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Ruth C. Wilson

California State University, San Bernardino

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ABRONIA: II. ANTHOCARP POLYMORPHISM AND
ANATOMY FOR NINE SPECIES OF ABRONIA
FOUND IN CALIFORNIA

RUTH C. WILSON

*Department of Biology, California State College
San Bernardino, California 92407*

INTRODUCTION

The highly diversified topography of California presents an ideal study area for an interpretation of morphological and anatomical divergence among species of a single genus. An attempt will be made here to correlate anthocarp structural differences with the ecological distribution of nine species of *Abronia* Juss.

Within the genus, the species of *Abronia* studied here represent the total range of habitats occupied by all species and include all representative anthocarp modifications. The nine species of *Abronia* found in California are placed in three major habitat categories: (1) coastal, including *A. maritima* Nutt. ex Wats., *A. latifolia* Eschs. and *A. umbellata* Lam.; (2) desert, including *A. villosa* S. Wats., *A. pogonantha* Heimerl. and *A. crux-maltae* Kell.; and (3) montane, including *A. nana* Wats. ssp. *covillei* (Heimerl.) Munz, *A. turbinata* Torr. and *A. alpina* Bdg. (Wilson 1970a, 1972).

Past anatomical and morphological studies of members of the Nyctaginaceae (e.g., Bhargava, 1932; Maheshwari, 1929; Rocen, 1927) were made to answer questions of taxonomic importance, but not questions related to dispersal. Of the *Abronia* species studied only *A. umbellata* was considered in terms of vascular tissue distribution primarily for taxonomic purposes. General descriptions of "typical" anthocarps are usually included in taxonomic keys, e.g., Munz and Keck (1959), and Standley (1909, 1911, 1918). What is not generally described is the polymorphism found among the anthocarps of a single inflorescence.

Throughout the Nyctaginaceae an accessory "fruit" is commonly developed about the gynoecium from the modified or expanded lower portion of the persistent perianth. A number of modifications of this "fruit," anthocarp, are illustrated for the nine species of *Abronia* found in California.

From the standpoint of functional anatomy, anthocarp anatomy is considered because it underlies morphological changes which may be correlated with dispersal and protection of the contained seed. A study of

anthocarp anatomy should provide clues to the distribution of weight and air spaces in the anthocarps relative to an understanding of anthocarp permeability, buoyancy, and possible potential for dispersal by wind. If natural selection results in economy, there will be little waste in the development of structures, especially in species evolved in the harsh xeric environments so often occupied by members of the Nyctaginaceae, and by species of *Abronia* in particular.

This paper hypothesizes that natural selection in *Abronia* acts on the structures involved with dispersal just as it does on structures related to processes necessary for individual survival and reproduction. The study of anthocarp and seed morphology and anatomy should provide clues for the interpretation of their function in eliminating or minimizing chances of dispersal or germination failure. The anthocarp is the vehicle of dispersal in space and germination-regulation mechanisms are the agents of dispersal in time.

This study is a step toward defining the possible adaptive value of the structural modifications observed in the indehiscent anthocarps of *Abronia*. In this effort we must keep in mind the fact that the structures which develop into the anthocarp, pericarp, and seed coat are involved not only with dispersal and germination but also with earlier processes of major reproductive importance, e.g., pollination, fertilization, and embryo development.

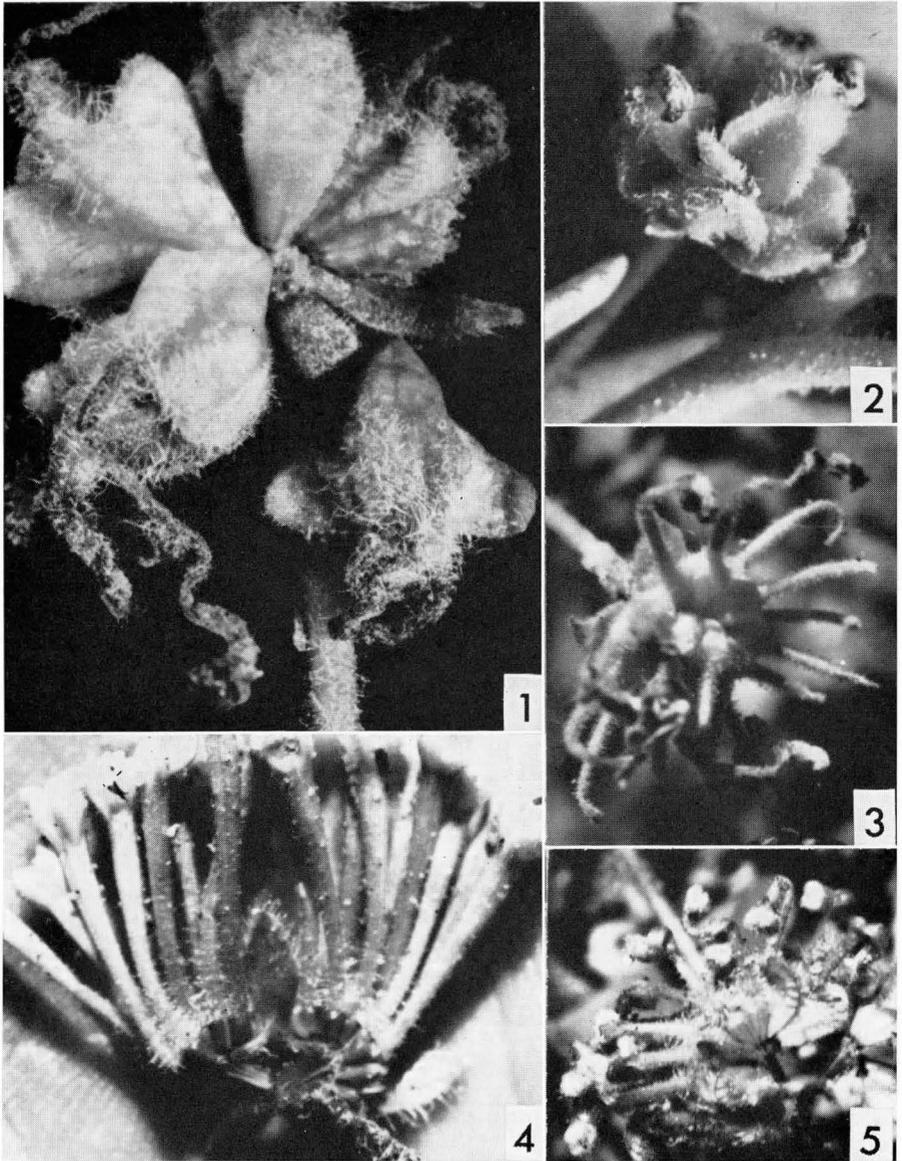
MATERIALS AND METHODS

Specimens of *Abronia* used for this study were collected from California, Nevada, and Arizona 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).

Variability of anthocarp size and shape within a single inflorescence was considered. When polymorphism of anthocarps was pronounced in an inflorescence, anthocarps of similar shape were measured together and recorded together in separate shape categories. The number of wings or lobes developed on each anthocarp provided the main criterion for the establishment of these categories.

Anthocarps, which were harvested and allowed to dry in paper bags, were used for weight and size measurements. Anthocarp measurements include length, width, and body diameter (diameter excluding wings or lobes where possible). Each anthocarp with its contained seed was weighed; later the seeds were removed and weighed separately. Although the seed coat is adherent to the pericarp—generally only a single layer of ovary wall in the mature seed stage—this complex of seed and pericarp will be referred to in this paper simply as the seed with the understanding that the term seed, generally used in most taxonomic keys, refers more specifically to a fruit type similar to a caryopsis.

Each anthocarp normally develops one seed but many do not develop any seeds. Therefore, anthocarps were opened and the seeds checked for size



Figs. 1-5. Headlike inflorescences with anthocarps for four species of *Abronia*.—1. Separated, developed anthocarps of *A. villosa*, $\times 3.5$.—2. Developed anthocarps of *A. maritima*, $\times 1.9$.—3. *Abronia turbinata* developing anthocarps with upper perianth beginning to twist and wither, $\times 1.9$.—4. Early stage of *A. pogonantha* anthocarp development with upper perianth still fresh, $\times 2.7$.—5. Later stage of *A. pogonantha* anthocarp development showing two-winged forms toward the outer edges and wingless forms in a central cluster of the inflorescence, $\times 1.9$.

and general condition. Data recorded for an anthocarp which was later found to be lacking a seed were eliminated from the calculations. Only mature, abscised anthocarps with a seed were used for anatomical studies to insure that any variation detected did not result from changes connected with seed abortion and subsequent failure of anthocarp development.

Sections of anthocarps fixed in FAA were prepared using the paraffin method and stained with safranin 0 and fast green (Johansen, 1940). From these sections, tissue arrangement, special cell types, and the formation of the cavity within the body of the anthocarp were taken as evidence of internal differences which may be related to general morphological differences seen among the nine species of *Abronia* studied.

Trichomes present on the surfaces of mature anthocarps were also examined. Camera lucida drawings of trichomes were made from macerated or sectioned anthocarps. Parenchyma cells were drawn from macerated anthocarp tissues.

MORPHOLOGY

DEVELOPMENT OF THE ANTHOCARP

After fertilization, an abscission layer forms approximately in the region where the perianth tube constricts above the ovary. Maheshwari (1929) described small cells with a tubular arrangement and dense cytoplasm in the region of abscission. In the species studied here, the lower portion of the perianth becomes cut off from the upper portion which soon withers, twists, and dies (Figs. 1-5). The top of the anthocarp becomes generally sealed off, completely enclosing the developing ovary wall and seed. Bhargava (1932) described the development of *Boerhaavia diffusa* L. perianths into anthocarps as following a sequence of events similar to that of *A. umbellata* as described by Rocen (1927). *Abronia* anthocarps are indehiscent, and may persist even after seedlings develop. Seedlings at the Rancho Santa Ana Botanic Garden were observed growing through the persistent anthocarp walls.

GENERAL MORPHOLOGY OF THE ANTHOCARP

When compared with other species of *Abronia*, the California species as a group show the greatest diversity of anthocarp shape, size, and weight. The anthocarp structure may be subdivided into two parts: (1) the body, and (2) the wings or lobes. The body wall directly surrounds the inner cavity which contains the seed which is adherent to the pericarp. The wings or lobes radiate outward from the body. Winged or lobed anthocarp conditions are differentiated morphologically by the formation of the inner cavity. If the inner cavity extends, even a short distance, into the expanded edge of the perianth, it is lobed. Although the exact point which separates lobes from body wall is sometimes only marked by an arbitrary imaginary line designated by the investigator, the distinction between the two is made wherever possible. If the inner cavity does not extend laterally and is cut off from the expanded perianth edges by bands of fibers, vascular tissue, and parenchyma, the anthocarp is winged.

Winged anthocarps occur in *A. umbellata*, *A. villosa*, *A. pogonantha*, and *A. crux-maltae*. The other species studied have lobed anthocarps, except *A. alpina*. *Abronia alpina* has an anthocarp which is so reduced that it has neither wings nor lobes and may be described as ridged at most (Wilson 1970b).

The anthocarp bodies of each species are described as follows: *A. maritima*, spongy to the touch; *A. latifolia* and *A. pogonantha*, coriaceous; *A. umbellata*, *A. villosa*, and *A. crux-maltae*, especially indurate with fibrous walls; *A. alpina*, thin but coriaceous; *A. turbinata*, thin and slightly hardened; and *A. nana covillei*, very thin and fragile.

The coarsely reticulate-veined anthocarp lobes in *A. maritima* are thin at the upper edges and often extend above the body. Anthocarps in *A. maritima* are generally truncate above and attenuate below.

In *A. latifolia* the reticulate-veined lobes are attenuate above and below giving the anthocarps a biturbinate shape.

The thin, faintly net-veined wings in *A. umbellata* are truncate above and attenuate below. These wings generally do not extend far above the short-beaked anthocarp body.

The wings in *A. villosa* are thin, faintly veined, and alternately convex and concave when viewed from one side. In the wind, these anthocarps spin along the ground turning like propellers. The anthocarps of *A. villosa* are unlike those of *A. umbellata* owing to their rugose-veined (pitted) bodies, and wings that often extend well above the body.

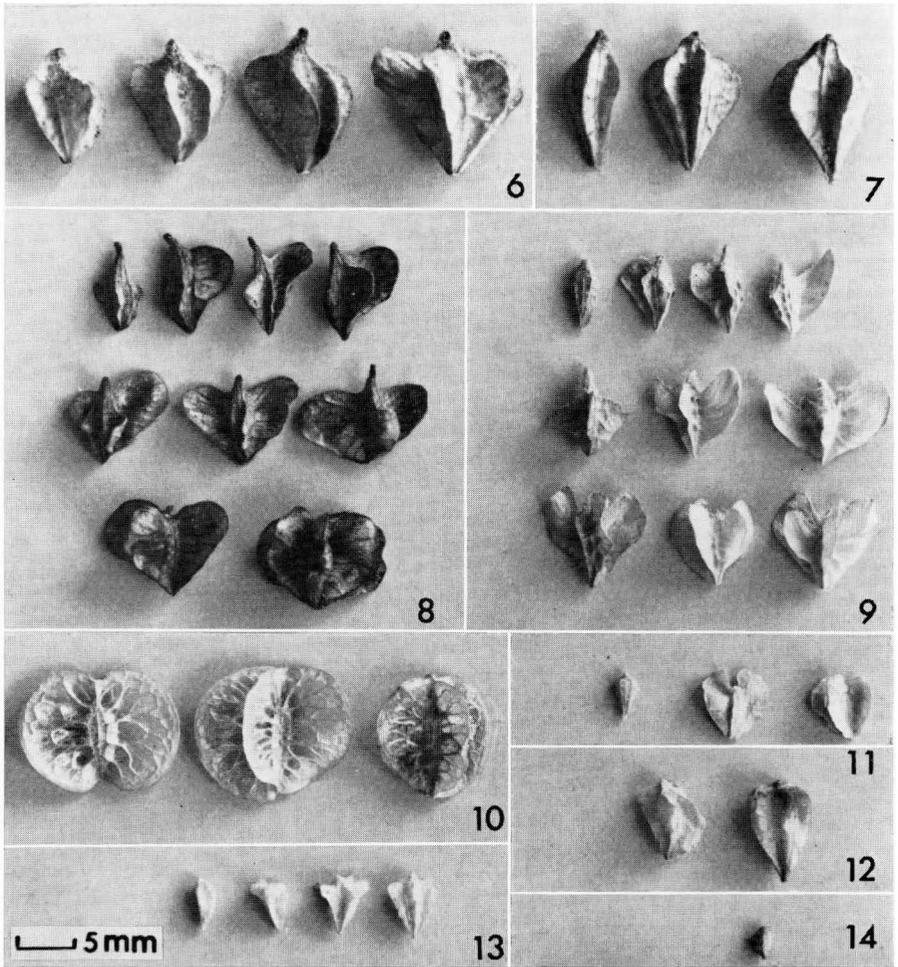
In *A. pogonantha* anthocarps have thin, obscurely veined wings. Typically two wings develop on opposite sides of the finely reticulate-veined body; these anthocarps have an orbicular-obcordate shape.

The membranous wings of *A. crux-maltae* anthocarps are coarsely net-veined. The veins are strikingly indurate. The wings are rounded both above and below the anthocarp body.

Abronia nana covillei anthocarps are turbinate or obcordate, with thin-walled, regular lobes. The top of each lobe is slightly inflated and perpendicularly flattened. This flattened crest on each lobe is an important modification which increases the surface area of the anthocarp.

The faintly net-veined lobes of *A. turbinata* anthocarps are acute, truncate above and extremely attenuated below, tapering abruptly to a sharp point at the base in populations from Deadman's Summit. Anthocarps from populations in the Mt. Pinos region have relatively rounded bases and slightly inflated upper edges along the lobes. A study of variation among the widely scattered and apparently isolated populations of *A. turbinata* could present some interesting problems.

The thin, reticulate-veined anthocarp bodies of *A. alpina* are narrowed at each end and are obtusely or acutely angled. *Abronia alpina* anthocarps are described as having no wings or lobes; but at least two pronounced, longitudinal, linelike ridges generally developed to one side in the upper half of the anthocarp. These ridges may represent wing vestiges. Five linelike thickenings are also visible on the surfaces of the anthocarps. These



Figs. 6-14. Polymorphism of *Abronia* anthocarps from nine species, all enlarged to the same scale, $\times 1.5$.—6. *Abronia maritima*.—7. *Abronia latifolia*.—8. *Abronia umbellata*.—9. *Abronia villosa*.—10. *Abronia crux-maltae*.—11. *Abronia pogonantha*.—12. *Abronia nana covillei*.—13. *Abronia turbinata*.—14. *Abronia alpina*.

thickenings correspond with the five major, longitudinal vascular bundles of the body wall.

POLYMORPHISM OF THE ANTHOCARP

An important implication to this series of studies is that polymorphism may be significant as it affects the potential of a species for dispersal to a wide range of distances under variable wind velocities and terrain relative

TABLE 1. Average (arithmetic mean) anthocarp size and weight characteristics relative to numbers of wings or lobes present for nine *Abronia* species found in California.

Species and habitat groups	Number of wings or lobes	Mean anthocarp				Mean total seed and anthocarp weight (g)
		Width (mm)	Length (mm)	Body diam. (mm)	Weight (g)	
COASTAL						
<i>A. maritima</i>	3-5	12.3	12.3	3.9	0.0439	0.0500
<i>A. latifolia</i>	5	8.2	10.1	4.0	0.0260	0.0320
<i>A. umbellata</i>	0	3.7	6.0	1.7	0.0039	0.0064
	3-5	9.1	6.8	1.6	0.0068	0.0094
DESERT						
<i>A. villosa</i>	0	4.7	8.3	2.0	0.0082	0.0104
	1-2	8.8	8.2	1.8	0.0076	0.0101
	3-5	10.7	9.6	1.8	0.0112	0.0139
<i>A. pogonantha</i>	0	1.7	4.0	1.7	0.0004	0.0017
	2	6.2	6.1	1.7	0.0017	0.0029
	3	5.7	5.9	1.7	0.0014	0.0031
<i>A. crux-maltae</i>	2-4	15.6	13.1	2.9	0.0096	0.0179
MONTANE						
<i>A. nana covillei</i>	5	5.8	7.9	1.7	0.0026	0.0046
<i>A. turbinata</i>	0	2.3	4.3	1.9	0.0007	0.0025
	3-5	4.1	5.5	2.0	0.0016	0.0033
<i>A. alpina</i>	0	1.9	3.2	1.9	0.0006	0.0030

to the variability of the anthocarp shapes, sizes, and relative weights. A study of these effects will be presented in a future paper.

Anthocarp polymorphism is of special interest in *Abronia* because it is pronounced in some species and not in others (TABLE 1, Figs. 6-14).

Anthocarp length and weight decrease as the number of wings decreases. A marked increase in weight is noted in *A. umbellata*, *A. pogonantha*, and *A. turbinata* anthocarps with the addition of wings. Weight increases in *A. villosa* anthocarps are not striking until three to five wings have been added. Even then, the weight increase of winged over wingless anthocarps in *A. villosa* is not as great as that recorded for the three species listed above. The wings of *A. villosa* anthocarps are very thin, most of the anthocarp weight is in the body. The anthocarps of coastal species are generally the heaviest and those of montane species are generally the lightest.

Body diameters do not change as the numbers of wings or lobes on the anthocarps change (TABLE 1). Except for *A. crux-maltae*, the body diameters recorded for *A. maritima* and *A. latifolia* anthocarps are twice the size recorded for the other species measured.

If the numbers of wings or lobes are used to describe polymorphism within a species, the desert species *A. villosa* (Figs. 1, 9) and *A. pogonantha* (Figs. 4, 5, 11), the coastal, weedy species *A. umbellata* (Fig. 8), and the montane species *A. turbinata* (Figs. 3, 13) all display significant variability

among their anthocarps. Of the four, *A. turbinata* anthocarps show the slightest degree of polymorphism.

Anthocarps are arranged from left to right (Figs. 6–14) to represent the variation common among the anthocarps within a single inflorescence from the outer edge of the head to the center, respectively except for *A. pogonantha* (Fig. 11). Unlike the other species illustrated, in *A. pogonantha* (Fig. 11) anthocarps without wings or with three wings may develop in the center of the head and the two-winged forms toward the edge or throughout the head. In some inflorescences only two-winged types are found.

The greatest variability in shapes is seen in *A. umbellata* (Fig. 8) and *A. villosa* (Fig. 9), with all shapes and sizes grading from wingless to five-winged forms. In *A. pogonantha* (Fig. 11) a more precise expression of polymorphism is seen with three distinct anthocarp types, wingless, two-winged, and three-winged.

At least two broad wings commonly develop on the anthocarps of *A. crux-maltae* (Fig. 10). As many as four wings may occur on the anthocarps of this species, the additional wings may be of various sizes.

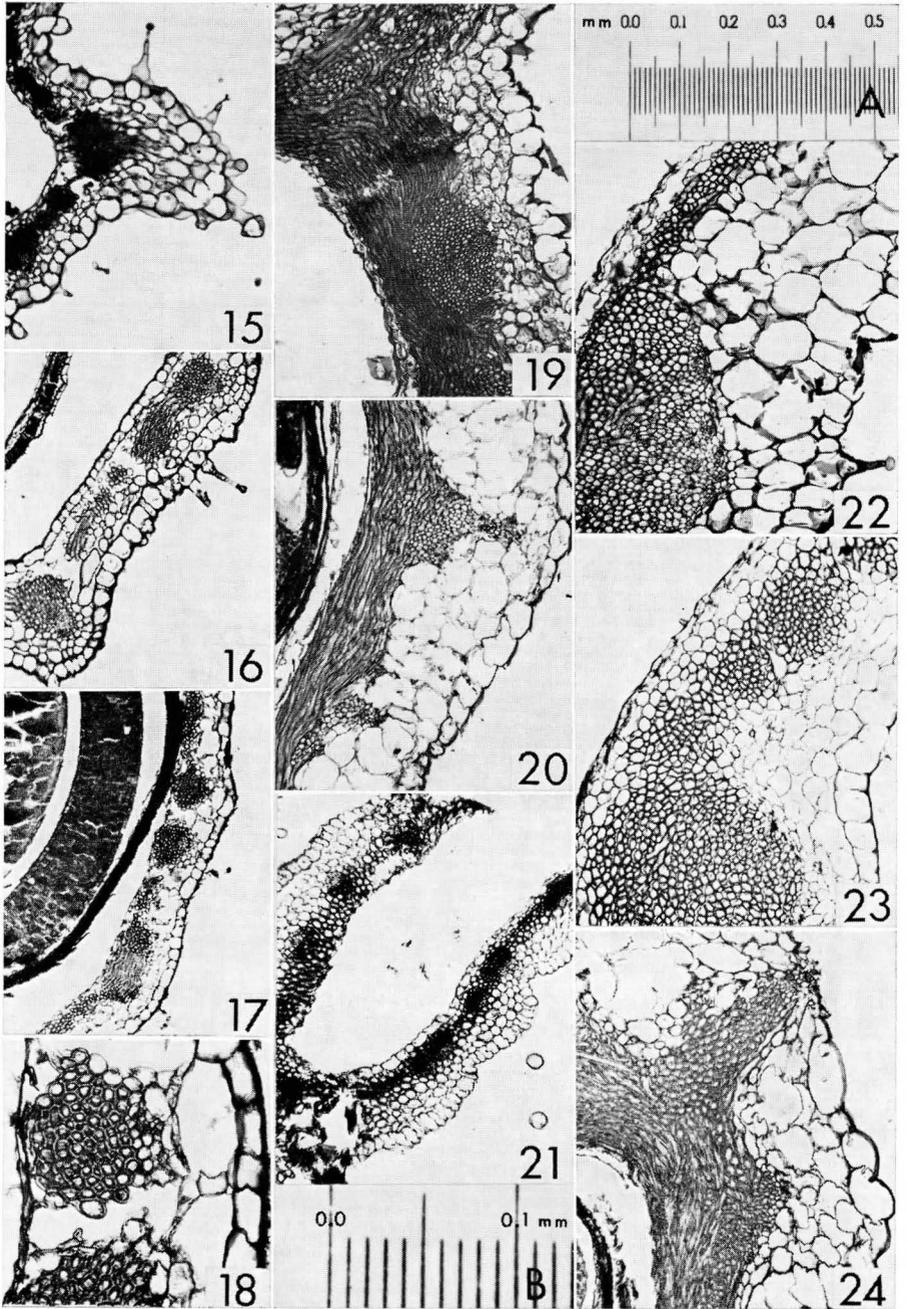
The anthocarps of *A. nana covillei* (Fig. 12) are relatively uniform.

Anthocarps of the outer series in *A. turbinata* are conspicuously reduced when compared to the innermost anthocarps. On the outer edges of the heads, anthocarps from Deadman's Summit populations often develop two horn-shaped lobes at their tops; a feature which is common to the majority of anthocarps in heads of plants from populations of the southern Sierra Nevada portion of the range near Lake Isabella.

One might suggest that because the anthocarps of *Abronia* species are developed in crowded headlike inflorescences (Figs. 1–5) it is not surprising to find differences in the development of wings and lobes relative to the position of the anthocarp in the inflorescence. Generally wings and lobes are best developed on the centermost anthocarps. The centermost anthocarps are often the most uniform in shape, and are the ones used taxonomically to represent the "typical" anthocarp type in keys to the species. Yet, does the congestion of anthocarps into dense headlike inflorescences or the position of these developing anthocarps sufficiently explain their tendency to produce asymmetrical anthocarps toward the outer edges of the head? Consider the facts that wingless anthocarps in *A. pogonantha* (Figs. 4, 5) develop in the centers of heads; that many species, with crowded anthocarps, still produce winged, relatively sym-

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Figs. 15–24. Anthocarp transections from nine species of *Abronia* showing amounts and arrangement of three major tissue regions: epidermis, parenchyma, and fibers and vascular bundles. Exterior anthocarp edges are positioned toward the right of the page. All figures are enlarged to scale A, except figure 18 which is enlarged to scale B.—15. *Abronia nana covillei*.—16. *Abronia turbinata*.—17–18. *Abronia alpina*.—19. *Abronia villosa*.—20. *Abronia crux-maltae*.—21. *Abronia pogonantha*.—22. *Abronia maritima*.—23. *Abronia latifolia*.—24. *Abronia umbellata*.



metrical, uniform anthocarps throughout; and that in groups such as *A. crux-maltae* wingless anthocarps are not developed. It soon becomes apparent that anthocarp polymorphism, seen in several species of *Abronia*, is not just the consequences of their maturation in a headlike inflorescence. Variability in symmetry evidently is under some genetic control since crowded, developing anthocarps in the different species do not all show the same degree of variability within their inflorescences (Figs. 6-14). Morphological variability of the anthocarps among species and within inflorescences of a species may be correlated with differential dispersibility both among the species and within a species. Anthocarp polymorphism may give the species a wider range of dispersal potentials which could be of adaptive value in some habitats.

ANTHOCARP ANATOMY

TISSUE ARRANGEMENT

For *Abronia* in general, I separate the anthocarp tissues into three categories; (1) epidermis, (2) parenchyma, and (3) vascular bundles associated with fibers. One to several layers of parenchyma occur beneath the outer epidermis. Inward from the outer layer of parenchyma, either bands, or discontinuous strands of fibers and vascular tissue develop. Vascular bundles are composed of small areas of phloem to the outside and large areas of xylem to the inside. Generally at least one layer of parenchyma develops adjacent to the inner epidermis. (See Figs. 15-24)

In the species examined, five vascular bundles are visible as distinct structures at the bases of anthocarps in all but *A. crux-maltae*. Only four vascular bundles occur at the bases of *A. crux-maltae* anthocarps. Observations of serial sections taken from the anthocarps of the nine *Abronia* species studied revealed that each vascular bundle divides into two a short distance from the base of the anthocarp. One main vascular bundle develops in each lobe or beneath each wing and one minor vascular bundle develops between the lobes or wings. The same patterns of vascular bundles are seen in transverse sections of wingless or lobeless anthocarps. The larger vascular bundles in the bodies of wingless and lobeless anthocarps may mark the position where wings or lobes might have developed. Continued subdivision of the vascular bundles is evidenced by reticulate venation patterns, visible on the surfaces of the anthocarp bodies. Distinct vascular bundles are often surrounded by heavy dense bands of fibers and are thus further obscured in the middle and upper anthocarp body walls. Only at the very tops of anthocarps, above the abscission layers in the perianth where fibers are absent, are the five main vascular bundles distinctly visible again.

Anthocarp surfaces, in all *Abronia* species studied, are covered by thin, uniform cuticles. Cuticles, on both exterior and interior surfaces, showed no signs of any special sculpturing or other features that might be uniquely related to dispersal.

Raphides of calcium oxalate are especially abundant in the inner epi-

dermal layers of all anthocarps. Pockets of raphides beneath the interior anthocarp surfaces are so large and numerous that they are readily visible to the naked eye as bright, glistening areas.

RELATIVE AMOUNTS OF TISSUE TYPES

The amount of parenchyma and fibers developed in anthocarp walls varies markedly among the species.

The crests at the tops of anthocarp lobes described for *A. nana covillei* under GENERAL MORPHOLOGY OF THE ANTHOCARP were examined from longitudinal and transverse anthocarp sections. Large cavities occur inside the crests, but they do not interconnect with the body cavity. The body cavity extends longitudinally into the lobes along the middle third of the anthocarp. The combination of thin anthocarp walls, inflated crests, and partially inflated lobes makes these anthocarps balloonlike.

Although the anthocarps of *A. nana covillei* (Fig. 15) are about three times larger than those of *A. turbinata* (Fig. 16) and at least five times larger than those of *A. alpina* (Figs. 17, 18), body wall thickness is similar in all three. The anthocarp walls in *A. alpina* are the thinnest of any *Abronia* species studied.

In transverse sections, the anthocarp walls of *A. alpina* are characterized by large intercellular spaces in the outer parenchyma layer and a band of discontinuous fibers and vascular tissue. By contrast, the outer parenchyma layers in *A. nana covillei* and *A. turbinata* are more compact.

Near the tops and generally to one side of *A. alpina* anthocarps radially broadened areas, composed primarily of parenchyma cells, are seen in longitudinal sections. These areas appear to correspond to the position on the anthocarp relative to the vascular bundles where wings would form in winged species, e.g., *A. villosa*.

In *A. villosa* narrow fibrous wings extend from a hard anthocarp body which is composed mostly of continuous bands of fibers and vascular tissue. Relatively little parenchyma occurs toward the outside of these anthocarps. Only a single layer of parenchyma cells develops inside the inner epidermis (Fig. 19).

Although placed with desert and waste-area species, *A. pogonantha* anthocarps are unlike those of *A. umbellata*, *A. villosa*, and *A. crux-maltae*. Continuous heavy bands of fibers do not occur in the small, thin, delicate anthocarps of *A. pogonantha*; one portion of the body wall may contain vascular bundles and dense bands of fibers, and another may contain vascular bundles and fibrous strands separated by parenchyma cells (Fig. 21). In *A. pogonantha*, fibers and vascular bundles are rarely seen in transverse sections of the wings. The wings are composed of irregularly shaped parenchyma cells and large intercellular spaces.

In the hard fibrous bodies of *A. crux-maltae* anthocarps, continuous heavy bands of fibers encircle the body cavities separated from the inner epidermis by a single intermittent layer of parenchyma (Fig. 20). Three to four layers of thin-walled parenchyma cells occur to the outside of the fibrous layers.

Anthocarps of *A. maritima* and *A. latifolia* contain large parenchyma cells which form an especially thick spongy outer layer in *A. maritima* (Fig. 22), and a thinner spongy layer in *A. latifolia* (Fig. 23). Because a wider band of fibers and vascular tissue occurs in *A. latifolia* anthocarp walls, they are harder in texture than those of *A. maritima*. The body cavities of these two species extend a short distance into the anthocarp lobes.

Although *A. umbellata* occurs on the coast, its anthocarp anatomy (Fig. 24) resembles that of the desert species *A. villosa* (Fig. 19) more closely than that of the two coastal species with which it grows. This possibly reflects anatomical modifications correlated to its dry, waste-area habitat (Wilson, 1972).

TRICHOMES ON THE INTERIOR AND EXTERIOR SURFACES OF ANTHOCARPS

Both glandular and nonglandular trichomes may be observed on the exteriors of anthocarps but only nonglandular trichomes are found on the interior surfaces. Only uniseriate trichomes were seen on the anthocarps examined.

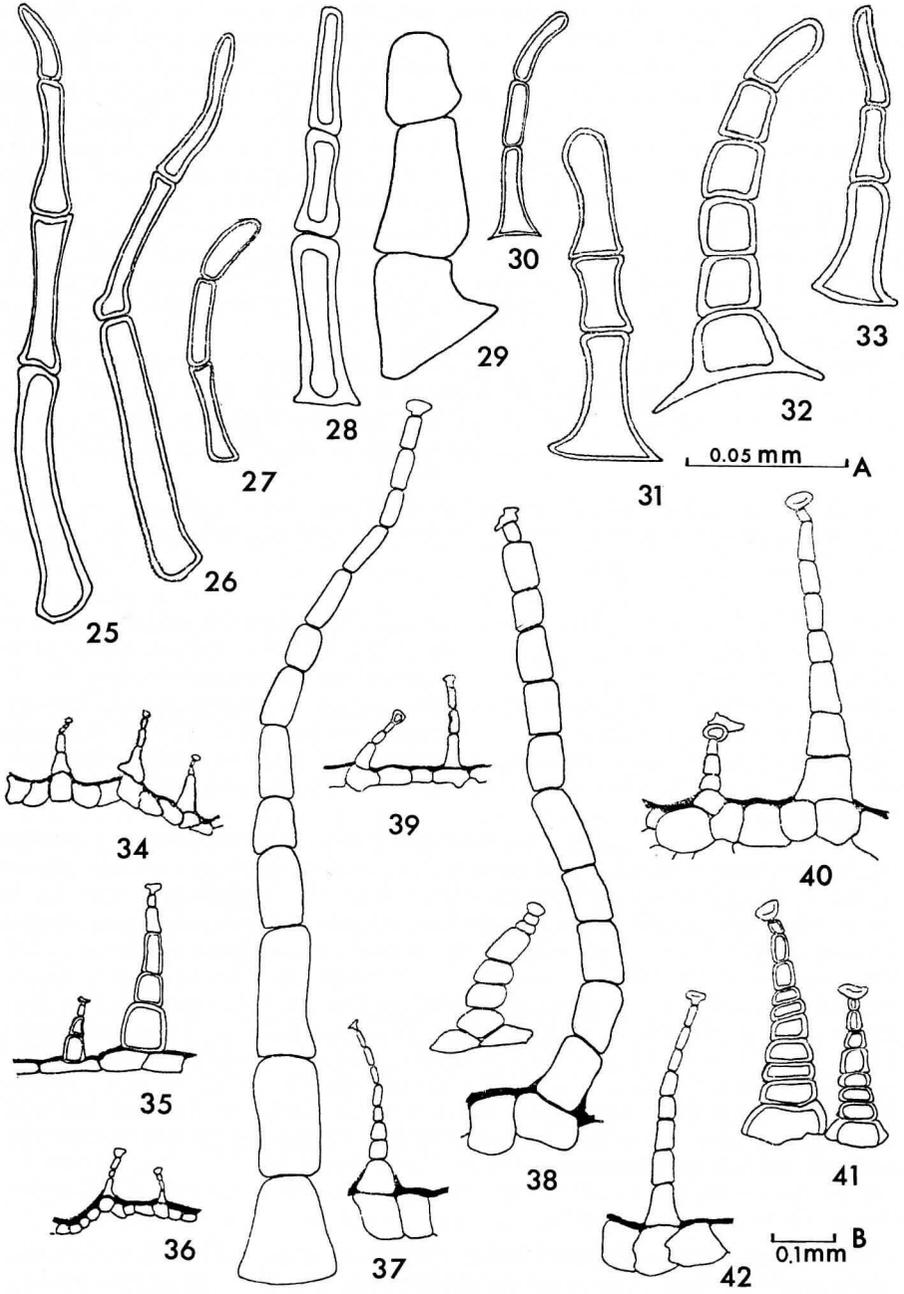
Trichomes on the interiors of anthocarps are distinctive for each of the species studied (Figs. 25–33). Apparently trichome lengths are affected by the space available between the ovary and anthocarp walls. Those species with a large body cavity and a large seed develop shorter trichomes than those species with an equally large cavity but a smaller seed, e.g., *A. maritima* (Fig. 31) contrasted to *A. nana covillei* (Fig. 25) respectively. Space in the anthocarp cavity around the seed of *A. crux-maltae* is especially limited compared to the other species, except *A. alpina*. The interior trichomes of *A. crux-maltae* (Fig. 29) are composed of unusually broad cells.

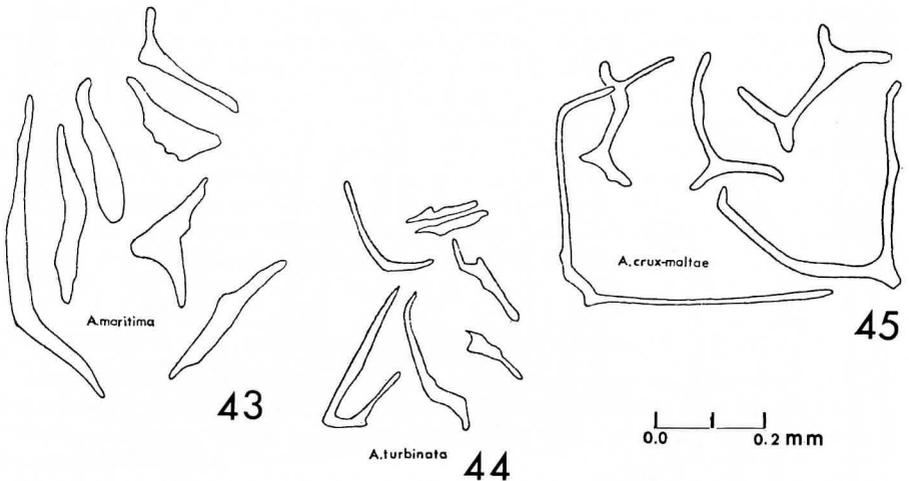
The more distinctive trichomes on the interior surfaces may prove to be taxonomically significant. Unfortunately, the presence of trichomes on the interiors of anthocarps suggests no obvious functional correlations.

When compared with trichomes on interior anthocarp surfaces, the anthocarp trichomes on the exterior surfaces are equally diversified in their structure or length (Figs. 34–42). Just below the glandular head of the trichomes in *A. nana covillei* (Fig. 34) a thickened collarlike portion develops which seems to aid in the detachment of the head from the stalk. In *A. turbinata* (Fig. 35) the stalk cells of the trichomes are slightly thickened and do not collapse. On air-dried anthocarps, the glandular heads of these trichomes will collapse but do not break off in contrast to those of *A. nana covillei*. Trichomes in *A. pogonantha* (Fig. 39) and *A.*

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Figs. 25–42. *Abronia*.—25–33. Trichomes from the interior anthocarp surfaces of nine species, drawn to scale A.—34–42. Trichomes from the exterior anthocarp surfaces of the same nine species as above, drawn to scale B.—25, 34. *Abronia nana covillei*.—26, 35. *Abronia turbinata*.—27, 36. *Abronia alpina*.—28, 37. *Abronia villosa*.—29, 38. *Abronia crux-maltae*.—30, 39. *Abronia pogonantha*.—31, 40. *Abronia maritima*.—32, 41. *Abronia latifolia*.—33, 42. *Abronia umbellata*.





Figs. 43–45. Parenchyma cells of three species of *Abronia* drawn to the same scale from macerated anthocarp tissue.—43. *Abronia maritima*.—44. *Abronia turbinata*.—45. *Abronia crux-maltae*.

alpina (Fig. 36) are similar, except those of *A. alpina* are slightly smaller. In *A. umbellata* (Fig. 42) and *A. villosa* (Fig. 37) the trichomes are quite similar only being shorter and less abundant on *A. umbellata* than on *A. villosa* anthocarps. The often large trichomes of *A. crux-maltae* (Fig. 38) are distinctively intermixed with much shorter trichomes. These trichomes are thin walled and either collapse or are sheared off in the dried anthocarps. In *A. latifolia* (Fig. 41) the trichomes have thick walls, which do not collapse.

Glandular trichomes make the developing perianth exteriors very sticky. In *A. maritima* glandular trichomes persist and impart a mucilage which remains sticky for several years, even when the anthocarps have been air-dried. Although these anthocarps can adhere to bird feathers or animal fur for short distances, attachment to animals as a major mechanism for the dispersal of the large *A. maritima* anthocarps must be ruled out. Quite possibly the mucilage is more important in making the anthocarps of this species less permeable to water in their fore-dune habitat. These trichomes (Fig. 40) neither collapse nor lose their glandular heads ontogenetically as is most often the case in the other species studied (Figs. 34–42). Therefore, viscidness does not appear related to dispersal in *Abronia* because the head of each glandular trichome is either emptied or lost before the time of anthocarp abscission.

TYPES OF PARENCHYMA CELLS

Three populations of parenchyma cells from wing and lobe tissues are illustrated for three species of *Abronia* (Figs. 43–45). All of the species

studied contained irregularly shaped parenchyma cells. Apparently these cells result from ontogenetic stretching and distortion of parenchyma cells during the expansion of the perianth edges into lobes or wings. Two purposes might be served by this expansion: (1) it increases the surface area exposed, perhaps related to wind dispersal; and (2) it forms a lighter anthocarp possibly capable of better dispersal by wind. Various degrees of lignification of the parenchyma cells was noted in each species studied.

In the coastal species *A. maritima*, parenchyma cells (Fig. 43) of the lobes are large, more regular, and relatively compact with small intercellular spaces. By contrast in the desert species *A. crux-maltae* (Fig. 45) the wings contain the most highly distorted parenchyma cells accompanied by the largest intercellular spaces developed among the nine *Abronia* species examined.

The membranous wings of *A. crux-maltae* are strengthened by prominent veins. These fibrous veins form a framework which supports a network of interconnected, distorted, parenchymatous and often sclerenchymatous cells; all covered by a thin layer of epidermal cells.

SUMMARY

Although marked similarities occur among the anthocarps of species of *Abronia* (Nyctaginaceae) growing in similar habitats, the anthocarps of each species have morphological modifications which are correlated with both habit and local ecological conditions.

The species studied are placed in three habitat categories: (1) coastal, (2) desert, and (3) montane.

Anthocarp morphology, polymorphism, and anatomy are described and illustrated for nine Californian species of *Abronia*. These species have evolved in widely diversified habitats. Morphologically their dispersal units (anthocarp with contained seed) are equally diversified.

Five main areas of anthocarp variation are considered: (1) morphological differences among the species; (2) polymorphism within single inflorescences of each species; (3) variation in the relative amounts and arrangement of the tissue types among the species; (4) variation of the trichomes present on both exterior and interior epidermal layers of the anthocarp walls; and (5) variation in the parenchyma cells of anthocarp lobes or wings of three species.

Clues regarding potential for anthocarp dispersal by wind or water can be taken from both anthocarp morphology and anatomy. Although the samples taken are not completely definitive for each species, the more outstanding morphological differences may be validly considered for each anthocarp to suggest its mode of dispersal.

A parenchyma, several layers thick, beneath the outer epidermis distinguishes the anthocarp walls of the coastal species from the anthocarp walls of *Abronia* species examined from other habitats.

Desert species are marked by slightly less parenchyma, and a wider band of fibers and other sclerified cells which surround the entire body cavity.

Anthocarp walls of montane species are significantly thinner in contrast to the walls of both coastal and desert species.

In montane species the fibers in combination with vascular tissue form an intermittent network interrupted by parenchyma, they do not form the same massive bands as seen in transverse sections from anthocarps of the coastal and desert species.

Although viscid trichomes on the exteriors of *A. maritima* anthocarps remain sticky even when air-dried, they are not believed sufficiently viscid to attach anthocarps to animals for significant distances. No other anatomical or morphological evidence is found in the anthocarps to suggest that they are transported either on or in animals. Fleishy, edible portions are not found on any of the mature anthocarps.

Divergent morphological and anatomical structures found among the nine *Abronia* species suggest at least four adaptive features: (1) a greater potential for wind dispersal among desert species and weedy coastal species from hind-dune waste areas due to their thinner, broader, and often numerous wings; (2) a reduced dispersibility among some montane species due to their smaller anthocarp bodies and walls; (3) a greater potential for buoyancy among fore- and mid-dune coastal species due to their large body cavities and greater relative amounts of parenchyma tissue; and (4) a greater diversity of dispersal potential among desert and coastal weedy species due to their pronounced anthocarp polymorphism.

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