Nesom, G.L. 2018. *Aquilula* (Asteraceae: Astereae), a new genus for *Ericameria riskindii*. Phytoneuron 2018-24: 1–11.
Published 30 May 2018. ISSN 2153 733X

AQUILULA (ASTERACEAE: ASTEREAE), A NEW GENUS FOR *ERICAMERIA RISKINDII*

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ABSTRACT

Aquilula Nesom, **gen. nov.**, is established to comprise the single species *Ericameria riskindii* ≡ *Xylothamia riskindii* ≡ *Gundlachia riskindii* as **Aquilula riskindii** (Turner & Langford) Nesom, **comb. nov.** It is segregated from a group of four North American species recently considered to be members of *Gundlachia*, based primarily on molecular evidence. The remaining three species are retained in the genus *Xylothamia* (as *X. diffusa*, *X. triantha*, and *X. truncata*). *Gundlachia* is regarded here a genus of seven species restricted to the Caribbean region. A phylogenetic hypothesis is proposed for these three genera, based on morphology and with the underlying assumption (based on molecular evidence) that they comprise a single clade. Photographs are provided for all of the taxa under consideration (*Aquilula*-1, *Xylothamia*-3, *Gundlachia*-7).

The genus *Xylothamia* was proposed to include nine species traditionally associated with *Ericameria* (Nesom et al. 1990; Nesom 1992). All but one (*X. riskindii*) are species of the Chihuahuan and Sonoran deserts. Molecular data show that these nine species are divided between two separate clades (Roberts 2002; Urbatsch et al. 2003; Brouillet et al. 2009). Five of the species, as the genus *Medranoa* Urbatsch & Roberts (Nesom 2007; mapped here in Fig. 11), are part of a clade that includes *Amphiachyris*, *Bigelowia*, *Euthamia*, *Gutierrezia*, *Gymnosperma*, and *Thurovia*. The other four species, including the *Xylothamia* type, are closely related to the Caribbean genus *Gundlachia* (sensu Lane 1996). The *Gundlachia* clade is sister to the *Amphiachyris* et al. clade.

Based primarily on the molecular data, Urbatsch and Roberts (2004) formally expanded *Gundlachia* to include the four North American species closely related to it — I suggested that morphological and geographical disparities support keeping *Xylothamia* and *Gundlachia* separate in taxonomy (Nesom 2007), with the caveat that the distinction of *X. riskindii* might justify its segregation from the other three North American species. The current paper formally recognizes *X. riskindii* at generic rank and retains the remaining three species within *Xylothamia* sensu stricto (mapped here in Fig. 10).

Molecular data (Roberts 2002; Urbatsch et al. 2003) did not resolve the topology of relationships among *Gundlachia* (represented in their analysis by only 1 species) and the four *Xylothamia* species. Results differed depending on optimality criteria used in the DNA sequence analysis. In the PAUP ratchet analysis of the combined ITS/ETS sequences, *X. riskindii* occupies a basal position in the *Gundlachia* clade. In the parsimony-derived trees that included indels, the Caribbean and North American species are resolved as sister lineages, with *X. riskindii* basal to the 3 desert species. When indels were excluded, *X. riskindii* is basal to all of the *Gundlachia* clade. *Gundlachia* sensu stricto is paraphyletic without the North American species in only one of their various analyses.

In any case, molecular data indicate that the four American species form a single clade with *Gundlachia*, thus their treatment as a single genus (i.e., *Gundlachia*) is reasonable. Three groups, however, are represented among them — the North American species are distinct from Caribbean *Gundlachia* in morphology, geography and ecology, and *X. riskindii* stands apart from the three desert species (*Xylothamia* sensu stricto). A phylogenetic hypothesis is presented in Figure 1, based on conspicuous apomorphies.

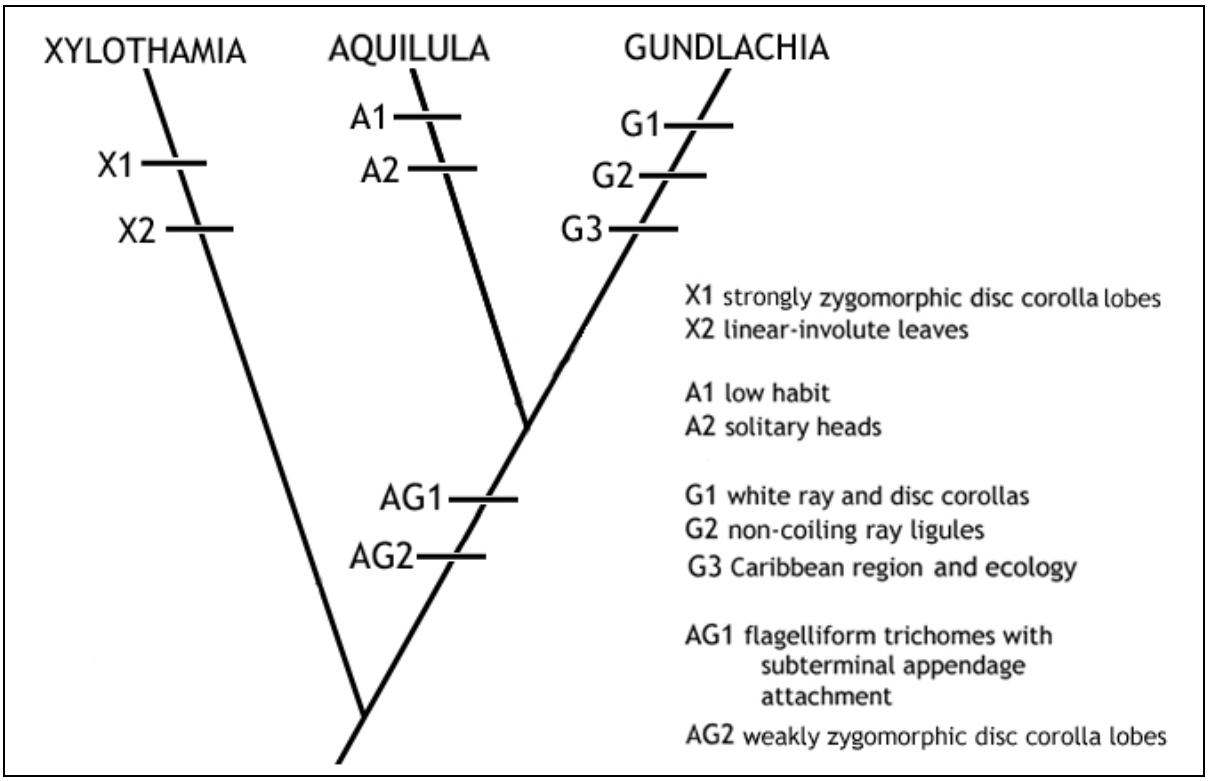

Figure 1. Phylogenetic hypothesis for the *Gundlachia* clade, based on conspicuous apomorphies. Zygomorphic disc corollas in this group were discussed by Nesom et al. (1990) and Nesom (2007). Variation in flagelliform trichomes was discussed and illustrated by Urbatsch et al. (2003) and Urbatsch and Roberts (2004). Strongly zygomorphic disc corolla lobes (X1) also are characteristic of *Medranoa*, seemingly in parallel.

Paired contrasts between Aquilula, Xylothamia, and Gundlachia

A. Leaves flat, narrowly obovate to spatulate; heads solitary; involucres 7–8 mm in diam.; ray florets 7–13; disc florets 30–50, corollas weakly zygomorphic; achenes strigose; montane habitats ... **Aquilula**

A. Leaves involute, appearing terete; heads sessile to subsessile, loosely arranged in weak corymbs or (in *X. truncata*) sessile in groups of 2–3 at branch apices; involucres 2.5–4 mm in diam.; ray florets 0 or 1–3 and obscured within the involucre; disc florets 3–7, corollas strongly zygomorphic (two of the sinuses cut nearly to the base of the throat, one very shallow [1/4–1/3 as deep as the former], and the other two intermediate in depth, the two short lobes erect, the others reflexed-coiling); achenes sericeous; desert habitats ..... **Xylothamia**

B. Plants ca. 8–15 cm tall; leaves 8–10 mm x 3–5 mm; heads terminal and solitary, sessile to subsessile; involucres broadly turbinate to subhemispheric, 7–8 mm in diam.; ray florets 7–13, disc florets 30–50, corollas yellow; disc corolla lobes cut ca. 1/5 the length of the throat; achenes without discernible nervation; Mexico ..... **Aquilula**

B. Plants 30–200 cm tall; leaves 10–80 mm x 2–11 mm; heads mostly short-pedicellate, densely arranged in distinctly corymboid clusters or (in *G. domingensis*) in dense, elongate-paniculate panicles; involucres cylindric to narrowly obconic, 2–4 mm in diam.; ray florets 3–8, disc florets 3–10, corollas white; disc corolla lobes cut ca. 1/3–2/3 the length of the throat; achenes 5-nerved; Caribbean region ..... **Gundlachia**

C. Plants 20–100(–150) cm tall; leaves more or less terete with involute margins, linear, 2–15(–25) mm x 0.3–1 mm; heads sessile to subsessile, loosely arranged in weak corymbs or (in *X. truncata*) sessile in groups of 2–3 at branch apices; ray florets 0 or 1–3 and obscured within the involucre; ray and disc corollas yellow; disc corollas zygomorphic (two of the sinuses cut nearly to the base of the throat, one very shallow [1/4–1/3 as deep as the former], and the other two intermediate in depth, the two short lobes erect, the others reflexed-coiling); xeric habitats in the Chihuahuan and Sonoran deserts ..... **Xylothamia**

C. Plants 30–200 cm tall; leaves distinctly laminar with flat margins, linear-lanceolate to narrowly spatulate, narrowly obovate-spatulate, obovate, or ovate, 10–80 mm x 2–11 mm; heads mostly short-pedicellate, densely arranged in distinctly corymboid clusters or (in *G. domingensis*) in dense, elongate-paniculate panicles; ray florets 3–8, conspicuous; ray and disc corollas white; disc corollas symmetrical; coastal thickets, dunes, pinelands, and river, pond, and swamp edges in the Caribbean region ..... **Gundlachia**

AQUILULA Nesom, **gen. nov.**

Type species, *Aquilula riskindii* (Turner & Langford) Nesom

Different from *Gundlachia* in its low habit and smaller leaves, relatively large, solitary heads, yellow corollas, coiling ray ligules. Different from *Xylothamia* in its flat, narrowly obovate to spatulate leaves, solitary, large heads with prominent ray florets, stiffly strigose achenes, and montane habit.

Aquilula is the Latinized form of "Aguililla" (little eagle), the name of the Hinton rancho in northern Nuevo León, from which James C. Hinton and George S. Hinton (the son and grandson, respectively, of botanist G.B. Hinton) have studied the flora of northeastern Mexico. George continues his studies there, especially focused on south-central Nuevo León and adjacent Coahuila. The herbarium at Rancho Aguililla houses collections made by the three generations primarily in Coahuila, Nuevo León, Tamaulipas, Oaxaca, Michoacán, Guerrero, and Edo. México.

Aquilula riskindii (Turner & Langford) Nesom, **comb. nov.** *Ericameria riskindii* B.L. Turner & Langford, Madroño 29: 234. 1982. *Xylothamia riskindii* (Turner & Langford) Nesom, Sida 14: 113. 1990. *Gundlachia riskindii* (Turner & Langford) Urbatsch & Roberts, Sida 21: 249. 2004. **TYPE**: **MÉXICO**. **Coahuila**. Ca. 28 air mi E of Saltillo, S side of the Sierra de la Viga, ca. 4 mi E of Jamé along woodcutters' road, in *Pinus arizonica*, *Quercus greggii*, *Pseudotsuga*, *Agave macroculmis*, *Pinus cembroides*, *Arbutus* woodland, 10,000 ft, exposed limestone areas, low-rounded aromatic shrublets, 15 May 1977, *J. Henrickson et al. 16156b* (holotype: TEX!; isotypes: MEXU, RSA).

Low, rounded subshrubs, aromatic. **Stems** ca. 8–30 cm high, hispidulous with short, translucent, papillose projections (erect, sharp-pointed, 3–5-celled hairs 0.05–0.1 mm long), internodes 1–5 mm long. **Leaves** linear-oblanceolate to narrowly obovate or spatulate with an attenuate to subpetiolate base, 8–10 mm long, 1.5–5 mm wide, 1-veined, flat or the narrower boat-shaped, relatively even-sized along the stems, both surfaces densely punctate with sunken glands, usually densely and evenly resinous, otherwise glabrous, margins scabrous with short trichomes like the stem, apex obtuse to acute, often falcate-apiculate. **Heads** terminal, solitary, sessile to subsessile, broadly turbinate to subhemispheric, 7–8 mm wide; phyllaries graduate in 3–4 series, ovate-lanceolate to oblong, oblong-oblanceolate, or oblong-lanceolate, base white, distal 2/3 with a broad, elongate, green patch, punctate, densely resinous, otherwise glabrous, innermost 6–7 mm long; receptacles deeply alveolate, cup margins with spike-like projections. **Ray florets** 12–16, ligules 4–5 mm long, yellow, becoming purplish upon drying, coiling. **Disc florets** 30–50, corollas yellow, 4.5–6 mm long, tube weakly delimited from throat, lobes triangular, three cut deeply (ca. 1/5 the length of the throat), two shallowly; style branches appendages linear-lanceolate, 2 mm long, collecting appendages 1–1.5 mm long. **Achenes** subcylindric, 2–2.8 mm long, without discernible nervation, densely strigose, the surface not obscured; pappus 3–5 mm long 1-seriate, persistent. Chromosome number, 2n = 18 (see Additional collections). Figure 2.

Figure 2. *Aquilula riskindii*. A. Holotype (*Henrickson 16156b*, TEX). B. Enlargement of paratype (*Hinton 18192*, MEXU 355123). C. Paratype (*Hinton 18192*, MEXU 807481). Ruler for A and C.

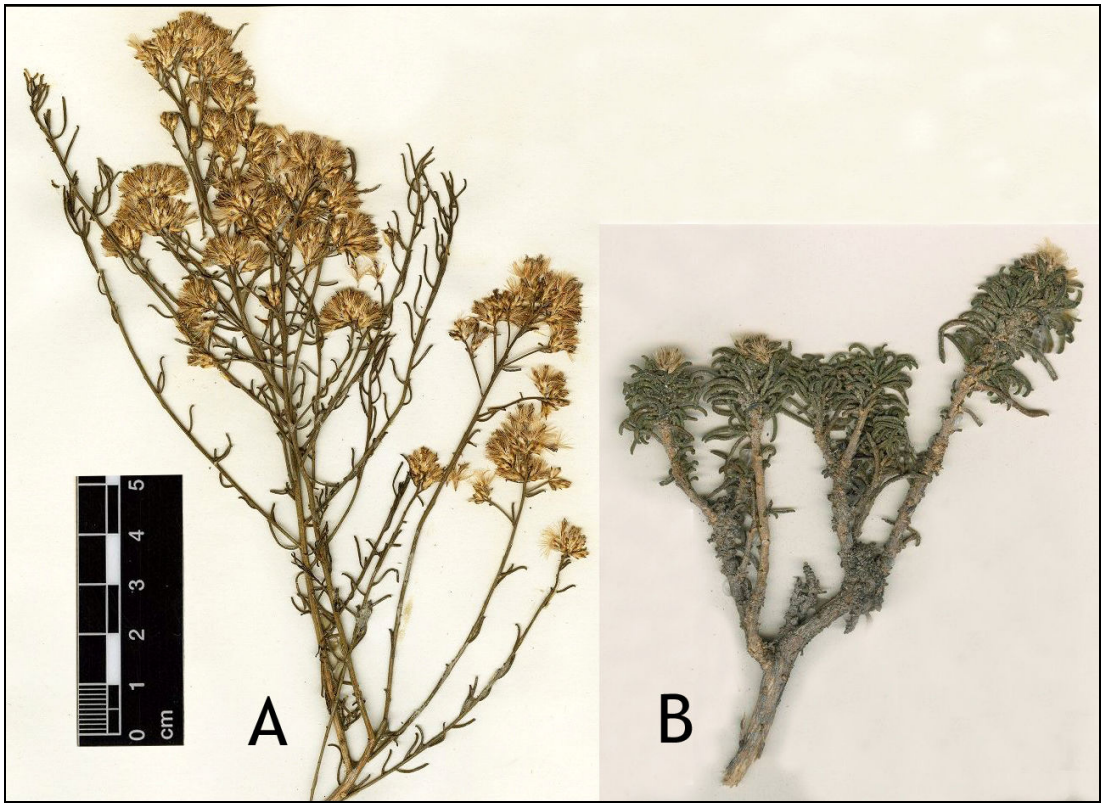

Figure 4. *Xylothamia* species. A. *Xylothamia diffusa* (holotype of *Linosyris sonoriensis*, *Palmer 11*, GH). B. *Xylothamia truncata* (from holotype, *Nesom 5254*, TEX). Ruler for both.

Figure 5. *Xylothama triantha* (holotype of *Haplopappus trianthus*, *Warnock 1126*, US). The type is from Brewster Co., Texas, the only place the genus *Xylothamia* reaches the USA.

Figure 6. Representative collections of *Gundlachia corymbosa* sensu stricto. Ruler for both.

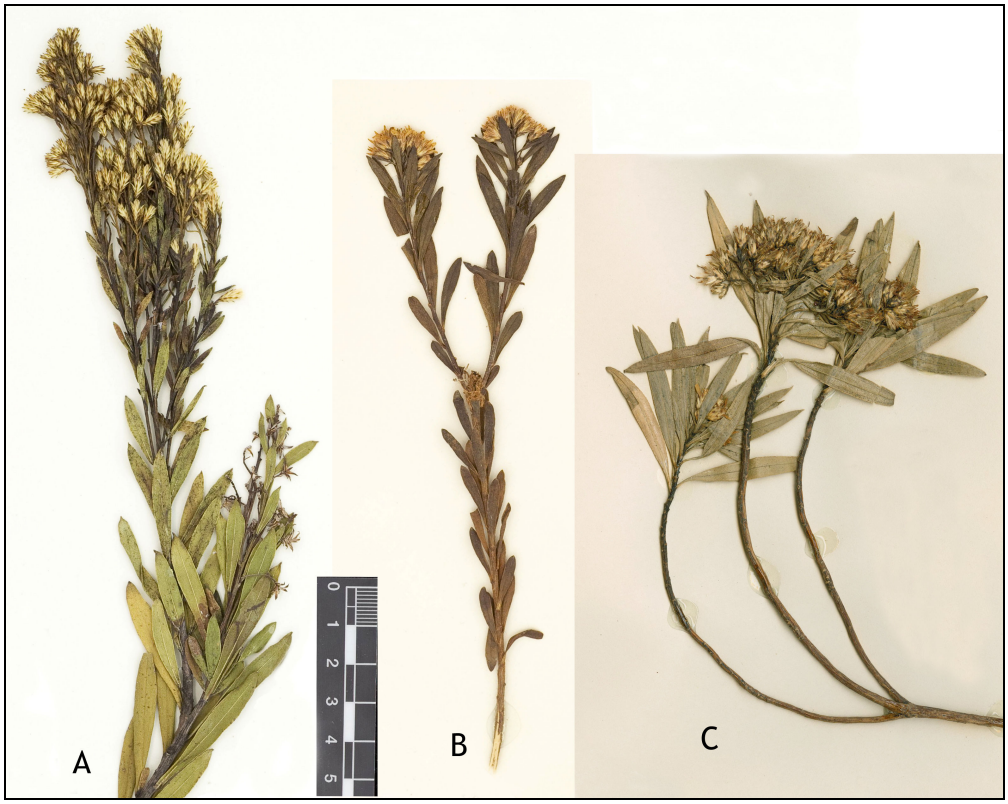

Figure 7. Representative collections of *Gundlachia*. A. *Gundlachia apiculata*. B. *Gundlachia cubana*. C. *Gundlachia ocoana*. Ruler for all three.

Figure 8. Representative collections of *Gundlachia*. A. *Gundlachia compacta*. B. *Gundlachia foliosa*.

Figure 9. *Gundlachia domingensis* (isotype of *G. floribunda*, *Ekman 3512*, S). The elongate-paniculate capitulescence probably is derived — in all the other species of *Gundlachia* it is strongly corymboid.

Coahuila, Nuevo León, Zacatecas; pine-fir-oak woodlands in limestone and gypsum areas, 2100–3000 m; flowering Apr–May. Figure 10.

Additional collections examined. **Nuevo León**. Mpio. Arteaga. Sierra Zapaliname, among rocks in rockslide, 2945 m, 19 May 1990, *Hinton 20261* (TEX-2 sheets). Mpio. Galeana: Santa Rita, rocky limestone hillside, 2100 m, 25 Apr 1981, *Hinton 18192* (TEX); above La Becerra, gypsum and limestone hillside, 2100 m, 12 Sep 1989, *Hinton 19683* (TEX); Santa Rita, gypsum hillside, 2030 m, 23 Mar 1993, *Hinton 22718* (TEX); ca. 20 km N of San Rafael, W-facing slope and W edge of mountains, ca. 2 km E of village of La Becerra, gypseous limestone, with pinyon pine, *Mortonia*, *Dasylirion*, *Yucca*, *Lindleya*, *Cowania*, *Ephedra*, and cacti, 2040 m, scattered, 21 Sep 1993, *Nesom 7697* with M. Mayfield and G.S. Hinton – voucher for chromosome count of n=9, not previously reported (TEX).

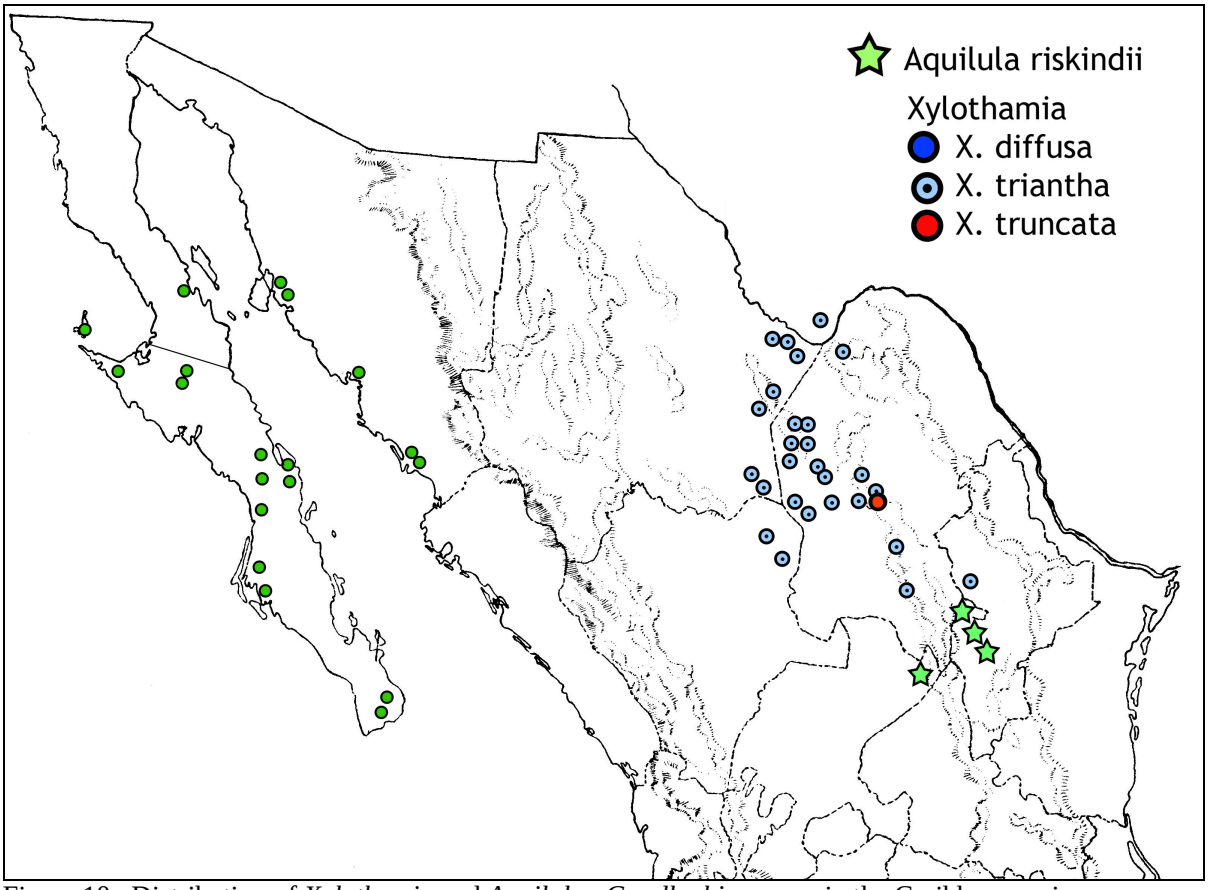

Figure 10. Distribution of *Xylothamia* and *Aquilula*. *Gundlachia* occurs in the Caribbean region.

Note on the taxonomy of *Gundlachia* sensu stricto

Lane (1996) collapsed the taxonomy of Caribbean *Gundlachia* into two species, *G. domingensis* (Spreng.) A. Gray and *G. corymbosa* (Urb.) Britt. ex Bold., the latter comprising 6 varieties. The rationale for her approach was given solely in the two paragraphs quoted here:

> "Examination of the technical characters of these specimens revealed seven taxa. Two groups of specimens differ sufficiently in reproductive characters to warrant recognition at specific rank, and are recognized here as *G. domingensis* and *G. corymbosa*. Among the specimens referable to the latter, differences in vegetative characters—coupled with geographic, topographic, and edaphic adaptations—provide the the basis for recognition of six taxa. The technical features of these groups of specimens, however, are so similar to one another that there is no justification for

giving these taxa specific rank. Therefore, *G. corymbosa* is treated below as having six varieties" (p. 532).

"Though the taxa presented below as varieties have been treated as species by other workers, I cannot find sufficient differences in their technical characters to warrant such status. Each of the characteristics used here to distinguish the varieties can also be found among specimens of the typical variety, though not consistently or in the same combinations. Most of the differences among the varieties are vegetative and attributable to effects of soil type and elevation; the number of florets and larger corollas of *Gundlachia corymbosa* var. *compacta* (more or less twice as many, and twice as large) are like gigas features correlated with polyploidy, but unfortunately the chromosome number is not known" (Lane 1996, pp. 536–537).

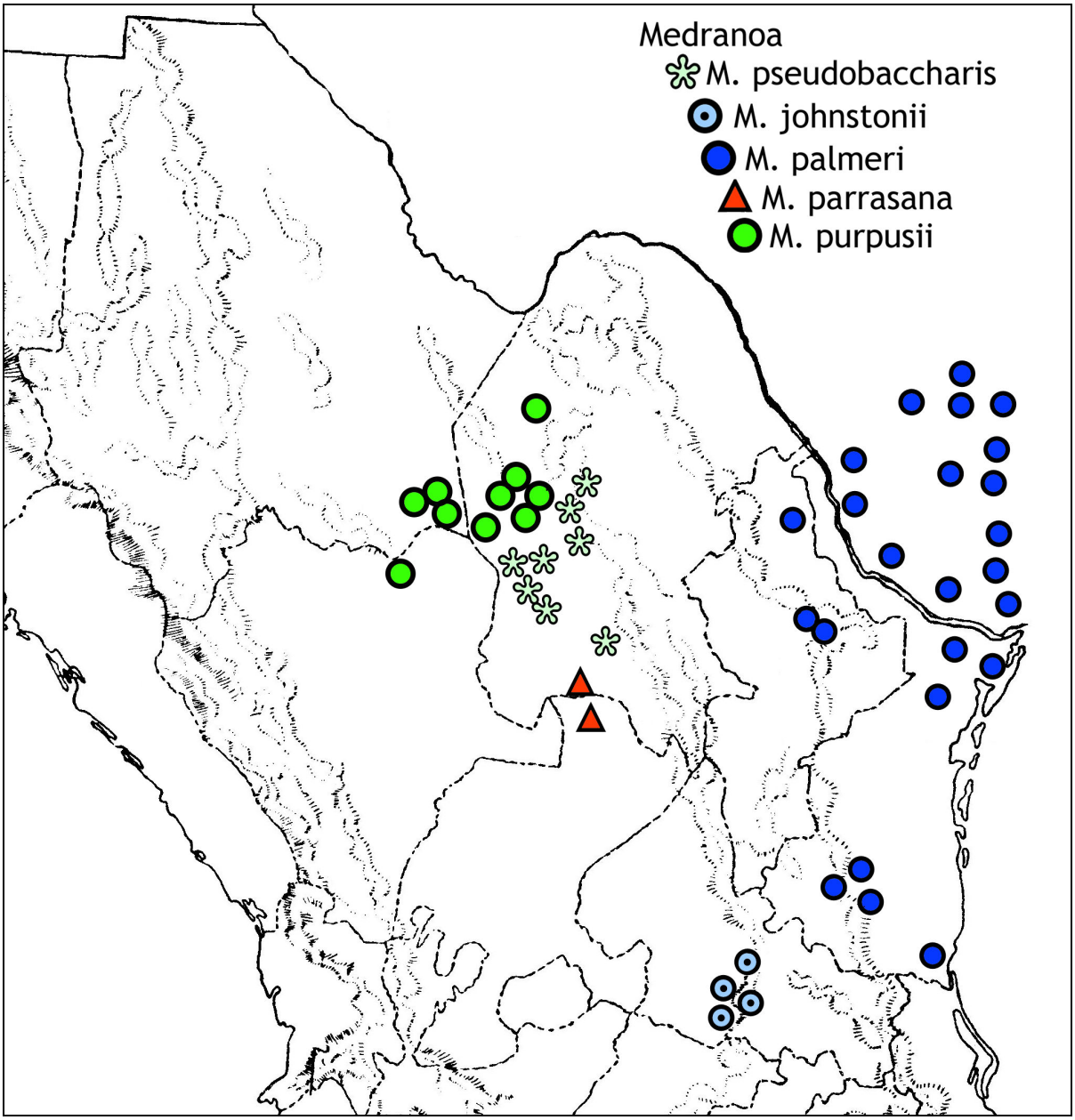

Figure 11. Distribution of the *Medranoa* species.

Reliance on the degree of morphological difference for assignment of rank (specific vs. infraspecific) is not suited to providing an accurate picture of the biological situation, especially without consideration of sympatry, hybridization, or intermediate forms. Species across many genera and families are known to be separated by a wide range of differences, quantitatively and qualitatively. Lane weighted "reproductive characters" (apparently alluding to the shapes of capitulescence, involucre, and phyllaries; see the 1st couplet in her key, p. 535) in deciding that only two species could be recognized. Varieties were distinguished by differences in "vegetative characters." Her observation that vegetative differences (presumably she meant as adaptive responses) among varieties reflect variation in soil type and elevation is without substantiation, and in any case, the point of the observation is not clear, as many evolutionary changes are adaptive.

I have not studied the full range of collections available to Lane, but there appears to be justification for the treatment of *Gundlachia* as a genus of 7 species (Figs. 6–9) — the widespread *G. corymbosa* and 6 others of narrower distribution — following botanical assessments prior to Lane's (e.g., Alain 1962) and as still followed (e.g., Acevedo-Rodríguez & Strong 2007). There perhaps are more than 7 species, as Urbatsch et al. (2003, p. 645) noted that "Branch lengths for the two populations of *G. corymbosa* var. *corymbosa* from different islands [Hispaniola vs. Puerto Rico, fide supplementary data] ... are as great as or greater than ones often observed for distinct species and indicate significant genetic differentiation and possibly cryptic species."

ACKNOWLEDGEMENTS

I'm grateful for the opportunities to study at TEX-LL and BRIT-SMU-VDB and the hospitality of the staffs there.

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