4-1992

A Survey of Mucilaginous Testa in *Chamaesyce*

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Recommended Citation

Jordan, Martha S., and W. John Hayden. "A Survey of Mucilaginous Testa in *Chamaesyce*." *Collectanea Botanica (Barcelona)* 21 (April 1992): 79-89.

A Survey of Mucilaginous Testa in *Chamaesyce*

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Resum

JORDAN, M. S. & W. J. HAYDEN (1992). Revisió dels mucílags de la testa en *Chamaesyce*. Collect. Bot. (Barcelona) 21:79-89.

Han estat estudiades les granes de *Chamaesyce* segons la presència o no de testa mucilaginosa. Les mostres van ésser seleccionades per tal de representar totes les principals seccions del gènere. Les observacions han estat fetes al microscopi de dissecció després d'hidratar breument les llavors; addicionalment s'han fet observacions en el MER de llavors seques, senceres i fracturades, de les espècies seleccionades. Amb poques excepcions, la major part de les subseccions de Boissier presenten els tests de presència de mucílags a les granes positius; no obstant, els mucílags generalment no es presenten en les subseccions *Gymnadeniae* i *"Sclerophyllae"*, per a les quals l'absència de mucílags és considerada com una pèrdua secundària a partir d'avantpassats mucilaginosos. Encara que la producció de mucílags s'associa amb les capes subepidèrmiques ben definides de les macroesclereides, en realitat és la capa de cèl·lules superficials la que secreta mucílags. Les cèl·lules secretores de mucílags i les macroesclereides de la testa madura s'interpreten com desenvolupades a partir de les capes epidèrmiques dels teguments extern i intern, respectivament. El mucílag de les granes possiblement juga un paper en la hidratació i/o dispersió de les granes.

Mots claus: testa, mucílag, *Chamaesyce*, MER, estructura de la grana.

Abstract

JORDAN, M. S. & W. J. HAYDEN (1992). A Survey of Mucilaginous Testa in *Chamaesyce*. Collect. Bot. (Barcelona) 21:79-89.

Seeds of *Chamaesyce* were studied for presence of mucilaginous testa. Samples were selected to represent all major systematic sections within the genus. Observations were made with a dissecting microscope following brief hydration of seeds; additional SEM observations of both intact and fractured dry seeds were made for selected species. With few exceptions, most of Boissier's subsections test positively for seed mucilage; however, mucilage is generally absent in subsections *Gymnadeniae* and *"Sclerophyllae"*, for wich absence of mucilage is regarded as secondary loss from mucilagionus ancestors. Although mucilage production is associated with a well-defined subepidermal layer of macroesclereids, it is the surface layer of cells that actually secrete mucilage. Mucilage secreting cells and macroesclereids of mature testa are interpretted to develop from the epidermal layers of outer and inner integuments, respectively. Seed mucilages may play a role in seed hydration and/or seed dispersal.

Keywords: Testa, Mucilage, *Chamaesyce*, SEM, Seed Structure.

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INTRODUCTION

The value of seed and testa morphology in the systematics of *Euphorbia* L., *sensu lato*, is well-known (KROCHMAL, 1952; EHLER, 1976). Size, shape, surface texture, and presence or absence of a caruncle are all routinely employed to help distinguish species and other subgeneric taxa in this exceptionally diverse and speciose group. Seed features are especially useful in the segregate genus *Chamaesyce* S. F. Gray (see e.g., BURCH 1966; MCVAUGH, 1961; WHEELER, 1941).

That seeds of some species of *Euphorbia* and *Chamaesyce* exude a mucilaginous surface layer following hydration has received sporadic comment in previous literature. MANDL (1926) described such a layer in species of *Euphorbia* subgenus *Tithymalus*, as did RÖSSLER (1943), who also made note of seed coat mucilages in several species of *Chamaesyce*. Correll and Johnston (1970) mention the mucilaginous layer exuded by hydrated seeds of *Chamaesyce revoluta* (Engelm.) Small. CARLQUIST (1966, 1980) has discussed the presence and absence of mucilaginous seeds in relation to the dispersal of *Chamaesyce* to the Hawaiian Islands. In only one species, *C. maculata* (L.) Small (JORDAN et al., 1985; reported as *E. supina* Raf.), has the structure of the mucilaginous layer been studied in detail.

The present study was stimulated by the observation that, while the ability to produce mucilaginous exudations from testa seems to be widespread in *Chamaesyce*, some species, in particular, *C. mesembrianthemifolia* (Jacq.) Dugand and certain Hawaiian species (CARLQUIST 1966, 1980; KOUTNIK, 1987), lack this capacity. In order to ascertain the taxonomic distribution of mucilaginous testa in *Chamaesyce*, we describe here the results of a preliminary survey of all major species groups of *Chamaesyce* as classified by BOISSIER (1862). We also compare mucilaginous and non-mucilaginous seeds in the dry condition as viewed with SEM.

MATERIALS & METHODS

For the most part, seeds were obtained from herbarium specimens. However, seeds of a few species were obtained from mass collections of whole live plants dried in covered cardboard boxes in order to retain the ballistically dispersed seeds.

Specimens tested and their documentation are included in Table 1. Subsectional taxonomy follows BOISSIER (1862) with some modifications. We follow SUBILS (1977) who transferred *C. selloi* (Kl. & Gke.) Croizat from subsection "*Pleiadeniae*" to subsection "*Chamaesyce*" and KOUTNIK (1987) who moved *C. degeneri* (Sherff) Croizat & Degener from "*Sclerophyllae*" to *Gymnadeniae* (Boiss.) Koutnik. Further, we tentatively include *C. lata* (Engelm.) Small in subsection "*Chamaesyce*", since MAYFIELD (1991) has argued for its exclusion from subsection "*Acutae*". We also depart from Boissier's (1862) treatment of these plants by according them generic status separate from *Euphorbia* and have used combinations in the genus *Chamaesyce* wherever possible. Although many species have nomenclatural combinations available in both genera, this is not true for all, and not all of Boissier's subsections have been formally adopted as subgeneric taxa of *Chamaesyce*; these circumstances pose nomenclaturally awkward consequences in communication of our morphological information. Some species, for example the recently described "*Euphorbia*" *johnstonii* Mayfield, appear so close to the boundary between *Euphorbia* and *Chamaesyce* that their ultimate inclusion in the latter may be doubted. Further, Boissier's subsections, although a useful framework for a preliminary survey, must be considered provisional at best in light of the years that have passed since their first proposal. For these reasons we forego perfunctory coining of nomenclatural novelties for taxa without published names in *Chamaesyce* and, further, as a temporary means of communication, we have resorted to placing such names in

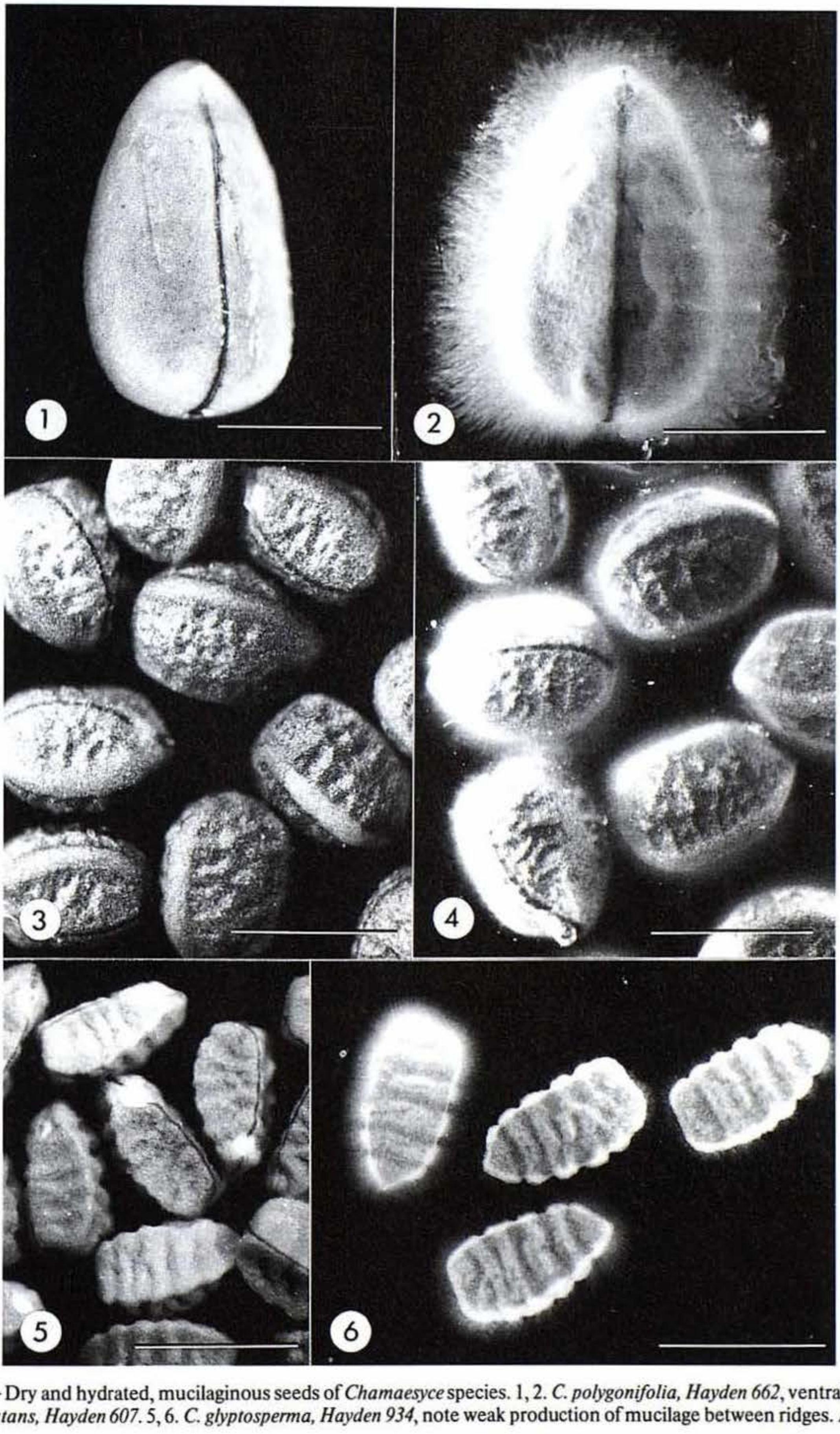

Fig. 1-6.— Dry and hydrated, mucilaginous seeds of *Chamaesyce* species. 1, 2. *C. polygonifolia, Hayden 662*, ventral views. 3, 4. *C. nutans, Hayden 607*. 5, 6. *C. glyptosperma, Hayden 934*, note weak production of mucilage between ridges. All bars = 1 mm.

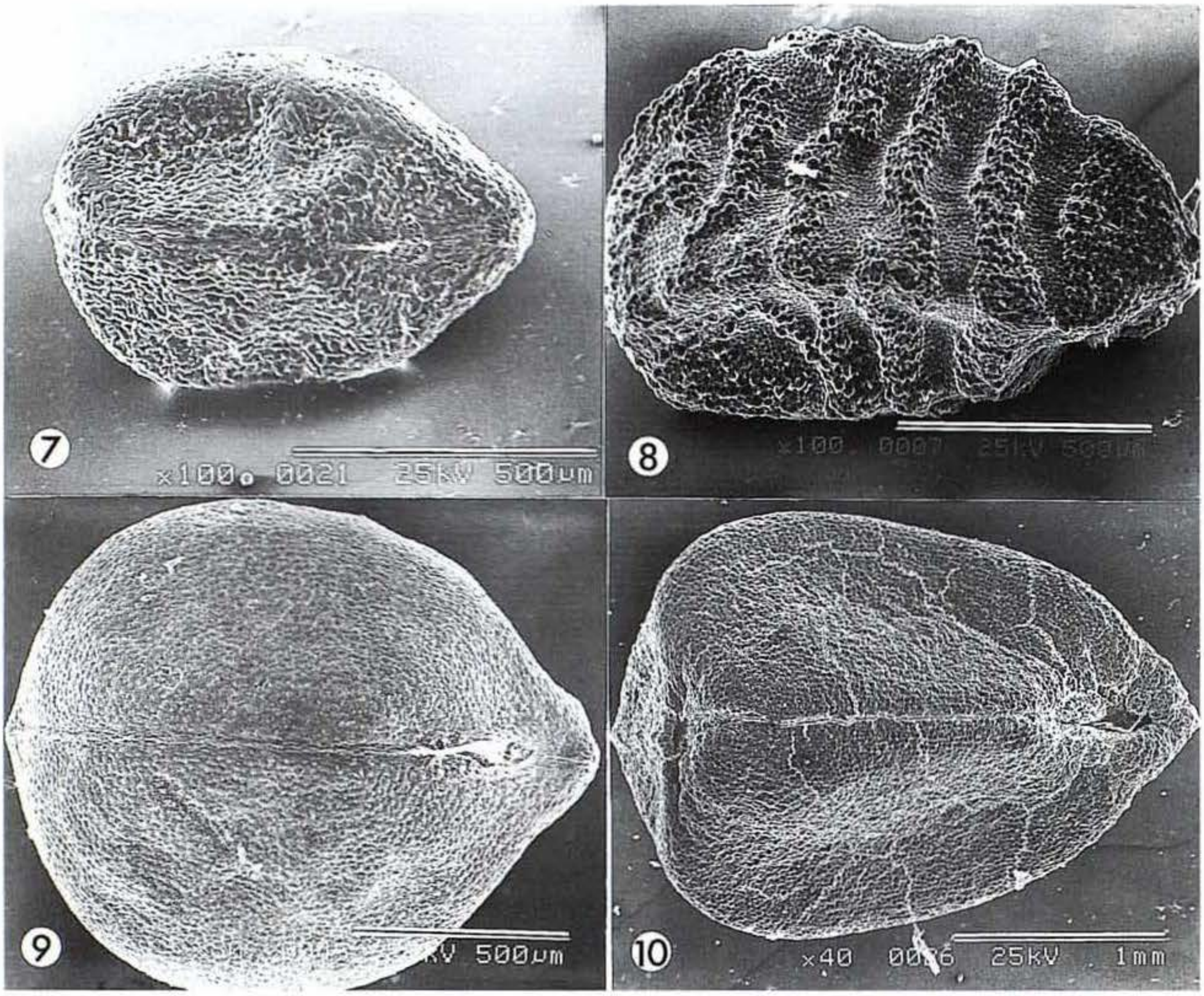

Fig. 7-10.— SEM of whole seeds of *Chamaesyce*. 7. *C. hypericifolia, Hayden 2050*, ventral view, potentially mucilaginous. 8. *C. glyptosperma, Hayden 934*, dorsal view; note contrast between potentially mucilaginous cells at ridges and non-mucilaginous cells between ridges. 9. *C. mesembrianthemifolia, Hayden 709*, ventral view, non-mucilaginous. 10. *C. acuta, Hayden 3140*, ventral view, potentially mucilaginous. 7-9, bars = 500 µm; 8, bar = 1 mm.

quotation marks. No new names, new combinations, nor new statuses are overtly intended in this publication.

Ability to produce a mucilaginous layer was assessed by placing several seeds from each collection in a drop of water and observing their reaction with a Nikon SMZ10 stereoscopic dissecting microscope at 10x to 40x. Seeds were kept moist and observations continued for a period of 5 minutes; if seeds showed no mucilaginous exudations within this time, mucilage was judged to be absent. Photomicrographs (Figures 1-6) were prepared from Kodak Tmax 100 film processed with Tmax developer.

Seeds of selected specimens were prepared for SEM as follows: Dry seeds were mounted directly on aluminum conductive tape affixed to specimen stubs. Intact seeds were mounted to expose both dorsal and ventral surfaces. Seeds of some species were sectioned transversely with a razor blade and mounted with the cut surface exposed. After mounting, seeds were placed on a 40 C warming tray in order to drive out residual moisture. Seeds were then sputter coated with 15 nm of gold-palladium mixture and observed with a Hitachi S-2300 SEM. Electronmicrographs (Figures 7-14) were prepared from 4" x 5" Kodak Tri-X film developed in Kodak HC110 developer at dilution "B."

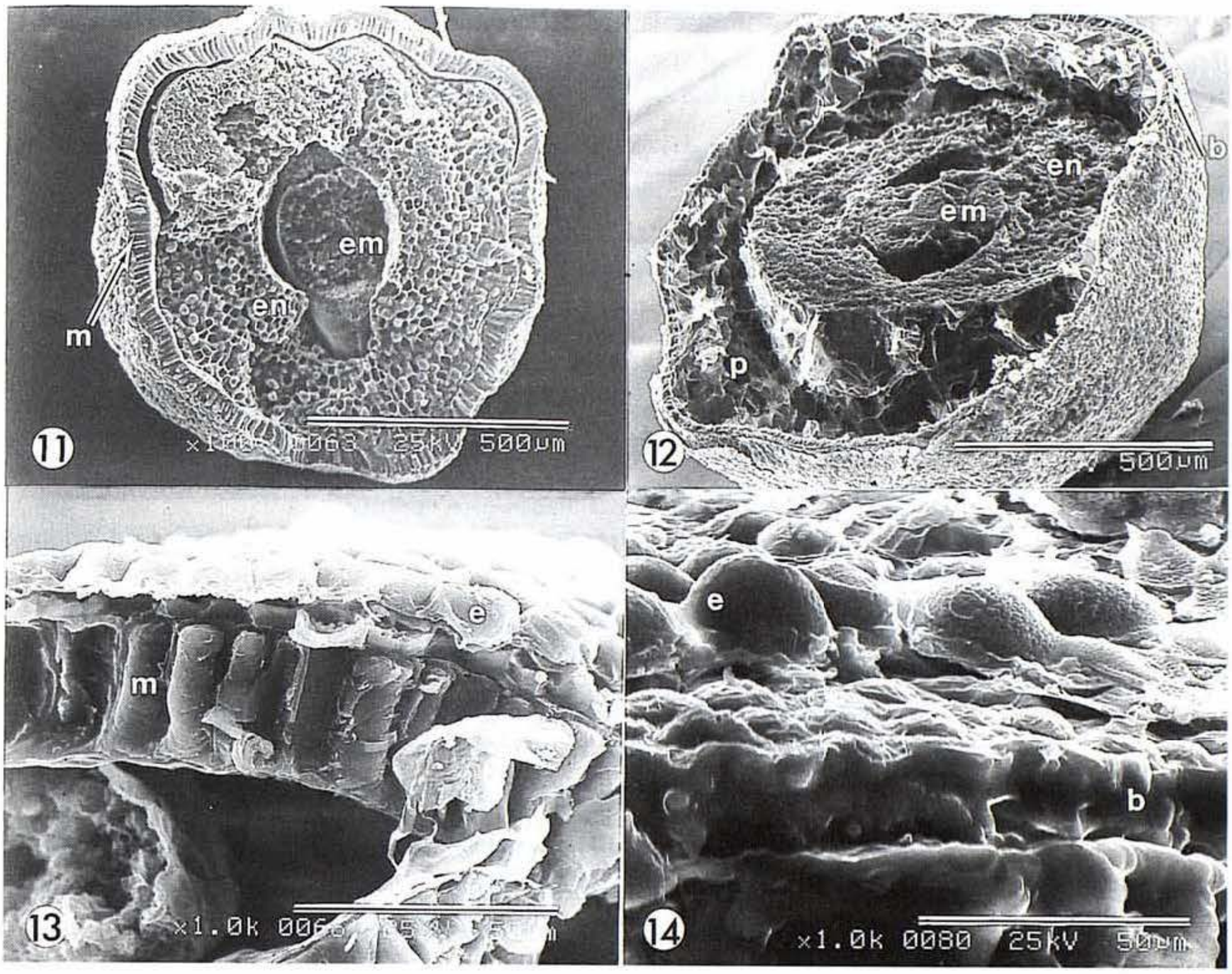

Fig. 11-14.— SEM of sectioned seeds of *Chamaesyce*. 11. *C. nutans, Hayden 607*, potentially mucilaginous seed xs. 12. *C. mesembrianthemifolia, Hayden 709*, non-mucilaginous seed xs. 13. *C. nutans, Hayden 607*, testa and subjacent tissue of potentially mucilaginous seed. 14. *C. halemanui, Koutnik s.n.*, testa and subjacent tissue of non-mucilaginous seed. 11 & 12, bars = 500 µm; 13 & 14, bars = 50 µm; b = brachysclereids, e = epidermis, em = embryo, en = endosperm, m = macrosclereids, p = parenchymatous cells.

RESULTS & DISCUSSION

Description of dry and hydrated seed surfaces. Many, but not all, species of *Chamaesyce* tested produce mucilage upon hydration of the seed coat. Reactions of the species tested are listed in Table 1, which also includes data for several species based on previous literature. Mucilaginous seeds generally react within 10 seconds following exposure to water. Cells of the surface layer of testa form opaque cylindrical projections extending at roughly right angles from the surface. Thickness of the mucilage layer varies from species to species, and can be roughly correlated with seed size. Individual mucilage strands from large seeds, such as *C. polygonifolia* (L.) Small (Figures 1, 2) or *C. acuta* (Engelm.) Millsp., approached 0.5 mm in length, whereas those of much smaller seeds, e.g., *C. hirta* (L.) Millsp., were less than 0.1 mm long. To the extent detectable at 40x mucilage layers observed were consistent with descriptions for *C. maculata* by JORDAN et al. (1985). We also confirm the report that the mucilaginous layer of this species can reform repeatedly under alternating cycles of wet and dry conditions (JORDAN et al., 1985); indeed, this capacity seems characteristic of all mucilaginous species examined.

Table 1. Presence (+) or absence (−) of mucilaginous layer derived from seed coats in response to externally applied water. Placement of species follows Boissier (1862), except as noted with an asterisk (*), see text for details. Herbarium acronyms follow Holmgren et al. (1990).

Mucilage	Species, specimen data, and/or reference.
	Subsect. *Gymnadeniae* (Boiss.) Koutnik
+	*C. celastroides* (Boiss.) Croizat & Degener. USA, Hawaii, Kauai: *Koutnik s.n.*
−	*C. clusiifolia* (Hook. & Arn.) Arthur. Carlquist (1980).
−	* *C. degeneri* (Sherff) Croizat & Degener. USA, Hawaii, Oahu: *Webster 13828* (DAV), *Carlquist 2377* (DAV).
−	*C. halemanui* (Sherff) Croizat & Degener. USA, Hawaii, Kauai: *Koutnik s.n.*
−	*C. remyi* (Boiss.) Croizat & Degener. USA, Hawaii, Kauai: *Koutnik s.n.* Carlquist (1980).
−	*C. rockii* (C. N. Forbes) Croizat & Degener. Carlquist (1980).
	"Subsect. *Sclerophyllae* Boiss."
−	*C. atoto* (Forst.) Croizat. Fiji: *Webster 14050* (DAV). New Hebrides: *Webster 19361* (DAV).
−	*C. laevis* (Poir.) Croizat. Australia: *Sauer 3403* (DAV).
−	*C. mesembrianthemifolia* (Jacq.) Dugand. Bermuda: *Webster 25470* (DAV). USA, Florida Keys: *Hayden 709* (URV). Mexico, Yucatan: *Davison 3* (DAV).
−	"*E. taitensis* Boiss." Society Islands: *Carlquist 661* (DAV).
	"Subsect. *Cheloneae* Boiss."
+	*C. recurva* (Hooker) Burch. Galapagos, N. Seymore I.: *Snodgrass & Heller 562* (US).
+	*C. punctulata* (Anderss.) Burch. Galapagos, Española: *Bentley 331* (US).
	"Subsect. *Acutae* Boiss."
+	*C. acuta* (Engelm.) Millsp. USA, Texas: *Hayden 3140* (URV), *Hinckley & Hinckley 169* (US).
−	*C. angusta* (Engelm.) Small. USA, Texas: *Hayden 3132* (URV), *Hinckley & Hinckley 42* (US).
+	"*E. johnstonii* Mayfield." Mexico, Tamaulipas: *Mayfield et al. 765* (URV).
	"Subsect. *Elegantes* Boiss."
+	*C. elegans* (Spr.) Soják. India: *Jacquemont 215* (US).
+	*C. fimbriata* Rao & Razi [see Rao & Prasad (1987) for synonymy]. India, Mysore: *Saldanha 15552* (US).
	"Subsect. *Hypericifoliae* Boiss."
+	*C. hirta* (L.) Millsp. Mexico, Guerrero: *Mayfield et al. 1026* (URV). USA, Virginia (greenhouse weed): *Hayden 2406* (URV).
+	*C. hypericifolia* (L.) Small. USA, Florida Keys: *Hayden 2050* (URV).
+	*C. nutans* (Lag.) Small. USA, Virginia: *Hayden, 607* (URV). Rössler (1943).
	"Subsect. *Chamaesyce*"

+		*C. cordifolia* (Ell.) Small. USA, Texas: *Hayden 3158* (URV).
+		*C. glyptosperma* (Englem.) Small. USA, Colorado: *Hayden 934* (URV). USA, Texas: *Hayden 3092* (URV).
+		*C. humifusa* (Willd.) Prokh. Rössler (1943).
+		*C. humistrata* (Gray) Small. USA, Virginia: *Hayden 2934* (URV).
+	*	*C. lata* (Engelm.) Small. USA, New Mexico: *Wooton s.n.* (US), *Fisher 183* (US).
+		*C. maculata* (L.) Small. USA, Virginia: *Hayden 608* (URV). Jordan et al. (1985) (as *E. supina* Raf.); Rössler (1943).
+		*C. peplis* (L.) Prokh. Rössler (1943).
+		*C. polygonifolia* (L.) Small. USA, Virginia: *Hayden 662* (URV).
+		*C. prostrata* (Ait.) Small. USA, Texas: *Hayden 3084* (URV). Rössler (1943).
+		*C. revoluta* (Engelm.) Small. Correll & Johnston (1970).
+	*	*C. selloi* (Kl. & Gke.) Croizat. Brazill, Rio Grande do Sul: *Filho 350* (URV).
+		*C. serpens* (H.B.K.) Small. USA, Texas: *Hayden 3169* (URV).
+		*C. serrula* (Engelm.) Woot. & Standl. USA, Texas: *Hayden 3119* (URV).
+		*C. stictospora* (Engelm.) Small. USA, Texas: *Hayden 3075* (URV).
+		*C. vulgaris* Prokh. Rössler (1943) (as *E. chamaesyce* L.).
	"Subsect. *Pleiadeniae* Boiss."	
+		*C. caecorum* (Mart. ex Boiss.) Croizat. Brazil, Goiás: *Irwin & Soderstrom 7571* (US). Brazil, Matto Grosso: *Eiten & Eiten 9027* (US).
+		*C. chamaerrhodos* (Boiss.) Croizat. Paraguay: *Jorgenson 4672* (US).

Seed size, shape, and surface topography vary widely within *Chamaesyce*. No obvious surface features were found that correlate consistently with ability to produce mucilage. For example, seeds over 2 mm long include both mucilaginous, e.g., *C. acuta*, and non-mucilaginous examples, such as *C. remyi* (Boiss.) Croizat & Degener. Similarly, many species with seeds less than 1.5 mm long are mucilaginous, whereas, *C. mesembrianthemifolia* (Figure 9), with seeds ca 1.3 mm long, is non-mucilaginous. Mucilage production was found on smooth seeds, e.g., *C. acuta* (Figure 10), *C. polygonifolia* (Figures 1, 2), as well as on wrinkled seeds, such as *C. glyptosperma* (Engelm.) Small (Figures 5, 6, 8) and *C. hypericifolia* (L.) Small (Figure 7). As viewed with SEM, some species with mucilaginous seeds, such as *C. nutans* (Lag.) Small (Figures 3, 4), have convexly protruding surface cells forming a densely pusticulate surface (Figure 13), but so do some non-mucilaginous seeds, e.g., *C. halemanui* (Sherff) Croizat & Degener (Figure 14). Similarly, seeds with a more or less smooth surface of closely tessellated cells proved to be either mucilaginous, e.g., *C. acuta* (Figure 10), or non-mucilaginous, e.g., *C. mesembrianthemifolia* (Figure 9). Seeds with sharply ridged surfaces, e.g., *C. glyptosperma* (Figure 5), often produced mucilage more copiously from the ridge crests than from the intervening crevices (Figure 6); SEM of dry seeds of this species (Figure 8) reveals surface cells of the mucilaginous ridges to be larger and somewhat more protrusive than cells of the non-mucilaginous regions.

Although surface features alone proved uninformative, sections reveal a striking difference between mucilaginous and non-mucilaginous seeds. Mucilage-producing seeds such as *C. acuta, C. glyptosperma*, and *C. nutans*, all show a prominent subepidermal layer of radially aligned macrosclereids (Figures 11, 13). These macrosclereids are well-known features of euphorb seed development (see below), and have been described previously in *C. hirta* (KAJALE, 1954; MANGALY et al., 1979), *C. thymifolia* (MANGALY et al., 1979), *C. cristata* (Heyne ex Roth) Webster (MUKHERJEE, 1967), and various species of *Euphorbia* (MANDL, 1926; SINGH, 1959; SINGH, 1969). In *C. nutans*, macrosclereids are 27-40 µm long and 8-15 µm wide. These macrosclereids are closely overlain with shorter cells (ca 12 µm tall) that give rise to the mucilaginous layer. From below, endosperm appears to extend to the base of the macrosclereid layer (Figure 11). While macrosclereids are correlated with mucilage production, there is no obvious causal connection between these two observations. Mucilage secretion is clearly a function of the surface layer.

In contrast, sectioned seeds of *C. halemanui* (Figure 14), *C. mesembrianthemifolia* (Figure 12), and *C. remyi*, all of which tested negatively for mucilage, also lack the prominent macrosclereid layer. Testa layers for these three non-mucilaginous species are not, however, identical. In *C. mesembrianthemifolia* a layer of brachysclereids ca 25 µm tall occupies a position comparable to that of the macrosclereids. Further, this species has a zone of thin-walled parenchymatous cells located between the brachysclereids and endosperm (Figure 12). *Chamaesyce halemanui* and *C. remyi* have an extremely thin testa, which appears as two poorly differentiated layers of relatively thin-walled cells directly enclosing the endosperm.

Developmental considerations. For the most part, all seeds within a collection and multiple collections of a species reacted similarly. Occasionally a single seed of an otherwise mucilaginous species failed to develop mucilage, further, some samples included both light and dark colored seeds with noteworthy differences in their capacity to produce mucilage. These examples of infrequent negative responses (no mucilage) in otherwise mucilaginous species can be attributed to differences in seed maturity. For example, the abundant light-colored mature seeds in a mass sample of *C. maculata* consistently develop mucilage; other, less abundant, darker seeds of the same collection frequently failed to produce mucilage. Dissection of young indehiscent capsules of *C. maculata* reveals dark seeds to be a sign of immaturity in this species. Although based on a much smaller sample size, similar results were observed in *C. glyptosperma*; see, for example, Figure 6, in which mucilage production varies considerably from seed to seed. Interestingly, opposite results were noted for *C. hypericifolia*, in which mature seeds are usually described as "brownish or reddish with a very thin whitish bloom" (CORRELL & JOHNSTON, 1970); darker seeds produced greater amounts of mucilage than did lighter seeds. It may be hypothesized that mucilage-producing ability develops late in testa ontogeny; thus weak mucilage production may indicate immaturity of the seed and copious mucilage (in mucilaginous species) is correlated with mature seed coloration.

Testa features observed in the present study are generally consistent with previous developmental literature, including studies of various species of *Chamaesyce* (e.g., KAJALE, 1954; MUKHERJEE, 1961; MANGALY et al., 1979), *Euphorbia* (e.g., BOR & KAPIL, 1975; Singh, 1959; SINGH, 1969), and other Euphorbiaceae (e.g., BOR & BOUMAN, 1974). Ontogenetic studies in *Euphorbia* and *Chamaesyce* show the ovules to be bitegmic, with portions of both integuments contributing to the mature testa. Each integument consists of three to four layers of cells initially, but during maturation some layers are lost. The ontogenetic literature suggests that outer epidermis of the inner integument always persists, forming the layer of macrosclereids that constitute the major protective layer of mature testa; we found these macrosclereids to be prominent in mucilaginous species (Figures 11, 13). It is interesting to note that, in at least some species, characteristic surface features such as crests, ridges, and reticulations have been attributed to unequal radial (anticlinal) elongation of macrosclereids (SINGH, 1969). This sclerified layer thus forms a useful landmark in interpreting mature testa structure. We propose that the brachysclereids of *C. mesembrianthemifolia* (Figure 12) are equivalent (homologous) to the macrosclereids commonly observed in other species. The nature of the wide zone of thin-walled parenchymatous cells located below the brachysclereids of this species (Figure 12) cannot be determined at this time. Conceivably, these cells could be derived from subepidermal regions of the inner integument or from nucellus.

The embryological literature (papers cited above) further suggest that as many as three layers of thin-walled cells derived from the outer integument may persist as the superficial covering over the sclerified layer of mature testa. Of the several species we sectioned and viewed with SEM, distinct well-defined cells are detectable at the surface of most seeds, but not in subsurface layers; i.e., only the epidermis of the outer integument is retained as a distinct cell layer. It is these epidermal cells that produce mucilage in mucilaginous species. *Chamaesyce acuta*, however, is notably different, with two distinct cell layers, presumed subepidermal cells of the outer integument, located between the surface and the macrosclereid layers. We interpret seeds of subsection *Gymnadeniae* as extreme products of testa reduction, consisting of a weakly sclerified layer and a thin, non-mucilaginous epidermis. Of course, we acknowledge that inference of developmental events from examination of mature structure is fraught with pitfalls. We thus urge careful studies of testa development in species which depart from the norm established by the earlier embryological literature.

Taxonomic and phylogenetic considerations. Mucilaginous seeds are present in at least some species of all but one of Boissier's subsections; mucilaginous seeds were not found in any species classified in subsection "*Sclerophyllae*". Lack of mucilage is also widespread in subsection *Gymnadeniae*. Only two subsections, "*Acutae*" and *Gymnadeniae*, were found to contain both mucilage-producing and non-mucilaginous species, otherwise, Boissier's subsections are consistent in regard to this character.

Testa anatomy and mucilage production has the potential to offer insight into aspects of the phylogeny of *Chamaesyce*. From presently available evidence, mucilage secretion and well-defined macrosclereids appear to be plesiomorphic for *Chamaesyce*, since both of these features are also found in species of *Euphorbia* (MANDL, 1926; RÖSSLER, 1943). *Gymnadeniae* and "*Sclerophyllae*" share certain obvious synapomorphies with most other subsections of *Chamaesyce*, notably C_4 photosynthesis (WEBSTER et al., 1975; ROBICHAUX & PEARCY, 1984) and terminal differentiation of the seedling epicotyl (DEGENER & CROIZAT 1938; KOUTNIK, 1987; HAYDEN, 1988); absence of mucilage and weak sclerification of testa in *Gymnadeniae* and "*Sclerophyllae*" is thus most parsimoniously viewed as synapomorphic loss in these subsections. The general absence of seed mucilage in *Gymnadeniae* and "*Sclerophyllae*" underscores their apparently close relationship (KOUTNIK, 1987). Absence of mucilage in *C. angusta* (Engelm.) Small, however, seems to be a different case. This C_3 species (WEBSTER et al., 1975) is reputedly near the transition between *Euphorbia* and *Chamaesyce* (MAYFIELD, 1991) and shows no obvious relationship with species of *Gymnadeniae* or "*Sclerophyllae*"; its lack of mucilage, if not an artifact of seed immaturity, is, most likely, the result of parallel loss (homoplasy).

Functional hypotheses. Two hypotheses, seed hydration and seed dispersal, have been proposed to explain the adaptive value of mucilaginous testa in *Chamaesyce* and *Euphorbia*.

JORDAN et al. (1985) suggested that seed mucilage in *C. maculata* plays a role in water absorption and thus, presumably, in germination. Although some seeds of this species may germinate shortly after dispersal, greatest rates of germination are achieved following cold stratification (KREUGER & SHANER, 1982). This experimental result conforms with observations in nature (W. J. Hayden, unpublished); in eastern North America, seedlings from naturally dispersed seeds are generally encountered only in early summer. Yet, in another study (HAYDEN, 1988), high rates of germination were obtained after just one week of stratification at 5 C. Thus, even though sufficient water absorption for germination can occur within a period as short as a week, many seeds in nature remain dormant until they have overwintered. Hydration appears to be a necessary, but may not always be a sufficient, factor for germination in this species. Details of the role of mucilage in hydration of seeds of *Chamaesyce* have yet to be investigated.

The dispersal function of mucilaginous euphorb seeds has been discussed by CARLQUIST (1966, 1980). The dispersal hypothesis is based largely on comparative data of Hawaiian and other Pacific species, and is, in part, a negative argument involving the contexts in which loss of dispersibility occurred. Noting that sticky mucilaginous seeds are widespread in *Chamaesyce*, Carlquist postulated that ancestors of Hawaiian *Chamaesyce* (subsection *Gymnadeniae*) reached the islands as dispersed seeds attached to feathers of birds. *Chamaesyce celastroides* (Boiss.) Croizat, a species of low altitude inland habitats and found on all major islands of the chain, has mucilaginous seeds, hypothetically the retention of a primitive character. Interestingly, KOUTNIK (1987) also interpreted this species as most primitive among the species of *Gymnadeniae.* Other species of *Gymnadeniae*, such as *C. clusiifolia* (Hook. & Arn.) Arthur, *C. degeneri, C. halemanui, C. remyi*, and *C. rockii* (C. N. Forbes) Croizat & Degener, have lost the capacity to form mucilaginous exudations. Despite the necessity of efficient dispersal for colonization, dispersibility is mal-adaptive once a species becomes established in an island setting (CARLQUIST, 1966). Both the presence of *Chamaesyce* species in the remote Hawaiian Islands and loss of mucilaginous seeds in many of them is, therefore, testimony to the effectiveness of mucilage in dispersal.

Loss of seed mucilage in the closely related subsection "*Sclerophyllae*" is proposed to be a different story. Many species of "*Sclerophyllae*" occur as plants of coastal strands, and are presumably dispersed as drift seeds (CARLQUIST, 1966) in which mucilage would be superfluous. Seeds of *C. atoto* (Forst.) Croizat are reputed to float in sea water by virtue of air spaces in its testa (GUPPY, 1906). Seeds of *C. mesembrianthemifolia* examined in this study also float in seawater, presumably by virtue of the broad zone of thin-walled parenchymatous cells (Figure 12) located below the band of brachysclereids, as described above. Loss of mucilage in "*Sclerophyllae*" may well be a consequence of an adaptive shift to dispersal by floatation. Studies on seed viability following floatation in sea water may well provide insight into the evolution of subsection "*Sclerophyllae*", especially in regard to its putatively close relationship with *Gymnadeniae.*

Acknowledgments

The research reported here was supported by grants from both the Undergraduate and the Faculty Research Committees, University of Richmond; we are grateful for their support. Daryl Koutnik, Mark Mayfield, Grady Webster, and the Smithsonian Institution provided seeds of several critical species; their assistance is greatly appreciated. Light microscopy and photomicrography were provided through NSF Grant BSR 8407594. Scanning electron microscopy was provided through NSF Grant USE 8952055 to Roni J. Kingsley.

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(Received 30 March, accepted 29 April 1992)