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Seed Morphology of *Euphorbia* Section *Tithymalopsis* (Euphorbiaceae) and Related Species

Ki-Ryong Park*
Department of Biology, Kyung-Nam University, Masan 631-701, Korea

Light and scanning microscopies were used to evaluate the sectional boundary of 17 species included by various authors in *Euphorbia* sect. *Tithymalopsis*. Based on seed shape, surface ornamentation, and mucilage formation, five seed morphological types were recognized in North American section *Tithymalopsis* and related species. These results did not provide added support for recent treatment of the sect. *Tithymalopsis* s.s. However, a close relationship was suggested among species of the *Tithymalopsis* subsection *Corollatae*. In addition, including species from subsections *Innocuae*, *Ipecacuanhae*, and *Sphaerorhizae* within sect. *Tithymalopsis* could not be justified, based on seed morphological data.

Keywords: *Euphorbia*, section *Tithymalopsis*, seed morphology

Euphorbia subgenus *Agaloma* section *Tithymalopsis* Boiss. comprises seven species of herbaceous perennials that are endemic to the southeastern USA (Park, 1998). These species possess glabrous cyathia, no vestigial sepals in the pistillate flowers, rounded leaf apices, and cylindrical roots. They form a monophyletic group based on morphological and isozyme data (Park and Elisens, 1997; Park, 1998). Each is described by unique morphological characters, and most of the species occupy distinct habitats.

Klotzsch (1859) segregated the genus *Tithymalopsis* from *Euphorbia*, based on its obovate, white petaloid appendages. It was later reduced to a sectional name in *Euphorbia* by Boissier (1862), who divided *Euphorbia* into 26 sections in de Candolle's Prodromus. Boissier recognized eight New World species in sect. *Tithymalopsis*.

Sectional boundaries and the number of species included in sect. *Tithymalopsis* have varied widely in taxonomic treatments. For example, Rafinesque (1836, 1840), Small (1903), Nieuwland (1912), and Park (1995) each restricted the section to include only species of the southeastern USA, and none used any subsectional classification. In contrast, Boissier (1862) and most recent authors (McVaugh, 1961; Webster, 1967; Huft, 1979) have expanded the sectional boundaries to include species from the USA, Mexico, and western Guatemala. Webster (1967) divided sect. *Tithymalopsis* into three subsections: *Corollatae*, *Innocuae*, and *Ipecacuanhae* (Table 1), with *Corollatae* mostly corresponding to Boissier's sect. *Tithymalopsis*. However, Webster suggested that several species in Texas and Mexico, such as *E. maysillesii*, *E. sphaerorhiza*, and *E. wrightii*, required a new subsection. Although Huft (1979) followed Webster's sectional delimitation, his intrasectional system was different. Here, much of Webster's subsect. *Corollatae* was subsumed into a broader subsect. *Ipecacuanhae*, while three species from subsect. *Corollatae* were transferred to two new subsections, *Scoparia* and *Sphaerorhizae* (Table 1).

Scanning electron microscopes (SEM) and light microscopes (LM) delineate many taxonomically useful characters, such as testal cell ornamentation, structure of intercellular space, and the shape of the seed and caruncle (Khan, 1964; Richardson, 1968; Ehler, 1976; Simon et al., 1992). The seed characteristics of *Euphorbia* have been used to recognize subgeneric (Webster, 1967; Carter and Radcliffe-Smith, 1988), sectional or subsectional (Khan, 1964; Ehler, 1976; Park et al., 1999), and species boundaries (Richardson, 1968; Hassall, 1977; Simon et al., 1992). The adaptive significance of some seed characters of *Euphorbia* species also has been examined (Jordan et al., 1985; Jordan and Hayden, 1992). In the current study, seed morphology was used to evaluate the sectional boundary of *Euphorbia* sect. *Tithymalopsis* and related species.

MATERIALS AND METHODS

Seeds of 17 species that had been included in sect. *Tithymalopsis* by previous authors (Webster, 1967; Huft,

*Corresponding author; fax +82-551-244-6504
e-mail park@kyungnam.ac.kr

Table 1. A comparison of major taxonomic treatments within *Euphorbia* section *Tithymalopsis*.

Webster (1967)	Huft (1979)	Park (1998)
Subsect. *Corollatae*	**Subsect. *Ipecacuanhae***	
E. corollata	*E. corollata*	*E. corollata*
E. curtisii	*E. curtisii*	*E. curtisii*
E. discoidalis	*E. discoidalis*	*E. discoidalis*
E. mercurialina	*E. mercurialina*	*E. mercurialina*
E. polyphylla	*E. polyphylla*	*E. polyphylla*
E. pubentissima	*E. pubentissima*	*E. pubentissima*
(= *E. apocynifolia*)	*E. ipecacuanhae*	*E. gracilior*
E. wrightii	*E. gracilior* (= *E. exserta*)	
E. sphaerorhiza	**Subsect. *Scoparia***	
E. maysillesii	*E. strictior*	
Subsect. *Ipecacuanhae*	*E. wrightii*	
E. ipecacuanhae	**Subsect. *Innocuae***	
E. gracilior (= *E. exserta*)	*E. innocua*	
Subsect. *Innocuae*	**Subsect. *Sphaerorhizae***	
E. innocua	*E. macropodoides*	
	E. sphaerorhizae	
	E. macropus	
	E. ixtlana	
	E. hintonii	

Table 2. Collection data and voucher deposition for specimens of *Euphorbia* species used as seed sources.

Euphorbia corollata L., Park 51 (KNUH). *E. curtisii* Engelm. ex Chapm., Park 63 (KNUH). *E. discoidalis* Chapm., Park 36 (KNUH). *E. gracilior* Cronguist, Park 20 (KNUH). *E. hintonii* Wheeler, Hinton et al. 6257 (MICH). *E. innocua* Wheeler, Park 1 (KNUH). *E. ipecacuanhae* L., Park 80 (KNUH). *E. ixtlana* Huft, Lundell 12288 (MICH). *E. macropodoides* Rob. & Greenm., Pringle 4713 (MICH). *E. macropus* (Kl. & Garcke) Boiss., McVaugh 17112 (MICH). *E. maysillesii* McVaugh, Maysilles 17112 (MICH). *E. mercurialina* Michix., Park 38 (KNUH). *E. polyphylla* Engelm. ex Holz., Park 52 (KNUH). *E. pubentissima* Michx., Park 37 (KNUH). *E. sphaerorhiza* Benth., Palmer 416 (MICH). *E. strictior* Holz., Park 25 (KNUH). *E. wrightii* Torr. & Gray, Park 28 (KNUH).

1982) were examined by light microscopy (LM) and scanning microscopy (SEM). Mature seeds had been collected in the field or obtained from herbarium specimens from the University of Michigan (MICH; Table 2). Observations and measurements at low magnification were made with a dissecting microscope. Production of a mucilaginous layer was tested using the method of Jordan and Hayden (1992). Seeds were placed in a moist Petri dish, hydrated in water for 5 min, then examined under a dissecting microscope for the presence of bright projections of mucilage. For SEM studies, seeds were affixed with double-sided cellophane tape to aluminum stubs, air-dried, sputter-coated with a gold-palladium mixture, and observed with an ETEC Autoscan SEM.

RESULTS

Seeds of sect. *Tithymalopsis* and related species are ovate, and either angular or round in cross-section. They vary in color from white to brown. The top (= proximal end of the hilum) of the seeds is narrowly acute; the other end (= distal end of the hilum) is round or flattened with a nipple-like structure (Figs. 1 and 2). The dorsal line of seeds is unclear in most species except *E. innocua*.

All of the species examined were ecarunculate. The shape of the hilum was mostly triangular, and the region of the hilum was abruptly depressed. The smallest seed (1.6-1.8 mm long) was produced by *E. macropodoides*; the largest seed (3.3-3.7 mm) by *E. strictior*. Seed surfaces were pitted, smooth, or tuberculate (Table 3). The surface pitting referred to circular depressions (e.g., Figs. 1B, 1H, 2G, and 2H). Smooth seeds lacked these depressions and tubercles. The testal cells usually were round, with several concentric circles (Fig.1, E and I), but they were elongate in *E. ixtlana* (Fig. 2E). The testal cells around the hilum were compactly arranged whereas the intercellular spaces were mostly well developed around the rest of the surface (Figs.1D, 1I, and 2I). Mucilaginous seeds were found only in *E. innocua* and *E. ipecacuanhae* (Table 3). Based on seed shape, surface ornamentation,

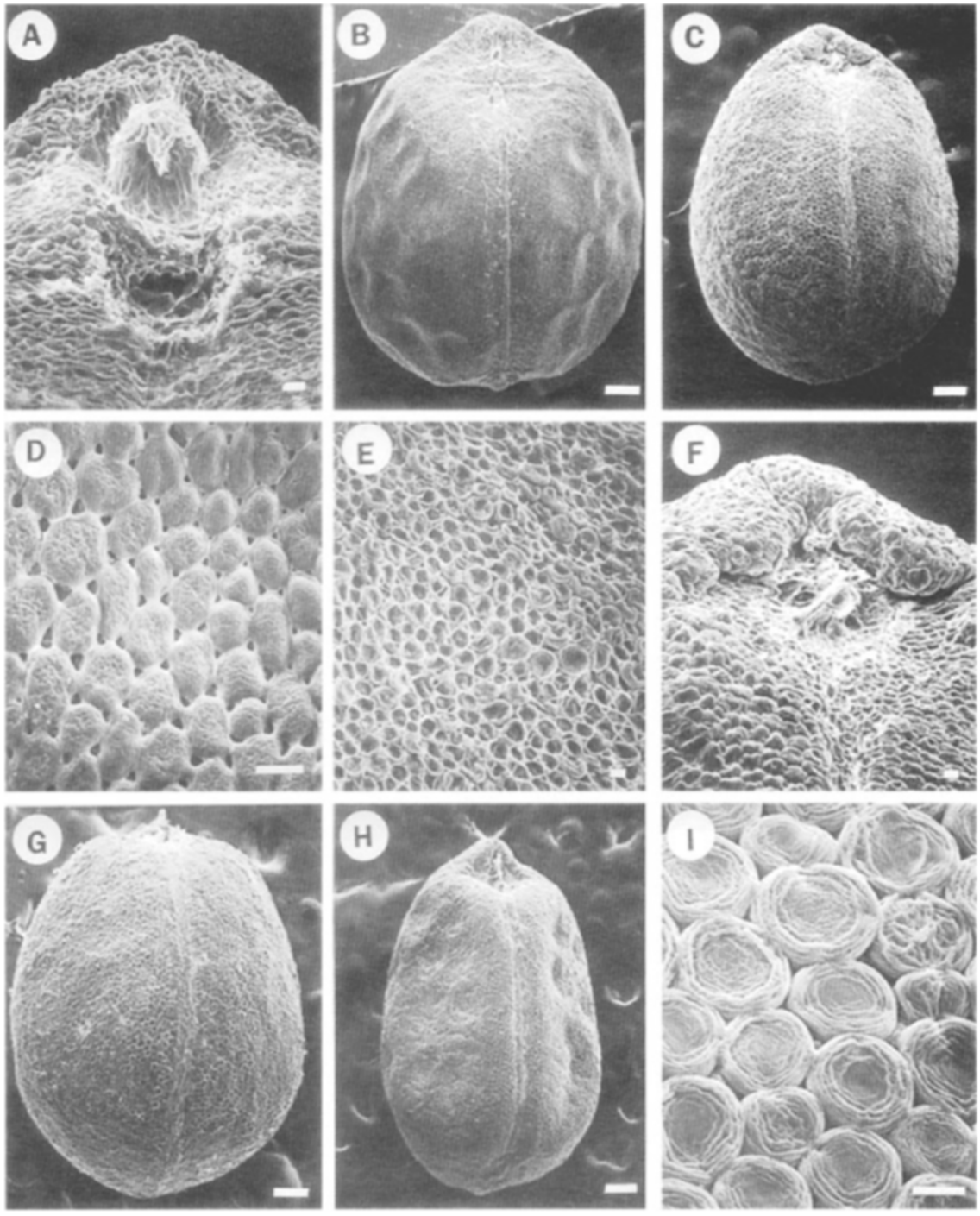

Figure 1. Scanning electron micrographs of whole seeds and portions of seed coats in North American *Euphorbia* subg. *Agaloma* species. A, *Euphorbia pubentissima*; B and D, *E. mercurialina*; C and F, *E. discoidalis*; E, *E. corollata*; G, *E. curtisii*; H, *E. gracilior*; I, *E. polyphylla*. (Scale bar = 100 μm in B, C, G, H. Scale bar = 10 μm in A, D-F, I).

and mucilage formation (Table 3), five seed morphological types are recognized in North American sect. *Tithymalopsis* and related species:

1) *E. corollata* type. The seeds of this type are ovate, with a round cross section. Their surfaces are either pitted (*E. corollata*, *E. mercurialina*, *E. pubentissima*, *E. gracilior*, *E. strictior*, and *E. wrightii*), or smooth (*E. curtisii*, *E. discoidalis*, *E. polyphylla*, *E. hintonii*, *E. may-*

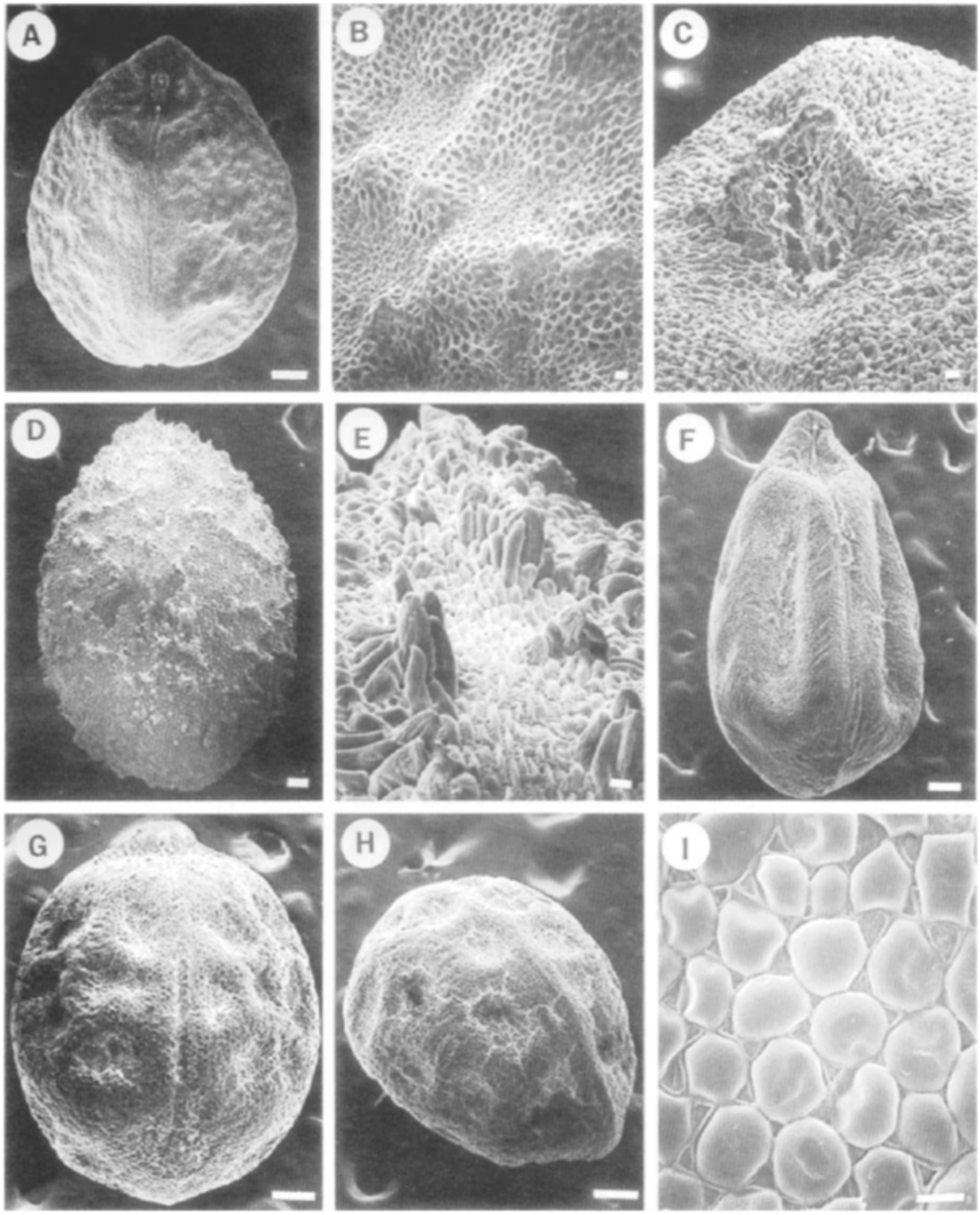

Figure 2. Scanning electron micrographs of whole seeds and portions of seed coats in North American *Euphorbia* subg. *Agaloma* species. A and B, *E. macropus*; C, *E. wrightii*; D and E, *E. ixtlana*; F, *E. ipecacuanhae*; G and H, *E. innocua*; I, *E. sphaerorhiza*. (Scale bar = 100 μm in A, D, F-H. Scale bar = 10 μm in B, C, E, I).

sillesii, and *E. sphaerorhiza*). These seeds produce no mucilage.

2) *E. macropus* type. Seeds are ovate, and round in cross-section. The proximal end of the hilum is acute. Tubercles consist of round testal cells (Fig. 2, A and B). This seed type produces no mucilage. Species include *E. macropus* and *E. macropodoides*, both of which are endemic to Mexico.

Table 3. Comparison of seed characters among species in section *Tithymalopsis* and related species.

Taxon	Length (mm)	Cross-Section	Sculpturing Pattern	Testal Cell	Mucilage Formation
Section *Tithymalopsis* (Park 1998)					
E. corollata	2.5-3.3	round	pitted	round	No
E. curtisii	2.3-2.6	round	smooth	round	No
E. discoidalis	1.8-2.4	round	smooth	round	No
E. gracilior	1.9-2.4	round	pitted	round	No
E. mercurialina	2.6-2.8	round	pitted	round	No
E. polyphylla	2.4-3.0	round	smooth	round	No
E. pubentissima	1.9-2.3	round	pitted	round	No
Related species					
E. innocua	1.7-1.8	round	pitted	round	Yes
E. ipecacuanhae	2.3-2.5	angular	pitted	round	Yes
E. ixtlana	2.5-2.8	round	tuberculate	elongate	No
E. hintonii	2.3	round	smooth	round	No
E. macropus	1.9	round	tuberculate	round	No
E. macropodoides	1.6-1.8	round	tuberculate	round	No
E. maysillesii	2.5	round	smooth	round	No
E. sphaerorhiza	2.5-2.8	round	smooth	round	No
E. strictior	3.3-3.7	round	pitted	round	No
E. wrightii	2.8-3.0	round	pitted	round	No

3) *E. ixtlana* type. Seeds are elliptic, and round in cross-section. In contrast to the *E. macropus* type, tubercles here consist of elongated and swollen testal cells (Fig. 2, D and E). Mexican endemic *E. ixtlana* is recognized only by this type.

4) *E. ipecacuanhae* type. Seeds are ovate, and angular in cross-section, with longitudinal grooves on ventral surfaces (Fig. 2F). Surfaces are pitted, and the seeds produce mucilage. *E. ipecacuanhae* was the only species found for this type in the current study.

5) *E. innocua* type. Seeds are round in cross-section, pitted, and mucilaginous. Prominent dorsal lines and mucilaginous seed coats (Fig. 2, G and H) characterize this type, of which *E. innocua* was the only member found here.

DISCUSSION

Park's (1998) restriction of the *Euphorbia* sect. *Tithymalopsis* to seven North American species of the *E. corollata* complex is well supported by morphological and isozyme data (Park and Elisens, 1997; Park, 1998). However, the seed micro-morphology of the 17 species of *Euphorbia* subg. *Agaloma* examined here does not provide added confirmation to this treatment. Instead, the resulting data suggest a close relationship among the seven species Park included in *Tithymalopsis* as well as *E. wrightii*, *E. strictior*, *E. hintonii*, *E. maysillesii*, and *E. sphaerorhiza*. This agrees with Webster's (1967) expended sect. *Tithymalopsis* subsection *Corollatae*.

Two subsections of sect. *Tithymalopsis*, *Innocuae* (*E. innocua*) recognized by Webster (1967) and *Ipecacuanhae* sensu Webster (1967) (*E. ipecacuanhae*), show unique morphological characteristics that do not support their inclusion in the section. Instead, their mucilaginous seeds and longitudinal grooves (in the case of *E. innocua*) suggest affinities with species in subg. *Chamaesyce* (Park, 1998). Evolutionary relationships within the New World Euphorbiinae group have also demonstrated the close association among the members, with a unique synapomorphy (Park, 1996).

Three Mexican species, *E. ixtlana*, *E. macropus*, and *E. macropodoides*, differ from species of sect. *Tithymalopsis* because of their tuberculate seeds (Park, 1996). Huft (1979) assigned these species to subsect. *Sphaerorhizae* of sect. *Tithymalopsis*, along with two other Mexican species, *E. sphaerorhiza* and *E. hintonii*. However, the seed morphological data support the exclusion of *E. ixtlana*, *E. macropus* and *E. macropodoides* from *Tithymalopsis*. Previous phylogenetic analysis suggests that the species of subsect. *Sphaerorhizae* are closely related with herbaceous members possessing tuberculate seeds, such as *Euphorbia* sect. *Zygophyllidium* (Park, 1996, 1998).

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