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Systematics of Nama (Hydrophyllaceae)

John D. Bacon

The University of Texas at Arlington

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SYSTEMATICS OF *NAMA* (HYDROPHYLLACEAE): REEVALUATION OF THE TAXONOMIC STATUS OF *LEMMONIA CALIFORNICA*

JOHN D. BACON

Department of Biology
The University of Texas at Arlington
Arlington, Texas 76019

ABSTRACT

Lemmonia has been maintained as a monotypic genus, despite the fact that it is morphologically very similar to several species of *Nama*. The major basis for this separation resides in the reportedly coalescent filament bases of *Lemmonia* as contrasted with the distinct filaments of *Nama*. Examination of corollas of *Lemmonia* with the scanning electron microscope has revealed that the filaments of the taxon are distinct. There is, then, no qualitative basis upon which to found *Lemmonia*, and the taxon is transferred to *Nama*.

Key words: Hydrophyllaceae, *Lemmonia*, *Nama*.

INTRODUCTION

Lemmonia californica A. Gray is a small, prostrate, dichotomously branched annual distributed from Lake County, California, southward into southern California and northern Baja California. [Munz and Keck (1959) indicate the taxon also is to be found in Nevada.] Gray (1877) placed *Lemmonia*, along with *Nama*, exclusive of *N. aretioides*, maintained by Gray as the monotypic *Conanthus*, and *Eriodictyon* in his *Nameae*, but reckoned, as well, that it was somewhat related to *Draperia* in his *Phacelieae*. Subsequently, *Lemmonia* has come to be viewed as most closely related to *Nama* (Hitchcock 1933; Jepson 1943; Constance 1963). Indeed, Jepson (1943:284), considering morphology, implied that *Lemmonia* might better be accommodated in *Nama*.

The dichotomous habit of *Lemmonia* is identical with that of seven species of *Nama*, all of which occur in the same general region as does the former. Recently, the outer seed coat of *Lemmonia* has been shown to have the same basic structural organization as the outer coat of seeds of nine species of *Nama* (Bacon 1987), which form one of six seed groups identified in *Nama* (Chance and Bacon 1984); the seven aforementioned Namas are within this group. Moreover, the two genera have been found to be essentially diploid (a very few Namas are tetraploid) with $n = 7$, a number found elsewhere within the family in only two additional species, each in a separate genus (see Constance 1963; Bacon 1987), neither closely related to either *Lemmonia* or *Nama*. Considering the above, Bacon (1987) doubted that *Lemmonia* could be maintained as distinct from *Nama*.

Nevertheless, there are some minor features by which *Lemmonia* can be differentiated from *Nama*. The former produces only four seeds per fruit, generally, while *Nama* produces many. The corolla of *Lemmonia* is shorter than those of *Nama*, and is campanulate-bowl shaped with a short basal tube. Corollas of *Nama* species that co-occur with *Lemmonia* are generally described as tubular-salverform. Jepson (1943) considered the corolla tube to be one of the few characters

by which *Lemmonia* could be separated from *Nama.* However, the most significant difference between the two taxa lies in the reportedly coalescent filament bases of *Lemmonia,* a feature unique within the family (Brand 1913; Jepson 1943; Munz and Keck 1959; Constance 1963). Certainly, this feature bears on the acceptance of *Lemmonia* as a genus (e.g., see Jepson 1943; Constance 1963). In fact, were it not for this character there would be essentially no qualitative basis upon which to found *Lemmonia,* and the submergence of *Lemmonia* in *Nama* would be warranted, if not mandated. Because the filament character is fundamental to the status of *Lemmonia,* attempts were made to visualize the character using light microscopy and the few available corollas found in seed packets on herbarium specimens; however, I was unable to satisfactorily evaluate the reported fusion. Recently, Dr. Lincoln Constance kindly supplied herbarium material of *Lemmonia* with several corollas attached. Therefore, corollas of *Lemmonia* and selected *Nama* species were examined using the scanning electron microscope (SEM) in order to compare corolla features between the two taxa and, particularly, to examine and evaluate the significance of the reportedly coalescent filament bases as it bears on the status/relationship of *Lemmonia* and *Nama.* Results and conclusions derived from that examination are contained in this report.

MATERIALS AND METHODS

Corollas of *Lemmonia* were removed from herbarium specimens (Appendix 1) and rehydrated in distilled water overnight. Rehydrated corollas were then dehydrated through successive overnight immersions in each of four aqueous ethanol mixtures, 50, 70, 80 and 95 percent ethanol, with a final overnight immersion in absolute ethanol. For purpose of comparison, corollas of selected *Nama* species (Appendix 1), which had been preserved in FAA, were dehydrated in a like manner, except that the rehydration procedure was omitted. Some corollas were opened, using a razor blade, parallel to their long axis so that filaments could be observed. Dehydrated corollas were then critical point dried in a Pelco Model H critical point drying apparatus. Corollas were mounted on aluminum stubs with carpet tape, coated in a Polaron E5100 or Hummer VI sputter coater, using gold-palladium target, and examined with a JEOL JSM 35-C SEM at an accelerating voltage of 15 kV.

RESULTS

The corolla of *Lemmonia* is essentially glabrous and has a short, but distinct, tube that abruptly expands and becomes campanulate above (Fig. 1), as clearly described by Jepson (1943:284). Filaments are equally-subequally inserted on the corolla tube approximately at its point of expansion (Fig. 2). At their point of insertion, and continuing slightly above, filaments are expanded and straplike but narrow abruptly and become elongate and rounded in their apical portion (Fig. 2, 3). Filaments are clearly distinct and not coalescent; this fact is apparent in young, unopened flower buds (Fig. 3), where even the adnate filament appears to be marginally free (narrowly winged) on some filaments, as well as in mature corollas (Fig. 2). The adnate portion of each filament separates readily from the tube with gentle teasing and there is no indication that one filament is laterally fused to another (Fig. 4). Moreover, throughout its length, the separated adnate

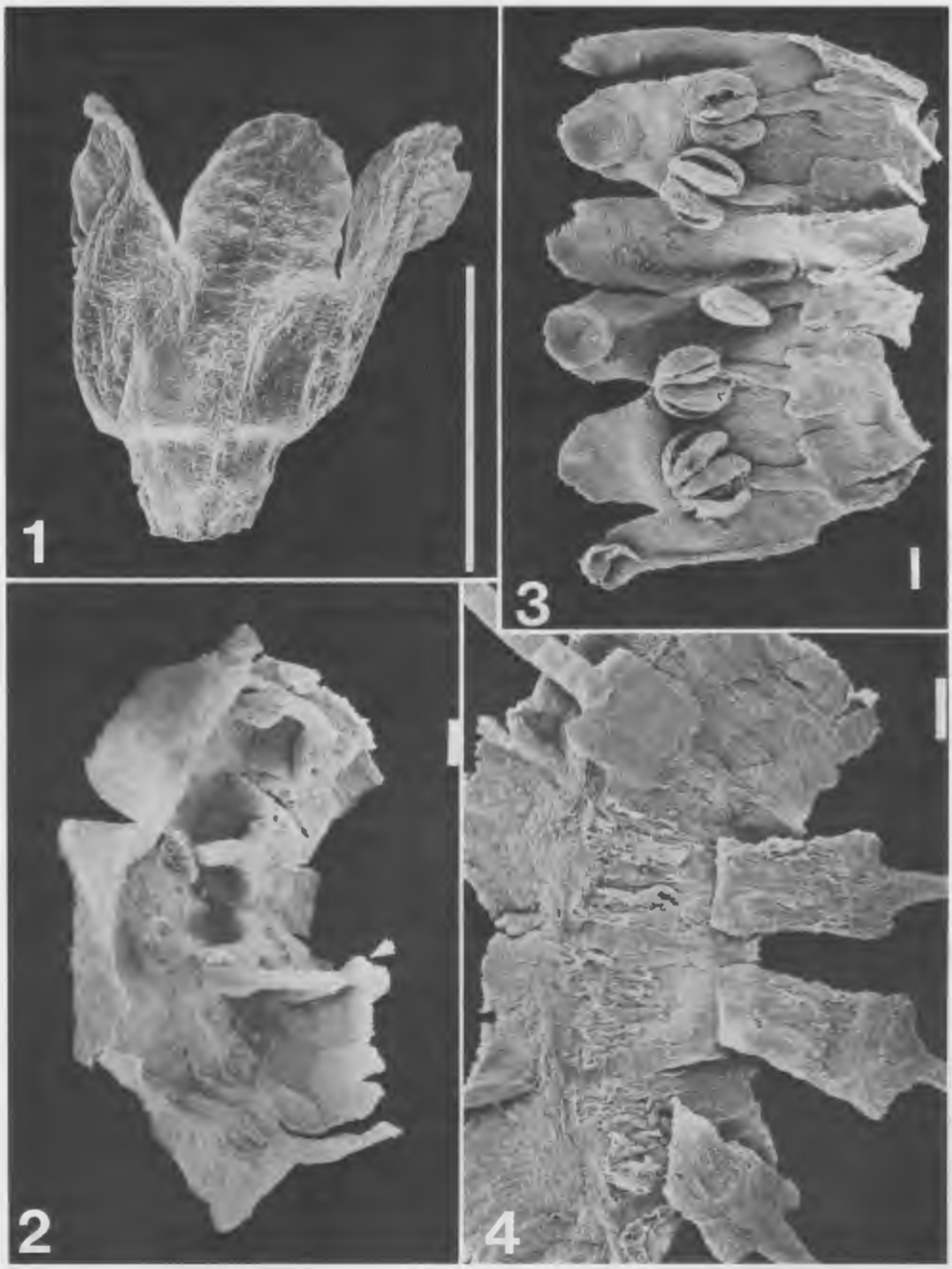

Fig. 1–4. Corolla and filaments of *Lemmonia californica* (*Munz 13229,* UC).—1. Whole corolla.—2. Longitudinal section of corolla showing point of filament insertion; note expanded free filament at arrowhead.—3. Opened flower bud; note free margins of adnate filament at arrows.—4. Corolla section with adnate filaments teased away from corolla. (Bar in Fig. 1 = 1 mm; bar in Fig. 2, 3, 4 = 100 μm.)

filament portion approximates the width of the expanded, free portion, and the adnate margins of each come away from the tube "cleanly," again arguing for the absence of lateral fusion among filaments (Fig. 4).

Corollas of examined Namas are sparsely to densely pubescent, and all are basically tubular-salverform. However, in corollas of *N. pusillum* (Fig. 5), *N. parviflorum,* and *N. densum* the tube is essentially the same width from the base to the throat. In corollas of *N. demissum* (Fig. 6) and *N. depressum* there is a short basal tube, somewhat constricted at its apex, that expands, much less abruptly than in *Lemmonia,* into an elongate funnelform-salverform apical portion. There is some variation in corolla shape in *N. aretioides* but, generally, the corolla has a definite but narrower, more elongate tube than in other *Nama* species and lacks the constriction at the point where it expands into the funnelform-salverform apical portion. Filaments in all examined Namas are distinct and subequally to unequally inserted (Fig. 7–10). In *N. demissum* (Fig. 7), *N. depressum,* and *N. aretioides* (Fig. 9), filaments insert about or slightly above the point of expansion of the basal tube; in the former two species, insertion of each filament is clearly marked externally by a groove in the corolla (Fig. 6). The free filament is rounded in all species; the adnate portion is narrowly winged in *N. pusillum* (Fig. 8), *N. demissum* (Fig. 7), and *N. depressum,* but lacks wings in *N. aretioides* (Fig. 9), *N. parviflorum* (Fig. 10), and *N. densum.* The adnate filament portion in all separates readily from the corolla with gentle teasing.

DISCUSSION

Bacon (1987) implied that Gray originally described the filament bases of *Lemmonia* as coalescent. However, Gray's (1877:162) original description concerning the stamens of *Lemmonia* reads as follows: ". . . Stamina brevia, tubo corollae brevissimo aequaliter inserta: filamenta subulata, ad insertionem subito dilatata, quasi appendiculata: . . ." In his discussion, Gray goes on to state of *Lemmonia*: "It is distinguished from *Nama* by the short campanulate corolla and correspondingly short styles and subulate filaments (the latter dilated and thickened at the very insertion in such manner as to form a sort of annulus to the corolla-tube), and by the single pair of ovules to each cell, forming large seeds." In later work regarding *Lemmonia* (e.g., Gray 1886), Gray repeats the above, essentially, and does not attribute coalescent filament bases to the genus.

It appears that Brand (1913:137) was the first to state that the filaments of *Lemmonia* were laterally connected; his description of the filaments of the taxon reads: ". . . Stamina inclusa, nuda, basi dilatata et linea transversa squamiformi inter se conjuncta." Also, Brand (1913:138, Fig. 25. D) includes a line drawing of the opened corolla of *Lemmonia* illustrating the filaments. He shows the rounded, free filaments arising from a narrow, lateral band, which inserts at the apex of the corolla tube. [Constance (1951:524, Fig. 4139) more clearly depicts the expanded portion of the free filament but again shows the expanded portions to be coalescent into a narrow lateral band which inserts at the apex of the corolla tube.] Brand's interpretation was apparently accepted/confirmed by later workers (e.g., Jepson 1925, 1943; Constance 1951, 1963; Munz and Keck 1959; Wiggins 1980), and *Lemmonia* has since been incorrectly characterized as having basally coalescent filaments.

It is not my intent to imply that the interpretations of earlier workers were

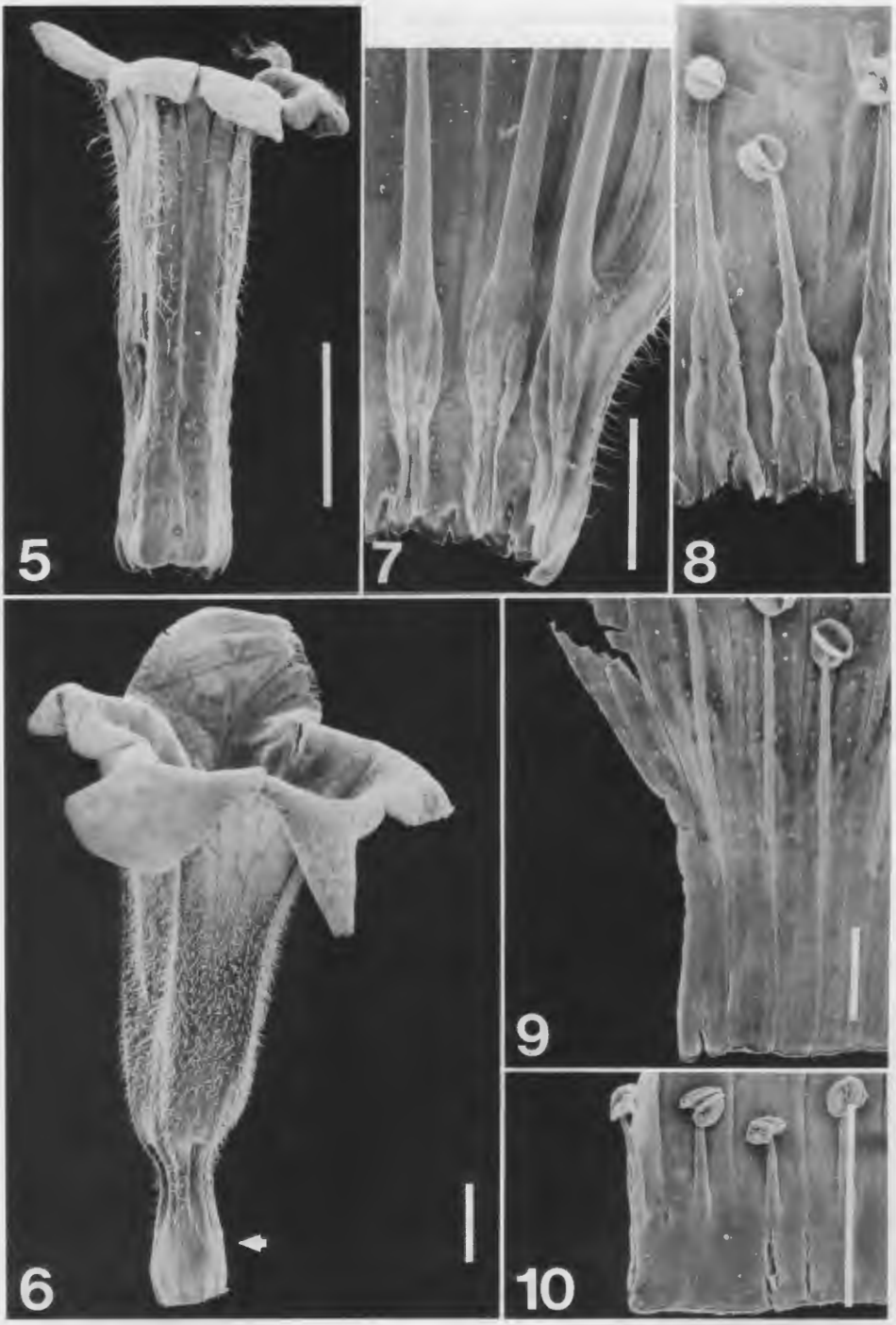

Fig. 5–10. Corollas and filaments of *Nama*.—5, 8. *N. pusillum* (*Bacon 1801*)—5. Whole corolla.—8. Corolla section with filaments.—6–7. *N. demissum* (*Bacon 1858*).—6. Whole corolla; note corolla tube at arrowhead.—7. Corolla section with filaments.—9. Corolla section with filaments of *N. aretioides* (*Bacon 1805*).—10. Corolla section with filaments of *N. parviflorum* (*Bacon 1810*). (Bar in all = 1 mm.)

based in careless observations. The corolla of *Lemmonia* is small, up to 2 mm long, the tube is about 0.5 mm in diameter, and the expanded free filaments, while small, more or less "fill" the tube, forming the "annulus" of Gray (1877). I was unable to confirm that the filaments were free using a dissecting scope (X50). Only by utilizing SEM is the true nature of the filaments of *Lemmonia* resolved.

Jepson (1943) considered that the generic status of *Lemmonia* resided in the "two slight technical characters" of its coalescent filaments and its possession of a corolla tube. It is my assumption that Jepson was considering *Lemmonia* from the point of view of the species of *Nama* co-occurring with the former because there are other species of *Nama* which possess a corolla tube, and the corolla of *N. prostratum* Brand, although much larger than that of *Lemmonia,* is campanulate with a short basal tube. Nevertheless, the basal tube is not unique to *Lemmonia,* even compared with those species of *Nama* co-occurring with the taxon, for a corolla tube also is found in *N. demissum* (Fig. 6) and *N. depressum.* Bacon (1987) has shown that the seed coat of *Lemmonia* is strikingly similar to that found in *N. demissum.* Jepson (1943) has commented on the remarkable similarity in morphology between *Lemmonia* and *N. pusillum.* It is, perhaps, significant that these two Namas, along with *N. depressum,* exhibit winged filaments (Fig. 7, 8), reminiscent of the expanded filament in *Lemmonia.*

One is left, then, with only the feature of seed number upon which to found *Lemmonia.* The import of seed number as regards the status of *Lemmonia* seems trivial, however, because there are differences in number of seeds produced per fruit among species of *Nama.* Moreover, Constance (1949, 1963) has shown that seed number is an arbitrary character as it applies to phyletic relationships in *Phacelia.*

It is my opinion that the similarities among the annual, dichotomous Namas and *Lemmonia* are such that *Lemmonia* cannot be maintained as a genus distinct from *Nama,* but must be submerged in the latter. The required transfer is as follows: **Nama californicum** (A. Gray) Bacon, comb. nov. Based on *Lemmonia californica* A. Gray, Proc. Amer. Acad. 12:162. 1877.

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APPENDIX 1

Source of Examined Specimens

Vouchers for *Nama* collections will be deposited at TEX; those for *Lemmonia* are deposited as indicated. Collection numbers are those of the author unless otherwise indicated.

Lemmonia californica A. Gray. CALIFORNIA. Kern Co.: 20 mi from Weldon on road to Walker Pass, *Munz 13361* (UC); Ventura Co.: Upper Sespe Creek, N of Wheelers Hot Springs, *Munz 13229* (UC).—*Nama aretioides* (H. & A.) Brand. CALIFORNIA. Inyo Co.: 1 mi NW off jct Aberdeen road and Hwy 395, *1799*; ca. 7 mi W of Bishop along Pleasant Valley Road, *1805*.—*N. demissum* A. Gray. CALIFORNIA. Inyo Co.: ca. 1 mi E of Hwy 395, ca. 11 mi S of Big Pine, *1802*; 5 mi W of Bishop, *1804*. NEVADA. Clark Co.: just W of Mountain Springs Summit on Hwy 160, *1858*.—*N. densum* Lemmon. CALIFORNIA. Mono Co.: 3 mi E of Hwy 395 on Hwy 120, *1861*; 0.5 mi N of Hwy 120 on Deep Wells Road, *1862*.—*N. depressum* Lemmon ex. A. Gray. CALIFORNIA. Inyo Co.: 1 mi NW of jct Aberdeen road and Hwy 395, *1800*.—*N. parviflorum* (Greenm.) Const. NEVADA. Washoe Co.: E side of Pyramid Lake, *1810*—*N. pusillum* Lemmon ex. A. Gray. CALIFORNIA. Inyo Co.: ca. 1 mi E of Hwy 395, ca. 11 mi S of Big Pine, *1801*. NEVADA. Clark Co.: 2 mi SW of jct Hwy 160 and road to Tecopa, *1859*.