



A Revision of *Thenardia* H.B.K. (Apocynaceae, Apocynoideae)

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A REVISION OF *Thenardia* H.B.K. (APOCYNACEAE, APOCYNODEAE)

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Abstract: A revision of the Mexican genus *Thenardia* H.B.K. is presented. Three species are here recognized: *T. chiapensis* J. K. Williams, *T. floribunda* H.B.K., and *T. galeottiana* Baillon. A complete account of synonymy, and typification is provided, as well as a key to species, photographs of types and pollen, and a distribution map of the species.

Resumen: Se presenta una revisión del género *Thenardia* H.B.K. Se reconocen tres especies: *T. chiapensis* J. K. Williams, *T. floribunda* H.B.K., y *T. galeottiana* Baillon. Se incluye un informe completo sobre la sinonimia de las especies y su tipificación, así como claves para las especies, fotografías de los tipos y el polen. También se incluyen mapas de distribución para todas las especies.

Keywords: *Thenardia*, Apocynaceae, Flora of Mexico

Thenardia H.B.K. is a neotropical genus of vines endemic to rain forests of southern Mexico. The genus is distinguished within the Apocynaceae by the combination of watery sap (shared with *Echites* R. Br. subg. *Pseudechites* and selected species of *Parsonsia* R. Br.), fully exerted anthers (shared with *Forsteronia* G. Mey., *Isonema* R. Br., *Pottsia* Hook. & Arn. and selected species of *Parsonsia*), subumbellate inflorescences, fused follicles (shared with various species of *Artia* Guillaumin, *Forsteronia*, *Mandevilla* Lindl. and *Parsonsia*) and one species (*T. floribunda*) with coiled filaments (shared with selected species of *Parsonsia* and *Dewevrella* De Wild.). Because of its combination of convergent characters the relationship of *Thenardia* within the Apocynaceae has been under considerable dispute (see Generic Relationships). The recognition of species, however, is facilitated by each taxon's possession of discrete morphological characters which help to readily separate it from other members of the genus.

TAXONOMIC HISTORY

Kunth (1819) established the genus

Thenardia as monotypic with the description of *Thenardia floribunda*. He named the genus in honor of his friend L. J. Thénard (1777–1857), chemist and plant physiologist. A second species of *Thenardia* (*T. suaveolens*) was described by Martens and Galeotti (1844), this species, however, was later reduced to synonymy under *T. floribunda* by Woodson (1936). Woodson's decision to not recognize *T. suaveolens* is followed here. Baillon (1890) described a third species of *Thenardia* (*T. galeottiana*), and discussed *Thenardia's* affinities with *Parsonsia* (see Generic Relationships).

Woodson (1936, 1938) provided the first taxonomic treatments of *Thenardia*, recognizing four species for the genus: *T. floribunda*, *T. galeottiana*, *T. gonoloboides*, *T. tubulifera*. The latter two species (*T. gonoloboides* and *T. tubulifera*) were described by him (Woodson 1932, 1936, respectively). The characters by which Woodson recognized these species, however, are regarded here as extremely variable and insignificant, and thus the species are regarded as synonyms under *T. galeottiana* and *T. floribunda*, respectively.

Williams (1995) subsequently described

an additional species in *Thenardia* (*T. chia-pensis*), and included a few taxonomic notes on the genus.

Five additional names proposed in *Thenardia* have been transferred to or synonymized under other genera (*Forsteronia*, and *Rhynchanthera* DC.) (see Excluded Taxa).

GENERIC RELATIONSHIPS

It is widely recognized that at present there is no modern intrafamilial classification system for the Apocynaceae (Fallen, 1983; Middleton, 1995). Treatments to date are not regarded by most authors as monophyletic. Schumann's treatment of the family in Engler and Prantl's *Die natürlichen Pflanzenfamilien* (1895) is perhaps the most universally accepted for the family. Pichon (1948a, 1948b, 1950) and Leeuwenberg (1994) have provided subsequent treatments of the family. Pichon's work includes more detailed descriptions of the genera as well as provides some of the first observations on pollen for the family, however, the overall taxonomic arrangement varies only slightly from that of Schumann's. The treatment of Leeuwenberg is mainly a checklist of genera arranged by their suspected subfamilies and tribes. His treatment includes very little discussion of characters and the placement of the genera within the family.

Although there is no universal agreement as to the recognition and arrangement of tribes, subtribes and genera within the Apocynaceae, most authors (Schumann, 1895; Rosatti, 1989; Leeuwenberg, 1994) accept two subfamilies, although some authors have argued for three (Pichon, 1948a; Fallen, 1983). The two subfamilies can be distinguished by the following key:

1. Trees, shrubs or herbs; stamens free from pistil head; aestivation of the corolla in bud to the left (occasionally to the right (*Alstonia*, *Haplophyton cimidum*, *Kopsia*, *Ochrosia*); seeds without coma or with both apical and basal coma (*Haplophyton*); plants with or without indole alkaloids; pollen colpiporate. Plumerioideae

1. Mostly lianas (rarely herbs *Apocynum* or shrubs *Nerium*); stamens adnate to the pistil head; aestivation of the corolla in bud to the right, occasionally valvate (*Parsonsia*); seeds with apical coma; plants lacking indole alkaloids; pollen porate.

Apocynoideae

Thenardia, as evidenced by its stamens fused to the style head, dextrorse aestivation and comose seeds, belongs in the Apocynoideae. The Apocynoideae has been divided into several different tribes by various authors (see below). Below is a brief history of the assignment of *Thenardia* within the family by various authors and a discussion of the genera most possibly related to *Thenardia*.

When Kunth (1819) erected *Thenardia*, a classification system of the Apocynaceae had not yet been established and he merely stated its resemblance to *Echites*. This is of little interest, however, because at that time *Echites* was nothing more than a grab-bag of miscellaneous Apocynoideae with over two hundred species. It was not until Woodson (1936) revised *Echites* that the genus ceased being artificial and became legitimately circumscribed, ultimately housing seven species.

De Candolle (1844) established the first classification system of the Apocynaceae, recognizing seven tribes in the family: Willughbeae, Carisseae, Plumereae, Parsonseae, Wrighteae, Alstoneae, and Echitideae. He placed *Thenardia* in the tribe Echitideae (= Apocyneae of Schumann) near *Haemadictyon* Lindl. (the species of which are at present divided between *Laubertia* and *Prestonia*). The Echiteae as viewed by de Candolle, however, appears to represent an unnatural amalgam of artificially arranged taxa.

Bentham (1873) recognized three tribes (Carisseae, Plumerieae, Echitideae) in the Apocynaceae. In his work he placed *Thenardia* in the Echitideae subtribe Parsonsineae (including, in this order; *Prestonia*, *Thenardia*, *Forsteronia*, *Vallaris*, *Parsonsia*, *Lysonia* (= *Parsonsia*), *Pottisia*, *Isonema*, *Wrightia*). The Parsonsiae of

Bentham is an expanded version of de Candolle's Parsonsieae, which included only four genera (*Vallaris*, *Parsonsia*, *Balfouria* and *Beaumontia*; the latter two genera were placed elsewhere by Bentham). The additional members of Bentham's Parsonsieae came from Wrightieae of de Candolle and selected genera of his Echiteae (*Prestonia*, *Thenardia*, *Forsteronia*, *Pottsia* and *Isonema*). What explains the discrepancy between the genera recognized in the Parsonsieae of de Candolle and in that of Bentham is that both authors had different concepts for the taxon. De Candolle separated the Parsonsieae from the other tribes by its ovary of two united carpels, while Bentham defined the Parsonsieae by its exerted anthers and rotate corolla.

Schumann (1895) essentially followed the same treatment of *Thenardia* as Bentham, placing it in his subfamily Apocynoideae tribe Parsonsieae. His tribe Parsonsieae would encompass the same definition (exserted anthers) and genera as Bentham's, although Schumann's separation of genera differed. Whereas Bentham keyed *Thenardia*, *Prestonia* and *Forsteronia* from *Parsonsia* because of their restriction to the New World (vs. restricted to the Old World), Schumann keyed *Thenardia*, *Prestonia* and *Forsteronia* from *Parsonsia* based on their ovary of two free carpels (vs. ovary of two united carpels).

Woodson never attempted a systematic treatment of the Apocynaceae as a whole. He did, however, tend to indicate relationships by constructing natural keys. In his key to the American genera of the Echitoideae (Woodson, 1933), he separated *Thenardia* along with *Echites* and *Prestonia*. He keyed *Thenardia* from *Echites* on its rotate corolla and exerted anthers (vs. salverform and included) and from *Prestonia* based on its lack of an annulate corolla mouth. *Forsteronia* was separated from the former genera based on its numerous col-leters ("squamellae" of Woodson) alternate the calyx lobes (vs. solitary and opposite), the same difference used by Schumann.

Pichon (1950) was the first to recognize that *Thenardia* had an ovary of two united carpels. Because of this, he placed *Thenardia*, with *Parsonsia* and *Artia*, in his tribe Parsonseae subtribe Parsonsiinae, which was defined by its ovary of two united carpels. He keyed *Thenardia* from *Parsonsia* on its possession of developed intrapetiolar stipules (vs. reduced or absent) and corolla size. *Artia* was keyed from the former genera by its bent filaments. It seems evident that, due to their lack of fruiting specimens both de Candolle and Schumann refrained from placing *Thenardia* with *Parsonsia*. Indeed, if they were to have observed either the fruits or ovary of *Thenardia* they would have most likely classified it near *Parsonsia*.

Leeuwenberg (1994) placed *Thenardia* in his subtribe Parsonsiinae following this order: *Delphyodon*, *Grissea*, *Parsonsia*, *Dewevrella*, *Thenardia*, *Artia*, *Pottsia*, and *Isonema*. He neither provided a key to the genera nor discussed the differences between them. Leeuwenberg also defined the Parsonsiinae in a broader sense than had previous authors. His Parsonsiinae was defined as including lianas, with short corolla tubes, exerted anthers, and an ovary of two free or united carpels. The expanded definition of the Parsonsiinae is probably explained by the variability that exists within *Parsonsia*, a genus which possesses species with and without united carpels.

Relation to *Parsonsia*: Baillon (1890) regarded *Thenardia* as little distinct from *Parsonsia*, suggesting that the only real difference was that *Thenardia* was restricted to Mexico. He thus proposed that *Thenardia* be regarded as a section of *Parsonsia* (Baillon, 1891). He explains the presence of *Thenardia* in Mexico as being an extremely "ancient" introduction from "oceanic archipelagos where [*Parsonsia*] is present in high number." An introduction of an Apocynaceae genus into the neotropics from Indonesia is not altogether improbable as the genus *Alstonia* shares members in

both the Neotropics (Mexico and Central America) and the Paleotropics (Africa, Australia and Indonesia) (Gentry 1983a).

The species of *Parsonsia* most similar to *Thenardia* is *P. rotata* Maiden & Betche. The characters that *P. rotata* shares with *Thenardia* are watery sap, glabrous habit (except corolla throat), coiled filaments, leaves with obscure secondary veins, five free nectary scales, older stems with corky outgrowths and fruits of two fused follicles 15–20 cm long (J. B. Williams, 1996). Indeed, an illustration (ibid.) of the inflorescence of *P. rotata* even shows the inflorescence as compact and umbel-like.

Parsonsia mainly differs from *Thenardia* in its geography (Indonesia vs. Central America), lack of intra-petiolar stipules, valvate (occasionally dextrorse) aestivation, number of calycine squamella (0–many vs. 1), pubescent corolla throat (vs. glabrous) and stamens attached to the base of the corolla (vs. attached to the apex). In a broad scheme these differences seem inconsequential, however, many of the genera in the Apocynoideae are defined by fewer and seemingly less important characters (e.g., *Mesechites* differs from *Mandevilla* in only one character: branched vs. unbranched inflorescence).

Relation to *Forsteronia*: The only similarities between *Thenardia* and *Forsteronia* (besides their restriction to the Neotropics) is their possession of exerted anthers and fruits with fused follicles. Hansen (1985) suggests that the fused follicles have “little phylogenetic significance” (at least within *Forsteronia*) since they have evolved independently in several unrelated lineages. He likewise suggests that the moliniform structure of the follicles also represents convergence. Hansen mentions that Bentham placed *Thenardia* near *Forsteronia* in the Parsonsieae, but does not suggest any close relation between two, supporting rather the relation of *Forsteronia* to *Mandevilla* on the basis of their shared colleters at the apex of the petiole along the

upper surface of the leaf.

Forsteronia also differs from *Thenardia* in having many colleters alternate to the sepals (vs. solitary and opposite), domatia on the underside of the leaves and thyriform inflorescence (vs. subumbellate cyme) and a different style head shape. Of the possible candidates related to *Thenardia*, *Forsteronia* seems the most improbable.

Relation to *Echites*: *Echites* is divided (Woodson, 1936) into two subgenera, *E. subg. Echites* and *E. subg. Pseudechites*, that are separated by their corolla lengths and sap (30–80 mm and milky vs. 12–25 mm and watery, respectively). *Thenardia* is more similar to *E. subg. Pseudechites* (represented by the species *E. agglutinata* Jacq. [*Prestonia agglutinata* (Jacq.) Woodson of some authors], *E. tuxtensis* Standley, *E. turbinata* Woodson, and *E. woodsoniana* Monach.).

Thenardia and *Echites* subg. *Pseudechites* share the following characters: watery sap, one colleter opposite each sepal, intra-petiolar stipules, leaves with obscure secondary veins, and an extensive growth form from woody terrestrial stems (the above observations were taken from a population of *E. woodsoniana* by the author), as well as a neotropical distribution. *Echites* subg. *Pseudechites* mainly differs from *Thenardia* in having a racemous inflorescence, included anthers and fruits of two free follicles.

In conclusion, I refrain from placing *Thenardia* within a subtribe due in part to the artificial nature of the tribes and subtribes as circumscribed to date and in part to the considerable convergence that exists within the Apocynoideae. I am inclined, however, to support a relation between *Thenardia* and *Echites* subg. *Pseudechites* (as described above). Ultimately, this is a hypothesis and I believe that until a thorough cladistic analysis as constructed by molecular evidence is formulated the relationship of many of the genera in the Apocynoideae will remain speculative.

MORPHOLOGY

LEAVES. The leaves of *Thenardia* are opposite and entire, as in all neotropical lianas of the Apocynoideae. *Thenardia* lacks colleters at the apex of the petiole and domatia on the underside of the leaves, typical of *Forsteronia*, a genus which *Thenardia* is often confused. The leaves have obscure secondary veins, which are alternate in formation.

Although the Apocynaceae is typically regarded as lacking stipules, *Thenardia*, and all other Mexican Apocynoideae, possess intra-petiolar stipules. These stipules are not to be confused with "colleters", they are in fact multi-cellular foliaceous structures arising from the leaf axil. Two of the species are pubescent along the petioles and midribs of the leaves beneath, while the third species (*T. chiapensis*) has wholly glabrous leaves. The leaves of *T. floribunda* are often two to three times longer and broader than the other two species. Field studies have shown that the above mentioned characters are uniform and consistent within a population.

INFLORESCENCE. The inflorescence in *Thenardia* is a pedunculate di- to trichotomously branched umbelloid axillary cyme. The inflorescences have a congested growth form which often makes them appear to be umbels. The umbel-like appearance of the inflorescence is a distinctive trait that helps to readily distinguish the genus from other neotropical viney Apocynoideae. The distinctiveness of the inflorescence lead Sessé and Mociño to name the species *T. umbellata* (see *T. floribunda* below).

The number of flowers per inflorescence ranges from 6–15 in *T. chiapensis* and *T. galeottiana* and between 20–30 for *T. floribunda*. The more congested inflorescence of the latter species helps to distinguish it from the former two species.

FLOWERS. The calyx in *Thenardia* is regular, pentamerous, and with a solitary colleter

opposite to the adaxial surface of each sepal. The sepals are narrowly triangular and 1–2 mm long in *T. chiapensis* and *T. floribunda*. In *T. galeottiana* the sepals are quite distinctive being narrowly elliptic, curled, and 4–6 mm long. The shape and dimensions of the sepals for each species corresponds to the shape and dimensions of the bracts subtending the pedicel.

The corolla is rotate, wholly glabrous and with wholly exerted stamens. The exerted stamens are a unique feature of *Thenardia*, helping to distinguish it from other Mexican Apocynoideae genera (ex. *Laubertia* and *Prestonia*) which have only their anther tips exerted past the corolla orifice. The filaments are attached to the apex of the corolla throat as opposed to *Parsonsia* which has its filaments attached to the bottom of the corolla tube. The filaments are coiled in *T. floribunda*. Coiled filaments were also observed in one of the specimens (Martinez 124) of *T. galeottiana*, while the filaments of *T. chiapensis* are apparently always straight. The aestivation of *Thenardia* is dextrorse as are all other members of the Mexican Apocynoideae.

FRUIT. The fruit of *Thenardia* is composed of two fused, herbaceous, pendulous, dehiscent follicles developing from two united ovaries. The follicles are moliniform and can reach a length of 40 cm (*T. floribunda*).

The seeds are 6–20 per follicle, fusiform 0.8–2.0 cm long, glabrous, and each with a micropylar coma. The surface is essentially smooth, lacking any surface sculpturing which could prove taxonomically useful. The overall structure of the seeds are essentially similar to the seeds of other genera of the Apocynoideae.

POLLEN. The pollen of *Thenardia* is spherical, triporate, and with a smooth perforate surface (Fig. 1). The diameter of the grains ranges from 30–60 μm (Table 1). *Thenardia chiapensis* and *T. galeottiana* have much smaller grains than *T. floribunda*, a difference correlated with the latter species also

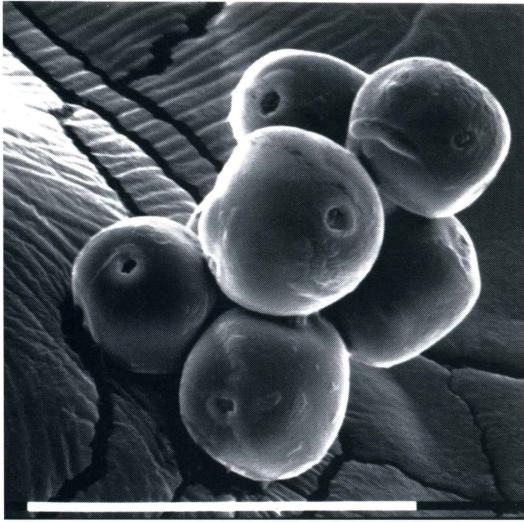


FIG. 1. Microphotograph of *T. chiapensis* pollen. Microbar = 100 μm .

having much larger anthers than the former two (6–7 mm vs. 2.5–5.0 mm). There is not a difference in the diameter of the pollen apertures between the three species. All species have round apertures ranging from 3.5–4.0 (5.0) μm .

The structure of pollen grains in the Apocynoideae is essentially uniform. The majority of species have spherical, 3–4-porate (occasionally 5 to polypantoporate) and with smooth perforate surfaces (Erdtman, 1952; Nilsson, 1990; Sampson and Anusarnsunthorn, 1990; Roubik and Moreno, 1991; Nilsson et al., 1993). Huang (1989) has shown that the number, arrangement and shape of the pores are occasionally useful diagnostic characters for recognizing genera. The latter characters can be

observed using either light or scanning electron microscopy (SEM). The same author also shows that species of a genus can in many cases be distinguished by their exine stratification using freeze/fracture methods with a transmission electron microscope (TEM). The present study and others (e.g., Roubik and Moreno, 1991) show that species of a genus can occasionally be identified by their pollen diameter.

A comparison of SEM photos of pollen in *Thenardia* (Fig. 6) with SEM photos of *Forsteronia* (Hansen, 1985; Nilsson et al., 1993) and *Parsonsia* (Sampson and Anusarnsunthorn, 1990) show the three genera to be little different from one another in pollen characters. Because of the uniform and convergent nature of pollen grains in the Apocynoideae, their study in *Thenardia* provides at present no further insight into its relationship with other genera.

CHROMOSOME NUMBERS. There have been no reported chromosome counts of *Thenardia*, and none were done during the present study. A cursory review of chromosome counts of the Apocynaceae up to 1991 (the last published account of the Index to Plant Chromosome Numbers; Goldblatt and Johnson, 1994) shows that at present the only chromosome counts for genera closely related to *Thenardia* are for *Echites* ($x=6$), *Parsonsia* ($x=9$), *Pentalinon* ($x=6$) and *Prestonia* ($x=9$). A chromosome count of *Thenardia* could help to resolve its placement within the family. However, because studies (Van der Laan and Arends, 1985)

Table 1. Pollen and pore size in *Thenardia* species.

Species	Diameter of pollen	Diameter of pore	Voucher specimen
<i>Thenardia floribunda</i>	50–60 μm	3.0–4.5 μm	<i>Machuca</i> 7337 (TEX)
<i>Thenardia chiapensis</i>	30–45 μm	3.0–4.5 μm	<i>Breedlove</i> 14910 (TEX)
<i>Thenardia galeottiana</i>	30–45 μm	3.0–4.5 μm	<i>Rzedowski</i> 21272 (TEX)

suggest that aneuploidy reduction from the family's basic number of $x=11$ might have occurred multiple times in the family, a count of either $x=6$ or $x=9$ for *Thenardia* could represent a case of convergence rather than a relationship to either of the above mentioned genera. It is of interest, however, that the chromosome count of *Prestonia* is from *P. acutifolia* (Benth.) K. Schum. a species that could be considered a member of *Echites* subg. *Pseudechites* based on its included anthers and reduced sepals (see Gentry (1983b) and J. K. Williams (1996) regarding the differences between *Prestonia* and *Echites*). The count of $x=9$ for both *Prestonia acutifolia* and *Parsonsia* suggests a possible chromosomal relation between the two and with the morphological similarities between *Thenardia* and *Echites* subg. *Pseudechites* acknowledged, a possible relation between *Thenardia* and *Parsonsia* can possibly be inferred. This relationship is highly speculative, however, with so few chromosome counts in the Apocynaceae to compare, (the count of $x=6$ for *Echites* was taken from a species in *E.* subg. *Echites*).

METHODS

The morphological study is based on field observations and the examination of approximately 80 herbarium specimens from the following institutions: F, GH, LL, MA, MEXU, MO, NY, TEX, US.

The pollen of the three species was collected from dried herbarium specimens, TEX/LL. The pollen was not rehydrated, acetolyzed or critical point dried. Observations of *Parsonsia* pollen by Sampson and Anusarnsunthorn (1990) suggest that the skipping of these procedures produces no significant change in either the diameter of the pollen grains or the pores. Pollen grains were mounted onto a SEM stub with double-sided adhesive tape placed in a dessicator for 24 hours and coated with gold using a LADD Sputter Coater. Observations of the pollen were made with a Phillips 515 Scanning Electron

Microscope (Cell Research Center, University of Texas at Austin) and photographed using Polaroid type 55 positive/negative film.

TAXONOMIC TREATMENT

Thenardia H.B.K., Nov. gen. sp. 3: 209. 1819; non Sessé and Moçño, Prodr. 3: 108. 1828. TYPE SPECIES: *Thenardia floribunda* H.B.K.

LIANAS, with multiple herbaceous green stems arising from woody terrestrial stems, sap watery not milky, stems glabrous. LEAVES opposite, petiolate, narrowly elliptic, those of a pair equal in size, pubescent along the base of the midrib below or glabrous, papery when dry; petioles, with a solitary intra-petiolar stipule and 2–4 col-leters at base of petiole; leaf blades entire, apex acuminate-caudate, base acute-obtuse, without colleters, lateral nerves alternate, 5–14. INFLORESCENCES pedunculate tri-chotomous subumbellate cymes. FLOWERS 8–30 per inflorescence; peduncles pubescent or glabrous; bracts narrowly elliptic, straight or curled, glabrous; pedicels puberulent-papillate or glabrous; flowers 5-merous, perfect, actinomorphic; calyx lobes triangular to narrowly elliptic, straight or curled, puberulent or glabrous; colleters ca. 1.0 mm, opposite the sepals, solitary, denti-form; corolla rotate, creamy white to bur-gundy, aestivation dextrorse; tube externally glabrous; lobes ovate; limb 10–30 mm in diameter; stamens wholly exerted, fila-ments five, twisted or straight, pubescent; anthers 2.5–7.0 mm, adnate to pistil head, sterile at apex and base, yellow, bases forked or sagittate with blunt lobes; pistil 3–11 mm long; ovary of two fused carpels united into a common style, superior, ovoid, glabrous, 0.8–2 mm long; pistil head 2–4 mm, fusiform; stigma at base of pistil head; nec-taries five, essentially free, as long as or shorter than the ovary. FRUIT of two united follicles, constricted between the seeds,

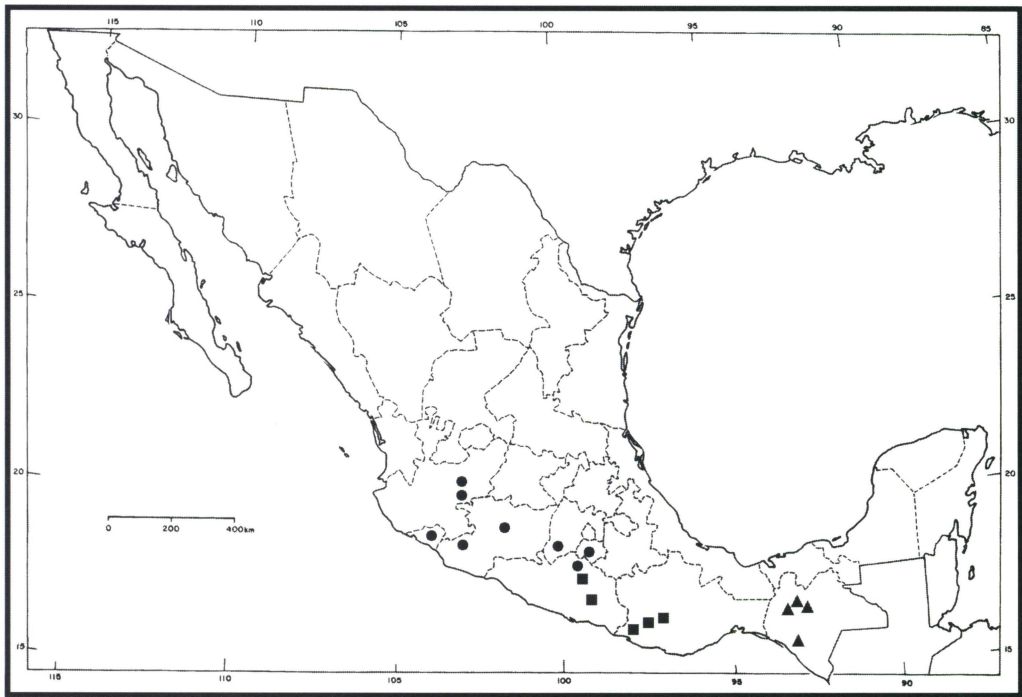


FIG. 2. Distribution map of *Thenardia*; circles = *T. floribunda*, squares = *T. galeottiana*, triangles = *T. chiapensis*.

moniliform, dark green, glabrous, pendulous, longitudinally dehiscent; seeds 6–20 per follicle, glabrous, with micropylar coma; coma white, directed toward the apex of the follicle. CHROMOSOME NUMBER unknown.

Three species endemic to southern and southwestern Mexico (Fig. 2). Zarucchi

(1991) speculated the genus to be in Guatemala, however, to date no specimens have been collected from that country. Flowering from July–October (December), fruiting from October–March, the fruits usually ripening within three months of fertilization.

Key to the species of *Thenardia*

1. Mature leaf blades 5–11 cm long, 2.5–5.5 cm wide; pedicels 15–27 mm long; 20–30 flowers per inflorescence; corolla lobes 8–15 mm long, maroon; filaments coiled. 1. *T. floribunda*
1. Mature leaf blades 2.7–9.2 cm long, 0.5–2.5 cm wide; pedicels 3–8 mm long; 6–15 flowers per inflorescence; corolla lobes 2.0–5.5 mm long, solid white or white with pinkish tinged tips; filaments straight or coiled.
 2. Leaves glabrous; peduncle 1.3–4.7 cm long; bracts 1–2 mm long, narrowly triangular, straight; sepals 1–2 mm long, narrowly triangular, straight; corolla tube 1–2 mm long, not constricted at the mouth; corolla lobes 2–3 mm long, erect; anthers 2.5–3.0 mm long. 2. *T. chiapensis*
 2. Leaves pubescent; peduncle 0.4–0.8 cm long; bracts 3–5 mm long, very narrowly elliptic, reflexed curled; sepals 4–6 mm long, very narrowly elliptic, reflexed curled; corolla tube 2–3 mm long, constricted at the mouth; corolla lobes 5.0–5.5 mm long, spreading; anthers 3.5–5.0 mm long. 3. *T. galeottiana*

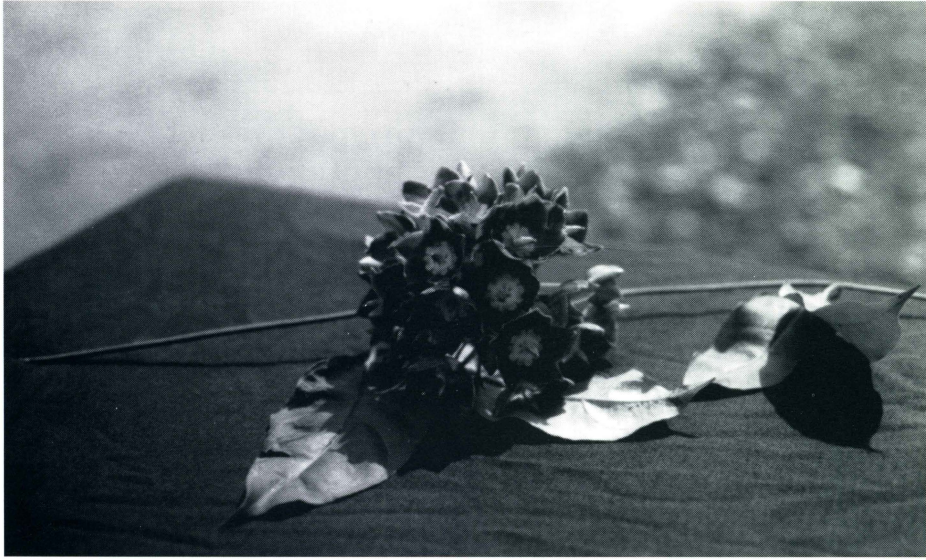


FIG. 3. Photograph of *T. floribunda*, by J. K. Williams.

1. THENARDIA FLORIBUNDA H.B.K.

Thenardia floribunda H.B.K., Nov. gen. sp. 3: 209. pl. 240. 1818. TYPE: MEXICO. "Crescit prope urben Mexici," 1170 m, Jul 1799–1804, F. W. H. A. Humbolt & A. J. A. Bonpland s.n. (HOLOTYPE: P, n.v; photo TEX!).

Thenardia suaveolens M. Martens & Galeotti, Bull. Acad. Roy. Sci. Burxelles 11: 359. 1844. TYPE: MEXICO. MICHOACAN: Uruapan, Sep 1844, H. G. Galeotti 1557 (HOLOTYPE: BR, n.v.).

Echites umbellata Sessé and Moç., Fl. Mexic. 43. 1887, non Jacq. Enum. Pl. Carib. 13. 1760. TYPE: MEXICO. Morelos: Chichipilco, between Amecameca and Ayacapixtla, Aug 1795–1804, M. Sessé & J. M. Moçino. 5074 (HOLOTYPE: MA!; ISOTYPE: F!).

Thenardia tubulifera Woodson, Ann. Missouri Bot. Gard. 19: 381. 1932. TYPE: MEXICO. JALISCO: no date; L. J. G. Diguet s.n. (HOLOTYPE: MO; ISOTYPE: US!).

STEMS glabrous. LEAVES 5.7–12.0 cm long, glabrous above, pubescent below along the midrib and lateral nerves; petioles 7–14 mm long, pubescent; blades oblanceolate, 5–11 cm long, 2.5–5.5 cm wide at middle. INFLORESCENCES with ca 20–30 flowers; peduncles 10–50 mm long, pubescent; bracts ca 1 mm long; pedicel 15–27 mm long, glabrous. SEPALS triangulate-lanceolate, 1–3 mm long, ca 0.6 mm wide, shorter than corolla tube, glabrous. COROLLA 12–17 mm long, maroon, margins of corolla lobes

white; tube 2–5 mm long, constricted at the mouth; lobes spreading, ovate, acuminate, 8–15 mm long, 5–10 mm wide, longer than tube. STAMENS 8–11 mm long; filaments 5–8 mm long, pubescent, coiled around each other; anthers ca 6–7 mm long, forked at base. PISTILS 10–11 mm long; styles 7–8 mm long, glabrous; ovary ovoid, ca 1.5 mm long, glabrous; pistil head fusiform, 2.5–3.0 mm long. NECTARIES to half the length of ovary. MATURE FOLLICLES to 25–40 cm long, 1.0 cm wide; seeds 15–20 per follicle, 1.8–2.0 cm long; coma 1.8–2.2 cm long.

DISTRIBUTION AND ECOLOGY: Semi-deciduous forest and tropical cloud forest of Central Mexico (Guerrero, Mexico, Morelos) and the Nueva-Galicia (Colima, Jalisco, Michoacán) region of Mexico (Fig. 1), 1200–2200 m. Usually growing along rivers and waterfalls with *Achimenes*, *Adiantum*, *Bursera*, *Ficus*, *Hedyosmum*, *Inga*, *Ipomoea*, *Juglans*, *Lopezia*, *Manihot*, *Oplismenus*, *Oxalis tetraphylla*, *Russelia*, *Senecio*, *Sida*, *Solanum*, *Tecoma stans*, *Thevetia thevetiodes*, and *Toxicodendron*.

ILLUSTRATION: Photo of flower (Fig. 3); reproduction of plate 240 in Kunth (1819) (Fig. 4).

Tab. 240.



Tuepin del. et litho.

THENARDIA floribunda.

FIG. 4. Reproduction of plate of *T. floribunda* from Kunth (1819).

REPRESENTATIVE SPECIMENS EXAMINED. MEXICO. Colima: Rancho El Jabalí, 22 km NNW of Colima in the SW foothills of the Volcán de Colima, clay soils on steep volcanic slopes and alluvial flats, humid montane forest (19° 27' N, 103° 40' W), 1300 m, margins of Lago Epazote, 6 Feb 1991, *Vázquez 443* (MEXU, MO). Guerrero: La Landa, 5 km al SW of Taxco, camino Taxco-Ixcateopan, ca 200 yards N of road along the W bank of ravine (18° 33' N, 99° 37' W), 15 Aug 1995, *Williams 80* (TEX). Jalisco: Parque de Barranca de Huentitán on northern outskirts of Guadalajara, microcuenca de las 7 cascadas, 2 km E of Tonalá, 1200 m, 29 Jul 1990, *Flores & Ramos 2401* (MO, MEXU, TEX); Mpio. Jocotepec, ladera S of Cerro Viejo, barranca del agua, 2200 m, 2 Jul 1996, *Machuca 7337* (TEX); Mpio. Jocotepec, cauce conocido con el nombre de Jaral, exposición sur, 2.5 km de Huejotitán, 2 Aug 1986 *Nuñez 3049* (MO); Mpio. Jocotepec, Ojo de Agua de Flores, ladera S enfrente de Santa Luciano, 2000 m, 31 Aug 1987, *Machuca 6051* (MO). Mexico: Nanchititla, Dist. Temascaltepec, 22 Aug 1935, *Hinton 8204* (F, NY, TEX). Michoacán: Zanzamora, Dist. Coalcomán, 1630 m, 26 Sep 1938, *Hinton 12253* (F, GH, MO, NY, TEX); Sierra Naranjillo, Dist. Coalcomán, 1500 m, 18 Oct 1941, *Hinton 15989* (GH, TEX); Dist. Coalcomán, Saltire-Masa, 1760 m, 30 Oct 1938, *Hinton et al. 12481* (F, NY). Morelos: Tepoxteco, Dec 1952, *Lyonnet 5212* (MEXU); Bluffs of barranca near Cuernavaca, 10 Aug 1898, *Pringle 6966* (F, MO, NY).

Thenardia floribunda is perhaps the most beautiful species of *Thenardia* (Figs. 2, 3). It is readily distinguished from the other two species by its densely congested inflorescences, maroon flowers (vs. white), wide leaves (2.5–5.5 cm vs. 0.5–2.2 cm) and long pedicels (15–27 mm vs. 3–8 mm). This species is quite distinct from the other two species, but, because of its distribution, coiled filaments and pubescent leaves, it seems likely that it is more closely related to *T. galeottiana*.

This species has been reported as having extremely fragrant flowers by various authors (Martens and Galeotti, 1844; Sessé and Moçño, 1887; Woodson, 1936) and field collectors (*Machuca 7337*). Field observations by the author, however, failed to uncover any flowers with a heady odor.

Woodson (1932, 1936) distinguished *T. tubulifera* from *T. floribunda* by its salverform corolla (vs. rotate), corolla tube 5–6 mm long (vs. 2–4 mm) and corolla lobes

7–8 mm long (vs. 10–13 mm). These differences were apparently based on data from only four herbarium specimens. An accumulation of herbarium specimens alongside field observations has allowed the author to observe the natural variation of *T. floribunda*, leading to the conclusion that the character differences between *T. tubulifera* and *T. floribunda* are not significant enough to warrant the recognition of two distinct species. The larger flowers of *T. tubulifera* appear to represent an extreme form of *T. floribunda*, and therefore it is here regarded as a synonym of the latter species.

Martens and Galeotti (1844) described *Thenardia suaveolens* from a single specimen (*Galeotti 1557*; BR) collected in Michoacán. They distinguished the species from *T. floribunda* on the basis of its rose colored flowers (vs. whitish-green) and its long corolla tube. They discuss in the protologue that the specimen was growing in the village of Uruapan at the base of a Lauraceae tree. The Indians of the village proudly displayed the liana to foreigners visiting the area. Galeotti remarks that the Indians were protective of the plant implying that he was not allowed to collect many samples. This perhaps explains why isotypes have not been distributed to other herbaria, as opposed to the type of *T. galeottiana* (*Galeotti 1565*; F, GH, MO, NY, US). I have not had an opportunity to observe the type of *T. suaveolens*. However, from the description, locality, and comments I am confident that it is a synonym of *T. floribunda*.

Sessé and Moçño (1887) described *Echites umbellata* from one locality in Morelos, Mexico stating that the corolla is "rotato-campanulata," and the leaves "ovato-oblonga." Indeed, there is one specimen (5074) of *Thenardia floribunda* H.B.K. in the Sessé and Moçño collections housed at MA with those exact same comments written on the label. Although the specimen is labeled *E. rota*, many of the names written on the specimen label were not followed in



FIG. 5. Holotype of *T. chiapensis* (TEX).

any of the posthumously published works of Sessé and Moçño. The description of *E. umbellata* also states that the flowers are fragrant and purple, characters associated with *T. floribunda*. The type locality (Morelos) of *E. umbellata* corresponds as well with the range of *T. floribunda*.

The species epithet refers to the profusion of flowers produced by each individual inflorescence.

2. THENARDIA CHIAPENSIS J. K. Williams

Thenardia chiapensis J. K. Williams, Brittonia 47: 403. 1995. TYPE: MEXICO. Chiapas: Moist gradual slope in the paraje of Mahosik, Mpio. Tenejapa, 4800 ft, 8 Aug 1966, *D. E. Breedlove 14837* (HOLOTYPE: TEX!; ISOTYPES F!, MEXU!, NY!).

STEMS glabrous. LEAVES 5.0–10.5 cm long, glabrous; petioles 6–18 mm long, glabrous; blades oblanceolate, 4.0–9.2 cm long, 5–22 mm wide at middle. INFLORESCENCES with ca 6–12 flowers; peduncle 13–47 mm long, pubescent; bracts 1–2 mm long, narrowly triangular, straight; pedicel 4–7 mm long, glabrous. SEPALS narrowly triangular, straight, 1–2 mm long, ca 0.5 mm wide, shorter than corolla tube, glabrous. COROLLAS 4–6 mm long, white, with reddish tinge at ends of lobes; tube 1–2 mm long, not constricted at the mouth; lobes ovate, acuminate, 2–3 mm long, ca 1 mm wide, equal in size to the tube, erect. STAMENS 3–4 mm long; filaments 0.8–1.2 mm long, pubescent, straight; anthers 2.5–3.0 mm long, bases sagittate with blunt lobes. PISTILS 3–4 mm long; styles ca 1–2 mm long, glabrous; ovaries ovoid, ca 0.8 mm long, glabrous; pistil heads fusiform, ca 2 mm long. NECTARIES as long as to slightly shorter than ovary. Mature FOLLICLES 14–18 cm long, glabrous; seeds 6–9 per follicle, 0.8–1.3 cm long; coma 1–1.3 cm long.

DISTRIBUTION AND ECOLOGY: Endemic to the wooded moist slopes of the Central Plateau region of Chiapas (Breedlove, 1981)

and the Sierra Madre of Chiapas, Mexico (Fig. 2), 1100–1700 m. Usually growing along waterways with *Acacia*, *Liquidamber*, *Nyssa*, *Pinus*, *Quercus*, and *Salvia*.

ILLUSTRATION: Photo of holotype (Fig. 5); line drawing of flower (J. K. Williams, 1995).

REPRESENTATIVE SPECIMENS EXAMINED. MEXICO. Chiapas: 2–4 km below Ixhualán, along road to Pichucalco, 27 Sep 1971, *Breedlove 19937* (MEXU); Paraje of Mahosik, 8 Aug 1966, *Breedlove 14910* (F, NY, TEX); Slope along the Río Hondo, 6.5 km N of Jitotol, along road to Pichucalco, Mpio. de Jitotol, 1700 m, 27 Oct 1971, *Breedlove 21372* (F, MEXU, NY, TEX); Steep walled canyon with seasonal evergreen forest and grassy slope below Burrero on road from Zinacantán Center to Ixtapa, Mpio. de Ixtapa, 1158 m, 25 Aug 1981, *Breedlove 52399* (TEX); Steep wooded slope on the bank of the Río Hondo, 4 mi N of Jitotol on the road to Pueblo Nuevo Solistahuacán, Mpio. de Jitotol, 5500 ft, 20 Aug 1965, *Breedlove 12046* (F, TEX); Kulaktik, Mpio. de Tenejapa, 5 Dec 1983, *Tøn 7041* (F, LL, TEX); Ojo del Río Cueva Yashanal, Mpio. de Tenejapa, 1500 m, 15 Oct 1982, *Tøn 4812* (F, TEX); Reserva El Triunfo, polígono Campamento, HQ-Finca Prusia (15° 39' N, 92° 48' W), 23 Jun 1990, *Heath & Long 1257* (MEXU).

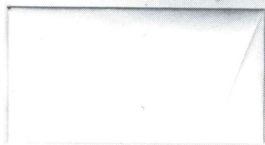
Thenardia chiapensis is readily distinguished from the other species by its glabrous leaves, erect corolla lobes, and smaller flowers. Because the corollas are highly reduced in size this species is often confused with *Cynanchum* (Asclepiadaceae) (Zarucchi, 1991). It can be readily distinguished from *Cynanchum* in the field by its watery sap (vs. milky), glabrous habit (vs. pubescent), eglandular leaves (vs. glandular at the apex of petiole) and vegetative parts with an overall shiny green appearance (vs. dull grayish-green).

Its short pedicels, thin leaves, sparse inflorescence, small corolla and pollen grains 30–45 µm in diameter, indicates that this species is most closely related to *T. galeottiana*.

The species epithet is in reference to the Mexican state to which the species is endemic.



UNITED STATES NATIONAL MUSEUM



N^o 1568 Coll. H. GALEOTTI.
 EX. HERB. BRUXELLENSIS
Clala
 Mexico, prov^o de
 h^orr^o
 Aug 1846. II.



STUDIES IN THE APOCYNACEAE
Thevardia galeottiana Baill.
 5/35 DET. R. E. WOODSON, JR.

PLANTS OF MEXICO
 RECEIVED BY THE U. S. NATIONAL MUSEUM IN 1907 FROM THE JARDIN BOTANIQUE DE
 L'ETAT, BRUXELLES
Thevardia galeottiana Baill.
 No. H. GALEOTTI, Collector

FIG. 6. Isotype of *T. galeottiana* (US).

3. *THENARDIA GALEOTTIANA* Baill.

Thenardia galeottiana Baill., Bull. Mens. Soc. Linn. Paris, ii: 819. 1890. TYPE: MEXICO. Oaxaca: Talea, 3000 ft, Aug 1844, *H. G. Galeotti 1565* (HOLOTYPE: BR n.v.; ISOTYPES F!, GH!, MO!, NY!, US!).

Thenardia gonoloboides Woodson, Ann. Missouri Bot. Gard. 23: 274. 1936. TYPE: MEXICO. Oaxaca: canyons of mountains near Oaxaca, 6500 ft, 20 Aug, 1894, *C. G. Pringle 4822* (Holotype: MO!; Isotypes: GH!, US!, MEXU!, NY!).

STEMS glabrous. LEAVES 3–9 cm long, glabrous above, pubescent below along the midrib and lateral nerves; petioles 4–12 mm long, pubescent; blades oblanceolate, 2.7–6.5 cm long, 6–20 mm wide at middle. INFLORESCENCES with ca. 6–15 flowers; peduncle 4–8 mm long, pubescent; bracts 3–5 mm long, very narrowly elliptic, reflexed curled; pedicel 3–8 mm long, glabrous. SEPALS very narrowly elliptic, reflexed curled, 4–6 mm long, ca. 0.6 mm wide, longer than corolla tubes, glabrous. COROLLA 7–9 mm long, white, tips of lobes occasionally pinkish; tube 2–3 mm long, constricted at the mouth; lobes spreading, ovate, acuminate, 4.0–5.5 mm long, 3–4 mm wide, longer than tube. STAMENS 5–6 mm long; filaments 2–3 mm long, pubescent, straight, occasionally coiled; anthers 3.5–5.0 mm long, forked at bases. PISTILS 4–5 mm long; styles ca 3 mm long, glabrous; ovaries ovoid, ca 1.5 mm long, glabrous; pistil heads fusiform, ca 2 mm long. NECTARIES as long as to slightly shorter than ovary. Mature FOLLICLES to 12 cm long, 1.0 cm wide; seeds unknown.

DISTRIBUTION AND ECOLOGY: Montane oak-juniper forest of Oaxaca and Guerrero (Fig. 2), 1250–1600 m, with *Bursera*, *Juniperus*, and *Quercus*.

ILLUSTRATION: Photo of isotype (Fig. 6); line drawing of flowers (J. K. Williams, 1995).

REPRESENTATIVE SPECIMENS EXAMINED. MEXICO. Guerrero: Iguala, 12 Aug 1905, *Rose 9424*

(F, GH, NY); Iguala Canyon, 21 Sep 1905, *Pringle 13585* (GH). Oaxaca: El Vado, Mpio. Ejutla, 71 km de la Oaxaca-Sola de Vega, 29 Sep 1965, *Rzedowski 21272* (TEX); Dist. Tehuantepec, recorrido Santa Lucía, a Las Cruces, al O de El Limón, 19 Aug. 1985, *Martínez 124* (MEXU); 15 km al SO de Buenos Aires, hacia Tenango, entrada por Hierba Santa, 10 km al NO de Tehuantepec, 13 Sep 1985, *Torres 7365* (MEXU); Mpio. Totolapan, 10 km de la desv. a Portillo San Dionisio rumbo a Totolapan, 12 Jun 1987, *Saynes 1283* (MEXU); Canyons of mountains near Oaxaca, 20 Aug 1894, *Pringle 4822* (GH); Rancho de Calderón, 13 Aug. 189, *Smith 151* (GH).

Thenardia galeottiana is readily distinguished from the other members of the genus by its short peduncle (4–8 mm vs. 10–50 mm), and reflexed curled sepals and bracts.

Thenardia galeottiana shares a combination of characters with both species. With *T. chiapensis* it shares nectaries as long as the ovary, follicles and pistil of the same length, pedicels 3–8 mm long, 6–15 flowers per inflorescence, white corollas with pinkish tips and pollen 35–50 μm in diameter (Table 1). With *T. floribunda*, *T. galeottiana* shares pubescent leaves, coiled filaments, distribution and spreading corolla lobes. Because *T. galeottiana* shares more reproductive features (e.g., pollen and pistil dimensions) with *T. chiapensis* it seems evident that the two are more closely related.

Woodson (1936) regarded *T. gonoloboides* as distinct from *T. galeottiana* on the basis of its obtuse corolla lobes (vs. acute), narrowly triangular episealous col-leters (vs. dentiform), nectaries half the length of ovary (vs. equal to or surpassing), and an overall larger corolla. These distinctions were based on Woodson's observation of only three herbarium specimens. After having examined both the types and additional collections of the above mentioned species the author concludes that above characters are merely extremes of the natural variation of *T. galeottiana*. Consequently, *T. gonoloboides* is here regarded as a synonym of *T. galeottiana*.

This species was named in honor of H. G. Galeotti (1814–1858) French born

botanist, geologist and field collector in Cuba and Mexico.

EXCLUDED TAXA

- Thenardia corymbosa* Benth., J. Bot. (Hooker) 3: 246. 1841. = *Forsteronia schomburgkii* A. DC. (fide Hansen, 1985); = *Forsteronia umbellata* (Aubl.) Woodson (fide Woodson, 1936).
- Thenardia laurifolia* Benth., J. Bot. (Hooker) 3: 246. 1841. = *Forsteronia laurifolia* (Benth.) A. DC. (fide Woodson, 1936; Hansen, 1985)
- Thenardia scabra* Spreng., Syst. iv. Cur. Post. 65. = *Lyonsia scabra* (Spreng.) A. DC. = *Parsonsia* sp.?
- Thenardia umbellata* (Aubl.) Spreng., Syst. 1: 636. 1825. (*Apocynum umbellatum* Aubl., Hist. pl. Guiane 1: 275. 1775.) = *Forsteronia umbellata* (Aubl.) Woodson (fide Woodson, 1936; Hansen, 1985)
- Thenardia rosea* Sessé and Moç. ex DC., Prodr. 3: 108. 1828. = *Rhynchanthera mexicana* DC. (Melastomataceae) (fide Renner, 1990)

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I would like to thank the curators of the following herbaria for allowing me the opportunity to examine their specimens: F, GH, MA, MEXU, MO, NY, TEX, US. Piero Delprete provided valuable literature as well as translations of French text. I would also like to credit the staff of the Cell Research Center (University of Texas at Austin) for allowing me access to their scanning electron microscope; in particular I would like to thank John Mendenhall for his instruction and help.

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LIST OF EXSICCATAE

- Breedlove, D. E. 12046 (2); 14910 (2); 19937 (2); 21372 (2); 52399 (2)
- Flores, A. and Ramos, P. 2401 (1)
- Heath, M. and Long, A. 1257 (2)
- Hinton, G. B. 2150 (1); 8204 (1); 12253 (1); 12481 (1); 15989 (1)
- Lott, E. J. 3018 (1)
- Lyonnet, P. 5212 (1)
- Machuca, J. A. 6051 (1); 7337 (1)
- Martinez, E. 124 (3)
- Nuñez, J. C. S. 3049 (1)
- Pringle, C. G. 4822 (3); 6966 (1); 7242 (1); 13585 (3)
- Rose, J. N. 9424 (3)
- Rzedowski, J. 21272 (3)
- Salas, E. 1228 (1)
- Sanders, A. C. et al. 10892 (1)
- Saynes, A. 1283 (3)
- Smith, J. D. 151 (3).
- Ton, A. S. 4812 (2); 7041 (2)
- Torres, M. L. 7365 (3)
- Williams, J. K. 40–95 (2); 80 (1); 120 (1)

NUMERICAL LIST OF SPECIES

1. *Thenardia floribunda* H.B.K.
2. *Thenardia chiapensis* J. K. Williams
3. *Thenardia galeottiana* Baillon