THE GENUS REVERCHONIA (EUPHORBIACEAE)

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Reverchonia, a monotypic genus of the subfamily Phyllanthoideae, has been placed in the subtribe Phyllanthinae adjacent to Phyllanthus (Pax and Hoffmann, 1931). The single species, R. arenaria A. Gray, is a highly specialized desert annual (fig. 2) found in disjunct sand-dune areas in the southwestern United States and northeastern Mexico. Gray, in the original description (1880), noted that "the relationship of this plant to Phyllanthus is so close, that, were it not for a combination of characters, it might be taken for an aberrant Phyllanthus." This character-complex, which has sufficiently impressed subsequent authors so that all have followed Gray's lead and maintained Reverchonia as distinct, includes features of both habit and reproductive organs. The aspect of the fruit-bearing plant, due

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University of Arizona (ARIZ); Chicago Natural History Museum (FH); Gray Herbarium (GH); Missouri Botanical Garden (MO); University of New Mexico (UNM); Oklahoma State University (OKLA); University of Oklahoma (OKL); Southern Methodist University (SMU); University of Texas (TEX); Texas Technological College (TT); United States National Museum (US); Utah State Agricultural College (UTC); and University of Utah (UT).

Voucher specimens for research described in this paper are deposited at the Kriebel Herbarium, Purdue University (FEL).
Fig. 1. Flowers of *Reverchonia* (Warnock 10723). A. Male flower, with one calyx-lobe removed. B. Male calyx-lobe, adaxial view. C. Disk of male flower (as seen from above, partially enclosing the filament bases). D. Female flower, with 2 calyx-lobes removed.
to the disproportionately large capsules hanging from slender lateral branches, is distinctive and unlike any other taxon of American Phyllanthoideae. Especially prominent reproductive features (fig. 1) include the dark reddish flowers with unusually shaped calyces (the male vaguely suggesting the flowers of certain Fumariaceae), the introrse stamens and central disk of the male flower, the large seeds with a subchalazal invagination, and the embryo with linear cotyledons.

As duly noted by Gray, the most anomalous character of Reverchonia is the narrow cotyledon shape, which would technically place the genus in the "series" Stenolobeae as conceived by Mueller Argoviensis (1866). The Stenolobeae, as delimited by Mueller and later by Pax (1890) and Gruning (1913), comprise a number of genera with more or less ericoid habit which are restricted to Australia and New Zealand. Except for the narrow cotyledons, however, most of these taxa seem to have little in common with Reverchonia. Micrantheum, which would probably key out the nearest, differs in having foliate stipules, extrorse anthers, a pistillode in the male flower, and (like most other Stenolobeae) carunculate seeds.

A search has been made among genera of American Phyllanthoideae other than Phyllanthus for any which might show similarities to Reverchonia. The only group in which any degree of resemblance can be detected is Tetracoccus. As recently revised by Dressler (1954), it comprises 4 taxa of desert shrubs which grow in southwestern desert areas adjacent to the range of Reverchonia. Although the species of Tetracoccus are completely dissimilar in overall habit (being intricately branched bushes), the leaves (when entire) have an aspect suggesting those of Reverchonia. The flowers show a considerable superficial resemblance, especially in the central male disk and the dilated style-tips. The likeness of the male disk is especially striking, since it is in this particular character that Reverchonia diverges most strongly from Phyllanthus.

In order to evaluate possible relationships of Reverchonia
with *Phyllanthus*, *Tetracoccus*, and other Phyllanthonoideae, we have carried out palynological, cytological, and anatomical studies. Punt (1962), in a valuable detailed study of Euphorbiaceous pollen, has described the microspores of most of the taxa in question. He shows that in most of the taxa of Stenolobeae, together with certain other Australasian taxa possessing broad cotyledons, the pollen grains are of a very characteristic echinate, non-corporate type (“*Aristogeitonia* configuration”). The microspores of *Tetracoccus ilicifolius*, with their 6-7 small colpi and prominent spines 3.5 μ long, definitely belong in this grouping. In contrast, the pollen grains of *Reverchonia* are prolate, tricolporate with a small colpus transversalis, and psilate (the tectate exine essentially smooth). Punt’s illustration (his Plate II, fig. 7) and that of Erdtman (1952: fig. 97D) agree well with our own observations (on microspores from Miller & Miller 1322, Webster 4615) except that the exine reticulation is much fainter than indicated in Erdtman’s drawing. Punt classified the grains of *Reverchonia* in his *Phyllanthus pentaphyllus* subtype along with those of several herbaceous species of *Phyllanthus* and *Savia erythroxyloides*. In the species of *Phyllanthus* sect. *Phyllanthus* examined by us the tectate exine is distinctly finely pitted (Punt describes the exine of *P. niruri* as “intra-reticulate”). and *Reverchonia* differs only in its somewhat more obscure ornamentation. However, despite the palynological similarity, the herbaceous species of *Phyllanthus* sect. *Phyllanthus* do not appear very similar to *Reverchonia*, as they are highly specialized vegetatively (i.e., with phyllanthoid branching) and dissimilar in floral details (e.g., male disk of distinct segments, anthers extrorse, seeds differently ornamented). *Reverchonia* shows a certain approach to the condition of phyllanthonoid branching (as defined by Webster. 1956: 104) in that flowers are borne only on the lateral determinate axes; however, it differs in the lack of reduction of leaf-blades on the main axis and in the spiral rather than distichous phylloxy of the lateral branchlets.

Chromosome counts have been made by the junior author.
from aceto-carmine squashes of root-tips and immature leaves. The chromosome complement of *Reverchonia* proves to be $2n = 16$ (fig. 3). This is a very striking result, in view of the fact that within the subfamily Phyllanthoideae this

Fig. 2. Habit of *Reverchonia*, sand dunes near Kermit, Texas, $\times 1/10$ (photograph by C. M. Rowell).

Fig. 3. Mitotic chromosomes of *Reverchonia*, showing $2n = 16$, $\times 2000$ (*K. and L. Miller 1322*).

Fig. 4. Longitudinal section of ovary, *Reverchonia*, showing ovule and associated parts (O, obturator; N, tip of nucellus), $\times 60$ (*K. and L. Miller 1322*).

Fig. 5. Longitudinal section of ovary, *Argithamnia mercurialina*, $\times 60$ (*K. and L. Miller 1174*).
number has been found only in *Phyllanthus polygonoides*, belonging to sect. *Isocladus* (Webster & Ellis, 1962). In most of the other Phyllanthoideae studied, the base number is 13; and in *Tetraocoecus* it appears to be 12 (Perry, 1943). The cytological evidence, therefore, strongly supports a closer relationship between *Reverchonia* and sect. *Isocladus*. The pollen grains of taxa in this section certainly would not negate such a relationship, since they show considerable similarity to *Reverchonia*. As observed in *P. platylepis* and *P. polygonoides*, they differ mainly in being less prolate and in having a less elongated colpus transversalis. However, all known species of sect. *Isocladus* are strongly dissimilar in certain floral details, including extrorse anthers, male and female disks of separate segments, stamens united by the filaments, female calyx-lobes herbaceous, stigmas subcapitate, columella persistent, and seeds small with verruculose ornamentation and lacking a hilar invagination.

Studies on the gynoecium in taxa of Phyllanthoideae have yielded most interesting results which suggest particular relationships between *Reverchonia* and other putatively related genera. Gray (1880) had noted that *Reverchonia* was unusual in having amphitropous ovules. Since Pax and Hoffmann (1931) flatly categorize the ovules of the Euphorbiaceae as anatropous, the situation in *Reverchonia* might seem unusual indeed. However, anatomical researches in progress indicate that amphitropous ovules occur in a considerable number of Phyllanthoideae, as was clearly pointed out long ago by Baillon (1858: 164). The ovule of *Reverchonia*, as seen in longitudinal section (fig. 4), resembles that in *Phyllanthus* and allied genera in having 2 well-developed integuments, a nucellar beak extending through the micropyyle and in contact with the obturator, and a funicle which departs from the placenta below the middle of the locule. The funicle is definitely attached to the ovule toward its base. In the sense of Goebel (1933: 2003), the ovule of *Reverchonia* would be classed as "hemitropous." In contrast, the ovule in most other Euphorbiaceae is definitely anatropous (fig. 5), with the funiculus departing from the upper
half of the locule and adnate to the ovule for most of its length (cf. Schweiger, 1905).

These ovular differences are usually also apparent in the seed, despite various ontogenetic changes in proportion. In the usual anatropous Euphorbiaceae seed the hilum is near the micropylar end and the raphe (funicle scar) traverses the length of the seed before ending at a chalazal area often marked by a depression. In the seed of Reverchonia and certain other Phyllanthoideae, the hilum is below the middle of the seed (subchalazal) and there is no definite raphe. In such seeds, as well as some anatropous ones, the chalazal pit may be the most conspicuous external mark on the seed-coat, and it has been described as the hilum by some investigators. Vindt (1953), for example, refers to the submicropylar attachment of the funicle as the “hile apparent” and its chalazal ending as the “hile vrai.”

A survey of ovular configurations in the Euphorbiaceae, although not yet complete, indicates that the two kinds of ovules are correlated with definite systematic groups. Amphitropous ovules are found in Reverchonia, Phyllanthus, and a number of other genera in the Phyllanthoideae, while anatropous ovules occur in other Phyllanthoideae and in all of the Crotonoideae and Stenolobae. Tetracoccus has carunculate anatropous seeds which, as pointed out by Croizat (1942), resemble those of Petalostigma and certain other Phyllanthoideae of Australasia. Thus the palynological, cytological, and anatomical data all speak strongly against any close relationship of Tetracoccus with Reverchonia; any similarities must be due to convergent evolution. For the same reasons Tetracoccus cannot be related to Securinega (in the usual sense) either, as suggested by Croizat. Securinega (including the closely related Fluggea) has tricolporate reticulate pollen grains, amphitropous ovules, and (at least in Fluggea virosa) a haploid chromosome number of 13 (Webster and Ellis, 1962). Certain species of Securinega, in fact, show a definite resemblance to Reverchonia; in the mediterranean S. buxifolia the male disk-segments are fused in a manner suggestive of the disk in Reverchonia. On
the other hand, all the species of *Securinega* have a definite pistillode in the male flower, and all are shrubby plants dissimilar in habit. Furthermore, as shown above, the base chromosome number in *Securinega* is 13 rather than 8 as in *Reverchonia* and *Phyllanthus* sect. *Isocladus*.

On the basis of the evidence in hand, it appears that *Reverchonia* definitely belongs in the subtribe Phyllanthinae, where it has much in common with both *Securinega* and *Phyllanthus* sect. *Isocladus*. Although the chromosomal evidence suggests a closer relationship to *Isocladus*, the chromosome numbers in subtribe Phyllanthinae are too poorly sampled for this to be considered conclusive. It is possible that the closest affinity of *Reverchonia* may turn out to be with some Old World taxon of Phyllanthinae rather than with any of the American groups considered in this paper. *Tetraococcus*, which should be excluded from the Phyllanthinae, may share with *Reverchonia* a similar migrational history; both genera appear to be relict groups surviving from an ancient dispersal of Phyllanthoideae through tropical or subtropical desert regions.

Johnston and Warnock (1963) have questioned the status of *Reverchonia* as a genus distinct from *Phyllanthus*, on the grounds of its lack of diagnostic morphological characters. It is true that except for the male disk there are no diagnostic features which would immediately separate the two genera. Gray's recognition of *Reverchonia* on the basis of its particular ensemble of characters still seems the most reasonable solution. Because of the isolated position of *Reverchonia*, its inclusion in *Phyllanthus* would extend further the boundaries of that already vastly diversified genus. For those who still prefer to base classification on phylogeny, inclusion in *Phyllanthus* would seem unwise in view of the possibility that *Reverchonia* may be more closely related to *Securinega*.

**SYSTEMATIC TREATMENT**

**REVERCHONIA A. Gray, Proc. Amer. Acad. Arts and Sci. 16:107. 1880.**

Annual herbs; phyllotaxy spiral on all axes, branches persistent; leaves entire, stipulate, petiolate. Monoecious; flowers pedicellate, in
dense axillary clusters (cymules) on lateral branches; cymules typically androgynous, with one central female and several lateral male flowers. Male flower: calyx-lobes 4, biseriate, inflated, constricted above the middle, the distal portion flaring abaxially; disk central, deeply 4-lobed, partially surrounding the bases of the stamens; stamens 2, opposite the outer calyx-lobes; filaments free; anthers introrse, dehiscing longitudinally and vertically; pollen grains prolate, tricolporate, tectate. Female flower: calyx-lobes 6, not inflated as in the male; disk subentire or angular; carpels 3, styles fused below, stigmas bilobed; ovules two in each cell, collateral, amphitropous. Fruit capsular, dehiscent, 6-seeded; columnella usually deciduous; seeds trigonous, with a conspicuous subchalaclazal invagination; embryo slightly curved, cotyledons very narrow.

Type species: Reverchonia arenaria A. Gray.

Reverchonia arenaria A. Gray, Proc. Amer. Acad. 16: 107. 1880

Glabrous annual herb becoming 2-5 dm. high, with sparsely branching taproot; main stem suberete, smooth, glaucous-white; lower lateral branchlets 2-3 dm. long (upper ones shorter), mostly 1.5-2 mm. thick. Leaves: stipules reddish, papery, lanceolate, acuminate, persistent, entire or irregularly toothed, (0.7-) 0.9-1.7 (-2.3) mm. long; leaf-blades elliptic to narrowly oblong-elliptic or nearly linear, thickish, c. (15-) 20-40 (-45) mm. long, (1.8-) 2.5-8 (-9) mm. broad, apiculate at the tip, narrowed at the base, veins more or less obscure; petiole 1-3 mm. long.

Flowers in reduced bracteolate cymules axillary to the leaves on lateral branchlets (never on main stem), each cymule typically producing 1 central female and 4-6 lateral male flowers. Male flower: pedicel slender, 1.5-2.5 mm. long; calyx-lobes 4, ovate-oblong, submedianly constricted, 1-veined, obtuse, purplish or pinkish with a narrow central stomatiferous greenish strip, c. 1.5-2.5 mm. long, 0.7-1.5 mm. broad; disk of 4 roundish lobes continuous across the center of the flower (between the stamens), with the outline of an I-beam; stamens 2, opposite the outer calyx-lobes; filaments free, subterete, 0.7-1.2 mm. long; anthers erect, oblong, c. 0.5-0.75 mm. long, dehiscing vertically; pollen grains very finely tectate-reticulate, with prominent colpus transversalis. Female flower: pedicel stout, c. 1.5-2 mm. long at anthesis, becoming (2.5-) 3.2-6.5 (-8.7) mm. long in fruit; calyx-lobes 6 (rarely 5), oblong, colored and distally constricted as in the male but not especially inflated, becoming (1.3-) 1.5-2.5 (-2.9) mm. long; disk flat, rather thin, 1.1-1.8 mm. in diameter, roundish or 6-angled in outline; ovary oblate-spheroidal, smooth, grooved; styles erect, 0.5-0.8 mm. high, united halfway or less, stigmas somewhat dilated, emarginate or slightly bilobed.

Capsule oblate-spheroidal, smooth, stramineous, 7-9.8 mm. in diameter; columnella usually deciduous. Seeds trigonous, dark- or reddish-brown, smooth on the back (tangential face), papillate on the lateral
(radial) faces, (4.4-) 4.7-6.2 (-6.6) mm. long; hilum subchalazal, deeply invaginated, with a raised thickened rim. Cotyledons (measured on seedlings) linear, c. 20-30 mm. long, 1.2-1.6 mm. broad.

Type: Texas, Baylor Co., sandy island in the Brazos River near Seymour, September 1879, Reverchon (GH, lectotype; F, MO, isolecotypes). Gray did not cite a collection number, but the duplicate sheets at Chicago and St. Louis bear the number 876. Gray also cited the collection made by Bigelow in 1853; this was apparently the first discovery of the genus. Judging from the map and itinerary of Whipple's exploring party (Gorman, 1941) Bigelow collected the plant along the bed of the Canadian River in northeastern Hutchinson County, Texas, between Spring Creek and the Roberts County line.

DISTRIBUTION:


NEW MEXICO. CHAVES CO.: Arroyo Ranch, near Roswell, Griffiths 5694 (MO, US); shinners E of Roswell, Goodding 6541 (ARIZ); sandy soil near Acme (c. 25 mi. NE of Roswell), Williams 9588 (UNM). DONA ANA CO.: Jornada Range Reserve, Hurt 49 (US); between Strauss and Anapra, Stearns 396 (US). OTERO CO.: dunes S of Alamogordo, Hershey 3653 (UNM); 18 mi. S of Alamogordo, Johnston 2727 (SMU). QUAY CO.: sandy roadside, 4.8 mi. W of Glenrio, Shinners 21077 (SMU). SOCORRO CO.: 7 mi. W of the atom bomb crater, Dunn 4851 (UNM); 12.5 mi. S of junction W of Carthage, red sand dune area, Dunn and Lint 5011 (UNM); north of Lava, Wooton (TEX, US); W of Bingham, Shinners 9589 (UNM).

ARIZONA. COCONINO CO.: Leupp Indian Reservation, with Hilaria and Sacaton, Casteter (UNM), Oakley 373 (ARIZ). NAVAJO CO.: Moki (= Moenkopi?) Reservation, and Little Colorado River, Hough 39 (US); Second Mesa, Hopi Reservation, Whiting 756 (ARIZ).

UTAH. KANE CO.: dunes WSW of Kanab, Harrison 11080 (US); 10 mi. N of Kanab, Hinckley (ARIZ); dunes 6 mi. N of Kanab, Hitchcock, Kethke, and van Raadshooven 4536 (GH, UTC); dunes N of Kanab, Milner 8849 (UT).

MEXICO. CHIHUAHUA: dunes, LeSueur Mex-287 (F, GH, SMU, TEX), 765 (F, TEX); 38 mi. S of Juarez, sandhills in mesquite desert, Gentry 8207 (GH, US); 40 mi. S of Juarez, dunes, Gentry 17900 (US); sandhills near Samalayuca, Pringle 3944 (F); dunes 6 mi. S of Samalayuca, Waterfall 12475 (US); sandhills near Paso del Norte, Pringle 792 (F, GH, US).

A very dubious collection — Texas, Tarrant Co., Fort Worth, Mar. 1890, Bodin (US) — has not been mapped, as the plant has not been recollected within 100 miles of Ft. Worth, and it never flowers as early as indicated on Bodin’s label.

Shinners (1952) has noted that in Texas and Oklahoma the distribution of Reverchonia is remarkably parallel to that of Euphorbia carunculata, which was originally described by Waterfall from the Waynoka sand dunes in northern Oklahoma. Shinners also records Reverchonia from the state of Durango, Mexico, but we have not been able to confirm this and suspect that the mention of Durango was a slip for Chihuahua. All of the Mexican records of Reverchonia seem to come from the same area of dunes south of Samalayuca; and judging from the map of Chihuahuan vegetation presented by LeSueur (1945), dune habitats suitable for Reverchonia occur only in the northeastern corner
of the state, adjacent to El Paso and Hudspeth counties in Texas. It seems unlikely, therefore, that Reverchonia will be found much further south in Mexico. The spotty records from Arizona and western New Mexico are more difficult to interpret; it is possible that the apparent rarity of the plant there is an artifact of the inadequate collection records.

The area occupied by Reverchonia is fundamentally discontinuous due to its very strong preference for (or restriction to) dune habitats. It covers a considerable spread of altitudes, from around 1000 ft. along the Red River in Texas-Oklahoma to between 5500 and 6000 ft. in northern Arizona and Utah. According to Dr. Robert Vickery (in litt.) the plant in Utah grows on brilliant red dunes surrounded by pine forest (north of Kanab); this suggests very different conditions from the dunes of pale sand with shinnery oak (Quercus havardii) and Prosopis where Reverchonia occurs in west Texas (in Crane and Ward counties). The differ-
ences in altitude and precipitation (varying from 25 to less than 10 inches per year) which occur within the range suggest that *Reverchonia* possesses some degree of adaptability.

In its flowering pattern, *Reverchonia* behaves as a long-day plant. The earliest flowering specimen seen was collected on May 28 (McVaugh 10707) and the latest on September 25 (Gould and Childress 7726); fruiting begins by mid-July (at least in Texas and Oklahoma) and continues into October. Germination of the large seeds is rapid and the first internodes elongate greatly; the conspicuous narrow cotyledons may persist on certain plants until they begin to flower. It seems possible that the failure of *Reverchonia* to extend westward into the Californian and Sonoran deserts might be correlated with the different seasonal distribution of precipitation there (i.e., very few summer rains). Along the other boundaries of the species range it is impossible to suggest correlations with any one climatic

### Table 1. Morphological Variation in *Reverchonia*  

<table>
<thead>
<tr>
<th>Character</th>
<th>N</th>
<th>Range (mm.)</th>
<th>$\bar{X}$</th>
<th>s (mm.)</th>
<th>C. V.</th>
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<td>seed length</td>
<td>60</td>
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<td>5.34</td>
<td>0.48</td>
<td>8.98</td>
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<td>length fruiting pedicel</td>
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<td>2.5-5.3</td>
<td>4.11</td>
<td>0.65</td>
<td>15.82</td>
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<td>capsule diameter</td>
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<td>8.43</td>
<td>0.91</td>
<td>10.81</td>
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<td>stipule length</td>
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<td>0.7-2.3</td>
<td>1.27</td>
<td>0.27</td>
<td>21.5</td>
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<td>leaf length</td>
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<td>1.2-2.1</td>
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<tr>
<td>leaf width</td>
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<td>1.7-9.1</td>
<td>4.78</td>
<td>1.58</td>
<td>33.14</td>
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<tr>
<td></td>
<td>21</td>
<td>2.5-8.8</td>
<td>5.12</td>
<td>1.45</td>
<td>28.28</td>
</tr>
</tbody>
</table>

*Parameters are based on one measurement of each character per specimen. The upper row for each character gives data based on measurements of specimens throughout the range of the species; the lower row is based on a single population sample from Winkler Co., Texas (Miller and Miller 1322), except that for seed and pedicel length and fruit diameter specimens were added from a nearby collection (Rowell 60-074).*
factor, which indicates that a complex of interrelationships is probably involved.

Comparison of specimens from all portions of the range indicates that there is relatively little geographic variation. A population sample from Winkler Co., Texas, shows a range of variation quite close to that of the species as a whole (Table 1). The only character with some suggestion of geographical differentiation is the length of fruiting pedicel, which tends to be somewhat longer in some of the Chihuahuan specimens than from other localities. However, although the pedicels are over 8 mm. long in Gentry's collection, they are within the usual range of variation in plants collected by Pringle and Waterfall in the same general area. The seeds of the Chihuahuan specimens may average somewhat longer than those of most populations, but the available samples are not large enough to be decisive. In any event, it is fair to say that on the whole Reverchonia arenaria is a rather homogeneous species, even though there is considerable random — i.e., non-geographic — variability (as indicated by the high coefficients of variability for the characters in Table 1). We suspect that this lack of geographic differentiation may be related to the fact that the plant is sufficiently well adapted for cross-country dispersal (perhaps by travelling along sandy stream-beds) so that the populations do not remain isolated.

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LITERATURE CITED


