

OBSERVATIONS ON ANTHOCARP ANATOMY IN THE SUBTRIBE MIRABILINAE (NYCTAGINACEAE)

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Flowers of Nyctaginaceae have a uniseriate perianth. The calyx is petaloid and of short duration throughout the upper portion and morphologically simple compared to the lower portion, which forms a persistent, fleshy to hard and leathery, glabrous or pubescent, often 5(-10) ribbed to winged accessory fruit, the anthocarp. Anthocarp is used here to designate "the accrescent perianth base comprising the accessory fruit enclosing the mature ovary, which is itself an achene or utricle" (Bogle, 1974). The terms anthocarp and diclesium (Lawrence, 1963) are used synonymously in reference to Nyctaginaceae fruit. We have chosen to use the former which is traditional in American botanical literature.

Within Nyctaginaceae anthocarp morphology has long been useful in distinguishing taxa (Standley, 1918; Heimerl, 1934). Recent delimitation of taxa at specific (Smith, 1975) and generic (Galloway, 1975) levels has also been partially based on anthocarp morphology. Anthocarp morphology and anatomy have been considered in ecological and taxonomic studies within subtribe Abroniinae (Wilson, 1972, 1974, 1975, 1976; Galloway, 1971, 1975) and in *Boerhavia*, (Bhargava, 1932; Maheshwari, 1929), but the scope of these investigations does not include comparative examination of anthocarp anatomy to determine the phylogenetic information these data may hold.

This paper reports results of preliminary investigations to determine the feasibility of utilizing anthocarp anatomy to elucidate phylogenetic and taxonomic relationships in subtribe Mirabilinae, tribe Mirabileae. The subtribe Mirabilinae was selected for preliminary investigation because we believe it is a natural group and because within this subtribe anthocarp structure is more diverse than in other subtribes. Morphological diversity of the anthocarp in subtribe Mirabilinae is expressed primarily by the formation of ridges or wings from a portion of the anthocarp wall. Anthocarps of subtribe Mirabilinae may be morphologically placed into 3 general types: 1) those with smooth walls or slightly rounded or angled ridges; 2) those with narrow wings acute in cross section; and 3) those with broad laminar wings (Fig. 1). The anatomical basis of this morphological diversity among species serves as the focal point of this study. We felt it was necessary in an anatomically based preliminary phylogenetic study of the subtribe Mirabilinae to include not only congeneric species which exhibit one or more anthocarp types, but species from different genera which exhibit the same general anthocarp type. The following species were selected: *Mirabilis oblongifolia* (Gray) Heimerl, *M. viscosa* Cav. and *Boerhavia coccinea* Mill.

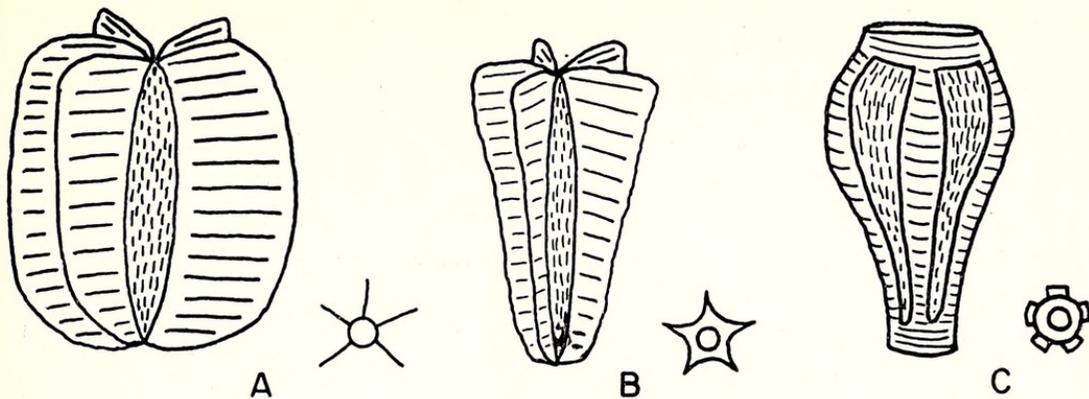


FIG. 1. Diagrammatic side views and cross sections of 3 general diclesium types. A, broad membranous wings. B, narrow wings. C, ridges.

exhibit rounded ridges; *B. intermedia* M. E. Jones and *B. spicata* Choisy have angled ridges; *B. alata* S. Wats. has narrow wings; *Selinocarpus lanceolatus* Gray and *Ammocodon chenopodioides* Standl. have broad laminar wings.

METHODS AND MATERIALS

Anthocarps in late stages of maturation were killed and fixed in the field using FAA (Sass, 1966), then transferred to tetrahydrofuran (THF) for dehydration (Leuty, 1964). Standard methods of paraffin infiltration, embedding, and sectioning at 12 μ m were employed (Sass, 1966). Sections were stained in toluidine blue (Feder and O'Brien, 1968), mounted in Permount, and drawn using a micro-projector. Several anthocarps from each plant or population were studied. Where advisable, confirmation of anatomical observations was made by examining anthocarps from geographically distant conspecific populations.

RESULTS

Anthocarp walls and accompanying wings or angles of each species are constructed from 5 common elements: epidermis, sclerenchyma, polyhedral parenchyma, vascular strands, and columnar parenchyma cells. Raphide bundles are common in all anthocarps but there is no trend in number or distribution. In *Selinocarpus* and *Ammocodon* no sclerenchyma is present in the walls between the wings, whereas in species of *Mirabilis* sclerenchyma is present in the wall between the angles in a band discontinuous from sclerenchyma within the angles. In species of *Boerkavia* sclerenchyma forms a continuous band, the sclerenchyma in the anthocarp wall contiguous with that of the wing or angle bases.

Graphic representation of transverse sections for each species is presented in Figs. 2-4. These illustrations are meant to replace complete and routine anatomical descriptions. Instead, a brief description of anthocarp morphology and citation for voucher specimens deposited at NMC

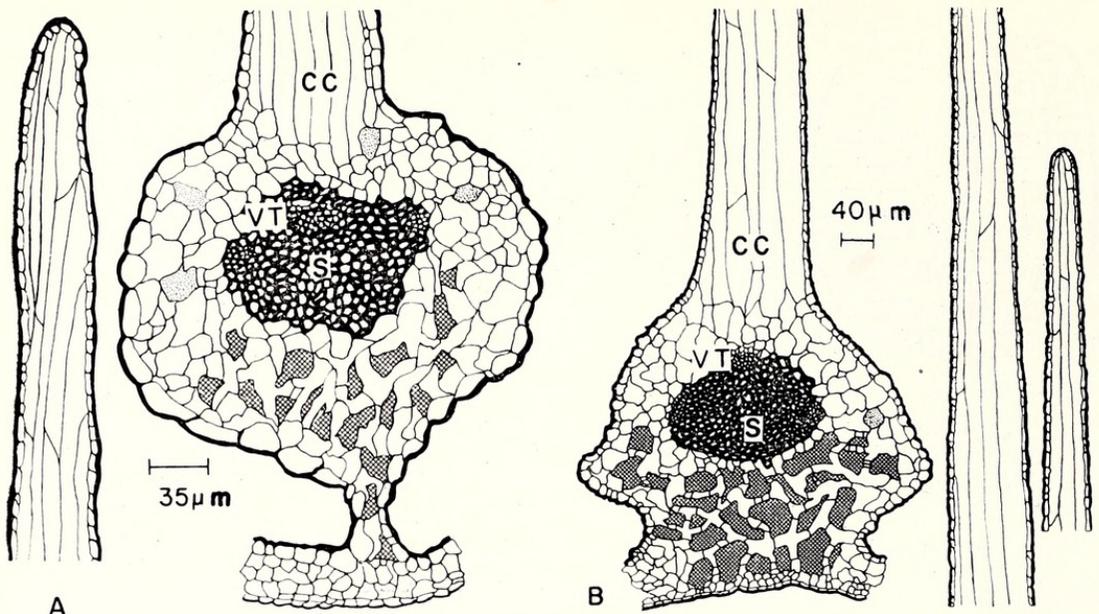


FIG. 2. Transverse sections of diclesium wings. A, *Ammocodon chenopodioides*. B, *Selinocarпус lanceolatus*. Cross hatched areas represent intercellular spaces within aerenchyma. CC = columnar cells, VT = vascular trace, S = sclerenchyma cylinder.

are followed by description of anatomical features which conspicuously differ between taxa.

Ammocodon chenopodioides (Fig. 2A): (USA, New Mexico, Doña Ana Co., Las Cruces, *R. Spellenberg* 2183). Anthocarp ca 5 mm long, wings ca 2 mm broad, glabrate, body sulcate between wings, sparsely puberulent. *Anatomy*: A single vascular strand is embedded in each sulcus region. Adaxial one-third of enlarged wing base filled with aerenchyma. Sclerenchyma cylinder in wing base with 3 vascular strands spaced equidistantly around abaxial edge of cylinder. Columnar parenchyma cells extend into each wing section filling wing lamina.

Selinocarпус lanceolatus (Fig. 2B): (USA, New Mexico, Doña Ana Co., NE tip of county, *R. Spellenberg* and *T. K. Todsén* 2640). Anthocarp ca 6–7 mm long, wings ca 2–3 mm broad, glabrate, body finely costate, truncate at both ends. *Anatomy*: A single vascular strand is embedded in each region between the wings. Adaxial half of enlarged hastate wing base filled with aerenchyma. Sclerenchyma cylinder in wing base with 3 equidistantly spaced vascular strands positioned around abaxial edge. Columnar parenchyma cells extend into each wing section filling wing lamina.

Mirabilis oblongifolia (Fig. 3A): (USA, New Mexico, Lincoln Co., 3 mi W of Alto, *R. Spellenberg* and *D. Jackson* 2657). Anthocarp obovoid, ca 3–5 mm long, minutely pilose, 5-angled, angles broad and usually tuberculate, sides coarsely or finely tuberculate. *Anatomy*: Sclerenchyma cylinder bordered laterally by sclerified parenchyma, and with a vascular strand at abaxial edge of cylinder. Columnar parenchyma cells extend to each ridge tip.

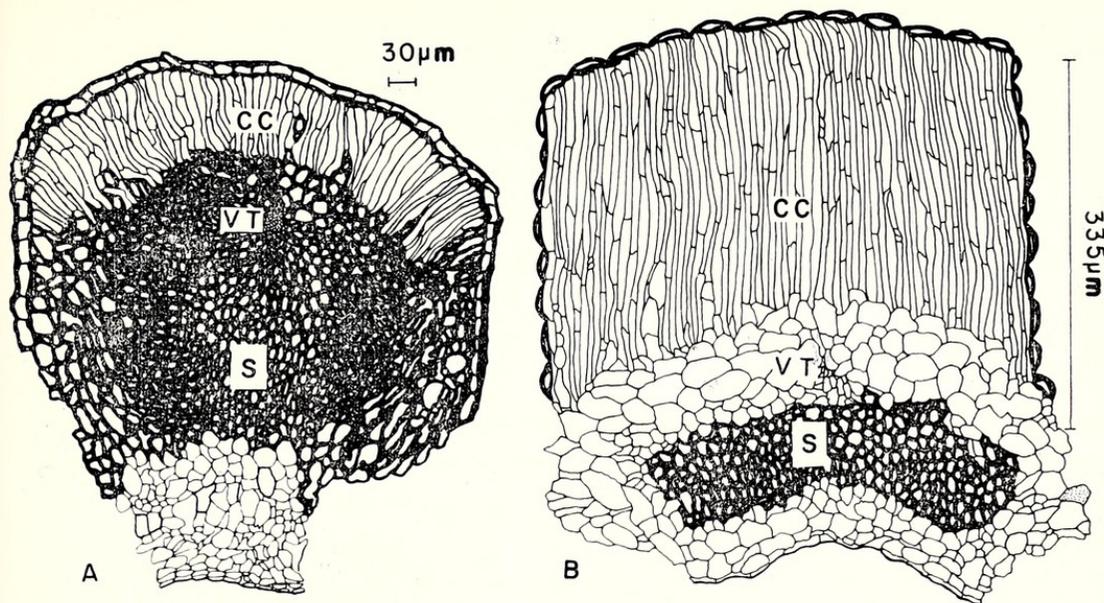


FIG. 3. Diclesium ridge anatomy. A, *Mirabilis oblongifolia*. Ridge anatomy with accompanying tubercule. B, *Mirabilis viscosa*. CC = columnar cells, VT = vascular trace, S = sclerenchyma cylinder.

Mirabilis viscosa (Fig. 3B): (Mexico, Guanajuato, just E of Silas, S of Cd. Guanajuato, *R. Spellenberg* 2969). Anthocarp obovoid, ca 5 mm long, angular, glabrous, densely covered with large coarse tubercles. *Anatomy*: Sclerenchyma band in basal region of ridge and contiguous with a vascular strand along abaxial edge of band. Columnar parenchyma cells extend into ridge and tubercule.

Boerhavia coccinea (Fig. 4A): (USA, New Mexico, Doña Ana Co., NMSU Campus, *R. Spellenberg* and *J. Willson* 3735). Anthocarp narrowly obovoid, ca 2.5–4 mm long, rounded at the apex, densely glandular-puberulent or glandular-pilose, 5-sulcate angles and sulci smooth. *Anatomy*: Sclerenchyma band thickened in ridge base, extending acutely into angle, and contiguous with a vascular strand at abaxial tip. Columnar parenchyma cells extend into angle.

Boerhavia spicata (Fig. 4B): (USA, Arizona, Maricopa Co., 5 mi SE of Morristown. *R.* and *M. Spellenberg* 2646). Anthocarp narrowly obovoid, ca 2.5 mm long, rounded at the apex, acute to acuminate at the base, stramineous, 5-angulate, angles from thick to thin, acute, sulci broad, open and rugulose. *Anatomy*: Sclerenchyma band broadened in angle base, projecting obtusely into angle. Four or 5 vascular strands present about the abaxial surface of the sclerenchyma cylinder. Columnar parenchyma cells extend into the angle.

Boerhavia intermedia (Fig. 4C): (USA, Arizona, Pima Co., 21.6 mi SE of Why, *R. Spellenberg* and *J. Willson* 3607). Anthocarp narrowly obpyramidal, ca 2–3 mm long, glabrous, truncate at apex, 5-angulate,

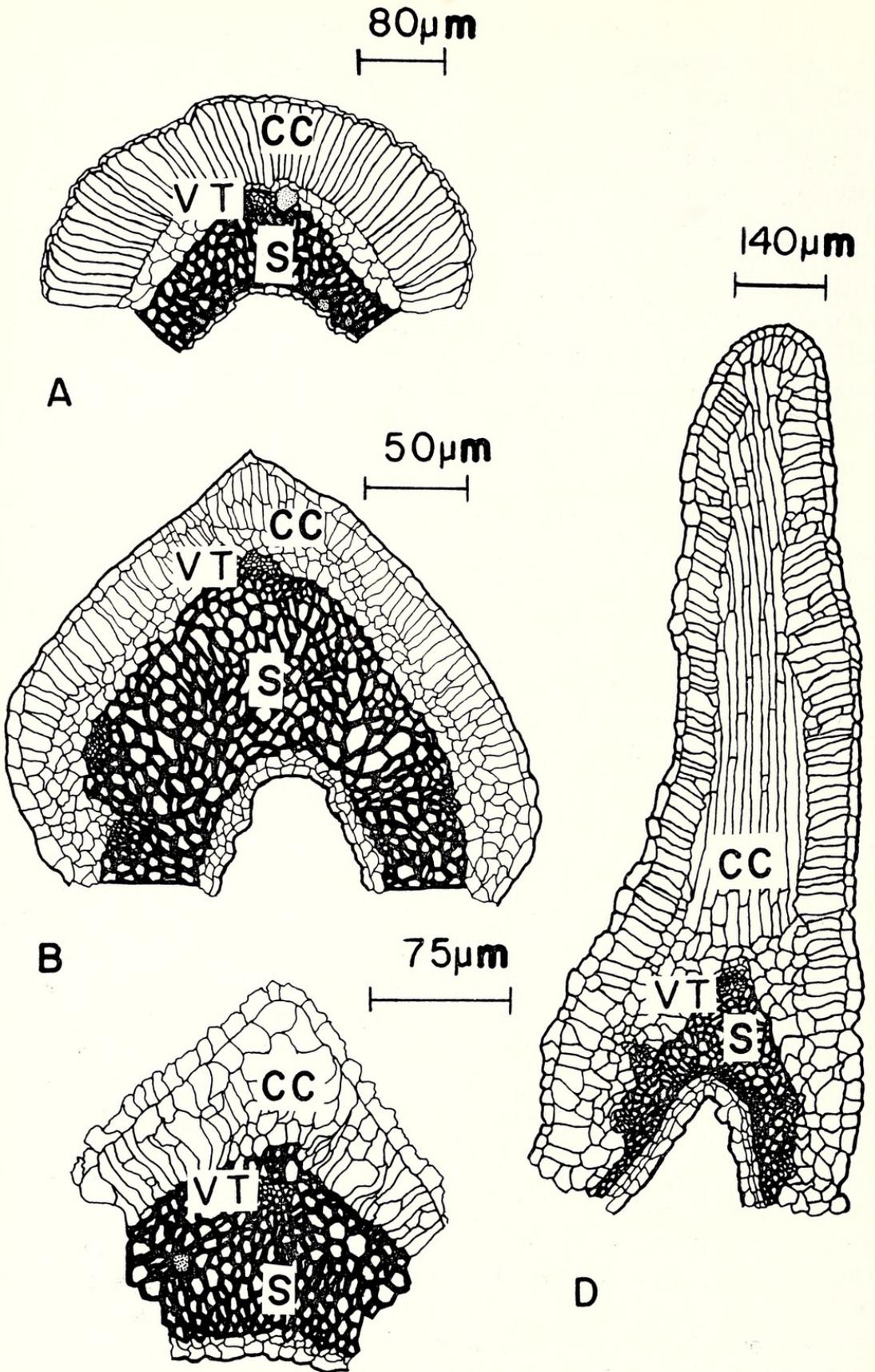


FIG. 4. Diclesium ridge anatomy. A, *Boerhavia coccinea*. B, *Boerhavia spicata*. C, *Boerhavia intermedia*. Diclesium wing anatomy. D, *Boerhavia alata*. CC = columnar cells. VT = vascular trace, S = sclerenchyma cylinder.

angles smooth, obtuse, sulci narrow, transverse-rugulose. *Anatomy*: Obtuse tip of sclerenchyma band barely projecting into angle where it is contiguous with a single vascular strand. Irregular columnar and isodiametric parenchyma cells fill angle.

Boerhavia alata (Fig. 4D): (Mexico, Sonora, Guaymas, SE section of city, R. Spellenberg, D. Jackson and D. Martin 2696). Anthocarp ca 4 mm long, sharply and broadly thin-winged, wings ca 1–1.5 mm wide, sulci narrow and transversely rugose. *Anatomy*: Sclerenchyma band thickened and forming a point in wing base, the point contiguous with 5 or 6 vascular strands about it abaxial periphery. Columnar parenchyma cells extend into the wing filling the interior wing lamina. Peripheral and laterally bordering the interior columnar cells is a second set of short columnar parenchyma cells.

DISCUSSION

The anatomical pattern within the wing or angle and corresponding anthocarp wall for each species suggests that wings or angles are modifications of the basic anthocarp wall structure. They are constructed from cells with similar position and morphology. The sclerenchymatous parenchyma of *Mirabilis oblongifolia*, the peculiar columnar parenchyma of *Boerhavia alata*, *Selinocarpus*, and *Ammocodon*, and the aerenchyma of *Selinocarpus* and *Ammocodon* are exceptions and are unique to wings or angles in those taxa.

Gray (1853) reported of *Pentacrophys wrightii* A. Gray (= *Acloisanthes*), subtribe Mirabilinae, that “. . . the superficial tissue of ribs abound in tubular cells, containing a spirally coiled thread, which is usually disengaged upon the application of moisture . . .” and that “. . . this structure was found in most Nyctaginaceae . . .” We did not observe this coiled thread in any species, but we did observe a discharge of mucilage or mucilage-like material when *Boerhavia* and *Mirabilis* anthocarps were placed in water. In *Selinocarpus* and *Ammocodon* the laminar portion of the wing exfoliates on contact with water, exposing the columnar cells, which separate like the bristles of a brush. *Phaeoptilum spinosum* Radlk. (subtribe Phaeoptilinae, tribe Mirabileae) possesses a broadly winged anthocarp somewhat similar to *Selinocarpus* and *Ammocodon* but these neither excrete mucilage nor exfoliate in water. The exact functional and ecological significance of the mucilage or mucilage-like material in *Boerhavia* and *Mirabilis* and the exposure of the columnar cells in *Selinocarpus* and *Ammocodon* is not known. However, mucilage excreted by wetted fruits or seeds may be involved with epizoochory and may be associated with germination (Kozłowski, 1972) or “carnivory” (Barber and Page, 1976). The rapid separation of the long tubular cells of the wings of the anthocarps of *Selinocarpus* and *Ammocodon* suggests (in addition to the importance of wings in seed dispersal) that these cells function in capillary retention of water near the seed. The absence of

both mucilage excretion and exfoliation in *P. spinosum* anthocarps suggests that wings in this species are associated primarily with wind dispersal.

Toluidine blue typically stains parenchyma walls pinkish-purple due to the binding of the stain with carboxylated polysaccharides and polyuronides. Walls containing polyphenolic compounds, such as lignified secondary walls, typically stain green, greenish-blue, or bright blue (O'Brien and McCully, 1969). The columnar cells in *B. coccinea*, *B. intermedia*, *B. spicata*, and *Mirabilis* and the exterior columnar cells of *B. alata* stain purple. The columnar cells of *Ammocodon*, *Selinocarpus* and the interior columnar cells of *B. alata*, however, stain blue. The parenchyma tissue adaxially adjacent to the columnar cells of *Ammocodon* and *Selinocarpus* and the short columnar cells of *B. alata* also stain bright blue rather than the purple of the polyhedral parenchyma within the wing or angle. These reactions indicate that in addition to similarity in morphology and position, interior columnar cells of *B. alata* and parenchymatous columnar cells of *Selinocarpus* and *Ammocodon* have similar wall composition. Also, the short columnar cells in *B. alata* and the columnar cells in *Mirabilis*, *B. coccinea*, *B. intermedia*, and *B. spicata* stain similarly and probably contain similar compounds in their walls or cytoplasm. Species that emit mucilage have purple-staining columnar cells and those that do not have blue-staining columnar cells. *Boerhavia alata* contains both types of columnar cells but those nearest the exterior surface and initially exposed to water are the purple-staining peripheral columnar cells; they enclose blue staining columnar cells. Since *B. alata*, *Selinocarpus*, and *Ammocodon* are in the same tribe (although the first seems fairly distantly related to the others), the presence of the similar blue staining columnar cells in *Boerhavia* may be a result of parallelism. Blue staining columnar cells in *Boerhavia* occur only in *B. alata*. It is not possible to ascertain whether wings of *Selinocarpus* and *Ammocodon* arose from the purple staining, mucilage-excreting columnar cells through development of a secondary set of elongate cells (as in *B. alata*) with subsequent loss of the mucilage-excreting cells, or in some other manner. Future studies of the ontogeny and ecology of Mirabilinae anthocarps may support one of these sequences and thus aid in elucidating phylogenetic relationships in these taxa.

The southwest African *Phaeoptilum spinosum*, the sole member of the subtribe Phaeoptilinae, has an anthocarp outwardly similar to *Selinocarpus* and *Ammocodon*. Limited material and difficulties in sectioning precluded a complete anatomical study of the mature anthocarp. However, it was noted that the laminar portion of the wing is filled with long, narrow, columnar cells that stain bright blue as in *Selinocarpus* and *Ammocodon*; these cells arise from polyhedral parenchyma cells, which also stain bright blue. A single, continuous band of sclerenchyma fibers is present in the anthocarp wall between the wings and forms a cylinder in the wing base, as in *Boerhavia*. Morphological and anatomical similari-

ties between the anthocarp of *P. spinosum* and the species with winged or ridged anthocarps of the Mirabilinae are probably also the result of parallel evolution. We concur with Nowicke (1970) who suggested that only a remote connection for *Phaeoptilum* and the Mirabilinae is possible when pollen type, endemism to southwest Africa, and the unisexual flowers of *P. spinosum* are considered.

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