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Author: Williams, Justin K.

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THOREAUEA (APOCYNACEAE: APOCYNOIDEAE), A NEW GENUS FROM OAXACA, MEXICO

Justin K. Williams
Department of Biological Sciences, Sam Houston State University, Huntsville, Texas 77341-2116

Abstract: Recent studies of Mexican Apocynaceae have uncovered a new species. The taxon is here viewed as generically distinct and accordingly the name ***Thoreauea paneroi*** J. K. Williams, **gen. et sp. nov.** is proposed. The species is from montane pine-oak cloud forests of the Santiago Juxtlahuaca area of northwestern Oaxaca, Mexico. Its relationship to *Thenardia* H.B.K. and other genera is discussed.

Keywords: *Echites, Forsteronia, Laubertia, Parsonsia, Prestonia, Thoreauea, Thenardia,* Apocynaceae.

Recently, a specimen of Apocynaceae from Oaxaca, Mexico was provided to me by one of the collectors, José L. Panero, for identification. After close examination, I determined that the specimen does not key out to any of the genera recognized in a key to the Mexican genera of Apocynaceae (J. K. Williams, 1996). This specimen keys out most favorably to *Thenardia* H.B.K., however, it possesses novel characters not found in *Thenardia* (e.g., dissected corona at the corolla mouth). A cladistic analysis (Fig. 5) based on morphological evidence indicates that if the new taxon were included in *Thenardia,* the genus would become paraphyletic, no longer representing a monophyletic lineage delimited by a shared consensus of characters. Thus, the problematic specimen is best regarded as representing a new genus.

Thoreauea paneroi J.K. Williams, gen. et sp. nov. (Figs. 1 and 2).

TYPE: MEXICO. OAXACA: Mpio. Santiago Juxtlahuaca, Dist. San Sebastián Tecomaxtlahuaca, 1.8 km N of the road Tecomaxtlahuaca—"Coicoyán, de Las Flores" along the road to Escopeta (17° 18′ 27.1″ N, 98° 07′ 51.5″ W), 4 Mar 1995, *J. L. Panero* with *I. Calzada* and *J. Kuijt 5583* (HOLOTYPE: IZTA!; ISOTYPE: TEX).

Thenardia affinis sed corollis urceolatus (vice rotatis) et corona corollae praesenti (vice carenti) et antheris inclusis (vice exsertis) differt.

VINE, twining, latex milky. STEMS terete, 3–3.5 mm in diameter, light green, glabrous, lenticellate with age; interpetiolar ridge moderately prominent. LEAVES opposite to subopposite, petiolate, membranous; petioles 20–23 mm, with a solitary bract and 2–4 colleters at base; colleters 0.8–1.0 mm long, linear lanceolate, dark brown when dried; leaf blade elliptic, apex acuminate with extended tip, base obtuse, margin entire, glabrous on both surfaces, chartaceous when dry, 10.5–14.0 cm long, 4.3–5.0 cm wide, without colleters, dark green above, light green below, midrib prominent below, slightly obscure above, lateral secondary veins 5–18, conspicuous, impressed alternate. INFLORESCENCE an axillary pedunculate, trichotomously-branched subumbellate cyme, glabrous; primary peduncle 23 mm long, 1.0–1.3 mm diameter; secondary and tertiary peduncles 5–18 mm long; bracts linear-lanceolate, 1.0–4.0 mm long, 0.2–0.4 mm wide, straight; pedicels 7.0–11.0 mm long. FLOWERS 20–25 per inflorescence, tightly clustered, pentamerous, actinomorphic, perfect. CALYX lobes equal, 0.9–1.0 mm long, separate nearly to the base, triangular, erect, glabrous; colleters ca. 0.5 mm long, opposite the sepals, solitary, thin, dentiform. COROLLA fused into a moderately

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HOLOTYPE OF:

`Thoreauea paneroi J.K.Williams`

FLORA DE OAXACA

ASCLEPIADACEAE

Metastelma

SANTIAGO JUXTLAHUACA: **San Sebastián**
Tecomaxtlahuaca. 1.8 km al N de la carretera
Tecomaxtlahuca-Coicoyán de Las Flores sobre la brecha a
Escopeta, 17° 18′ 27.1″ N, 98° 07′ 51.5″ W. Enredadera de 3-
5 m de largo, corolas crema. Bosque de pino-encino/mesófilo
de montaña. 2625 m

José L. Panero 5583 4 Mar 1995
con Ismael Calzada y Job Kuijt

Herbario Nacional de México (MEXU)
Michigan State University Herbarium (MSC)

Bajo el patrocinio de Grupo Bacardi, México,
Fundación UNAM y NSF DEB 91-14798, 94-96174

FIG. 1. Holotype of *Thoreauea paneroi*.

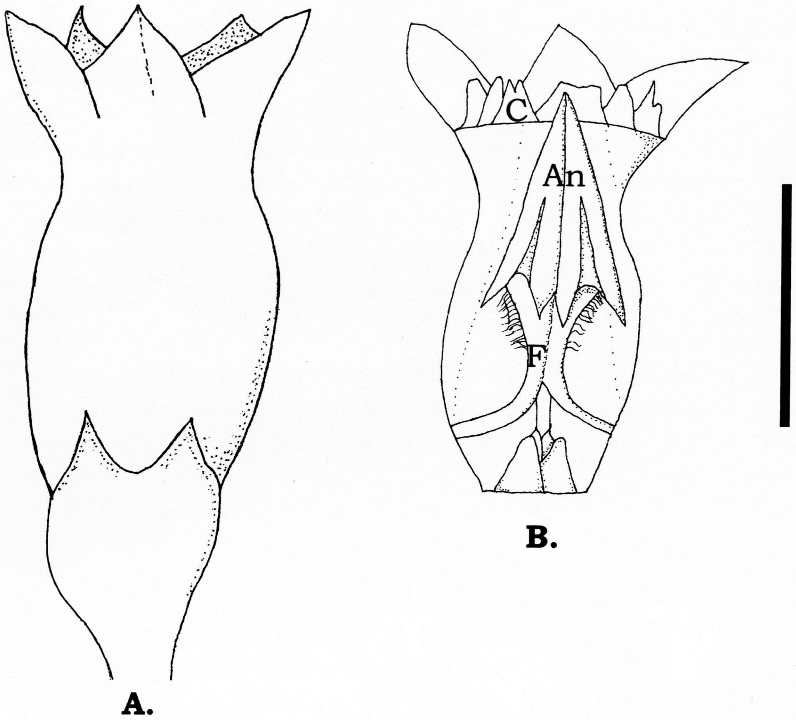

FIG. 2. *Thoreauea paneroi.* A. Flower. B. Longitudinal section of open flower. An = anthers. C = dissected corona around the mouth. F = filaments. Black bar represents 5 mm.

erect tube, urceolate, aestivation dextrorse, creamy white; tube 5–6 mm long, 2.7–3.1 mm wide, slightly constricted at the base and at the distal four-fifths of tube, glabrous, mouth of tube surrounded by a deeply dissected corona annulus, linear-lanceolate, both opposite and alternate the corolla lobes; lobes 1.0–2.0 mm long, 0.6–0.8 mm at widest point, triangular, erect; limb 3.0–4.0 mm in diameter. STAMENS 5.5–6.0 mm long, included; anther tips slightly below the corolla mouth to occasionally exserted ca. 0.2 mm above the rim, filaments 3.0–3.3 mm long, bending inward, and closely encircling the style head, pubescent; anthers 2.5–3.0 mm long, yellow, base sagittate, fertile in the upper part, the lower part enlarged, sterile and equipped with sclerenchymatic guide rails on the ventral face firmly agglutinated to the style-head secretions by thick brushes of hairs, forming a pseudo-gynostegum, in addition thecae agglutinated to the upper slopes of the style-head, forming five separate pollen chambers. PISTIL 3.0–3.5 mm long; ovary of two fused carpels united into a common style, superior, ovoid, glabrous, 0.8–1.5 mm long; style head 1.5–2.0 mm, spool-shaped, slender in the middle and greater in diameter at the base, with developed membranous collar at base; stigmattic zone located on underside of style head beneath collar; nectaries five, free, pressed closely together, tightly surrounding the ovary, as long or slightly shorter than the ovary. FRUIT unknown.

Thoreauea is a member of the subfamily Apocynoideae as evidenced by its anthers agglutinated to the style head, dextrorse aestivation of the corolla bud, and triporate pollen grains. Within the Apocynoideae *Thoreauea* belongs to the tribe Echiteae, as delineated by Endress and Bruyns (2000). Members of the Echiteae are characterized by the thecae agglutinated to the style head at two levels and by the spool-shaped style head that is slender in the middle and greater in diameter at the base.

DISTRIBUTION AND ECOLOGY: *Thoreauea paneroi* is a moderately sized liana known only from the type collection from the cloud forests of the district of Santiago Juxtlahuaca area of northwestern Oaxaca, Mexico. The species is found in a mesophytic habitat of montane pine-oak forest at 2625 m elevation. Flowers were collected in March but its phenology is unknown.

Thoreauea was included, together with 24 additional genera, in an unpublished morphological cladistic analysis of the Apocynoideae (Williams, 1999). A portion of this analysis (Fig. 5) is discussed below. Because additional results of the analysis are outside the scope of this paper, the full tree is not included or discussed.

METHODS

COLLECTION OF DATA. With the exception of selected species of *Parsonsia* (see below), a representative specimen is deposited at the Plant Resources Center for each of the species examined in the morphological cladistic analysis. Observations and data were collected from material borrowed from or observed at the following herbaria: BM, BRIT, CHAPA, F, FLAS, G, GH, K, MA, METPEC, MEXU, MO, NY, P, SHST, TAMU, TEX, US, WIS.

The pollen of all genera was studied using a light microscope as well as a scanning electron microscope (Philips 515). All genera were examined and measured under the SEM at the Cell Research Center of the University of Texas at Austin.

A total of 37 taxa, representing 25 genera, were included in the original cladistic analysis (Williams, 1999). Character measurements and states for the data matrix were obtained from living material and herbarium specimens for all of the representative species included in this study. Subsequently, three species of *Parsonsia* (*P. latifolia* (Benth.) S. T. Blake; *P. praeruptis* Heads & de Lange; *P. purpurascens* J. B. Williams) have been added to the study in order to represent better the diversity of *Parsonsia* (a genus with many superficial similarities to *Thenardia*). Morphological data for the three species of *Parsonsia* were obtained from literature descriptions (J. B. Williams, 1996; Heads & de Lange, 1998)

SELECTION OF CHARACTERS. Forty-five characters and 119 character states (Table 1) were utilized in this study. Informative character states were selected from those utilized in previous studies (Endress et al. 1996; Sennblad et al. 1998; Struwe et al. 1994; Potgieter and Albert, 2001). New characters not included in the above works, but uncovered during the course of this study were also included. A discussion of the characters utilized in this study is provided in Williams (1999). Table 2 lists the characters and character states for each of the taxa shown in this analysis.

CLADISTIC ANALYSIS. The characters and character states (Table 2) used in the analysis were entered into a data matrix using MacClade 3.0 (Maddison & Maddison, 1992). A phylogenetic analysis was then performed in PAUP 3.1 (Swofford, 1993). A heuristic search by stepwise addition of random trees was performed with 100 random addition sequences. The heuristic search was performed with the ACCTRAN, MULPARS and TBR options in effect. Taxa with multi-state characters were recognized as polymorphic for those characters. Characters were treated as unordered and of equal weight. At the end of the analysis the stored trees were rooted, with both the outgroup and ingroup directed as monophyletic. A majority rule consensus tree of the stored trees was then produced. Bootstrap values were calculated using 100 replications.

RESULTS

The heuristic search yielded a total of 337 equally parsimonious trees with 185 steps. The large number of trees is attribut-

TABLE 1. Characters and character states used in the cladistic analysis.

1. Latex
   0-milky
   1-watery
2. Predominate growth habit
   0-woody shrub
   1-liana
   2-suffruticose herb
   3-herb
3. Leaf arrangement
   0-opposite
   1-alternate
4. Colleters around the stem
   0-absent
   1-present
5. Colleters at base of upper leaf blade surface
   0-absent
   1-present
6. Colleters along the upper leaf blade surface
   0-absent
   1-present
7. Colleters along the petiole
   0-absent
   1-present
8. Leaves with domatia
   0-absent
   1-present
9. Secondary venation of leaves
   0-visible
   1-obscure
10. Tertiary venation of leaves
    0-visible
    1-obscure
11. Calyx size
    0-minute (0–3 mm)
    1-foliaceous (5–15 mm)
12. Calycine colleters
    0-absent
    1-numerous and alternate with the sepals
    2-solitary and opposite the sepals
13. Aestivation
    0-sinistrorse
    1-dextrorse
    2-valvate
14. Corolla shape
    0-salverform
    1-urceolate
    2-infundibuliform
    3-rotate
15. Corolla color
    0-white
    1-yellow
    2-maroon

TABLE 1. Continued.

16. Corolla with epistaminal appendages
    0-absent
    1-reduced to a callused ridge
    2-extended into a staminode
17. Corona between petal sinuses
    0-absent
    1-present
18. Corolla tube size
    0-minute (1–4 mm)
    1-small (6–10 mm)
    2-medium (1–20 mm)
    3-large (21–50 mm)
19. Infrastaminal appendages
    0-absent
    1-present
20. Filaments
    0-minute (0–1 mm)
    1-medium (3–6 mm) and running along the style
    2-long (10 mm and greater) and separate from the style
21. Anthers from ribs
    0-no
    1-yes
22. Stamen exopsure
    0-included
    1-anther tips exserted
    2-stamens fully exserted
23. Anthers with apical appendages
    0-absent
    1-present
24. Anther dehiscence
    0-introrse
    1-latrorse
25. Anther type
    0-*Thevetia*-type
    1-Apocynoideae rounded bases
    2-Apocynoideae forked bases
    3-*Mandevilla*-type
26. Anther-style head relationship
    0-anthers free from style head
    1-anthers fused to style head
27. Style type
    0-*Thevetia*-type
    1-*Mandevilla*-type
    2-*Echites*-type
28. Nectary
    0-absent
    1-5 free nectaries
    2-nectaries fused into a cup, *Echites*-type
    3-nectaries fused into a cup, *Thevetia*-type

TABLE 1. Continued.

29. Inflorescence position
0-axillary
1-terminal
30. Inflorescence morphology
0-raceme
1-corymbose
2-reduced cyme
31. Inflorescence branching
0-absent
1-present
32. Fruit type
0-linear follicle (2–15 mm in diameter)
1-robust follicle (30–60 mm diameter)
2-drupe
33. Follicle orientation
0-spreading
1-fused only at the apical tips
2-fused throughout entire length
3-fruit not a follicle
34. Follicles moliniform
0-no
1-yes
35. Follicle color
0-tan
1-red
2-black
36. Fruit dehiscent
0-no
1-yes
37. Fruit texture
0-herbaceous
1-woody
2-leathery
38. Seeds with coma
0-absent
1-present and sessile
2-present and rostrate
39. Pollen poration
0-tricolporate
1-triporate
40. Exine pattern
0-smooth
1-microreticulate
41. Pollen shape
0-spherical
1-triangular
42. Pollen diameter
0-20–35 μm
1-40–75 μm
2-75– 110 μm

TABLE 1. Continued.

43. Chromosome numbers
0-x=11
1-x=10
2-x=9
3-x=6
44. Distribution
0-South Mesoamerica
1-North America
2-Caribbean
3-Australia-New Guinea
45. Filaments
0-straight
1-coiled

ed to the fact that the characters used in this analysis are informative mainly at the generic level. Examination of a majority of the parsimonious trees indicated that the most stable branches were the terminal ones, and that the unstable branches were the basal ones. This is acceptable considering that the main focus of this study was to test the monophylly of problematic genera of Mexican Apocynoideae, in this case *Thoreauea.* One clade in the majority rule consensus tree (Fig. 5) includes *Thoreauea* and its relatives, *Forsteronia* G. Mey., *Laubertia* A. DC., *Parsonsia* R. Br., *Prestonia* R. Br., *Echites* R. Br. and *Thenardia* and will be referred to here as the "*Prestonia*" clade. To date no cladistic analysis has included all of the above genera. In their study, Sennblad et al. (1998) included only *Parsonsia* and *Prestonia.* Their tree (based on morphology and molecular evidence) supports the results presented here of a relationship between the two genera. Sennblad and Bremer (2002) presented a second phylogenetic analysis of the Apocynaceae based on molecular evidence. This study again included only *Parsonia* and *Prestonia* and, as before, their results showed the two genera as sister to one another. Potgieter and Albert (2001) included *Forsteronia, Parsonsia, Prestonia* and *Echites* in their combined morphological and molecular analysis. Their results support the relationship between *Parsonsia, Prestonia* and *Echites,* however, *Forsteronia*

TABLE 2. Data matrix of the 45 informative characters used in the phylogenetic analysis[a,b] presented in this study.

	Character number and character states				
	0000000001	1111111112	2222222223	3333333334	44444
Species	1234567890	1234567890	1234567890	1234567890	12345
Echites agglutinata	1100000001	0210100010	0000212101	1011010200	00?00
Echites turbinata	1100000011	0210130011	0000212101	1011010200	00?00
Echites woodsoniana	1100000011	0210100010	0000212101	1011010200	00?00
Forsteronia sp.	0100010010	0113a00001	0200212101	10b0011100	0a?d0
Laubertia contorta	1100000000	0010231021	0100212101	0011010100	01?00
Parsonsia latifolia	0101000000	0323000001	0200212111	1020011100	00231
Parsonsia praeruptis	1001000011	0323000000	02002121a1	1020011100	00230
Parsonsia purpurascens	1101000000	0323100000	0000212101	1020010100	00230
Parsonsia straminae	1101000000	0323100000	0100212101	1020011100	0?230
Prestonia acutifolia	0101000000	0210121011	0100212101	1010011100	01200
Prestonia mexicana	0101000000	1210131021	0100212101	1100011100	02?00
Prestonia tomentosa	0101000000	1210121021	0100212101	1100011100	01?00
Prestonia portobellensis	0101000000	1210221021	0100212101	1010011100	02?00
Rhabdadenia biflora	0100000000	1012000020	0000112102	0000011100	02?c0
Thenardia chiapensis	1100000001	0213000001	0200212101	1021010100	00?00
Thenardia floribunda	1100000001	0213000001	0200212101	1021010100	01?01
Thoreauea paneroii	0100000000	0211001001	0000212101	10??01?100	00?00

[a] Character numbers and character states correspond to those in Table 1.

[b] Polymorphic character states are represented by letters as follows: a = 0, 1; b = 1, 2; c = 0, 1, 2; d = 0, 2 (within the data matrix character states for polymorphic characters were entered as 0/1 etc. Letters are used here for the convenience of aligning the table).

appeared in a separate clade paired with *Cycladenia.* An examination of the tree presented here indicates that *Thoreauea* is the sister group to a clade comprised of *Parsonsia, Thenardia* and *Forsteronia* with all four genera monophyletic.

DIAGNOSTIC FEATURES AND GENERIC PLACEMENT

Table 3 presents a list of taxonomically useful characters for distinguishing *Thoreauea* from other closely related genera. Based on these characters and the results of the cladisitic analysis (Fig. 5), *Thoreauea* appears most related to *Thenardia,* sharing a trichotomously branched, cymous inflorescence, relatively small flowers, and triangular corolla lobes. *Thoreauea* differs from *Thenardia* in its possession of an annular, corolline corona in the mouth of the corolla, urceolate corollas, and included stamens (vs. rotate and exserted)'. *Laubertia* and *Prestonia* are two New World genera that also possess an annular corolline corona in the mouth of the corolla. However, they differ from *Thoreauea* in that their corona is continuous (vs. dissected; Figs. 3 and 4, respectively). *Laubertia* and *Prestonia* also differ from *Thoreauea* by their racemiform cymous inflorescences and salverform corollas. In addition, *Laubertia* and some species of *Prestonia (P. mexicana* A. DC.) possess an epistaminal corona abaxial to the anthers. In *Laubertia* the lobes of the second corona appear as five separate swollen calluses each abaxial to the point of divergence of each filament (Figure 3). In *Prestonia portobellensis* (Beurling) Woodson, the epistaminal corona is comprised of five separate linear protuberances each abaxial to the anther (Figure 4) resembling a staminode.

Table 3 indicates that the Paleotropical

TABLE 3. Morphological comparisons of the genera *Thoreauea, Thenardia, Prestonia, Laubertia, Forsteronia* and *Parsonsia, Echites.*

	Thoreauea	*Thenardia*	*Prestonia*	*Laubertia*	*Echites*	*Forsteronia*	*Parsonsia*
Latex	White	Clear	White	Clear	Clear	White	Clear
2° venation visible	Yes	Yes	Yes	Yes	No	Yes	Yes
Leaves with domatia	No	No	No	No	No	Yes	No
Glands at apex of petiole	No	No	No	No	No	Yes	No
Glands around stem at axils	None	None	Yes	None	None	None	Yes
Sepals foliaceous	No	No	Yes	No	No	No	No
Calycine colleters	One	One	One	None	One	Many	Many
Corolla aestivation	Dextrorse	Dextrorse	Dextrorse	Dextrorse	Dextrorse	Dextrorse	Valvate
Corolla shape	Urceolate	Rotate	Salverform	Salverform	Salverform	Rotate	Rotate
Corolla mouth corona	Dissected	None	Continuous	Continuous	None	None	None
Epistaminal corona	None	None	Staminode/none	Callused ridge	Calused ridge/none	None	None
Stamen exposure	Included	Fully exserted	Anther tips exposed	Anther tips exposed	Included	Fully exserted	Fully exserted
Corolla color	Cream	Cream	Yellow & Maroon	Maroon	Yellow	Cream & Yellow	Cream
Filaments fused along style	Yes	Yes	Yes	Yes	No	Yes	Yes
Follicles	Unknown	Fused throughout	Spreading/Fused at apex	Fused at apex	Fused at apex	Fused at apex & throughout	Fused at apex & throughout
Follicle shape	Unknown	Moliniform	Straight	Moliniform	Moliniform	Straight	Straight
Pollen diameter	30–45 μm	30–60 μm	(45)74–95 μm	50–65 μm	23–35 μm	30–75 μm	20–35 μm

genus *Parsonsia* also shares many similar characters with *Thoreauea.* Both genera have similar stamen architecture (filaments along the style and inserted at the base of the corolla), corolla color, and pollen diameter. *Thoreauea* differs from *Parsonsia* mainly in the number of calycine colleters (1 vs. many), corolla aestivation (dextrorse vs. valvate), and geography (Neotropics vs. Paleotropics). The cladistic analysis presented in Fig. 5, indicates that *Forsteronia* is sister to *Parsonsia.* The relation between *Parsonsia* and *Forsteronia* is supported by their shared rotate corolla and numerous calycine colleters. Endress and Bruyns (2000), however, included *Forsteronia* in a different tribe (Apocyneae Rchb.) from *Parsonsia* (Echiteae Bartl.). In addition, mo-

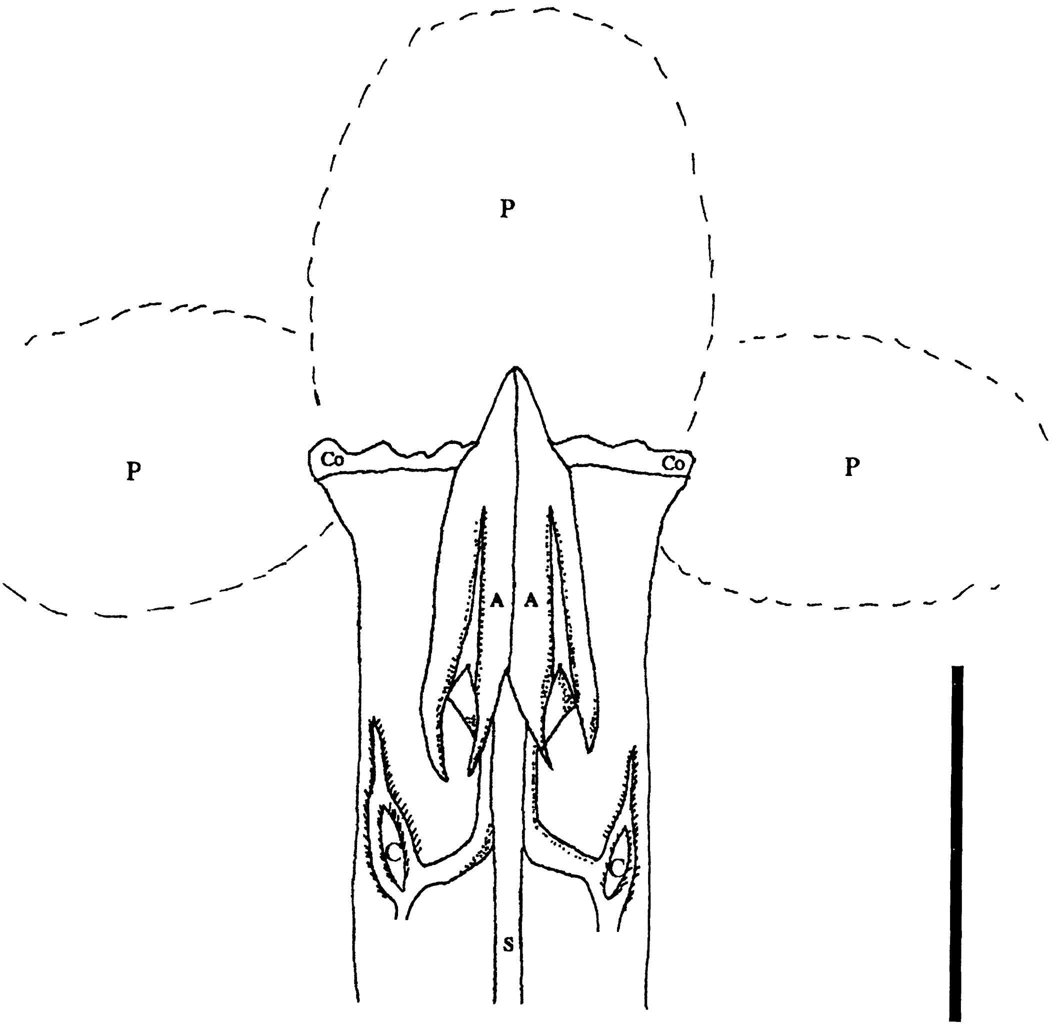

FIG. 3. Longitudinal section of a flower of *Laubertia contorta.* Note how the epistaminal corona is reduced to a callus ridge. A = anthers. C = epistaminal corona. Co = corona around the corolla mouth. P = petals. S = style. Black bar represents 5 mm.

lecular evidence presented by Potgieter and Albert (2001) clearly showed *Forsteronia* and *Parsonsia* distinct from one another, with *Parsonsia* more closely related to the "*Prestonia*" clade. Table 3 also shows many similarities between *Thenardia* and *Parsonsia.* This relationship was suggested by Baillon (1890), and is supported by the cladistic analysis (Fig. 5) that shows *Thenardia* sister to the clade containing *Parsonsia* and *Forsteronia.*

The surface morphology of pollen grains in the Apocynoideae is essentially uniform. The majority of genera have grains that are spherical, triporate (occasionally 4–5; *Telosiphonia*) and with smooth perforate surfaces (Erdtman, 1952; Nilsson, 1990; Sampson and Anusarnsunthorn, 1990; Roubik and Moreno, 1991; Nilsson et al., 1993; Williams, 1999). Huang (1989) showed that the number, arrangement and shape of the pores are occasionally useful diagnostic characters for circumscribing genera. Williams (1998) and Roubik and Moreno (1991) also showed that species of a genus can occasionally be identified by

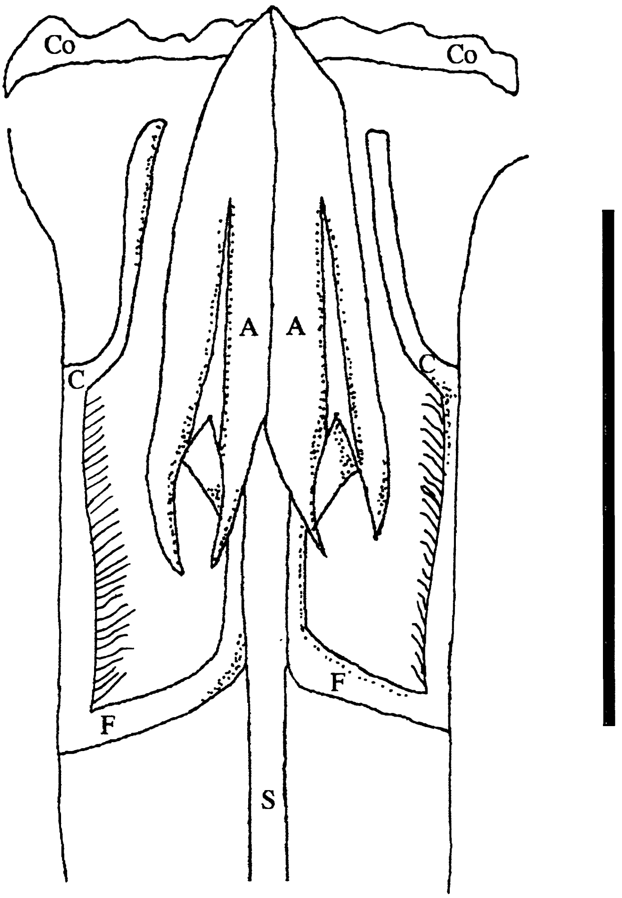

FIG. 4. Longitudinal section of a flower of *Prestonia portobellensis.* Note how the epistaminal corona appears as a linear protuberance. A = anthers. C = epistaminal corona. Co = corona along the corolla mouth. F = filaments. S = style. Black bar represents 5 mm.

their pollen diameters. It is speculated that pollen diameter may also be a useful character in resolving generic relationships. Measurements of the pollen grains of *Thoreauea paneroi* (under light microscopy and SEM) show the diameter to be between 30–45 μm. Interestingly, the pollen grain diameter of *Thenardia chiapensis* J. K. Williams falls within this range. The second species of *Thenardia, T. floribunda* H.B.K., in this study has grains 45–60 μm wide (Williams, 1998).

Fruiting specimens of *Thoreauea* will certainly aid in its taxonomic positioning within the Apocynoideae. Observations of fertilized ovaries suggest that the follicles, as in *Thenardia,* will be fused to one another.

The combination of vegetative and floral characters in this new species is so unique that including it in a currently recognized genus is not justified. Consequently, the new genus *Thoreauea* is proposed. I have not located any types or specimens of Neotropical Apocynaceae in the following herbaria that resemble this new species (Williams, 1999): BM, BRIT, CHAPA, F, FLAS, G, GH, K, MA, METPEC, MEXU, MO, NY, P, SHST, TAMU, TEX, US, WIS.

It is an honor to name this new genus after Henry David Thoreau (1817–1862), noted essayist and naturalist (Angelo, 1985; Egerton and Walls, 1997). His loving, and often unrecognized, commitment to botany inspired me to undertake the subject.

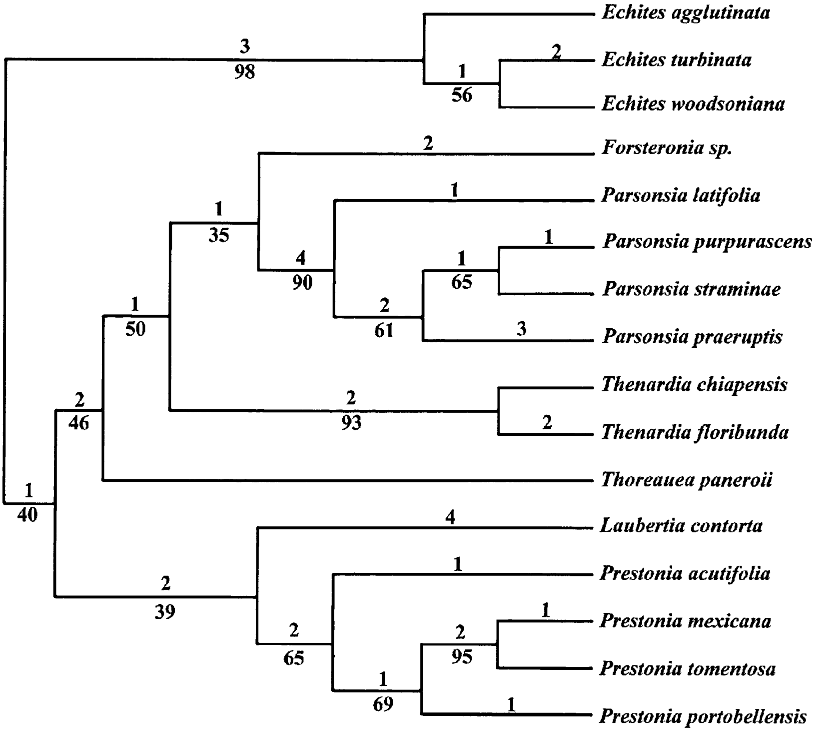

FIG. 5. "*Prestonia*" clade of majority rule consensus tree calculated from 337 most parsimonious trees (length = 185, CI = 0.53, RI = 0.76, RC = 0.40). Numbers above the lines indicate branch length and the numbers below the branches are bootstrap values greater than 50%.

The species epithet honors José L. Panero, Professor of Integrative Biology at the University of Texas at Austin and collector of the type specimen.

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