

SEED COAT MORPHOLOGY OF *DRAPERIA* *SYSTYLA* (HYDROPHYLLACEAE) AND ITS IMPORTANCE TO THE SYSTEMATICS OF *NAMA*

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ABSTRACT

Seeds of *Draperia systyla*, sometimes considered to be a close relative of *Nama*, have been examined using scanning electron microscopy. Seeds are ovate-elliptic in outline, average 1.8 mm in length and exhibit an alveolate surface pattern. Secondary deposits are found in the outermost testa cells. The deposits fill the lower $1/3 - 1/2$ of each cell and continue upward as a veneer of decreasing thickness to the apex of radial walls. Removal of deposits, by sonication, reveals that radial walls of these outermost cells have both pits and thickenings, a radial wall pattern not found in seeds of any species of *Nama*. Seeds of *D. systyla* are distinct from those of *Nama* and do not suggest the two genera are closely related.

INTRODUCTION

An important aspect of continuing revisionary studies of *Nama* is the determination of relationships with other genera. The nearest relatives of *Nama* generally have been held to be *Eriodictyon*, *Turricula* and *Lemmonia* (Hitchcock 1933; and see Constance 1963). As surmised by Hitchcock (1933), the alliance of *Nama* with *Eriodictyon* and *Turricula* (the latter included in *Eriodictyon* by Hitchcock), was to be traced through the anomalous *N. lobbii* A. Gray, placed by Hitchcock in his monotypic *Nama* sect. *Arachnoidea*. Recently, the relationship of *N. lobbii* to *Eriodictyon*, *Turricula* and the remainder of *Nama* has been assessed using seed coat structure (Bacon, Bragg and Hannan 1986a; Chance and Bacon 1984) and flavonoid chemistry (Bacon, Fang and Mabry 1986b; and see Bacon et al 1986c). These studies suggested that *N. lobbii* should be placed in its own genus, with affinities nearer to *Eriodictyon* than to *Nama*. Bacon (1989, 1987) has examined seed coat structure and floral characters of *Lemmonia* and selected species of *Nama* and concluded that *Lemmonia* must be united with *Nama*. Therefore, relationships of *Nama* appear to be more obscure than traditionally proposed, and that *Nama* has close relatives elsewhere within the Hydrophyllaceae should be considered.

Draperia systyla (A. Gray) Torr. ex A. Gray is a perennial herb with opposite leaves that is endemic to California (Jepson 1943; Munz and Keck

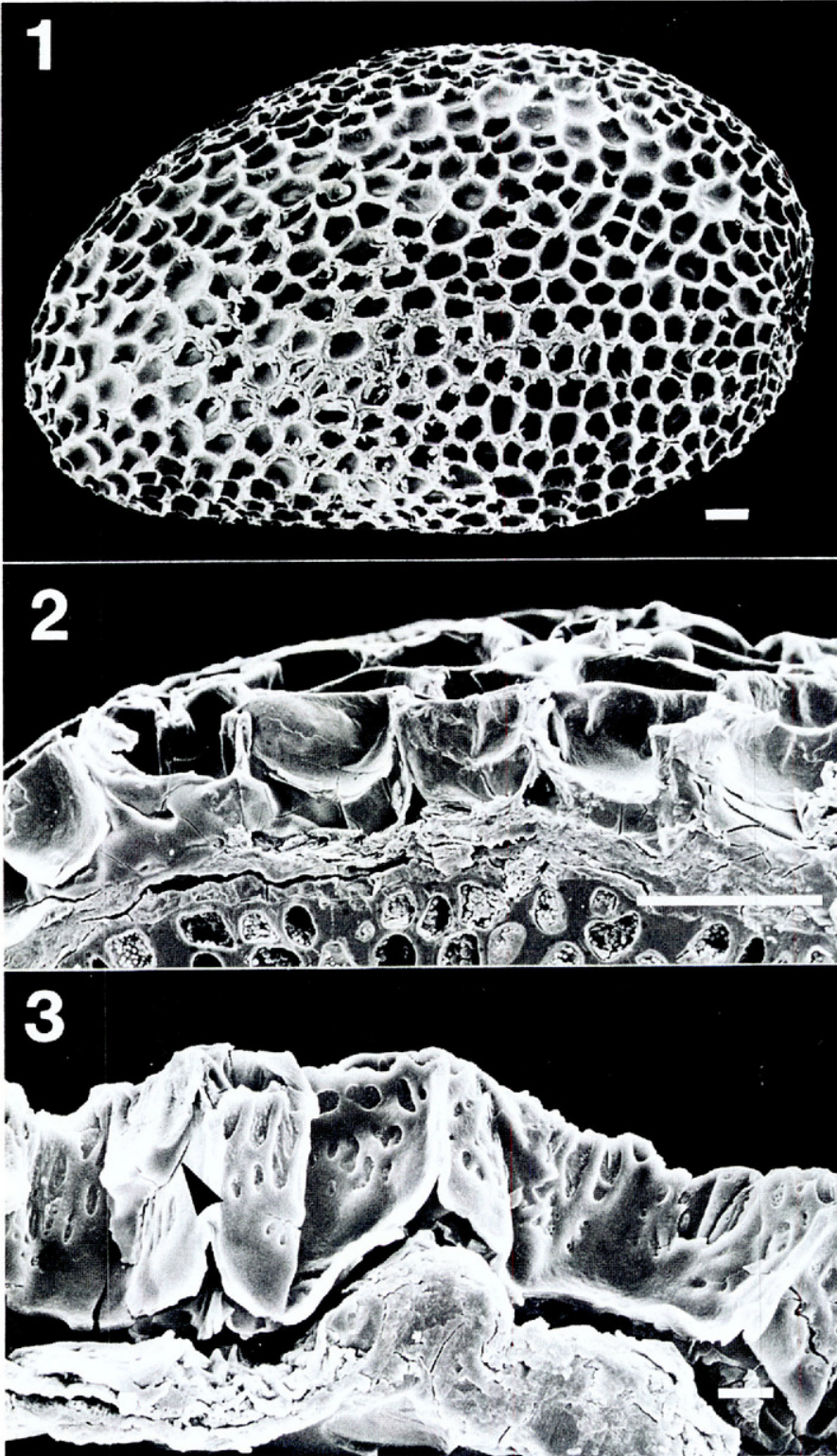
1959). Originally described by Gray (1862) as *Nama systyla* A. Gray, the taxon was subsequently established as the monotypic genus *Draperia* by Torrey (in Gray 1868) and placed in Gray's tribe *Phacelieae* (Gray 1875). Nevertheless, Gray (1877) maintained an indirect relationship between *Nama* and *D. systyla* when he founded *Lemmonia*, placed it in his tribe *Nameae*, along with *Nama* and *Eriodictyon* and stated that it was "somewhat related to *Draperia*". Also, Hitchcock (1933) cited *Draperia* as a close relative of *Nama*. However, because *Draperia* and *Nama* are dissimilar both morphologically and cytologically—in *Draperia* $n = 9$ (see Constance 1963), in *Nama* $x = 7$ (Bacon 1984, 1974; Constance 1963)—the potential relationship of the two genera has not been fully explored. With the submergence of *Lemmonia* in *Nama*, this potential relationship requires assessment. Seed coat features have proven valuable in assessing relationships within *Nama* (Chance and Bacon 1984) and among *Nama* and its suggested relatives (Bacon 1987; Bacon et al 1986a). Therefore, seeds of *D. systyla* have been examined using the scanning electron microscope (SEM), with the aim of assessing seed coat features as they bear on the relationship of *Nama* and *Draperia*. Results of that study are presented here.

MATERIALS AND METHODS

Mature, whole seeds were removed from herbarium specimens of *D. systyla* (see Appendix). For examination of internal structure, seeds were sectioned free-hand with a single-edge razor blade, placed in a 1/4 dram screw cap vial and extracted for about two minutes in acetone to remove obscuring oils. Additionally, some whole seeds and seed sections were placed in a 1/4 dram screw-cap vial, covered with acetone and sonicated in a Branson 12 Ultrasonic Cleaner for 120–180 seconds in an effort to remove the outer tangential wall and contents of reticulum cells (outermost testa layer) to reveal radial walls. Whole seeds and sections were mounted on aluminum stubs with carpet tape. Specimens were coated in an Anatech Hummer VI sputter coater using a gold-palladium target and examined with a JEOL JSM 35-C SEM at an accelerating voltage of 15 kV.

RESULTS

Seeds of *D. systyla* are dark red brown in color and generally ovate-elliptic in outline (Fig. 1). Examined seeds range from 1.6 to 2.1 mm in length, and average 1.8 mm ($N=15$). The outer testa is "moderately reticulate" as interpreted by Chance and Bacon (1984). Reticulum cells are irregularly angular, quadrangular to hexagonal (Fig. 1), generally as broad as long and radial walls—those at right angles to the long axis of the



FIGS. 1–3. Seeds of *Draperia systyla*. (Bar in Figs. 1 and 2 = 100 μm ; bar in Fig. 3 = 10 μm .) 1. Whole seed. 2. Unsonicated seed section showing secondary deposits in reticulum cells. 3. Sonicated seed section with secondary deposits removed (except at arrow) showing pits and thickenings on reticulum cell radial walls.

seed—are of equal height. In other examined species with angular reticulum cells the cells tend to be narrower in one dimension than the other and radial walls are unequal in height (Bacon et al 1986a; Chance and Bacon 1984). There is no definite pattern in the arrangement of reticulum cells in *D. systyla*, in contrast to the regular patterns found in *Eriodictyon* and *Turricula* (Bacon et al 1986a) and some groupings of *Nama* (Bacon 1987; Chance and Bacon 1984). Sections reveal that reticulum cells of *D. systyla* contain secondary deposits that adhere to but are not a part of reticulum cell walls, and, in fact, obscure details of wall structure. These deposits fill the lower $1/3 - 1/2$ of each cell and continue upward as a veneer of decreasing thickness to the apex of radial walls (Fig. 2,3). The deposits are not removed from cells of sonicated whole seeds, but are removed in some cells of sonicated seed sections, revealing that radial walls have both pits, of varying size and shape, and thickenings (Fig. 3).

DISCUSSION

In overall features, seeds of *D. systyla* are distinctive when compared to those of *Nama*. Seeds of *D. systyla* are larger than those of *Nama* proper, those of the latter ranging from 0.3 mm to about 1 mm in length, and there is little similarity in general reticulum organization between the two. The deposits found in reticulum cells of *D. systyla* are absent in the latter species, and the radial wall pattern found in reticulum cells of *D. systyla* is not found in species of *Nama*. Pits but not thickenings characterize reticulum cell radial walls in some species of *Nama*, while thickenings but not pits are found in several others (Bacon 1987; Chance and Bacon 1984). Pits in *D. systyla* are less rounded and of less uniform size and thickenings are more irregular in size and shape than those found in *Nama*. The pattern of both pits and thickenings on reticulum cell walls in *D. systyla* is unlike any found among species of *Nama*.

Deposits similar to those in *D. systyla* are found in reticulum cells of *N. lobbii* and *N. rothrockii* A. Gray, another anomalous species of *Nama* (Hitchcock 1933) whose placement has been challenged (Bacon et al 1986a; Chance and Bacon 1984). However, whereas those of *D. systyla* fill no more than half of each cell, those in the latter two species characteristically fill each cell. Nevertheless, seeds of *D. systyla*, *N. lobbii* and *N. rothrockii* are all comparable in size and larger than those of other species of *Nama*.

The differences between seeds of *D. systyla* and most species of *Nama* are consistent with morphological and cytological differences between the two taxa. In addition to its opposite leaves, *D. systyla* produces herbaceous, upright stems which arise from "horizontal, rooting branches of a large

root crown" (Jepson 1943). Its inflorescences are terminal, branched, scorpioid cymes. Its capsules contain 1–4 but typically 4 seeds.

Two species of *Nama* produce opposite leaves, but this arrangement appears sporadically elsewhere within the family and appears to be of little taxonomic importance at the generic level. There are no species of *Nama* that produce the horizontal, rooting branches characteristic of *D. systyla*, but, perhaps significantly, *N. lobbii* and *N. rothrockii* initiate stems from horizontal rhizomes. Inflorescences in *Nama* are cymose but never scorpioid. With the exception of *N. californicum* (A. Gray) Bacon (= *Lemmonia californica*), all species of *Nama* produce more than four seeds per capsule (see below).

Torrey (in Gray 1868) stated that *D. systyla* had the corolla and "nearly the androecium" of *Nama* while possessing the seeds and gynoecium of *Phacelia* proper. [Indeed, in overall size and reticulum organization, seeds of *D. systyla* are similar to seeds of some species of the Crenulatae group of *Phacelia* (Constance 1963), but they lack the excavations and salient ridge found on the ventral surface of seeds of the latter (see Atwood 1975).] In his generic description, Torrey noted that corollas of *D. systyla* are tubular-funnelform and that the stamens are unequal and unequally inserted, the typical conditions in *Nama*. Gray (1877), erecting *Lemmonia*, simply noted that *Lemmonia* was ". . . somewhat related to *Draperia* . . ." but was properly placed in his tribe *Nameae*. He pointed out that *Lemmonia* had a campanulate corolla and noted differences in stamen features which distinguished *Lemmonia* from *Nama*, and therefore, from *D. systyla*. He then noted that *Lemmonia* produced only two ovules per locule and formed large seeds. Thus, it seems that Gray's association of *Draperia* and *Lemmonia* must have been based in large part on ovule/seed number, a feature which he emphasized in his reorganization of *Phacelia* (Gray 1875), but which has since been shown to be unreliable (see Constance 1963).

In conclusion, evidence from morphology, cytology and seed structure supports recognition of *Draperia* and *Nama* as separate and perhaps unrelated genera.

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APPENDIX: SOURCE OF SEED SAMPLES.

California: Siskiyou Co.: White Ridge, S. Fork Sacramento River, *Crampton* 3839 (UC);
Tulare Co.: Old Colony Mill, K. *Brandegge* s.n. (UC).

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