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SYSTEMATICS OF *NAMA* (HYDROPHYLLACEAE): SEED COAT
MORPHOLOGY OF *LEMMONIA CALIFORNICA* AND *NAMA*
SPECIES ALLIED WITH *NAMA DEMISSUM*

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ABSTRACT

Seed coat morphology of *Lemmonia californica*, long held to be a relative of *Nama*, was examined using scanning electron microscopy. Its seed coat exhibits reticulum cells with undulate cell walls and columnar radial wall thickenings. Seed coat structure in nine species of *Nama*, *N. demissum*, *N. aretioides*, *N. densum*, *N. parviflorum*, *N. pusillum*, *N. depressum*, *N. dichotomum*, *N. sericeum* and *N. organifolium*, members forming one of six seed groups in *Nama*, also exhibit reticulum cells with undulate walls and columnar wall thickenings. The *Nama* species and *Lemmonia* are remarkably similar in testa organization, suggesting that the relationship of the two may well be closer than the generic status accorded *Lemmonia* would indicate.

Key words: Hydrophyllaceae, *Nama*, *Lemmonia*, seed coat morphology.

INTRODUCTION

The genus *Nama* (Hydrophyllaceae) includes a diverse assemblage of some 50 annual and perennial species distributed primarily in the drier regions of western United States and Mexico. As hypothesized by Hitchcock (1933), the genus is structured of five sections, *Arachnoidea*, *Cinerascentia*, *Zonolacus*, *Conanthus*, and *Nama* (= *Eunama* of Hitchcock); the former three sections are monotypic, the fourth houses but three species, and sect. *Nama* shelters the remainder, an assorted community itself. Indeed, Chance and Bacon (1984) have found that sect. *Nama* comprises five species groups based on seed coat morphology, and in seed features species of sects. *Conanthus* and *Zonolacus* singly conform with two of those groupings. Species of sects. *Arachnoidea* and *Cinerascentia*, *N. lobbii* A. Gray and *N. rothrockii* A. Gray, respectively, form a sixth seed group, but their distinctive features argue that any relationship between the two or of either to the bulk of *Nama* is remote (Chance and Bacon 1984; Bacon, Bragg, and Hannan 1986), an argument countenanced by their flavonoid chemistry (Bacon, Fang, and Mabry 1986) and chromosome number (Bacon 1984; Constance 1963). In fact, accumulated evidence argues convincingly that these latter two species are best viewed as distinct phyletic elements within Hydrophyllaceae with affinities nearer to *Eriodictyon* than to *Nama* (Bacon, Fang, and Mabry 1986; Bacon, Bragg, and Hannan 1986).

Traditionally, the nearest relative of *Nama* has been identified as *Eriodictyon*. *Nama lobbii* is critical for this alignment since it is through this taxon that Hitchcock (1933) allied the genus with *Eriodictyon*. Acceptance of recent evidence, however, portraying *N. lobbii* as well removed from the bulk of *Nama*, severs the direct relationship of the two genera and requires that relatives of *Nama* proper be sought elsewhere within the family. While Hitchcock (1933) addressed directly

only the perceived relationship of *Nama* and *Eriodictyon*, he did briefly note the monotypic genera *Draperia* and *Lemmonia* as close relatives of *Nama*. Although *Nama* and *Draperia* are chromosomally divergent (Constance 1963), their relationship has yet to be fully explored. *Lemmonia*, on the other hand, is chromosomally harmonious with *Nama* (Constance 1963). Moreover, Gray (1877) observed that the seeds of *Lemmonia* "are very like those of *Nama demissa* (sic) and of *Conanthus*" (= *N. aretioides* (H. & A.) Brand in sect. *Conanthus* of Hitchcock). Seed coat morphology has proven informative in discerning relationships within *Nama* proper (Chance and Bacon 1984) and in assessing relationships among *N. lobbii*, *Eriodictyon* and *Turricula* (Bacon, Bragg, and Hannan 1986). Therefore, seeds of *Lemmonia* have been examined using the scanning electron microscope (SEM) with the aim of evaluating seed coat features as they pertain to the relationship of the former taxon and *Nama*. Also, ultrastructural features of the *Lemmonia* seed coat revealed the need for re-evaluation of cell wall ultrastructure in one of the six seed groups of *Nama* as identified by Chance and Bacon (1984). Implications of these seed features as they bear on systematics-relationships of *Nama* are considered herein.

MATERIALS AND METHODS

Mature, whole seeds removed from herbarium specimens (see Appendix) were mounted on aluminum stubs with double-stick carpet tape. For examination of internal features of cells forming the outermost testa layer (reticulum cells), seeds were sectioned free-hand with a single-edge razor blade, extracted for about two minutes in acetone to remove obscuring oils, and mounted as for whole seeds. Additionally, whole seeds were placed in a ¼-dram screw-cap vial, covered with acetone and sonicated for 60–150 sec to remove the outer tangential wall and reveal radial wall features of cells composing the reticulum; sonicated seeds were mounted as for whole seeds. Specimens were coated to a thickness of approximately 50 nm in a Polaron E5100 sputter coater using gold-palladium target and examined with a JEOL JSM 30-C SEM at an accelerating voltage of 15 kV.

RESULTS

Seeds of *Lemmonia* are dark brown to black and generally ovate-ovoid (Fig. 1). Seed size and shape are variable, however, as is the case in *Nama* and most other examined groups (see Chance and Bacon 1984). The outer testa is obviously cellular and surface patterning is shallowly reticulate as defined by Chance and Bacon (1984). Reticulum cells generally are elongate and tend to be oriented at right angles to the long axis of the seed (Fig. 1); however, some cells approach being as broad as long (Fig. 2) and orientation is obscured. Reticulum cell walls are undulate (Fig. 1, 2) and in section exhibit what appear to be pores in radial walls. Indeed, this impression can be gained in some sonicated seed preparations where sonication has removed much of the cell wall, leaving only fragments (Fig. 11). However, even in some sections the pores are clearly occluded by a thin wall (Fig. 5), suggesting that they are an artifact of the sectioning process and that walls are possessed of thickenings, instead. Examination of seeds sonicated for a shorter period reveals that radial walls do indeed include columnar thickenings (Fig. 12). Thickenings are irregularly placed and their positioning reflects the undulate nature of the wall.

Fig. 1-6. Seeds of *Lemmonia* and *Nama*. — 1-2. *L. californica* (Dudley 345, NY). — 1. Whole seed. — 2. Seed surface showing undulate reticulum cell walls. — 3. *N. demissum* var. *deserti*, whole seed (Bacon 1803). — 4. *N. depressum*, whole seed (Bacon 1800). — 5. *L. californica*, seed section showing porelike aperture occluded by thin cell wall (Dudley 345, NY). — 6. *N. densum*, seed section showing porelike apertures (Bacon 1865). (Bar in whole seed photographs = 100 μm ; bar in surface view and sections = 10 μm .)

Seeds with outer testa cells exhibiting undulate radial walls that show pores in sections characterize one seed group in *Nama* (Chance and Bacon 1984). Species included in this grouping are *N. demissum* A. Gray (Fig. 3), *N. depressum* Lemmon ex A. Gray (Fig. 4), *N. densum* Lemmon, *N. aretioides* (Fig. 7), *N. parviflorum* (Greenm.) Const. (Fig. 8), *N. dichotomum* (R. & P.) Choisy, *N. organifolium* H.B.K. (Fig. 9), *N. pusillum* Lemmon ex A. Gray (Fig. 10) and *N. sericeum* Willd. ex Roem. & Schult. In the light of results from *Lemmonia*, review of reticulum cell radial wall features in these species was mandated. Reexamination of seeds of species in this group confirms features as reported by Chance and Bacon (1984), including the presence of pores in seed sections (Fig. 6). Examination of sonicated seeds, however, shows that reticulum walls of these species include columnar thickenings (Fig. 13–18) rather than pores, and affirms that the pores as reported for this grouping by Chance and Bacon (1984) are indeed artifacts of sectioning.

Generally, wall structure is strikingly similar among examined *Namas* and between them and *Lemmonia*. Variations occur among species, nevertheless. Thickenings in *N. depressum* are not so pronouncedly distinct as in other species (Fig. 15) but are clearly present. Those of *N. dichotomum* (Fig. 18) are not so rounded nor as frequent and often they are broader than those of other taxa. Thickenings in *N. aretioides* (Fig. 16), *N. densum*, *N. parviflorum* (Fig. 17) (all in sect. *Conanthus* of Hitchcock) and, to a lesser degree, *Lemmonia* (Fig. 12) appear to occur as “double sets,” as if adjacent cells produce each its own set of non-contiguous wall thickenings.

Wall structure of *N. pusillum* has yet to be fully confirmed. Sonication, generally removes completely the outer testa layer or leaves the collapsed outer tangential wall intact, obscuring radial walls. A few wall portions have been observed and I believe thickenings are present although weakly defined. However, additional study is needed before such can be stated with certainty.

Overall, seeds of *Lemmonia* are more similar, remarkably so, to those of *N. demissum* than to those of any other *Nama*. Seeds of both exhibit markedly undulate radial walls and their reticulum cells show similar variations in size and shape. Additionally, wall thickenings of the two are similar in shape, more so than with other species examined. All in all, seed features of these two taxa are strikingly alike.

DISCUSSION

Emendation of characters defining the *Nama* seed group proposed by Chance and Bacon (1984) does not negate the grouping as proposed; in fact, it places it on a more solid basis, both conceptually and pragmatically, because wall thickenings are more readily explained than are pores. Moreover, Chance and Bacon (1984) were less than certain that *N. demissum* and *N. dichotomum* were to be included in this seed group, despite their obviously undulate walls, since seed sections of the two rarely yield clearly interpretable wall patterns and they were unable to observe pores in the walls of either taxon. As well, Chance and Bacon (1984) were concerned as to placement of *N. organifolium* and *N. sericeum* within this group owing largely to the woody habit of both, but also due to the presence of what appeared to be thickenings traversing the lower reticulum cell walls in *N. organifolium* (such thickenings characterize yet another seed group in *Nama*); they attributed these apparent thickenings to folds in the collapsed upper tangential

Fig. 7–11. Seeds of *Nama* and *Lemmonia*.—7. *N. aretioides*, whole seed (Bacon 1809).—8. *N. parviflorum*, whole seed (Weber & Salamun 12623, NY).—9. *N. organifolium*, whole seed (Bacon & Dillon 1759).—10. *N. pusillum*, whole seed (Bacon 1801).—11. *L. californica*, surface of sonicated seed showing wall remnant with porelike aperture (Dudley 345, NY). (Bar in whole seed pictures = 100 μ m; bar in surface view = 10 μ m.)

Fig. 12–18. Radial walls of testa cells of *Lemmonia* and *Nama*.—12. *L. californica* (Dudley 345, NY).—13. *N. demissum* var. *deserti* (Bacon 1802).—14. *N. organifolium* (Bacon & Dillon 1759).—15. *N. depressum* (Bacon 1800).—16. *N. aretioides* (Bacon 1809).—17. *N. parviflorum* (Weber & Salamun 12623, NY).—18. *N. dichotomum* var. *dichotomum* (Bacon 1704). (Bar in all figures = 10 μm .)

wall where it contacted more prominent wall undulations. The fact that only radial wall thickenings were observed in all examined *Nama* species removes much of the organizational uncertainty voiced by Chance and Bacon (1984) and affirms their proposed grouping.

Lemmonia californica A. Gray is a small, prostrate, dichotomously branched, white-flowered annual distributed in the southern portion of California, adjacent Nevada, western Arizona, and Baja California. The taxon also is possessed of unique floral features; its corolla is campanulate and its stamens are basally coalescent "... in such manner as to form a sort of annulus to the corolla-tube." (Gray 1877). Also, the taxon generally produces only four seeds. Gray (1877) noted that the genus was "... somewhat related to *Draperia* among the *Phacelieae*, yet belonging properly to the *Nameae*."

Since its establishment by Gray (1877), *Lemmonia* has been consistently maintained as a monotype (Gray 1880, 1886; Peter 1892; Brand 1913; Jepson 1925, 1943; Hitchcock 1933; Munz and Keck 1959; Constance 1963); this treatment is surprising since, except for the two woody taxa, the species of *Nama* in the above seed group are all very similar to *Lemmonia*; they occur in the same region, all are dichotomously branched annuals and four of the seven annuals have white flowers. Moreover, the annuals are generally small and, except for *N. dichotomum*, prostrate in habit. Indeed, even more markedly divergent elements have been included in *Nama* by many of the same authorities who accepted *Lemmonia* as distinct, e.g., *Draperia* (Gray 1862) and *Turricula* (Gray 1875, 1880, 1886; Peter 1892; Brand 1913), the placement of the latter problematical even in recent years (Hitchcock 1933; Jepson 1943). (However, much of the seeming inconsistency in this regard almost certainly is due to the positioning of *N. lobbii*—see Bacon, Bragg, and Hannan [1986] and Bacon, Fang, and Mabry [1986] for a full discussion of this situation.) Gray's treatment of *Lemmonia* as a distinct genus seems consistent, nevertheless, since, owing to its connate styles, Gray continually held *N. aretioides* to be generically distinct from *Nama*. Additionally, Gray (1875) considered ovule number as fundamental to certain groupings in his reorganization of *Phacelia*; to what extent this stance influenced his perception of the status of *Lemmonia* is unclear, but it seems reasonable to assume that, along with floral characters, the fewer, larger seeds of the latter, as compared to those of *Nama*, would have enhanced his evaluation. (Ovule-seed number may also account for Gray's suggestion that *Lemmonia* is "somewhat related" to *Draperia*, which also produces but four seeds; in all other aspects the two are distinct.) However, Constance (1949, 1963) has shown that ovule number is generally an arbitrary character and not indicative of phyletic origin in *Phacelia*. Recent evidence from seed morphology regarding sect. *Conanthus* suggests that, in some instances at least, floral features may be misleading when used to adjudge phyletic status. In fact, Jepson has implied as much regarding floral features of *Lemmonia*, while accepting the genus, by noting (Jepson 1943, p. 284):

"The tube of the corolla of *Lemmonia* is very short but distinctive and rather conspicuous. It is constricted at the top, at the point of stamen attachment. The bowl-shaped throat, markedly expanding above the tube, is twice as long as the tube. The ovary and capsule, described by Gray (Proc. Am. Acad. 12:162; Bot. Cal. 2:468) as 2-celled, are really 1-celled with closely parietal narrow placentae. In no way does *Lemmonia* differ in fruit from the species of *Nama* as a whole. Indeed, *Lemmonia californica* resembles *Nama pusillum* so closely that for the generic validity of *Lemmonia*, one must look to the corolla character newly described above and to the peculiar

structure joining the bases of the filaments. In all other essential respects, in habit, aspect, foliage, inflorescence and capsules, the similarity of *Lemmonia californica* to *Nama pusillum* is remarkable. *Lemmonia* as a genus rests mainly on two slight technical characters—that of the corolla-tube and the dilation-joined filaments.”

In addition to morphological similarities, chromosome number of both *Lemmonia* and *Nama* is $n = 7$ (see Constance 1963; Bacon 1974, 1984;). Hydrophyllaceae have been thoroughly surveyed chromosomally (Cave and Constance 1942, 1944, 1947, 1950, 1959; Constance 1963), and $n = 7$ is found elsewhere in the family only in one species of *Phacelia*, *P. racemosa* (Kell.) Brandeg., and one of *Nemophila*, *N. phacelioides* Nutt. ex Barton (see Constance 1963); the number is clearly derived in each of these taxa and its origin in each certainly is phyletically unrelated to that in either *Nama* or *Lemmonia*. Indeed, *N. phacelioides* has the largest chromosomes yet encountered in Hydrophyllaceae (Constance 1963) while those of *Nama* and *Lemmonia* are small.

Conformity of seed features of *Lemmonia* to those of the aforementioned *Namas* is apparent. It seems unlikely, given the degree of agreement in other features, that these similarities are simply fortuitous. Indeed, seed features among the few hydrophyllaceous taxa examined in depth, *Nama*, *Turricula* and *Eriodictyon* (Chance and Bacon 1984; Bacon, Bragg, and Hannan 1986), accentuate the unique organization exhibited by these species. Moreover, preliminary observations have been completed on seeds of *Phacelia* (25 spp.), *Emmenanthe* (1 sp.), *Ellisia* (1 sp.) and *Tricardia* (1 sp.), and testa organization in all is distinct as contrasted with that in the taxa discussed herein. Seed features confirm Gray's observation of the similarity of *Lemmonia* seeds and those of *N. demissum* and *N. aretioides*; indeed, seed similarities of the former and *N. demissum* would portray the two as more closely allied than are *Lemmonia* and *N. pusillum*, as might be inferred from the statement of Jepson (1943). However, the uniformity in testa organization among all species examined herein poses somewhat of a paradox; it strongly supports the alliance of *Lemmonia* with *Nama* but also places the generic status of *Lemmonia* in doubt.

My intent is not to suggest that seed coat features are the ultimate arbiters of taxonomic status in Hydrophyllaceae. However, in those few genera studied in depth, all in Gray's Nameae, seed coat indications correspond remarkably with other features of morphology and cytology. (Seed coat features of examined species of *Phacelia* correlate strongly with subgenera and species groups proposed by Constance [1963].) Therefore, results of those studies might be instructive in evaluating the taxonomic significance of seed features of *Lemmonia*. Indeed, a similar situation exists in *Turricula* and *Eriodictyon* (Bacon, Bragg, and Hannan 1986). Seeds of *Turricula* are, essentially, identical to those found in *Eriodictyon* species; on the basis of seed features alone, *Turricula* could easily be accommodated in *Eriodictyon*. However, the former is a malodorous, herbaceous perennial while the latter is an aromatic, shrubby genus. Additionally, *Turricula* has a chromosome complement of $n = 13$, while *Eriodictyon* is uniformly $n = 14$ (see Constance 1963). Seed features would affirm that the two are to be allied while morphological and cytological features support their accepted status. In the case of *Lemmonia* and *Nama* there is no chromosomal or morphological basis supporting of generic maintenance of the former. I tend to the opinion that *Lemmonia*

cannot be maintained as distinct from *Nama*. Nevertheless, I have no field experience with *Lemmonia* and hesitate to alter its status until seeds of other potential relatives of it and *Nama*, including *Draperia*, have been examined. But whatever its status, seed features argue cogently that relationships of the taxon lie with the mentioned seed group in *Nama*.

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APPENDIX

Source of Seed Samples

Vouchers for *Nama* collections will be deposited at TEX; those for *Lemmonia* are deposited as indicated. Collection numbers of the author are indicated by *B.* or *B. & D.* (=Bacon and Dillon).

Lemmonia californica: California. Kern Co.: Tehachapi Mts., *Dudley* 345 (NY); 8 mi N of Tehacapi (sic) on Hwy 202, *Dunn, Morris & Conrad* 20828 (NY); 20 mi from Weldon on road to Walker Pass, *Munz* 13361 (UC).—*Nama aretioides*: Nevada. Washoe Co.: E side of Pyramid Lake, *B.* 1809; Steamboat Springs, *Constance* 3290 (NY).—*N. demissum* var. *deserti*: California. Inyo Co.: 11 mi S of Big Pine on Hwy 395, *B.* 1802; 4 mi E of Big Pine on Hwy 168, *B.* 1803.—*N. densum*: California. Mono Co.: 2 mi past research station on road to Cottonwood Creek, White Mts., *B.* 1814; 3 mi E of Hwy 395 on Hwy 120, *B.* 1861; 0.5 mi N of Hwy 120 on Deep Wells Road, 26 mi E of jct Hwy 120 and 395, *B.* 1862; 41 mi E of Hwy 395 on Hwy 120, *B.* 1864.—*N. depressum*: California. Inyo Co.: Gooddale Creek Recreation Area, near Aberdeen, *B.* 1800.—*N. dichotomum* var. *dichotomum*: Arizona. Coconino Co.: Coconino Natl. Forest, *B.* 1702; 13 mi N of Flagstaff on Hwy 89, *B.* 1703. New Mexico. Sierra Co.: 18 mi W of Hillsboro on Hwy 180, *B.* 1704.—*N. organifolium*. Mexico. Durango: 16 mi W of Durango on hwy to Mazatalan, *B.* 1840. Hidalgo: 4 mi N of Mezquititlan, *B. & D.* 1759. San Luis Potosi: 2 mi S of Santa Maria del Rio on Hwy 57, *B. & D.* 1715.—*N. parviflorum*: Colorado. Moffat Co.: Between Greystone and Gates of Lodore, *Weber & Salamun* 12623 (NY). Oregon. Lake Co.: 64 mi NE of Lakeview on Hwy 395, *B.* 1865. Nevada. Washoe Co.: E side of Pyramid Lake, *B.* 1810.—*N. pusillum*: California. Inyo Co.: 11 mi S of Big Pine, *B.* 1801. Nevada. Clark Co.: 33 mi NE of Tecopah, *B.* 1859.—*N. sericeum*: Mexico. Hidalgo: 14 mi N of Zimapan on Hwy 85, *B. & D.* 1724; 4 mi N of Mezquititlan, *B. & D.* 1758.