

NEW COMBINATIONS IN THE GENUS *GUNDLACHIA* AND FOUR NEW GENERA OF ASTEREAEE (ASTERACEAE) FROM NORTHERN MEXICO AND THE SOUTHERN UNITED STATES

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ABSTRACT

New combinations and new genera for species in *Xylothamia* are provided, reflective of recent phylogenetic data indicating the polyphyletic nature of that genus and the need to revise its taxonomy. Four species of *Xylothamia* are subsumed under the genus *Gundlachia*, necessitating the following new combinations: *G. diffusa*, *G. riskindii*, *G. triantha* (the type for *Xylothamia*), and *G. truncata*. Four new genera are recognized for lineages without available generic names. *Neonesomia* includes *N. johnstonii* and *N. palmeri*. Each of the other three genera are monotypic, *Chihuahuana*, *Medranoa*, and *Xylovirgata*, and they accommodate *C. purpusii*, *M. parrasana*, and *X. pseudobaccharis*, respectively.

KEY WORDS: Asteraceae, Astereae, *Xylothamia*, *Chihuahuana*, *Gundlachia*, *Medranoa*, *Neonesomia*, and *Xylovirgata*, Chihuahuan Desert, Sonoran Desert, Caribbean plants

RESUMEN

Las nuevas combinaciones y los nuevos géneros que se ofrecen para las especies en *Xylothamia* son el reflejo de los datos filogenéticos recientes que indican la naturaleza polifilética de ese género y de la necesidad de revisar su taxonomía. Cuatro especies de *Xylothamia* se incluyen en el género *Gundlachia* que hace necesarias las nuevas combinaciones siguientes: *G. diffusa*, *G. riskindii*, *G. triantha*, (la tipo para *Xylothamia*), y *G. truncata*. Se reconocen cuatro nuevos géneros para los linajes sin nombres genéricos disponibles. *Neonesomia* incluye *N. johnstonii* y *N. palmeri*. Cada uno de los otros tres géneros es monotípico, *Chihuahuana*, *Medranoa*, y *Xylovirgata*, e incluyen a *C. purpusii*, *M. parrasana*, y *X. pseudobaccharis*, respectivamente.

INTRODUCTION

Xylothamia, a genus of nine shrubby species from northern Mexico, Baja California, and southern Texas, was proposed by Nesom et al. (1990) to accommodate certain species of *Haplopappus* (sensu Hall 1928) and certain *Ericameria* (sensu Urbatsch 1978), plus similar and more recently described taxa. Studies designed to evaluate relationships among North American Astereae using parsimony analysis of external (ETS) and internal transcribed (ITS) DNA sequence data has shown *Xylothamia* to be polyphyletic (Urbatsch et al. 2003). Four of the nine species in *Xylothamia* and *Gundlachia* formed a robustly supported clade in this sequence-based study. The other five species were, in general, unresolved in a clade that also contained species in the genera *Amphiachyris*, *Bigelowia*, *Euthamia*, *Gutierrezia*, *Gymnosperma*, and *Thurovia* (Urbatsch et al.

2003). Figure 1 summarizes the phylogenetic relationships among taxa treated in the present study and those related. The tree is derived from figure 4 published in Urbatsch et al. (2003) where additional, explanatory information may be found. The purpose of this paper is to provide names for species of *Xylothamia* reflective of their phylogenetic placement in this sequence based study with consideration for their morphological and cytological variation as well.

Gundlachia, according to Lane (1996), who last considered its taxonomy, is restricted to the Caribbean region and consists of two species, *G. domingensis* and *G. corymbosa*. The former is known from the Bahamas, Cuba, and the Dominican Republic, while the latter consists of six varieties, and ranges from coastal Venezuela northward through the Greater and Lesser Antilles to the Bahamas and Cuba (Lane 1996). Although *Gundlachia* had not been included in their cpDNA-based study, Lane et al. (1996) and Nesom (1991, 1993) were in general agreement on its placement within the *Gutierrezia* lineage sensu Nesom (1993). *Gundlachia* is expanded herein to accommodate *X. diffusa*, *X. riskindii*, *X. triantha*, and *X. truncata*. *Gundlachia* now encompasses six species. Its geographic range is expanded from the Caribbean and northern South America to include parts of mainland Mexico, the Baja California peninsula, and southwestern Texas. Formal nomenclatural combinations for these *Xylothamia* are made in keeping with the botanical code (Greuter et al. 2000). Generic synonymy for *Gundlachia* as treated herein is also updated because it encompasses *X. triantha*, the type for *Xylothamia*.

With regard to the other five species of *Xylothamia*, *X. johnstonii*, and *X. palmeri* constitute a robustly supported clade (Urbatsch et al. 2003) that is herein proposed as the new genus *Neonesomia*. The three remaining species of *Xylothamia* are each treated as monotypic genera because they are not unambiguously supported as monophyletic or placed within existing genera based on DNA sequence data (Urbatsch et al. 2003), and they are each morphologically unique. *Chihuahuaana*, *Medranoa*, and *Xylovirgata* are the generic names proposed for each of the three taxa.

Gundlachia as reconstituted in this study and its sister clade containing the five former species of *Xylothamia* plus *Amphiachyris*, *Bigelowia*, *Euthamia*, *Gutierrezia*, *Gymnosperma*, and *Thurovia* are supported as a monophyletic lineage based on ITS/ETS sequences (Urbatsch et al. 2003) and approximates what Nesom (1991) called the *Gutierrezia* group. Nesom (1991) credited the cpDNA enzyme restriction studies of Suh (1989) and Suh and Simpson (1990) for initially helping to define this group as monophyletic. Although *Gundlachia* had not been part of the aforementioned DNA investigations, Nesom (1991) aligned it with this group because of its sharing several anatomical and morphological features discussed in part by Anderson and Creech (1975). *Chrysoma* and *Sericocarpus* were subsequently aligned with the former ten genera of the *Gutierrezia* lineage (Nesom 1993) which Nesom subdivided into two groups. *Amphiachyris*, *Gutierrezia*,

Gymnosperma, and *Thurovia* were assigned to the redefined *Gutierrezia* group. Features shared by most taxa in this group are reduced pappus, short disc corolla lobes, annual life cycle in certain species, and base chromosome numbers of $x = 4, 5$ (Nesom 1993). The remaining six genera were designated the *Euthamia* group (Nesom 1993) that are typically perennial herbs or shrubs with pappus of capillary bristles and a base chromosome number of $x = 9$.

Chrysoma and *Sericocarpus* in the ETS + ITS sequence based phylogenies were placed more closely to *Solidago* and allies (Urbatsch et al. 2003) and not part of the *Gutierrezia* lineage sensu Nesom (1993). Results by Noyes and Rieseberg (1999) for *Sericocarpus* were similar while *Chrysoma* was not included in their study. Lane et al. (1996), based on cpDNA restriction site data, provided support for a clade containing six of the ten genera of the *Gutierrezia* lineage. *Chrysoma*, *Gundlachia*, and *Sericocarpus* were not investigated and *Xylothamia* constituted part of their *Ericameria* lineage (Lane et al. 1996). Branch support and decay index scores for *Xylothamia*'s inclusion in the *Ericameria* lineage ranged from one to zero (Lane et al. 1996).

Sequence support for the *Gutierrezia* group within the *Gutierrezia* lineage (sensu Nesom 1993) is equivocal based investigations of Urbatsch et al. (2003), depending on optimality criteria and databases analyzed. *Amphiachyris*, *Gutierrezia*, and *Gymnosperma* constitute a robustly supported lineage in the Bayesian ITS + ETS tree. However, *Thurovia* appears as an unstable member of the *Gutierrezia* group sensu Nesom (1993). Only when this data set is analyzed with PAUP* ratchet are *Thurovia* and *Amphiachyris* sisters (Urbatsch et al. 2003). Otherwise *Thurovia* was not affiliated with the *Gutierrezia* group. It was sister to *Bigelowia* in PAUP* ratchet of the combined ITS + ETS + indels and to *Neonesomia* in the Bayesian tree resulting from the combined ITS + ETS. Sequence data offered no support for the *Euthamia* group of the *Gutierrezia* lineage sensu Nesom (1993).

Characters that support and diagnose the *Gutierrezia* lineage as delineated in Urbatsch et al. (2003) i.e., without *Chrysoma* and *Sericocarpus*, include leaves showing xerophytic adaptations such as often being filiform or otherwise reduced in size, somewhat coriaceous in some taxa, usually punctate and resin coated, and often supporting a variety and abundance of trichomes; capitula generally small, borne in sessile clusters or on short peduncles; phyllaries basally indurate with a thickened apical patch; stamen insertion below the apex of disk corolla tube; cypselae small, cylindrical to turbinate, and often sericeous.

NOMENCLATURAL TREATMENT

1. **Chihuahuana** Urbatsch & R.P. Roberts, gen. nov. TYPE: *Ericameria purpusii* Brandege, Univ. Calif. Publ. Bot. 4:191. 1911. = *Chihuahuana purpusii* (Brandegee) Urbatsch & R.P. Roberts, combination made herein].

Fruticulus ramosus, folia lineari-lanceolata ca. 2 mm longa acuminata in axillis filiorum 3–10 mm

longorum linearium acuminatorum decurrentium demum cinereorum spinescentium fasciculatis; capitula ramos terminantibus 6–7 mm alta fere sessilia discoidea; corollae 8–10, luteola in lobos ovato-lanceolata inaequaliter sectis.

Densely branching shrubs to 30 cm tall; stems mostly concealed by the persistent closely spaced leaves with small axillary clusters; leaves sessile, acicular, narrowly triangular with a thickened midrib composed mainly of a large bundle of fibers, erect, 3–10 mm long, ca. 1 mm broad at base, hirtellous due to a dense covering of uniseriate conic trichomes, bases somewhat decurrent, apices sharply acute; capitula discoid, solitary, campanulate, 4–5 mm wide; phyllaries graduated, the inner 5–6 mm long; eradiate; disk flowers 8–10, corollas hairy 4.2–5.0 mm long; cypselae densely sericeous; $x = 9$.

Prominent features, distribution, and relationships.—*Chihuahuana*'s needle-like, non-resinous, hirtellous leaves with a large midvein consisting of a bundle of fibers is unique in the *Gutierrezia* clade where its relationships are not fully resolved (Urbatsch 1975; Urbatsch et al. 2003).

Etymology.—The generic name was selected because it is a member of the Chihuahuan Desert flora.

1a. *Chihuahuana purpusii* (Brandege) Urbatsch & R.P. Roberts, comb. nov.
 BASIONYM: *Ericameria purpusii* Brandege, Univ. Calif. Publ. Bot. 4:191. 1911.
Haplopappus [*Aplopappus*] *purpusii* (Brandege) S.F. Blake. Contr. U.S. Natl. Herb. 23:1491. 1926. *Xylothamia purpusii* (Brandege) G.L. Nesom, Sida 14:112 1990. TYPE: MEXICO. COAHUILA: Cerro de Macho, Jun 1910, *Purpus* 4479 (HOLOTYPE: UCI).

Distribution, ecology, and relationship.—Chihuahuan Desert region in southwestern Coahuila and adjacent locales in Chihuahua and Durango, rocky hills in gypseous or limestone soils (Nesom et al. 1990). Detailed descriptive information and distributional data for this species (as *X. purpusii*) are provided in Nesom et al. (1990).

Chihuahuana purpusii was originally described in *Ericameria* then transferred to *Haplopappus* by Blake (1926). Hall (1928) placed the species in *Haplopappus* section *Asiris* with five other species mostly of Great Basin distribution. This species was then reinstated in *Ericameria* (Urbatsch 1978) and subsequently placed in the newly created genus *Xylothamia* (Nesom et al. 1990). Foliar anatomy, morphology, and flavonoid profiles for *C. purpusii* are unique (Urbatsch 1978; Urbatsch et al. 2003). ETS/ITS sequence-based phylogenies indicate the affinities of *C. purpusii* are with the *Gutierrezia* clade rather than with species in section *Asiris* (Urbatsch et al. 2003).

2. *Gundlachia* A. Gray, Proc. Amer. Acad. Arts 16:100. 1880. TYPE: *Solidago domingensis* Spreng., Syst. Veg. 3:539. 1826].

Xylothamia G.L. Nesom, Y.B. Suh, D.R. Morgan & B.B. Simpson, Sida 14:106. 1990. TYPE: *Aplopappus trianthus* S.F. Blake, J. Wash. Acad. Sci. 28:485. 1938. *Gundlachia triantha* (S.F. Blake) Urbatsch & R.P. Roberts.

Evergreen shrubs to 2.0 m tall, stems unbranched to abundantly branching, angular to minutely ridged; leaves usually evenly spaced along the stems, spreading to occasionally appressed, sessile to short petiolate, narrowly to broadly linear to obovate, flat to involute-terete, punctate, resinous; capitula usually clustered at branch tip, clusters few and sometimes hidden by the subtending leaves or numerous and organized into racemes or paniculate to corymbiform capitulescences; involucre cylindric, turbinate, or narrowly obconic, phyllaries 2-5 seriate, linear-lanceolate to ovate with an apical resin pocket, basally chartaceous, indurate, margins translucent; ray flowers 0-13, corollas 1-6.5 mm long, white to yellow; disk flowers 3-50, corollas 4.0-5.5 mm long, white to yellow, lobes 1.0-2.5 mm long, slightly irregular, usually laxly recurved, style branches 1.0-2.2 mm long, linear lanceolate to ovate, ratio of appendage/stigmatic length variable with different species; cypselae turbinate to cylindrical, 1.0-2.5 mm long sparsely to densely pilose to sericeous; pappus of ca. 40, slender, flattened, barbellate bristles, 3.5-5.0 mm long; $x = 9$

Prominent features, distribution, and relationships.—*Gundlachia* as treated in this study consists of six species known from the Caribbean, northern South America, northern Mexico, Baja California, and southwestern Texas. Its monophyly was robustly supported by DNA sequence data as a lineage sister to one consisting of several other taxa primarily from western North America. All taxa in this genus are shrubs usually with resinous, punctate leaves that are linear lanceolate to spatulate in three species, *G. corymbosa*, *G. domingensis*, and *G. riskindii* and filiform in the other three. Capitulescences are often large, corymbose to paniculate in *G. corymbosa*, *G. domingensis*, and *G. diffusa*; they are more reduced and cymose in *X. triantha*. *Gundlachia riskindii* has solitary capitula whereas *G. truncata* has two or three capitula clustered at their twig apices. Phyllaries in *Gundlachia* are resinous to glutinous and basally indurate.

All species are xerophytes. *Gundlachia corymbosa* and *G. domingensis* inhabit mainly sandy or stony soils in or near coastal habitats of various Caribbean islands, while *G. diffusa* occupies similar habitats of the Gulf of California region of Sonora and Baja California. *Gundlachia riskindii* appears to be restricted to exposed limestone areas in pine-oak woodland at around 2100 m in Coahuila and adjacent Nuevo León, Mexico. The other two species occur in the Chihuahuan Desert region associated with elements more typical of that flora such as *Atriplex*, *Larrea*, *Prosopis*, *Suaeda*, etc. Specific descriptions, distributional data, and supporting documentation for the species of *Xylothamia* here considered as *Gundlachia* are provided in Nesom et al. (1990). Similar data for *Gundlachia truncata* as a species of *Xylothamia* can be found Nesom (1992). Lane (1996) provided detailed species descriptions, distributional data, other pertinent information, and keys to varieties of *G. corymbosa*.

There is no indication whether the *Gundlachia* clade first evolved in the Caribbean, in Mexico, or elsewhere since species relationships within it are not

well-resolved (Urbatsch et al. 2003). The clade sister to *Gundlachia* consists of North American taxa. These two clades taken together also appear to be related to North American species, although few Central and South American species have been investigated (Urbatsch et al. 2003). Regardless of where the *Gundlachia* clade first appeared, dispersal rather than plate tectonics must have been a factor in its evolution since the approximate present position of the Caribbean islands relative to North and South America predates the estimated age of the Asteraceae (Graham et al. 2000; Bohm & Stuessy 2001).

KEY TO SPECIES OF GUNDLACHIA

1. Leaves linear-lanceolate to spatulate, laminar, more than 2 mm wide.
 2. Capitula typically solitary at branch tips; plants of Coahuila and Nuevo León, Mexico _____ **G. riskindii**
 2. Capitula generally in large, dense, corymbose or paniculate clusters several cm broad; plants of the Caribbean.
 3. Capitula in corymbose clusters; involucre cylindric; ray corollas <4 mm long; Bahamas, Greater and Lesser Antilles _____ **G. corymbosa**
 3. Capitula in paniculate clusters; involucre obconic or turbinate; ray corollas >4 mm long; plants of northern Bahamas, Cuba, and Hispaniola _____ **G. domingensis**
1. Leaves filiform, less than 2 mm wide, nearly as thick as broad
 4. Leaves densely clustered along the terminal 2–3 cm of the branches, surfaces glutinous, not evidently punctate; capitula eradiate, in clusters of 2–3, mostly concealed by foliage; disk flowers 3–5; Coahuila, Mexico, Cuatro Ciénegas basin _____ **G. truncata**
 4. Leaves more widely spaced on stems, internodes generally much >2 mm long, surfaces resinous, somewhat punctate; capitula eradiate or rays 1–3, rays mostly concealed by the involucre; disk flowers 3–7.
 5. Stems glabrous; ray flowers 0–3; coastal habitats of the Gulf of California region, Baja California and Sonora, Mexico _____ **G. diffusa**
 5. Stems papillate, scabrous; rays absent; disk flowers 3(–7); widespread in the Chihuahuan Desert of southwestern Texas, Chihuahua, Coahuila, Durango, and Nuevo León, Mexico _____ **G. triantha**

New specific combinations in *Gundlachia*

- 2a. *Gundlachia triantha*** (S.F. Blake) Urbatsch & R.P. Roberts, comb. nov. BASIONYM: *Aplopappus*[*Haplopappus*] *trianthus* S.F. Blake, J. Wash. Acad. Sci. 28:485. 1938. *Ericameria triantha* (S.F. Blake) Shinnars, Field & Lab. 19:133. 1951. *Xylothamia triantha* (S.F. Blake) G.L. Nesom, Sida 14:113. 1990. TYPE: UNITED STATES. TEXAS. BREWSTER CO.: Chisos Mountains area, along road from Study Butte to Terlingua, 31 Aug 1937, B.H. Warnock 1126, (HOLOTYPE: US!; ISOTYPE: LL!).

Distribution, ecology, and relationships.—This species is widespread in the Chihuahuan Desert region ranging from Brewster County, Texas, to eastern Chihuahua, Coahuila, northeastern Durango, and west central Nuevo León, Mexico. It grows on gyp-seous, calcareous, igneous, or saline soil substrates on slopes or desert flats generally associated with *Atriplex*, *Prosopis*, *Larrea*, *Suaeda*, and various desert species at elevations 700–1500 m. Flowering normally occurs from July to October

which undoubtedly depends on the timing and abundance of rainfall. Its resinous, ad-axially caniculate, filiform leaves, and often three-flowered capitula are diagnostic.

Based on sequence data *G. triantha* and *G. truncata* are strongly supported as sisters (Urbatsch et al. 2003) (see Fig. 1). Nesom (1992) indicated that the two are similar in having linear, involute leaves, eradiate, few-flowered capitula, and similar style appendages. *Gundlachia diffusa* receives moderate support as the sister to this clade in most analyses except for parsimony analysis of the ETS + ITS data sets where it is sister to *G. domingensis* (Urbatsch et al. 2003). When describing *G. triantha* Blake, (1938) discussed its morphological similarity to *G. diffusa*. Urbatsch (1978) noted the similarity in flavonoid profiles between these two taxa. At the time these studies were made *G. truncata* was unknown. Nesom et al. (1990) commented on the *Euthamia*-like inflorescences of *G. triantha* and *G. diffusa*. Sequence data show that *Euthamia* is but distantly related to these taxa, indicating possible convergence in this feature (Fig. 1).

2b. *Gundlachia diffusa* (Benth.) Urbatsch & R.P. Roberts, comb. nov. BASIONYM: *Ericameria diffusa* Benth., Bot. Voyage H.M.S. Sulphur 2:23. 1844. non *Aplopappus diffusus* DC. 1836. *Solidago diffusa* (Benth.) A. Gray, Proc. Amer. Acad. Arts 5:159. 1861. *Bigelovia diffusa* (Benth.) A. Gray, Proc. Amer. Acad. Arts 8:640. 1873. *Chrysoma diffusa* (Benth.) E. Greene, Erythea 3:10. 1895. *Xylothamia diffusa* (Benth.) G.L. Nesom, Sida 14:109. 1990. TYPE: MEXICO. BAJA CALIFORNIA SUR: Magdalena Bay, 1839, R. Barclay & B. Hinds s.n. (HOLOTYPE: BM?).

Linosyris sonoriensis A. Gray, Proc. Amer. Acad. Arts 8:291. 1870. Basionym: *Haplopappus* [*Aplopappus*] *sonoriensis* (A. Gray) S.F. Blake, Contr. U.S. Natl. Herb. 23:1490. 1926. *Aster sonoriensis* (A. Gray) Kuntze, Rev. 1:317. 1891. TYPE: MEXICO. SONORA: District of the Yaqui River, 1869, E. Palmer s.n. (HOLOTYPE: GH!).

Distribution, ecology, and relationships.—*Gundlachia diffusa* occurs in Baja California Sur and coastal regions of Sonora, Mexico, where it inhabits various soil types including coastal sand dunes, gravel plains, and salt flats from near sea level to around 100 m. Its habitat preferences appear to be similar to the two species of *Gundlachia* from the Caribbean. Based on leaf morphology the species resembles the two Chihuahuan Desert species in this genus. When well-developed, its inflorescences can be large and paniculate and appear similar to those in *G. corymbosa*. Its species relationships are somewhat equivocal but appear to be closest to *G. triantha* and *G. truncata* and are discussed under to the former.

2c. *Gundlachia riskindii* (B.L. Turner & Langford) Urbatsch & R.P. Roberts, comb. nov. BASIONYM: *Ericameria riskindii* B.L. Turner and Langford, Madroño 29:234. 1982. *Xylothamia riskindii* (B.L. Turner and Langford) G.L. Nesom, Sida 14:113. 1990. TYPE: MEXICO. COAHUILA: ca. 24 km E of Saltillo, S side of Sierra La Viga, ca. 6.5 km E of Jamé along wood cutter's road, 10,00 ft, 15 May 1977, Henrickson et al 16156b (HOLOTYPE: TEX!; ISOTYPE: MEXU, RSA).

Distribution, ecology, and relationships.—This apparently rare species is known from southeastern Coahuila and adjacent Nuevo León where it occurs on ex-

posed limestone areas and in gypseous soils in pine-fir-oak woodlands at 2100–3000 m elevation. It is distinctive in having small spatulate leaves and radiate capitula with a large number of disk and ray florets. Originally, *G. riskindii* was described as *Ericameria* but then transferred to *Xylothamia*. Concerning its sister taxon relationships, results differ depending on optimality criteria used in DNA sequence analysis. In the PAUP ratchet analysis of the combined ITS/ETS sequences support is provided for its basal position in the *Gundlachia* clade. In the parsimony derived trees that included indels, the Caribbean and Mexican species are resolved as sister lineages, where it is basal to the latter (Urbatsch et al. 2003). When indels were excluded, the species is basal in the *Gundlachia* clade (Fig. 1). Flagelliform trichomes having a subterminal appendage attachment characterize the Caribbean species and similar trichomes are seen in *G. riskindii*. This unusual trichome type, along with spatulate leaves and certain DNA evidence suggest that *G. riskindii* may represent the ancestral state for *Gundlachia* or may be a link connecting the Caribbean and the Mexican species.

2d. *Gundlachia truncata* (G.L. Nesom) Urbatsch & R.P. Roberts, comb. nov.
 BASIONYM: *Xylothamia truncata* G.L. Nesom, *Phytologia* 73:318. 1992. TYPE: MEXICO. COAHUILA: Mpio. Cuatro Ciénegas, ca. 2 km W of town of Cuatro Ciénegas, along dirt road paralleling railroad, hard packed gypseous sand, 18 Oct 1985, Nesom 5254 (HOLOTYPE: TEX!).

This rare species is known only from the Cuatro Ciénegas basin in Coahuila, Mexico, where it was collected on alluvial, gypseous sands. It is readily recognized by its involute linear leaves crowded near the branch apices that largely conceal its flowering capitula (Nesom 1992). The nearly identical ITS/ETS sequences of *G. truncata* and *G. triantha* robustly support their sister relationship despite their distinctive morphologies. Nesom (1992) had suggested the possibility of *G. truncata* being an abnormal growth form of the latter, but field observations offered no evidence supporting this hypothesis.

Distribution, ecology, and relationships.—Both *Gundlachia corymbosa* and *G. domingensis* grow in the Caribbean region. The former occurs in eastern Cuba, the Bahamas, the Greater and Lesser Antilles, and northern Venezuela. It is distinguished from its counterpart by its corymbose capitulescences, cylindric involucre, ovate phyllaries, and ray corollas shorter than 4 mm. Six varieties are recognized within the species. Three of these, *G. corymbosa* varieties *apiculata*, *cubana*, and *foliosa*, have corymbs reduced to a few capitula concealed by the leaves, which is a feature seen in two species in Mexico, *G. riskindii* and *G. truncata*. The leaves of *G. corymbosa* var. *apiculata*, a taxon from the mountains of eastern Cuba, are similar in form to those of *G. riskindii* but larger. *Gundlachia domingensis* is known from the northern Bahamas, Cuba, and Hispaniola and is distinguished by its paniculate capitulescences, turbinate involucre, linear-lanceolate phyllaries, and ray corollas about 5.0 mm long. Both species appear to grow on well-drained sandy and stony substrates from near

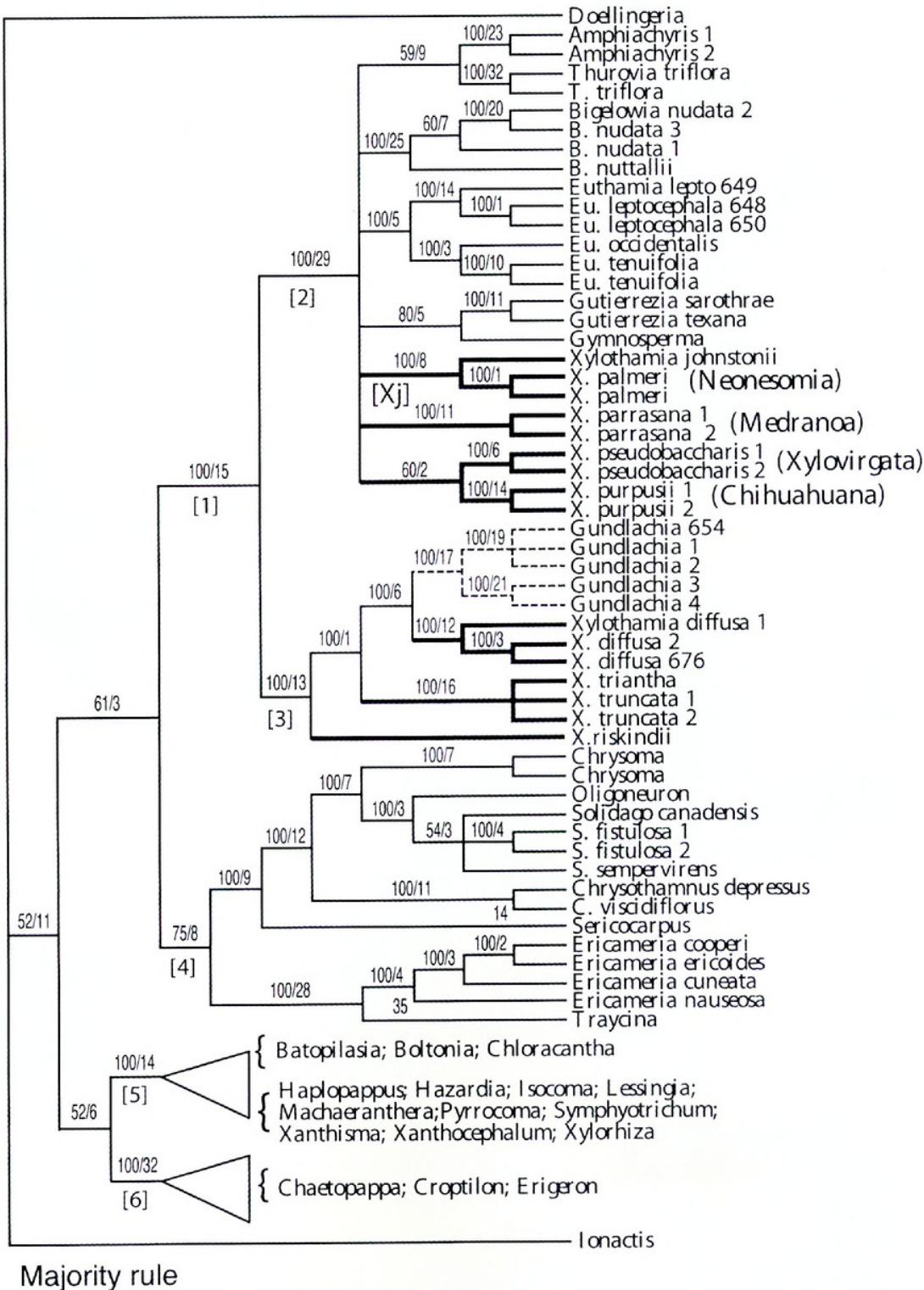


FIG. 1. 50% majority rule consensus tree derived from PAUP* ratchet analysis of the combined ETS + ITS data sets with-out indels and based on Fig. 4 published in Urbatsch et al. (2003). Fractional numbers designate branch support/branch length. Branches in bold highlight taxa traditionally treated as *Xylothamia*. Dash line branches highlight taxa tradi-tionally treated as *Gundlachia*. Generic names proposed in the present study are indicated parenthetically. Taxa of the lower most clades not immediately relevant to the present study are merely listed for each major lineage.

sea level to 2500 m elevation. Greater details for these two species are provided in Lane (1996).

3. *Neonesomia* Urbatsch & R.P. Roberts, gen. nov. TYPE: *Aster palmeri* A. Gray, Proc. Amer. Acad. Arts 17:209. 1882. = *Neonesomia palmeri* (A. Gray) Urbatsch & R.P. Roberts.

Frutices ad 3 m alta; caules ramosissimi aliquantum aromatici, ramunculis foliosis valde porcatis; folia 1–4 cm longa 1–2(–5) mm lata linearia elliptica ad anguste oblanceolata, laminis complanatis cum costis elevatis abaxialibus; capitula radiata solitaria vel in cymis fasciculatis ad apices ramulorum, paniculis laxis; involucria plerumque turbinata 4–6 mm longa; phyllaria valde gradata linearia; flosculi radii 5–15, corollae ca. 2–5 mm longa alba ad flava; flosculi disci 8–20, corollae 3.5–5 mm longa alba ad flava, limba aliquantum asymmetrica 5-lobata; pappi setosi; cypselae ca. 1.5 mm longae dense strigosae ad sericeas.

Shrubs to 3 m tall; much-branched, somewhat aromatic, leafy twigs strongly ridged, internodes 2–10 mm long; leaves 1–4 cm long, 1–2(–5) mm broad, linear, elliptic to narrowly oblanceolate, blades flat with conspicuously raised midvein abaxially, pubescent with flagelliform trichomes, margins entire to minutely ciliate; capitula solitary or in cymose clusters at branch tips these arranged in loose panicles; involucries usually turbinate, 4–6 mm long; phyllaries strongly graduated, linear, blunt to somewhat acute, thick, firm, resinous, mostly stramineous but with an apical glandular patch occupying much of the tip region; rays flowers 5–15 corollas ca. 2–5 mm long, white, pale yellow, or yellow; disk flowers 8–20, corollas 3.5–5 mm long, with a tube 1–1.8 mm long and poorly differentiated from the asymmetrical 5-lobed limb, shorter lobes 0.9–1.5 mm long, longest up to 3.3 mm long; pappus of setose bristles; cypselae ca. 1.5 mm long, densely strigose to sericeous; $x = 9$.

Prominent features, distribution, and relationships.—*Neonesomia* contains two species, *N. palmeri* from Nuevo León, Tamaulipas, and southern Texas and *N. johnstonii* from San Luis Potosí, which grow on rocky hillsides, brushy shrublands, and coastal dunes (Johnston 1970; Nesom et al. 1990). Species in this genus are characterized by their shrubby habit, ridged twigs, flat leaf blades with prominent midveins, small radiate capitula, and white to yellow corollas with somewhat zygomorphic disc corollas. They resemble the herbaceous perennials in *Euthamia* in leaf and growth form, but differ in being non-rhizomatous shrubs with deeply lobed, somewhat zygomorphic disc corollas.

Etymology.—*Neonesomia* commemorates Guy Nesom, Botanical Research Institute of Texas, zealous student of the Astereae and other Asteraceae who has significantly contributed to understanding their systematics. Additional information for these taxa is found in Nesom's treatment of *Xylothamia* (Nesom et al. 1990).

The genus *Neonesomia* is strongly supported as a clade in the gene-based phylogenies of Urbatsch et al. (2003). Based on parsimony analyses of ITS + ETS + INDEL data it is basal to a clade consisting of several xerophytic, mainly western North American taxa, including *Amphiachyris*, *Bigelowia*, *Chihuahuana*,

Euthamia, *Gutierrezia*, *Gymnosperma*, *Medranoa*, *Thurvoia*, and *Xylovirgata* (Urbatsch et al. 2003). Weak support for its sister relationship to *Thurvoia* was seen in the ITS/ETS Bayesian tree derived in that study. Otherwise its sister relationship was unresolved (Fig. 1) and kinship among the above cited genera is uncertain (Urbatsch et al. 2003).

KEY TO SPECIES OF NEONESOMIA

1. Ray and disk flowers 12–15 and 15–20, respectively; corollas yellow; flowering May to June; San Luis Potosí, Mexico _____ **N. johnstonii**
1. Ray and disk flowers 5–11 and 9–14, respectively; corollas white to very pale yellow; mainly flowering August to October; southern Texas and Nuevo León and Tamaulipas _____ **N. palmeri**

New combinations in *Neosomia*

- 3a. *Neonesomia palmeri*** (A. Gray) Urbatsch & R.P. Roberts, comb. nov. BASIONYM: *Aster palmeri* A. Gray, Proc. Amer. Acad. Arts 17:209. 1882. TYPE: UNITED STATES. TEXAS. MAVERICK CO.: Eagle Pass on the Rio Grande, Sep–Oct, 1879. *E. Palmer* 516 (LECTOTYPE: GH!; ISOLECTOTYPES: PH, US; Johnston 1967). *Isocoma palmeri* (A. Gray) Shinnery, Field & Lab. 18:2. 1950. *Ericameria austrotexana* M.C. Johnston, nom. nov., SouthW. Naturalist 12:106. 1967, non *E. palmeri* (A. Gray) H.M. Hall. *Xylothamia palmeri* (A. Gray) G.L. Nesom, Sida 14:110. 1990, non *X. palmeri* var. *pachylepis* (H.M. Hall) G.L. Nesom ex M.A. Lane & R.L. Hartman, Amer. J. Bot. 83:364. 1996

Distribution, ecology, and relationships.—This species is known from most counties in southern Texas, i.e., Atascosa, LaSalle, and San Patricio cos. southward into the states of Nuevo León and Tamaulipas, Mexico, mostly of open, brushy habitats on or near the Gulf Coast in sandy or saline soils from near sea level to 600 m. *Neonesomia palmeri* is distinguished from its sister species in having fewer flowers per capitula and paler yellow corollas. Its ITS/ETS sequences showed little differentiation from *N. johnstonii* in Urbatsch et al. (2003). *Neonesomia palmeri* was first described as a species of *Aster* and subsequently placed in various other genera including *Isocoma* (Shinnery 1950), *Ericameria* (Johnston 1967), and *Xylothamia* (Nesom et al. 1990). Nesom et al. (1990) proposed a close relationship of *N. palmeri* to *Medranoa* (*Xylothamia*) *parrasana* and *Xylovirgata* (*Xylothamia*) *pseudobaccharis*, a hypothesis not robustly supported by analyses of DNA sequences.

- 3b. *Neonesomia johnstonii*** (G.L. Nesom) Urbatsch & R.P. Roberts, comb. nov. BASIONYM: *Xylothamia johnstonii* G.L. Nesom, Sida 14:110. 1990. TYPE: MEXICO. SAN LUIS POTOSÍ: Bagre, Minas de San Rafael, May 1911, C.A. Purpus 5021 (HOLOTYPE: GH!; ISOTYPE: US).

Distribution, ecology, and relationships.—This taxon is known from central San Luis Potosí, Mexico where it apparently grows on steep slopes at elevations of 120–1500 m. In addition to the diagnostic features presented under *N. palmeri*, flowering times also differ with *N. johnstonii* blooming in the spring and *N.*

palmeri in the fall. Habitat preferences for the two taxa differ: *N. johnstonii* grows on steep hillsides at higher elevations than *N. palmeri*, which inhabits the Gulf coastal plain often on sand dunes near the water. Based on sequence data *N. johnstonii* and *N. palmeri* form a robustly supported clade, but the two taxa differ little from one another in sequence data indicating their close affinity (Urbatsch et al. 2003).

4. *Medranoa* Urbatsch & Roberts, gen. nov. TYPE: *Ericameria parrasana* S.F. Blake, Contr. Gray Herb. 52:26. 1917. = *Medranoa parrasana* (S.F. Blake) Urbatsch & R.P. Roberts.

Frutex ramosus caule tenui cortice griseo glabro donato, ramulis uventate viridibus dense papilloso-glandulosis viscosis non puberulis dense foliosis; folia linearia mucronulata ut ramuli punctata et viscosa complanata supra suprana vel paullum concave sutus subconvexa; involucri 3-seriati paullulum gradati 3.5–4 mm alti praecipue supra glandulari-viscosa ceterum subglabra infra valde indurate coriacea albida apice appendice appressa subherbacea lanceolata munita.

Shrubs to 2 m tall, much branched; branches ascending, mostly terete or remotely ribbed, bark smooth, becoming slightly fissured, tan becoming dark gray; twigs numerous, to 8 cm long, internodes smooth to obscurely sulcate, 1–4 mm long, green resinous, scabridulous; leaves evergreen, sessile, crowded, 5–12 mm long \leq 1.5 mm wide, narrowly elliptic-oblongate, flat to canaliculate, decurrent on stem, surfaces resinous, punctate; capitulescence somewhat corymbiform, capitula solitary or cymose at branch tips; involucre 2–3 seriate, campanulate, 3–5 mm high, 4–7 mm wide; phyllaries imbricate, moderately graduated, mostly chartaceous, 2.5–4 mm long; capitula radiate, with ca 30 flowers, ray flowers 5–11, pappus bristles ca. 80, setose, subequal, 2.5–4 mm long, silvery tan, corollas 5–8 mm long, ligules elliptic, 3–7 mm long, 1–2 mm wide; disk flowers ca 20, corollas pale yellow, 4–5 mm long, lobes spreading to recurved, unequal in length, shortest 0.8–1.2 mm long, longest 1.5–2.2 mm long, style branches 2–3 mm long, appendages narrowly linear, apices acute, 1.5–1.8 mm long, pappus same as on ray flowers; cypselae turbinate, ca. 2 mm long, pilose; $x = 9$.

Prominent features, distribution, and relationships.—*Medranoa* is unispecific with its only species occurring in the Sierra de Parras region of Coahuila and Zacatecas. Shrubby habit, deeply pitted, resin coated leaves, relatively large capitula, and thickened style branches are features diagnostic for this taxon. Sequence based data robustly support its placement in the *Amphiachyris*/*Gutierrezia* clade (Urbatsch et al. 2003). Weak support is provided in that study for a sister relationship with *Chihuahuana* (*X. purpusii*) or with a clade composed of *Chihuahuana* plus *Xylovirgata* (*Xylothamia pseudobaccharis*).

Etymology.—The generic name *Medranoa* is in honor of Francisco Gonzalez Medrano, MEXU. He has worked for many years on desert and dryland floras of Mexico—mostly Tamaulipas and Tehuacan, and has trained several young botanists. Additional information about this taxon can be found in the treatment of *Xylothamia* by Nesom et al. (1990).

- 4a. *Medranoa parrasana*** (S.F. Blake) Urbatsch & R.P. Roberts, comb. nov.
 [BASIONYM: *Ericameria parrasana* S.F. Blake, Contr. Gray Herb. 52:26. 1917].
Haplopappus parrasanus (S.F. Blake) S.F. Blake, Contr. U.S. Natl. Herb. 23:1490. 1926.
Xylothamia parrasana (S.F. Blake) G.L. Nesom, Sida 14:111. 1990. TYPE: MEXICO.
 COAHUILA: Sierra de Parras, rocky slopes, Mar 1905, *Purpus* 1005 (HOLOTYPE: GH!).

Distribution, ecology, and relationships.—The single species in this genus grows on rocky slopes in the Sierra de Parras region of southern Coahuila and northern Zacatecas. Originally it was described in *Ericameria* by Blake (1917) who later transferred it to *Haplopappus* (Blake, 1926). Subsequently, it was placed in *Xylothamia* (Nesom et al. 1990). In the DNA sequence-based trees, it is placed in the clade composed of *Amphiachyris*, *Bigelowia*, *Chihuahuana*, *Euthamia*, *Gutierrezia*, *Gymnosperma*, *Neonesomia*, and *Thurovia* (Urbatsch et al. 2003). *Medranoa* is basal to a clade of *X. pseudobaccharis* and *Chihuahuana purpusii* in parsimony analyses of the ETS/ITS/INDEL data set place. It is a weakly supported sister of *Chihuahuana purpusii* in the Bayesian analysis (Urbatsch et al. 2003).

Medranoa parrasana is distinguishable from other taxa in the *Amphiachyris*/*Gutierrezia* clade by the combination of its shrubby habit, narrowly elliptic-oblongate, flat-canaliculate, resin-covered leaves with numerous, well-organized depressions, and its campanulate capitula bearing 5–11 ray and 15–22 disk flowers. The thickened style branches wherein the vascular trace bifurcates or expands in size distally in each branch is unique among taxa in this clade. Additional information about this taxon can be found in the treatment of *Xylothamia* by Nesom et al. (1990).

- 5. *Xylovirgata*** Urbatsch & R.P. Roberts, gen. nov. TYPE: *Haplopappus pseudobaccharis* S.F. Blake, J. Wash. Acad. Sci. 40:47. 1950. = *Xylovirgata pseudobaccharis* (S.F. Blake) Urbatsch & R.P. Roberts.

Frutex scoparium metralis glaberrimus modice resinosus, ramis et ramulis multis erectis pallide viridibus striato-angulatus; folia anguste linearia integerrima plano paulum incrassata omnino non vel solum supra obscurissime punctata usque ad 1.4 cm longa 1 mm lata.

Intricately branched, broomlike shrubs to 1 m tall; stems slender, bark becoming whitish with age; branches and twigs strongly ridged and angled; leaves present mainly on present years growth, widely spaced, somewhat erect, blades 2–15 mm long, ≤ 1 mm wide; capitula radiate solitary at branch apices arranged in loose racemes; involucre campanulate to turbinate, 3–4 mm wide, phyllaries graduated, the inner 3–5 mm long, thickened subapical glandular structure present; ray flowers 3–6, ligules apically 2–3 denticulate, 2.3–3.0 mm long, ca. 1 mm wide; disk flowers 7–14, corollas 4.0–4.5 mm long unequally 5 lobed, shorter lobes ca. 1.3 mm long, longer lobes ca. 2.3 mm long; cypselae ca. 1.3 mm long, sericeous; pappus similar on disk and ray cypselae, ca. 30 subequal setose bristles; $x = 9$.

Prominent features, distribution, and relationships.—*Xylovirgata* is unispecific and known only from western Coahuila, Mexico. It is recognized by its

broom-like appearance due to its woody, erect, intricately branched habit, as referenced by its generic name, and its conspicuously ridged stems, reduced, widely spaced, inconspicuous leaves. This entity is clearly related to taxa in the *Amphiachyris*/*Gutierrezia* clade, where there is weak support for its sister relationship to *Chihuahuana* in trees resulting from parsimony analysis of ETS/ITS sequence data (Urbatsch et al. 2003). When indel data were added to the data set support for this relationship is supported more robustly. Bayesian and bootstrap analyses resulted in its placement as one of several unresolved basal elements in the *Amphiachyris*/*Gutierrezia* clade (Urbatsch et al. 2003). Additional descriptive data for this taxon can be found in Nesom et al. (1990).

5a. *Xylovirgata pseudobaccharis* (S.F. Blake) Urbatsch & R.P. Roberts, comb. nov.

BASIONYM: *Haplopappus pseudobaccharis* S.F. Blake. J. Wash. Acad. Sci. 40:47. 1950. *Ericameria pseudobaccharis* (S.F. Blake) Urbatsch, Sida 7:299. 1978. *Xylothamia pseudobaccharis* (S.F. Blake) G.L. Nesom, Sida 14:112. 1990. TYPE: MEXICO. COAHUILA: arid limestone hills of Sierra Paila, Valle Seco, General Cepeda, 1700 m, 4 Jul 1944, J.C. Hinton (G.B. Hinton et al.) 16546 (HOLOTYPE: US!; ISOTYPES: GH!, NY!).

Distribution, ecology, and relationships.—*Xylovirgata pseudobaccharis* is known only from western Coahuila, Mexico, where it grows on limestone or gypsum slopes. Its suggested relationships to *Neonesomia* (*Xylothamia palmeri*, *X. johnstonii*), *Medranoa* (*X. parrasana*), and *Gundlachia riskindii* (*X. riskindii*) (Nesom et al. 1990) are not supported by sequence-derived phylogenies (Urbatsch et al. 2003). Sequence data provides some support for its sister relationship with *Chihuahuana purpusii*. Additional descriptive and distributional data for this taxon as *Xylothamia pseudobaccharis* are presented in Nesom et al. (1990).

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