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ABRONIA: III. PERICARP AND SEED COAT ANATOMY AND ITS ECOLOGICAL IMPLICATIONS FOR NINE SPECIES OF *ABRONIA*

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INTRODUCTION

In *Abronia* Juss. each seed contained in its anthocarp is conveyed to its site of germination relatively unexposed. Because both anthocarps and seed coats may exert an influence on embryo germination by regulating gas and water exchange between the embryo and the soil, or influencing its light requirements, etc., I present the hypothesis that variations in pericarp and seed coat cell size, shape, or contents may represent special adaptations of the species to their individual habitats.

As pointed out by Crosley (1966), effective reproduction involves germination and growth to maturity and not seed production alone. Structural modifications which would lead to this end might be considered to have a positive selective value. With this in mind, an attempt will be made here to correlate pericarp and seed coat structural differences among the species of *Abronia* with their ecological distribution.

From the standpoint of functional anatomy, pericarp and seed coat anatomy are considered because they are believed to underlie morphological and physiological changes which may be correlated with dispersal and germination of the seed.

MATERIALS AND METHODS

Specimens of *Abronia* used in this study were collected from California and Nevada during 1968 and 1969, and identified in accordance with Munz and Keck (1959). Voucher specimens have been deposited at the Rancho Santa Ana Botanic Garden, Claremont, California (Wilson, 1972). Special emphasis was given to species of *Abronia* found in California.

Portions of plants were preserved as pickled material in a standard FAA solution (Johansen, 1940). Pickled specimens were sectioned using materials from the following collections (collected by R. C. Wilson from California unless otherwise indicated): *A. maritima* Nutt. ex Wats. (1182 from Oso Flaco Dunes, San Luis Obispo Co.); *A. latifolia* Eschs. (1176 from Oso Flaco Dunes); *A. umbellata* Lam. (1172, Ventura State Park, Ventura Co.); *A. villosa* S. Wats. (1043, Coyote Wells, Imperial Co.); *A. pogonantha*

Fig. 1. Generalized illustration of a developed *Abronia* anthocarp and contained pericarp-seed unit.

Heimerl. (1088, Antelope Valley, Los Angeles Co.); *A. crux-maltae* Kell. (1135, dunes 10 miles north of Winnemucca, Humboldt Co., Nevada); *A. nana* Wats. ssp. *covillei* (Heimerl.) Munz (1171, north of Big Bear Lake, San Bernardino Co.); *A. turbinata* Torr. (1169 from Deadman's Summit on Hwy. 395, Mono Co.); and *A. alpina* Bdg. (1294, Ramshaw Meadows, Tulare Co.)

Both longitudinal and transections of anthocarps containing a seed were prepared using the paraffin method and stained with safranin 0 and fast green (Johansen, 1940). From these sections, transectional analysis of the pericarp and seed coat were made. Cell types, numbers, and thickness were recorded for each species. Photomicrographs and camera lucida drawings were prepared from the transections. Longitudinal sections were observed to better understand the position of the structures. The longitudinal sections were helpful in preparing a generalized diagram of the anthocarp, pericarp and seed (Fig. 1).

Relative percentages for thickness were calculated by considering each species as a percentage of the species with the highest total thickness for each of two categories: (1) integument thickness; and (2) integument plus pericarp thickness. Thus, the species with the highest total thickness will equal 100 percent.

SEED MORPHOLOGY

The anthocarp is an accessory "fruit" which develops about the gynoecium from the lower portion of the persistent perianth (Fig. 1). Consequently, the ovary wall does not differentiate into an elaborate fruit but rather remains as a thin single pericarp layer adherent to the seed coat.

Abronia spp. normally contain one seed within each anthocarp. When two seeds occur in an anthocarp; e.g., as noted in some *A. umbellata* anthocarps, one is usually abortive. Other normal-looking anthocarps may be empty and show no signs of either seed or ovary development.

Lubbock (1892) reported the presence of two cotyledons on the embryos and seedlings of some species but not on others, and in some seeds but not in other seeds of the same species. Seeds of *A. latifolia* examined from Oso Flaco Dunes contained embryos which had two cotyledons in part and only a single cotyledon in part. One of the two cotyledons observed on *A. latifolia* embryos was smaller. The smaller cotyledon was only half as long as the larger one.

Individual variability is a striking feature of many *Abronia* spp., e.g., anthocarp polymorphism was noted for several species (Wilson, 1974). Although the general appearance, size and weight of the seed-pericarp unit seems relatively uniform within each species, the differences among the species are clearly evident (TABLE 1, Figs. 2-10).

Salisbury (1942) noted a tendency for small seed size in dune and open habitat plants. The total range of weights recorded for *Abronia* (TABLE 1) falls within the range suggested by Salisbury (1942) as typical for dune or open habitat plants. *Abronia crux-maltae* has the heaviest seeds, 0.008 g, as compared to 0.002 g for the other species and 0.0013 g for the seeds of *A. pogonantha* which developed in wingless anthocarps. Although seeds from wingless anthocarps may be slightly lighter than those from winged anthocarps of the same species, seed weights in general do not correlate with changes in numbers of anthocarp wings or lobes.

Two seed-size classes are noted from the data in TABLE 1: (1) 0.006-0.008 g for *A. maritima*, *A. latifolia*, and *A. crux-maltae*; and (2) 0.0017-0.003 g for the other species listed. The extremely light seeds, 0.0013 g, of *A. pogonantha* are a variation in this species which also produce larger seeds, 0.0017 g.

When compared to other desert species as well as to montane species, *A. crux-maltae* is larger by about a 4 : 1 seed weight ratio. Interestingly, the next largest seeds are found among the coastal species.

PERICARP AND SEED COAT ANATOMY

DEVELOPMENT OF THE PERICARP AND SEED COAT

Because the ontogeny of *Abronia* carpels and ovules was not part of this study, I must rely on Rocen's (1927) descriptions of seed coat differentiation and pericarp development. He described a single integument in the developing ovules of *A. umbellata*. The development of this integument resembles the development of single integuments in both *Boerhaavia*

Figs. 2-10. Seeds of nine *Abronia* spp. showing the appearance and major size differences.—2. *Abronia maritima*.—3. *Abronia latifolia*.—4. *Abronia umbellata*.—5. *Abronia villosa*.—6. *Abronia pogonantha*.—7. *Abronia crux-maltae*.—8. *Abronia nana covillei*.—9. *Abronia turbinata*.—10. *Abronia alpina*.

TABLE 1. Average (arithmetic mean) seed-pericarp weight and length characteristics for nine *Abronia* species.

Species and habitat group	Number of wings or lobes per anthocarp	Mean seed-pericarp	
		Weight (g)	Length (mm)
COASTAL			
<i>A. maritima</i>	5	0.0067	5.0
<i>A. latifolia</i>	5	0.0063	4.5
<i>A. umbellata</i>	0-5	0.0025	4.0
DESERT			
<i>A. villosa</i>	0-2	0.0025	3.0
	3-5	0.0028	
<i>A. pogonantha</i>	0	0.0013	2.0
	2-3	0.0017	
<i>A. crux-maltae</i>	2-4	0.0083	7-7.5
MONTANE			
<i>A. nana covillei</i>	5	0.0020	3.0
<i>A. turbinata</i>	0-5	0.0018	2.5
<i>A. alpina</i>	0	0.0025	2-2.5

repanda Willd. and *B. diffusa* L., described by Bhargava (1932) as exceptions for Nyctaginaceae.

Five to six cell layers occur in the integument of *A. umbellata* at the mature embryo sac stage. One enlarged, outer layer (containing aleurone grains) and three elongated inner layers remain in the fully differentiated integument (Rocen, 1927).

Two cuticular layers occur on the integument, one on the outer edge and one on the inner edge. The cuticular layer on the inner edge of the integument fuses with the cuticle of the outer layer of the nucellus. The outer layer of nucellus may separate from the rest of the nucellus tissue and adhere to the integument by its cuticle. The double-layered cuticle is evident in all nine species of *Abronia* as a clear white band (Figs. 11-19, 20-28). The waxy nature of this layer is evident in stained sections because it does not stain with either safranin or fast green.

After fertilization the ovary wall begins to dissociate and eventually fuses to the integument as a single layer of cells (Rocen, 1927). I have labeled the layer between the pericarp and the integument, where fusion takes place, the fusion layer (Figs. 1, 20). The fusion layer appears to contain lignin, possibly cutin from the outer cuticle of the integument, and other darkly stained, unidentified substances. Outer pericarp surfaces are covered by thin cuticles. In some species the pericarps are often fragmented or stretched. In other species pericarp cells not only remain intact, but appear somewhat enlarged and may contain aleurone grains.

Longitudinal sections of *A. nana covillei* and *A. latifolia* fruits revealed fragments of styles at the tops of seeds. In most *Abronia* species the styles are short and thin.

Figs. 11-19. Pericarp and seed coat transections from nine species of *Abronia*.—11. *Abronia maritima*.—12. *Abronia latifolia*.—13. *Abronia umbellata*.—14. *Abronia villosa*.—15. *Abronia pogonantha*.—16. *Abronia crux-maltae*.—17. *Abronia nana covillei*.—18. *Abronia turbinata*.—19. *Abronia alpina*.

Figs. 20-28. Camera Lucida drawings of pericarp and seed coat transections from nine species of *Abronia*.—20. *Abronia maritima*.—21. *Abronia latifolia*.—22. *Abronia umbellata*.—23. *Abronia villosa*.—24. *Abronia pogonantha*.—25. *Abronia crux-maltae*.—26. *Abronia nana covillei*.—27. *Abronia turbinata*.—28. *Abronia alpina*.

TABLE 2. *Pericarp, seed coat and nucellus dimensions in microns taken from trans-sections of Abronia fruits.*

Species and habitat groups	Characters								
	Pericarp (μm)	Fusion layer (μm)	Integument		Total ^a (μm)	Total ^b (μm)	Double cuticle (μm)	Total ^c (μm)	Nucellus (μm)
			Outer layer (μm)	Inner layer (μm)					
COASTAL									
<i>A. maritima</i>	8	4	42	11	53	61	1.8	67	18
<i>A. latifolia</i>	6	4–12	32	8	40	46	2.0	52	4–7
<i>A. umbellata</i>	4	3–7	16	4	20	24	0.9	28	4
DESERT									
<i>A. villosa</i>	16	2–3	20	8	28	44	1.5	47	8–10
<i>A. pogonantha</i>	5	7	20	3	23	28	1.5	36	8–10
<i>A. crux-maltae</i>	2	5	16	10	26	28	1.0	34	4–8
MONTANE									
<i>A. turbinata</i>	8	3	18	7	25	33	1.0	37	5–12
<i>A. nana covillei</i>	5–7	3	11	4	15	21	1.3	26	6–10
<i>A. alpina</i>	3	6	8	2	10	13	0.9	20	3

^a Total thickness for outer and inner layers of the integument combined.^b Total thickness for pericarp and integument combined.^c Total thickness for pericarp and seed coat components combined excluding the nucellus.

PERICARP AND SEED COAT VARIABILITY

The more striking pericarp and seed coat structures of each species are compared in this section. Anatomical differences of pericarps and seed coats described here appear to be correlated with both the habitat and habit of any given species.

Pericarp, cuticle, and fusion layer thickness, outer layer and inner layers of the integument, and the nucellus layer adhering to the integument, all vary among the species (TABLE 2; Figs. 11-19, 20-28).

Four cell layers occur in the integuments of the *Abronia* spp. studied, except *A. crux-maltae* which had only three. Cells of the outer layer are generally enlarged and contain aleurone grains.

Cells of the outer layer of the integument are elongated anticlinally in *A. maritima*, *A. latifolia*, *A. umbellata*, *A. villosa*, and *A. turbinata*; and periclinally in *A. crux-maltae*, *A. nana covillei*, and *A. alpina*. The same cells are elongated in both directions in *A. pogonantha*.

Three layers of cells occur in the inner layers of the integument in the species studied, except *A. crux-maltae* which generally develops only two inner layers. Cells in the inner layers are periclinally elongated, stretched, collapsed or compressed, and may contain a substance resembling aleurone in solid masses.

The inner layers of the integument in *A. pogonantha* are discontinuous. In parts of the integument, extremely compressed cells are found between the outer layer of integument and the double cuticle.

Data from experiments using fluorochromide as a marker, indicate that seed coats combined with cuticles show a reduced penetrability (Esau, 1967). In addition to the integumentary cuticles, seeds of *Abronia* species develop a fusion layer which varies in thickness from species to species. The relatively thick cuticular layer may function to make the seeds of *Abronia* species more impermeable to water as it does for many legume seeds with hard seed coats (Esau, 1967).

Aleurone occurs in the perianths of *Boerhaavia* (Kajale, 1938) as well as in the seed coats of other members of the Nyctaginaceae, and is prevalent in seed coats of *Abronia*. The distinctive granular nature of the aleurone grains is visible in the sections of *A. maritima* seed coats (Fig. 11) as well as in the seed coats of other species sectioned in this study (Figs. 12-19). Although the mobilization of aleurone might physiologically regulate embryo dormancy in some way, the actual effect of aleurone in the seed is not known. Aleurone may have some effect on germination, seed coat permeability, or starch digestion in the perisperm.

If total thickness is taken as an indicator of significant pericarp and integument modifications, variations among the species studied appear correlated with habitat (TABLE 2, Fig. 29).

The fusion of the pericarp to the integument in *Abronia* is not unlike that found in other genera of the Nyctaginaceae.

The fusion layer of *A. alpina* appears unusually thick relative to the size of the cells in the pericarp and outer layer of the integument.

Unlike the other species *A. nana covillei* has only small amounts of aleurone grains deposited in the outer layer of its integument (Figs. 17, 26). All desert species show a marked accumulation of aleurone grains not only in seed coats but also in the margins of cotyledons, radicles, and funicles.

The pericarp cells of *A. turbinata* are relatively thick walled and persist in the seed as a well-developed layer. The outer integument layer of *A. turbinata* accumulates aleurone grains that form solid masses (Figs. 18, 27). These characteristics are intermediate between those of pericarps and integuments of desert and montane species. This may be directly correlated with the distribution of *A. turbinata* which truly may fall between the categories delimited in this paper as desert and montane.

The two coastal species *A. maritima* and *A. latifolia* have the thickest integuments (TABLE 2, total 1). Species characteristic of waste areas behind the coastal dunes, in deserts, and along the dry slopes of the desert edge, all have integuments ranging from 20 to 30 μm thick, e.g., *A. umbellata*, *A. villosa*, *A. pogonantha*, and *A. turbinata*. The isolated and specifically montane groups have the thinnest integuments, e.g., *A. nana covillei* and *A. alpina*. When total thickness of the pericarp in combination with the integument is considered (TABLE 2, total 2, Fig. 29), all but *A. villosa* fall into size categories with the same species as before.

The total thickness of *A. villosa* pericarp and integument comes close to that for *A. latifolia*. The extremely thick pericarp of *A. villosa* is distinctive. Unlike the pericarps of the other species, it contains large accumulations of aleurone grains. The thick, relatively impermeable pericarps

Fig. 29. Relationship of integument thickness to integument and pericarp thicknesses combined for nine *Abronia* spp. from three major habitat categories.—Circle: open, dot, and solid represent *A. maritima*, *A. latifolia*, and *A. umbellata* respectively.—D: open, dot, and solid represent *A. villosa*, *A. pogonantha*, and *A. crux-maltae* respectively.—Triangle: open, dot, and solid represent *A. turbinata*, *A. nana covillei*, and *A. alpina* respectively.—Relative percentages calculated from totals 1 and 2 on TABLE 2.

and integuments of *A. villosa* may be correlated with its distribution near bodies of salt water. Thinner, permeable pericarps and integument layers containing less aleurone may be correlated with slightly more mesic habitats away from saline areas.

SUMMARY

Several differences are shown for the seed morphology and for the anatomical structures of the pericarps and seed coats of nine species of *Abronia*. Striking differences in cell size and cell contents of the pericarps and integuments are especially apparent in four species.

In *A. maritima*, the pericarp is not especially thick ($8\text{ }\mu\text{m}$), but its integument is the thickest ($53\text{ }\mu\text{m}$) measured. Integument cells are filled with solid masses of aleurone.

In *A. villosa*, the pericarp is notably well developed and is the thickest ($16\text{ }\mu\text{m}$) measured whereas the integument is intermediate in thickness ($28\text{ }\mu\text{m}$). Both pericarp and the outer integument layer are filled with aleurone grains.

In *A. alpina*, both pericarp ($3\text{ }\mu\text{m}$) and integument layers ($10\text{ }\mu\text{m}$) are the thinnest measured.

In *A. nana covillei*, pericarp ($5\text{--}7\text{ }\mu\text{m}$) and integument ($15\text{ }\mu\text{m}$) combined are among the thinnest measured. Although the pericarp persists intact in the mature seed, it does not contain aleurone grains. The outer layer of the integument contains small amounts of aleurone in contrast to the desert and coastal species.

An attempt was made to correlate pericarp and seed coat differences with the ecological distribution of the species. Three species can be listed to represent extremes in variation for pericarps and integuments: (1) *A. maritima*, a coastal species, thickest integument; (2) *A. villosa*, a desert species, thickest pericarp; and (3) *A. alpina*, a montane species, thinnest pericarp and integument.

Although the actual functions of the various parts of the pericarps and seed coats are unknown, the morphological and anatomical data suggest that they may have evolved as modifications correlated with adaptations to saline or dry conditions.

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