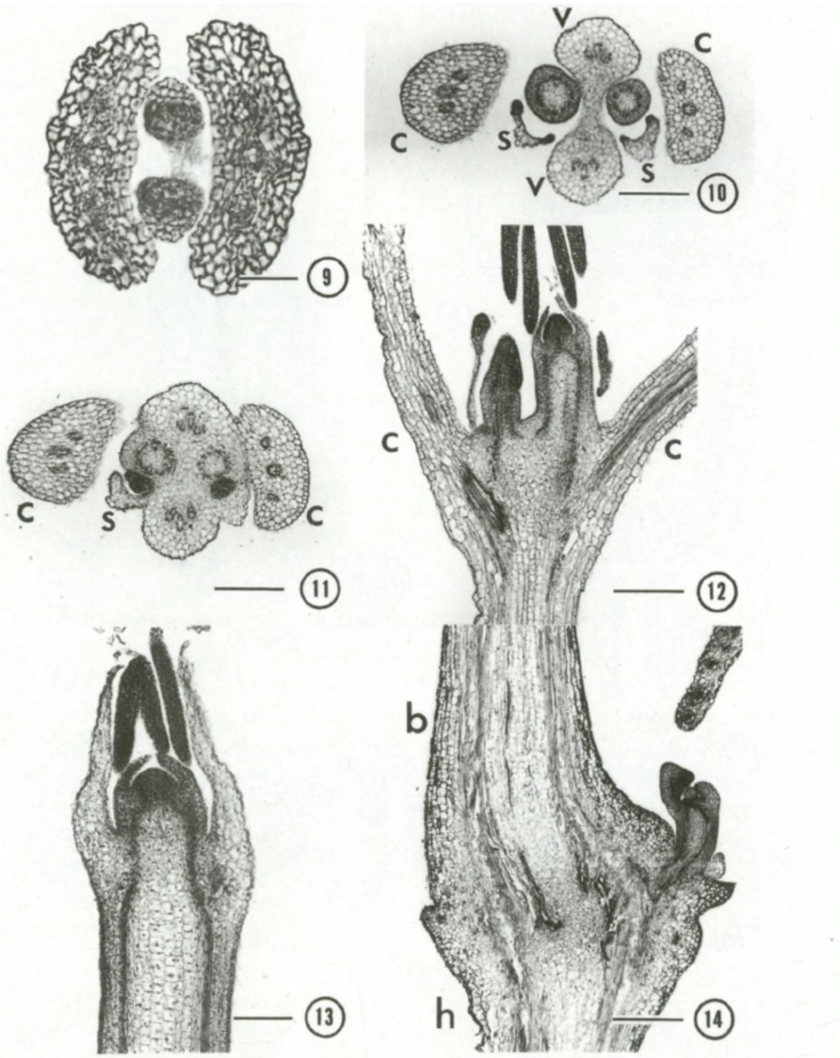
Mangaly et al. (1979) reported on seedling development in *Chamaesyce hirta* and *C. thymifolia* (L.) Millsp. We find their illustrations consistent with the anatomy and morphology of the species reported here and in Hayden (1988). We differ, however, in the interpretation of certain aspects of seedling structure and developmental processes. For example, Mangaly et al. (1979) failed to notice the absence of an epicotylar apical meristem upon development of the v-leaves. Thus, they interpreted the first lateral branch, which actually develops from the axil of a cotyledon, to be the "main axis" and they also described the second lateral branch, which develops from the axil of the other cotyledon, as "extra-axillary." On the basis of gross external morphology, numerous authors have expounded on the significance of the absence of true epicotyl development (main axis) in *Chamaesyce* (e.g., Wheeler 1941; Degener & Croizat 1938; Webster 1967). Both the absence of epicotyl and the axillary origin of the first two branches are clearly indicated by the LM and SEM evidence presented here. Hayden (1988) earlier refuted other evidently erroneous ontogenetic interpretations of seedling structure in *Chamaesyce* found in Veh (1928) and Degener and Croizat (1938).

We hypothesize that seedling form in *Chamaesyce* is derived from plants with growth habits that are widespread in *Euphorbia* subgenus *Agaloma* and subgenus *Esula*. Such plants produce ordinary, vegetative stems from the seedling epicotyl that eventually terminate in a single cyathium followed by a pleiochasial and dichasial pattern of cyathium production; they also produce additional vegetative axes from the cotyledonary node which also become pleiochasial or dichasial (Fig. 21-A). *Euphorbia helioscopia* L., as illustrated in Korsmo (1954; fig. 111) or Holm et al. (1997; fig. 41-2), provides a good example of this growth habit in an annual species. Reduction of the epicotyl to the first pair of leaves and accelerated proliferation of branches from the cotyledonary node (Fig. 21-C) would result in the growth habit found in *Chamaesyce*. By this interpretation, the majority of the shoot system in *Chamaesyce* would be homologous with proliferative cotyledonary branches in species of *Euphorbia*.

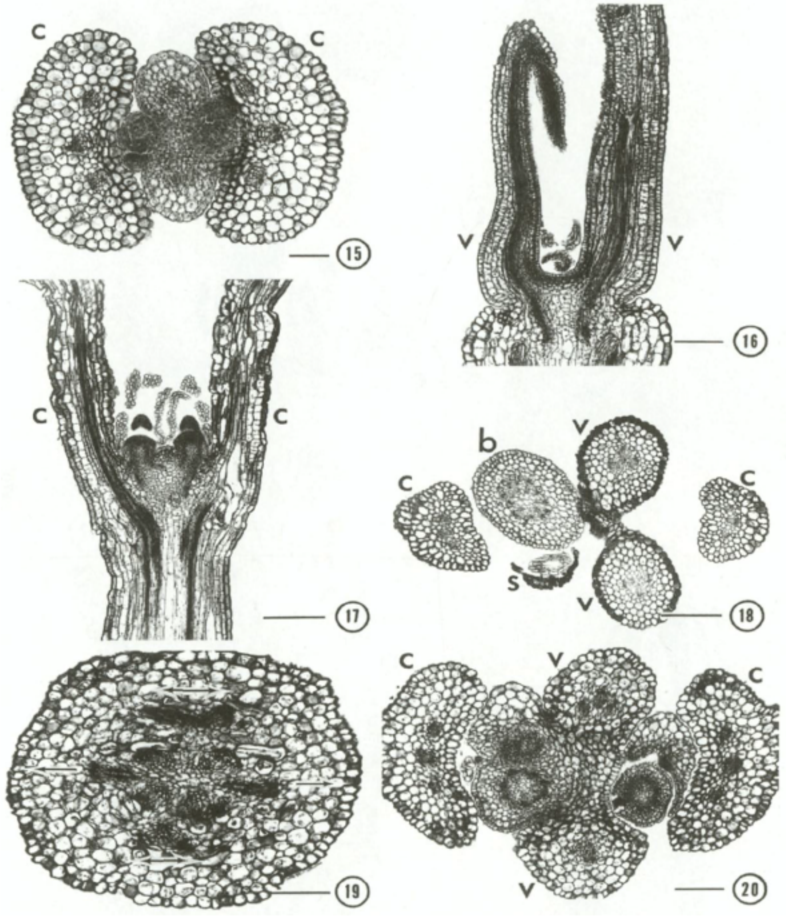
The hypothesis of homology at the cotyledonary node described above stands in partial contradiction to the oft-cited hypothesis of Roeper (1824) (Fig. 21-A,-B,-D) who said that foreshortening of the epicotyl results in development of pleiochasial branches (inflorescence axes) at ground level (see, for example, Wheeler 1941; Webster 1967). Pleiochasial branches in *Euphorbia* arise individually from the axils of a whorl of leaves at the apex of the epicotyl-derived main axis of the plant (Hayden 1988). If lateral branches in seedlings of *Chamaesyce* developed also from the axils of the v-leaves, then Roeper's hypothesis could be supported. However, this paper provides additional confirmation of the fact that lateral branches in *Chamaesyce* are strictly axillary to the cotyledons and never arise from axils of the v-leaves (Hayden 1988).

Plants with well-developed epicotyls and proliferative branches from the cotyledonary node, the hypothesized condition in ancestors of *Chamaesyce*, are common in *Euphorbia*. This growth habit occurs in both hemicryptophytic perennials and annuals. Among the hemicryptophytic forms, some familiar garden examples from subgenus *Esula* include *Euphorbia myrsinites* L. and *E. epithymoides* L. (*E. polychroma* A. Kern.); *Euphorbia corollata* L., widespread in eastern North America, and its close relatives in subgenus *Agaloma* section *Tithymalopsis* (Klotzsch & Garcke) Boiss., also proliferate from the cotyledonary node. Examples of annual species with proliferative branches from the cotyledonary node include *E. helioscopia* from subgenus *Esula*, *E. exstipulata* Engelm. from subgenus *Agaloma*, and *E. dentata* Michx. from subgenus *Poinsettia* (Graham) House. In *Chamaesyce*, species with proliferative cotyledonary nodes include hemicryptophytic perennials (Simmons & Hayden 1997), prostrate annuals (Hayden 1988), erect to ascending annuals (present study), sub-shrubs (present study), and small trees (Koutnik 1987). In contrast to the situation in *Chamaesyce*, *Euphorbia* species possess well-developed epicotyls.

Despite the uniformity of form and development that seems to be emerging from studies of *Chamaesyce* seedlings, examination of a few additional critical taxa appears warranted. Based on our unpublished observations of very limited material, seedlings of *C. acuta* (Engelm.) Millsp. appear to possess a relatively normal pattern of seedling development, with well-developed epicotyls. *Chamaesyce acuta* also lacks C4 photosynthesis (Webster et al. 1975) and its inclusion within *Chamaesyce* might thus be doubted. Confirmation



FIGS. 9–14. Seedlings of *Chamaesyce hypericifolia*, LM; 9, 13, *Hayden 3252*; 10–12, 14, *Hayden 3281*. 9. Petioles of cotyledons and v-leaf primordia, cross section at the epicotyl apex; bar = 50 µm. 10. Petioles of cotyledons, their lateral buds, and petioles of fully expanded v-leaves, cross section at the epicotyl apex; bar = 200 µm. 11. Same seedling as Fig. 10, cross section just above insertion of cotyledons; bar = 200 µm. 12. Petioles of cotyledons and their axillary buds, longitudinal section in the cotyledonary plane; bar = 200 µm. 13. Apex of lateral branch, longitudinal section; bar = 100 µm. 14. Cotyledonary node of seedling dominated by one lateral branch, longitudinal section in the intercotyledonary plane; bar = 200 µm. b = branch from axil of cotyledon, c = cotyledon, h = hypocotyl, s = stipule-like flap, v = v-leaf.



FIGS. 15–20. Seedlings of *Chamaesyce mesembrianthemifolia*, *Hayden* 709, LM. 15. Petioles of cotyledons, their lateral buds, and petioles of v-leaves, cross section below the epicotyl apex; bar = 50 µm. 16. v-leaf primordia, longitudinal section in the intercotyledonary plane; bar = 100 µm. 17. Petioles of cotyledons and their lateral buds, longitudinal section in the cotyledonary plane; bar = 200 µm. 18. Base of lateral branch arising from cotyledon axil and adjacent petiole bases of cotyledons and v-leaves, cross section at the epicotyl apex; bar = 200 µm. 19. Cotyledonary node from seedling with expanded v-leaves, note median traces (single arrows) and split lateral traces (double-headed arrows) to the cotyledons; bar = 100 µm. 20. Petioles of cotyledons, their lateral buds, and petioles of v-leaves; bar = 100 µm. b = branch from axil of cotyledon, c = cotyledon, s = stipule-like flap, v = v-leaf.

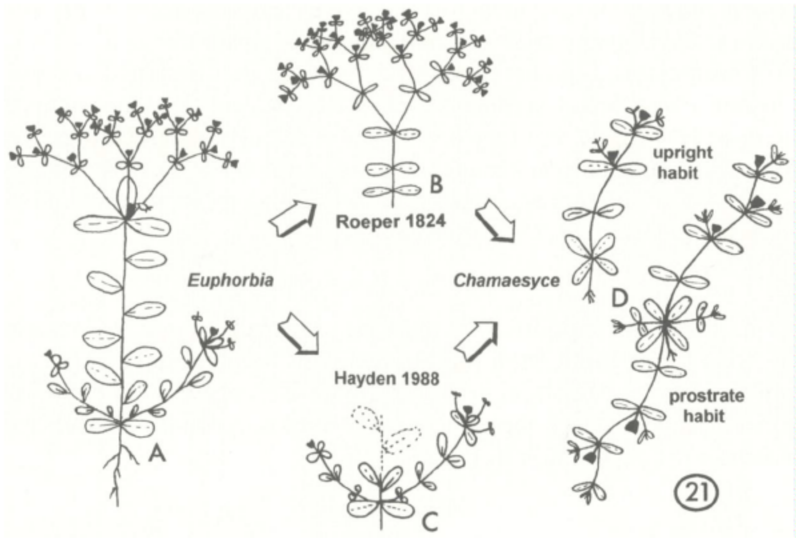


FIG. 21. Comparison of Roeper's (1824) and Hayden's (1988) hypotheses concerning the origin of the plant body in *Chamaesyce*. A. Hypothetical ancestor with habit common in *Euphorbia* subgenus *Agaloma* or subgenus *Esula*, i.e., epicotyl well-developed, with terminal cyathium/pleiochasium system and reiterative lateral branches from the cotyledonary node. B. Hypothetical intermediate (Roeper's Hypothesis) with reduced epicotyl development and no reiterative lateral branches. C. Hypothetical intermediate (Hayden's Hypothesis) with epicotyl aborted above the first node. D. Erect and prostrate growth habits in *Chamaesyce*.

of seedling development in this and supposedly related species of section Acutae (Boiss.) Webster (see discussion in Mayfield 1991) would thus prove useful. Also, seedling development in *C. potentilloides* (Boiss.) Croizat [=*C. caecorum* (Mart. ex Boiss.) Croizat] of southern Brazil and adjacent regions is completely unknown; because this is a hemicryptophyte species that routinely produces pleiochasial inflorescences reminiscent of the reproductive branches in subgenus *Agaloma* and Esula of *Euphorbia* (Simmons & Hayden 1997), a developmental study of its seedlings may provide useful phylogenetic insight for the genus as a whole. Finally, certain Hawaiian *Chamaesyce* species endemic to the island of Kauai appear to have ordinary seedling development with well-developed epicotyls (Koutnik 1987); anatomical comparisons between these epicotyl-present and epicotyl-absent species of *Chamaesyce* should prove critical in assessing relationships among the Hawaiian species of *Chamaesyce*.

A developmental mutant known in *Arabidopsis* Heynh. (Brassicaceae) results in a pattern of epicotyl deletion reminiscent of this hallmark feature of seedling ontogeny in *Chamaesyce*. In *Arabidopsis*, plants homozygous for the *WUSCHEL (WUS)* allele form a pair of leaves above the cotyledons but fail to develop any other ordinary epicotylar structure (Clark 1997). In *WUS* mutants, the epicotyl apex remains somewhat flattened and essentially non-meristematic, although it can initiate adventitious meristems that reiterate the abruptly terminated structure of these mutant seedlings (Clark 1997). Evidently, ordinary branches do not form at the cotyledonary node in these *WUS* mutants of *Arabidopsis*, so the analogy with developmental events in *Chamaesyce* is only approximate.

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