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The Systematic Significance of Seed Morphology in *Portulaca* (Portulacaceae) under Scanning Electron Microscopy

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ABSTRACT. Seeds of seven southeastern and one southwestern United States species of *Portulaca* were examined with the scanning electron microscope. Some species could be characterized by the external seed morphology while others could not. Those species with the largest geographical ranges and ecological diversities showed the greatest variation in morphology. Comparisons between species often showed significant overlap of morphological characteristics. Seed morphology in *Portulaca* can be used as a taxonomic trait, but should be combined with other traits for the diagnostic determination of species.

Since Davis and Heywood (1963) proposed seed morphology as a potential taxonomic character, an increasing number of papers have reported on the scanning electron microscopy of seed surface patterns. Brisson and Peterson (1976, 1977) provide a complete bibliography through 1977.

In general, the findings until now have supported the following groupings regarding seed surface taxonomic implications.

1. Intrageneric consistency complete, so that seed surface characters are predictable from species to species (Chuan and Heckard 1972; Hill 1976; Clark and Jernstedt 1978; Crow 1979).
2. Intrageneric consistency high, some species variability (Newell and Hymowitz 1978; Canne 1979, 1980; Wofford 1981; Elisens and Tomb 1983; Chance and Bacon 1984).
3. Intrageneric variability of some species, related to ecological conditions (Hauptli et al. 1978).
4. Intraspecific variability, showing different expressions over geographical range and ecological conditions (Wyatt 1984; Matthews and Levins 1985a).
5. Intraspecific consistency, involving subspecies, related to ploidy level (Danin et al. 1978).

These varied findings have resulted in the following conclusions, listed in historical sequence.

1. SEM photographs have not provided sufficient evidence to sustain a taxonomic innovation not held before (Brisson and Peterson 1976).
2. A distinctive seed coat morphology usually allowing identification of species solely on the basis of seed characters (Clark and Jernstedt 1978).
3. Both inter- and intrapopulational variation; some species monomorphic and some polymorphic with small populations tending to be monomorphic and widespread taxa polymorphic (Hauptli et al. 1978).
4. Seed morphology being subject to the same uncertainties and ambiguities as any other morphological attribute used in taxonomic studies (Newell and Hymowitz 1978).
5. Monomorphic seeds with variation in those species with the largest distribution (Canne 1979).
6. External seed morphology distinctive and valuable for species distinctions (Wofford 1981).
7. High levels of infraspecific variation suggesting caution in using SEM-level features to characterize species or taxa (Wyatt 1984).
8. Species specific seed coat morphologies that do not correspond well with the more classical treatments and suggest a restructuring of the intrageneric and even the generic taxonomy (Chance and Bacon 1984).
9. Variability in seed surface patterns occurs within geographic regions and within the species (Matthews and Levins 1985a).

A recent study (Matthews and Levins 1985a) concentrated on the variation in seed surface morphology of *Portulaca pilosa* over its southeastern and southwestern United States range. The present report will analyze the six other species occurring in the southeastern United States, which constitute the seven southeastern species of *Portulaca* (Matthews and Levins 1985b), plus one species from the southwest.

Materials and Methods

Seeds were examined from dried specimens from the following herbaria: ALU, ASTC, DUR, FLAS, FSU, G, GA, JSU, KNK, KY, LAF, LL, MO, NCU, NLU, NO, NY, SMS, SMU, TENN, TEX, UARK, UNA, UNCC, US, USAM, USCH, USF, VDB, VPI, VSC, and WILLI. Representative specimens from which seeds were taken for microscopy are listed in table 1. For the electron microscope, seeds were sputter coated with gold-palladium on a Hummer V and viewed at 100× with a Jeol JSM-35CF scanning electron microscope.

Results and Discussion

Seeds were examined with a 10× handlens to determine whether the surface was smooth or rough. At 25×, tubercles could be seen on the dorsal spine and the lateral surfaces could be determined to be smooth or rough, the tubercles producing the rough surface. However, the relation of the tubercles to the remainder of the surface cells was not easily detected. In addition, the seeds of some species were covered with an iridescent coating which often obscured the surface patterns. To better interpret the primary and secondary structures of the seeds, they were examined at 100× with an SEM.

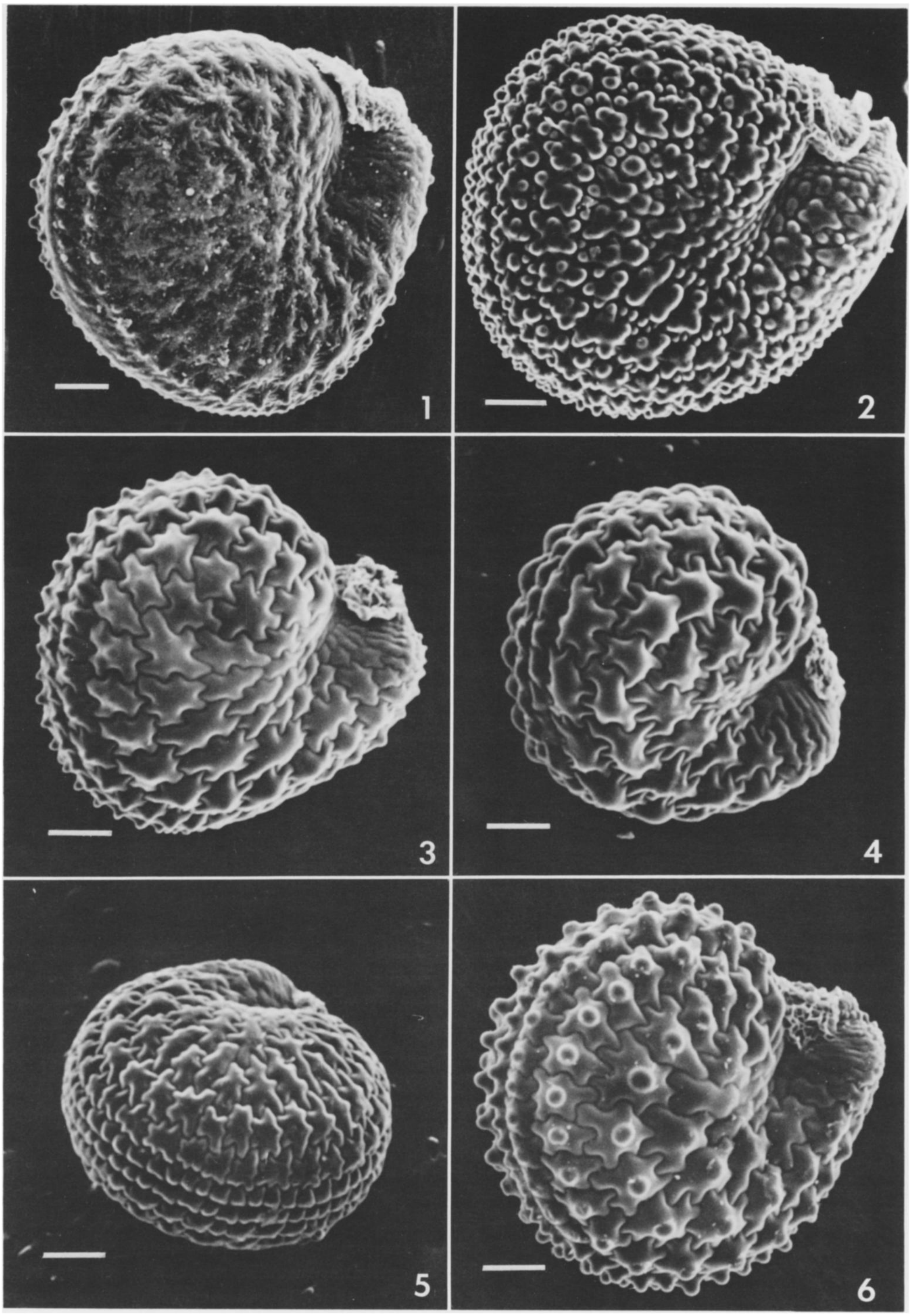
Using the classification of Barthlott (1984) for the microstructural features of the seed surfaces of *Portulaca*, the primary structure of the anticlinal walls of the isodiametric seed coat cells is S-undulate (in earlier reports, Matthews and Levins 1985a and 1985b, the term "stellate" was used to describe the S-undulate pattern). The secondary structure exhibited by the seeds is produced by channelled anticlinal walls, with periclinal walls varying from flat (smooth surfaces) to convex, to papillate, to tuberculate.

Portulaca oleracea. The most widespread species of *Portulaca* in the southeast, as well as in the world, is *P. oleracea* L., a species with yellow flowers, flat leaves and sparse pubescence. Legrand (1962) reported that the surfaces of *P. oleracea* seeds varied widely. Danin et al. (1978) demonstrated a correlation between ploidy level and seed coat morphology of *P. oleracea*. Seed surfaces of this taxon (figs. 1, 2) from the southeast show that the surfaces vary from nearly smooth to very granulate. Tubercles on the dorsal spines are minute or indistinct. While Legrand (1962) questioned the use of seed surface texture as a character to delineate varieties of *P. oleracea*, Danin et al. (1978) used seed size and seed coat morphology to describe nine subspecies. Cytotaxonomic comparisons of these subspecies showed that each had a fairly distinct distribution which may indicate their specialization to certain climatic and edaphic conditions. Although there was some subspecific variation in seed coat morphology, seed size and/or ploidy level were used to assist in the final identification. In our examination of *P. oleracea*, no attempt was made to determine how many of their subspecies could be identified in the southeastern United States, only that variation within *P. oleracea* was clearly evident. Our figure 1 is their *P. oleracea* subsp. *nitida*, figure 2 is their subsp. *granulato-stellulata*.

Portulaca pilosa. *Portulaca pilosa* L., the second most common species in the southeast, exhibits a wide variation in seed surface and tex-

TABLE 1. Voucher data for representative specimens of *Portulaca* used for SEM studies.

Fig. 1. *P. oleracea* L. **Alabama:** Mobile Co., 26 Aug 1965, *Deramus D732* (ALU).
Fig. 2. *P. oleracea* L. **Louisiana:** Rapides Parish, 19 Jul 1979, *Pias 4345* (NLU).
Fig. 3. *P. pilosa* L. **Florida:** Citrus Co., 13 Aug 1958, *Kral 7825* (NY).
Fig. 4. *P. pilosa* L. **Arkansas:** White Co., 14 Oct 1974, *Demaree s.n.* (GA).
Fig. 5. *P. pilosa* L. **Oklahoma:** Cimarron Co., 4 Aug 1977, *Taylor 25255* (NLU).
Fig. 6. *P. pilosa* L. **Texas:** Brewster Co., 23 Aug 1970, *Semple 408* (MO).
Fig. 7. *P. umbraticola* Kunth. **South Carolina:** Lancaster Co., 25 Sep 1973, *Hatley* and *Sowers s.n.* (UNCC).
Fig. 8. *P. rubricaulis* Kunth. **Florida:** Lee Co., 21 Jul 1954, *Cooley 2316* (G).
Fig. 9. *P. retusa* Engelm. **Texas:** Williamson Co., 16 Aug 1961, *Walker 73* (TEX).
Fig. 10. *P. smallii* P. Wilson. **Georgia:** Hancock Co., 22 Oct 1952, *Duncan 14481* (VSC).
Fig. 11. *P. amilis* Spegaz. **Georgia:** Echols Co., 23 Aug 1961, *Faircloth 4786* (VSC).
Fig. 12. *P. grandiflora* Hooker. **South Carolina:** Kershaw Co., 6 Oct 1957, *Radford 30004* (NCU).



FIGS. 1–6. Scanning electron micrographs of seeds of *Portulaca*. Scale = 100 μm. 1. S-undulate surface pattern of *P. oleracea*. 2. Granulate pattern of *P. oleracea*. 3. S-undulate pattern of *P. pilosa* with short tubercles. 4. S-undulate pattern of *P. pilosa* with rounded tubercles. 5. S-undulate-smooth pattern of *P. pilosa*. 6. S-undulate-tuberculate pattern of *P. pilosa*.

ture. *Portulaca pilosa* has red to purple flowers, terete leaves, and is densely pubescent. Numerous plants were examined from Florida, the Gulf Coast and westward into Texas, Oklahoma, Arkansas, and Missouri. The detailed results of this study have been reported elsewhere (Matthews and Levins 1985a), and are briefly summarized here.

In Florida, *P. pilosa* seeds have smooth to papillate lateral surface patterns and secondary tubercles on the dorsal spine (fig. 3). The Gulf Coast examples are very similar to those of Florida, but may have a reduction in tubercles on the dorsal spine. Specimens from northern Texas, Arkansas (fig. 4), Oklahoma (fig. 5), and Missouri exhibit fewer dorsal tubercles but retain the smooth to papillate lateral surface. In west Texas, an area of diverse habitats, surface texture varies from very tuberculate on both the spine and lateral surfaces (fig. 6) to few dorsal spines and lateral tubercles (figs. 4 and 5). We have interpreted these variations as responses correlated with ecological conditions, with a reduction in tubercles in dry habitats.

Geesink (1969), in a study of the portulacas of Indo-Australia and the Pacific, commented on the variability of *P. pilosa*, characterizing it as a very complex species into which he synonymized about 60 names. However, he did recognize eight subspecies which probably were originally geographically separate, but now through the activity of man are intermixed. For the American taxa, he stated that there were some 150 names recognized by von Poellnitz (1934) and Legrand (1962) that should be subordinated to the *P. pilosa* complex.

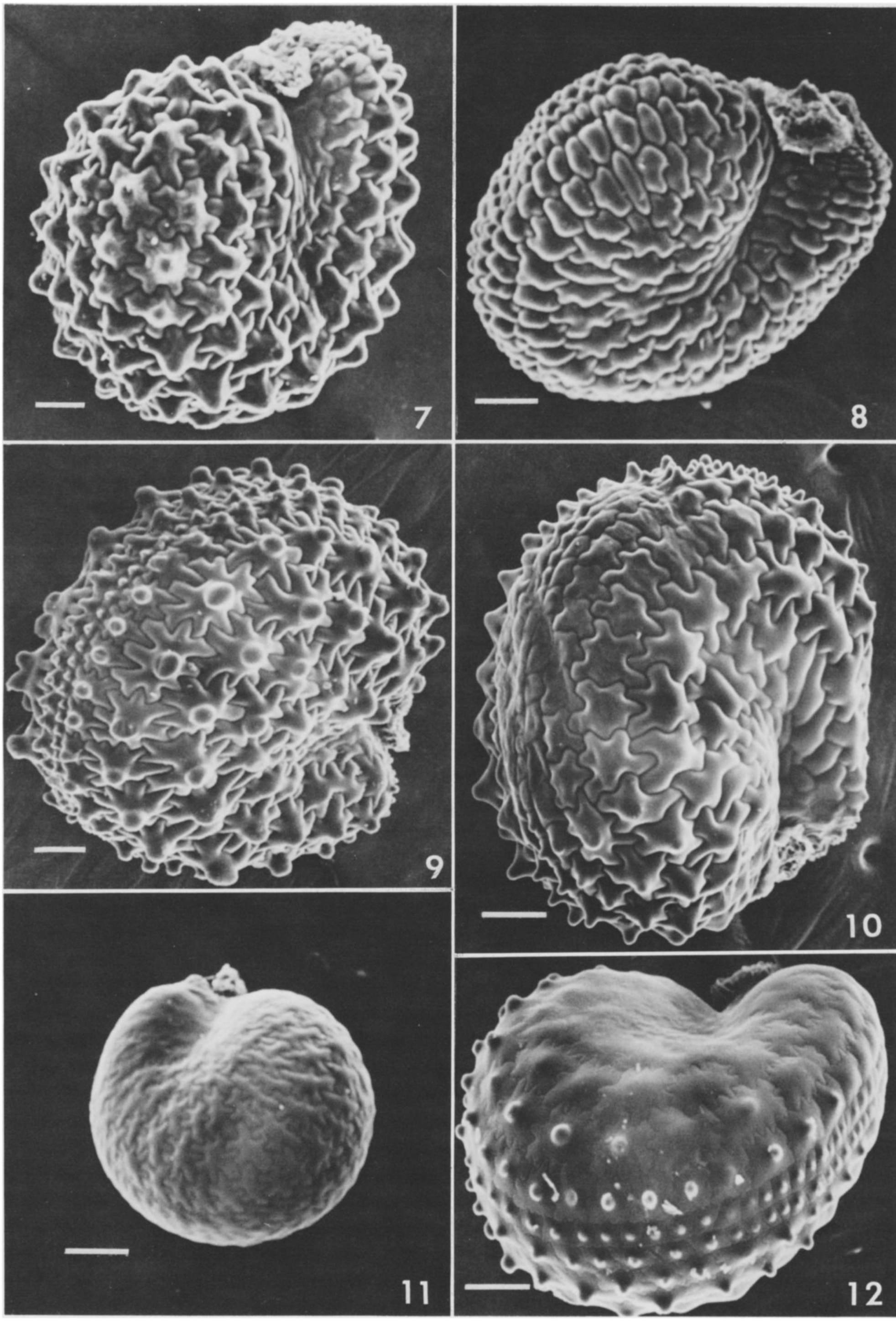
From these conclusions regarding *P. pilosa*, the characterization of seeds from specimens that do not represent the total range of a species may provide misleading concepts of the species by giving improper weight to only one type of seed morphology. This is not to say that seed coat morphology is not a good taxonomic character, but rather that it should be considered in combination with other morphological traits. Unfortunately, in some families and genera, particularly the succulent ones which do not make good dried specimens, there is a tendency to rely on a single feature, such as a hard seed coat, as a primary character for identification. The following comparisons illustrate the potential problems by pairing similar seeds of different species of the southeastern portulacas.

Portulaca umbraticola. Portulaca umbraticola Kunth (fig. 7) is easily identified by its yellow to orange flowers, flat leaves, sparse pubescence, and a membranaceous wing on the capsule. However, the seeds of *P. umbraticola* more closely resemble the tuberculate specimens of *P. pilosa* (fig. 6) although the tubercles are not quite as strongly developed.

Portulaca rubricaulis. The flattened surfaces of the seeds of the yellow- to orange-flowered, terete-leaved, pubescent *P. rubricaulis* Kunth (fig. 8) approximate those of *P. pilosa* from western Oklahoma (fig. 5). However, mature *P. rubricaulis* seeds are gray or brown while those of *P. pilosa* are black.

Portulaca retusa. Portulaca retusa Engelm. is closely related to *P. oleracea* (e.g., yellow flowers, flat leaves, and sparse pubescence), but differs from it by retuse leaves and a highly tuberculate seed coat. The distribution for *P. retusa*, derived from the specimens we examined, is limited to central and west Texas, and Oklahoma. Steyermark (1963) lists *P. retusa* from Missouri, but we saw no specimens from there. It has been assigned to Arkansas (Steyermark 1963; Correll and Johnston 1970), but Smith (1978) questions its presence, based on lack of documentation. A comparison of the seeds of *P. retusa* (fig. 9) with the highly tuberculate seeds of *P. pilosa* from the Big Bend and south-central Texas (fig. 6) shows a striking similarity. We are not suggesting a relationship between two species with very different flower colors, leaf shapes, and pubescence, but merely a similarity in seed coat morphology. Danin et al. (1978) in their characterization of nine subspecies of *P. oleracea*, described one, subsp. *impolita* (Type: Texas: Hartley Co., sandy soil along Punta de Agua Creek, between Romero and Middle Water, 9.X.1964, *Correll 30330*, holotype UC; isotype, GH) that has a seed coat morphology very similar to that of *P. retusa*. The range of *P. oleracea* subsp. *impolita* given by Danin et al. overlaps our observed Texas distribution of *P. retusa*. A study of *P. oleracea* and *P. retusa* should be made to determine whether the taxon now called *P. retusa* is a distinct species or falls within the range of *P. oleracea*.

Portulaca smallii. Portulaca smallii P. Wilson (fig. 10) is a red-flowered, terete-leaved, pubescent endemic of the granitic outcrops of the southeast. Seeds of *P. smallii* and *P. pilosa* were similar in morphology (fig. 3). *Portulaca smallii* is separated from *P. pilosa* by its ecological niche and consistently large (0.6–0.85 mm) elongate



FIGS. 7–12. Scanning electron micrographs of seeds of *Portulaca*. Scale = 100 μm. 7. S-undulate-tuberculate pattern of *P. umbraticola*. 8. Lightly S-undulate-smooth pattern of *P. rubricaulis*. 9. S-undulate-tuberculate pattern of *P. retusa*. 10. S-undulate-tuberculate pattern of *P. smallii*. 11. S-undulate pattern of *P. amilis*. 12. Lightly S-undulate-dorsally tuberculate pattern of *P. grandiflora*.

seed. All of the granitic outcrop specimens labeled *P. smallii* had seeds larger in size than any of the *P. pilosa* seeds that were measured.

Portulaca amilis. The small seeds of *P. amilis* Speg. have very smooth lateral surfaces and no tubercles (fig. 11). Over its southeastern geographical range very little seed surface variation is found. The identification of this red-flowered, flat-leaved, pubescent, newly introduced southeastern species (Judd and Wunderlin 1981) and the hypothesis of its introduction and spread (Matthews and Levins 1985b) suggest a reason for the lack of variability. Being introduced into the United States within the past 50 years from South America, probably from only a few seeds, the southeastern gene pool of *P. amilis* may be small.

Portulaca grandiflora. The final species is *P. grandiflora* Hook., the common rose moss of rock gardens, with variable flower colors, terete leaves, and pubescence. Limited herbarium specimens of this species, as escapes from cultivation, were available for study. The large seeds (0.75–1 mm) are smooth, except for dorsal tubercles (fig. 12). Our limited sample may not represent the total range of variability in this widely cultivated species, so comparison with the native and naturalized noncultivated species is not helpful.

Conclusion

As shown in the introduction to this study, there are indications that variability in seed surface morphology may be linked to diversity in geography, ecology, and ploidy level. In *Portulaca,* it may be that all three factors affect the expression of the surface morphology. Seed coat morphology is a useful character, one that needs to be included as part of the description of the species. However, it does not appear to be diagnostic for each species, so must be combined with other taxonomic characters in determining the systematic relationships within the genus.

It is unfortuate that seed coat morphology is not reliable at the species level, since determinations are often difficult from herbarium specimens. However when other features are lacking, this has been used, often with mixed results. With some familiarity of *Portulaca* and the morphological traits that assist in identification of species, the seed coat can be helpful. In *Portulaca,* taxonomic decisions become increasingly more accurate when the data available include the leaf morphology, vestiture of the stem and inflorescence, flower color, capsule structure, and seed morphology. Decisions are less accurate as these characters are less available. Working with difficult taxa like *Portulaca* is easier when herbarium label data include some of the more transient features, such as flower color, or comments on the ecological conditions of the habitat.

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Literature Cited

Barthlott, W. 1984. Microstructural features of seed surfaces. Pp. 95–105 in Systematics Association Special Vol. No. 25, *Current concepts in plant taxonomy*, eds. V. H. Heywood and D. M. Moore. London and Orlando: Academic Press.

Brisson, J. D. and R. L. Peterson. 1976. A critical review of the use of scanning electron microscopy in the study of seed coat. Ill. Inst. Techn. Res. Inst./SEM/1976/II:477–495.

——— and ———. 1977. The scanning electron microscope and X-ray microanalysis in the study of seeds: A bibliography of the period 1967–1976. Ill. Inst. Techn. Res. Inst./SEM/1977/II:697–712.

Canne, J. M. 1979. A light and scanning electron microscope study of seed morphology in *Agalinis* (Scrophulariaceae) and its taxonomic significance. Syst. Bot. 4:281–296.

———. 1980. Seed surface features in *Aureolaria, Brachystigma, Tomanthera,* and certain South American *Agalinis* (Scrophulariaceae). Syst. Bot. 5:241–252.

Chance, G. D. and J. D. Bacon. 1984. Systematic implications of seed coat morphology in *Nama* (Hydrophyllaceae). Amer. J. Bot. 71:829–842.

Chuan, T. I. and L. R. Heckard. 1972. Seed coat morphology in *Cordylanthus* (Scrophulariaceae) and its taxonomic significance. Amer. J. Bot. 59: 258–265.

Clark, C. and J. A. Jernstedt. 1978. Systematic studies of *Eschscholzia* (Papaveraceae). II. Seed coat microsculpturing. Syst. Bot. 3:386–402.

Correll, D. C. and M. C. Johnston. 1970. *Manual of the vascular plants of Texas.* Renner, Texas: Texas Research Foundation.

Crow, G. E. 1979. The systematic significance of seed morphology in *Sagina* (Caryophyllaceae) under scanning electron microscopy. Brittonia 31: 52–63.

Danin, A., I. Baker, and H. G. Baker. 1978. Cytogeography and taxonomy of the *Portulaca olera-*

cea L. polyploid complex. Israel J. Bot. 27:177–211.

DAVIS, P. H. and V. H. HEYWOOD. 1963. *Principles of angiosperm taxonomy*. London: Oliver and Boyd.

ELISENS, W. J. and A. S. TOMB. 1983. Seed morphology in new world *Antirrhinae* (Scrophulariaceae): Systematic and phylogenetic implications. Pl. Syst. Evol. 142:23–47.

GEESINK, R. 1969. Account of the genus *Portulaca* in Indo-Australia and the Pacific (Portulacaceae). Blumea 17:275–301.

HAUPTLI, H., B. D. WEBSTER, and S. JAIN. 1978. Variation in nutlet morphology of *Limnanthes*. Amer. J. Bot. 65:615–624.

HILL, R. J. 1976. Taxonomic and phylogenetic significance of seed microsculpturing in *Mentzelia* (Loasaceae) in Wyoming and adjacent western states. Brittonia 28:86–112.

JUDD, W. S. and R. P. WUNDERLIN. 1981. First report of *Portulaca amilis* (Portulacaceae) in the United States. SIDA 9:135–138.

LEGRAND, C. D. 1962. Las especies americanas de *Portulaca*. Anales Mus. Nac. Montevideo 7:1–147.

MATTHEWS, J. F. and P. A. LEVINS. 1985a. *Portulaca pilosa* L., *P. mundula* Johnst., and *P. parvula* Gray in the southwest. SIDA 11:45–61.

——— and ———. 1985b. The genus *Portulaca* in the southeastern United States. Castanea 50:96–104.

NEWELL, C. A. and T. HYMOWITZ. 1978. Seed coat variation in *Glycine* Willd. subgenus *Glycine* (Leguminosae) by SEM. Brittonia 30:76–88.

POELLNITZ, K. VON. 1934. Versuch zur einer Monographie der Gattung *Portulaca*. Feddes Repret Z. Bot. Taxon. Gebot. 37:240–320.

SMITH, E. B. 1978. *An atlas and annotated list of the vascular plants of Arkansas, + supplements.* Fayetteville, Arkansas: Published by the author.

STEYERMARK, J. A. 1963. *Flora of Missouri.* Ames: Iowa St. University Press.

WOFFORD, B. E. 1981. External seed morphology of *Arenaria* (Caryophyllaceae) of the southeastern United States. Syst. Bot. 6:126–135.

WYATT, R. 1984. Intraspecific variation in seed morphology of *Arenaria uniflora* (Caryophyllaceae). Syst. Bot. 9:423–431.

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Announcement

International Organization of Plant Biosystematists. The Executive and Council of the International Organization of Plant Biosystematists (IOPB) will meet during the IOPB 1986 Symposium, "Differentiation Patterns in Higher Plants", Zurich, Switzerland, 13–18 July 1986. Anyone wishing to place an item on the agenda for discussion should write to Dr. Liv Borgen, Secretary, IOPB, Botanical Garden and Museum, Trondheimsveien 23B, N-OSLO 5, NORWAY.

Information on participation may be obtained from the Chairperson, Dr. Krystyna Urbanska, Geobotanisches Institut, ETH, Stiftung Rubel, Zurichbergstrasse 38, CH-8044, ZURICH, SWITZERLAND.

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