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# A New Penicillate-Stigma Species of *Waltheria* (Sterculiaceae, Hermannieae) Endemic to Belize

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**ABSTRACT.** *Waltheria belizensis* J. G. Saunders, a new distinctive Sterculiaceae species known only from Mountain Pine Ridge National Forest Reserve, Cayo District, Belize, and potentially distylous by floral morphology, is described and illustrated. It is placed in section *Waltheria* L. in the *W. cinerescens* A. St.-Hilaire alliance by its penicillate stigma and loculicidal capsule with an extensive corneous endocarp. It is closest to the distylous *W. petiolata* K. Schumann in Martius from Brazil (Rio de Janeiro) by the decomposite inflorescences; the shape, venation, and vestiture of calyces; and the shapes of petal apices and seeds. *Waltheria belizensis* differs from *W. petiolata* by leaves with minute, appressed vestiture, revolute teeth margins, and a greater number of lateral veins; corymbiform inflorescences; and a seed less lobed and less pustulate. The contrasting characters are detailed in a key. Thrum-like pollen of *W. belizensis* and thrum pollen of confirmed *W. petiolata* are reported for the first time. These data suggest the thrum-like pollen of the Belizean species is less derived than that of the Brazilian one. A key is provided to separate *W. belizensis* from the only other species of *Waltheria* in Belize, *W. indica* L. s.l. The present and additional studies concur with previous exclusion of *W. glomerata* C. Presl from the flora of Belize, based solely on Dwyer & Liesner 12292, the type of *W. belizensis*. Other Belizean plant endemics found in the Mountain Pine Ridge National Forest Reserve are listed, and the region is discussed.

**Key words:** Belize, Byttnerioideae, Hermannieae, Malvaceae, Mountain Pine Ridge Reserve endemics, pollen morphology, Sterculiaceae, *Waltheria*.

Revision of material of *Waltheria* L. (Sterculiaceae<sup>1</sup>) for *Flora Mesoamericana* and a generic monograph (Saunders, 1995) have revealed a very distinctive undescribed species known only from Belize, as well as the first *Waltheria* species endemic to Mesoamerica. It is presented in detail here because

the new taxon is not included in the monograph and is possibly rare or relictual (Saunders, unpublished obs.), with only one known collection from 1974.

The new species possesses floral morphology consistent with thrum flowers and thrum pollen of distylous species of *Waltheria*, suggesting that it is potentially distylous. It is placed in the *W. cinerescens* A. St.-Hilaire alliance (= *W. cinerescens* clade sensu Saunders, 1995; Saunders, unpublished phylogenetic analysis) close to *W. petiolata* K. Schumann in Martius.

A key is provided to distinguish the new species from *Waltheria indica* L. s.l. seen from Belize (*Schipp* 504, NY; *Hill* 20386, NY; *Gentle* 8457, NY; and *Gentle* 1054, NY). *Waltheria indica*, as used in America, is not monophyletic (Cristóbal et al., 2005; Saunders, 2005) and needs more study.

***Waltheria belizensis*** J. G. Saunders, sp. nov. TYPE: Belize. Cayo District: Mt. Pine Ridge, 4.5 mi. S of Blancaneaux Lodge, 29 Jan. 1974, *John D. Dwyer & R. L. Liesner* 12292 (holotype, MO 2248285). Figures 1, 2A–G.

Haec species *Waltheriae petiolatae* affinis, sed pedicellis florum praesentibus; pubescentia vegetativa minuta, adpressa, rigida, ferrugineo-hyalina; foliorum nervis lateralibus pluribus (8 ad 13 paria) et dentibus marginalibus revolutis; aspectu apicali seminis minus lobato et cuticula seminali minus pustulata differt.

Shrubs ca. 1 m tall; stems straight, terete, sub-foliose apically, completely beige-covered; vestiture 2-tiered, the trichome overlayer sparse, deciduous, stellate-tomentose, the trichomes stalked, the radii spreading, twisted at tips, thinner and longer than underlying ones, to 0.5 mm, the underlayer densely stellate-tomentulose, persistent, the radii 10 to 12, 0.2(0.4) mm, rigid, appressed, conical, hyaline tinged ferruginous, brown contents basally; trichome stalks persistent after rays shed at times, 0.1–0.2(0.4) mm, castaneous, cylindrical to conical; cortex castaneous,

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<sup>1</sup> Hermannieae, including *Waltheria*, formerly in Sterculiaceae s.l., is now placed along with Theobromateae, Byttnerieae, and Lasiopetaleae in the Byttnerioideae, basal to the Grewioideae, formerly in Tiliaceae, in an expanded Malvaceae s.l. (Bayer & Kubitzki, 2003; Whitlock et al., 2001).



Figure 1. *Waltheria belizensis* J. G. Saunders. —A. Flowering branch. —B. Detail of revolute abaxial leaf margin. —C. Involucre, two stipules, and bradytelic leaf, from node below D. —D. Primary sympodial cyme with flower pair and two bracts above and below, developing cyme buds removed. —E. Thrum-like flower, opened, minus one calyx lobe, minus petals above base, minus pistil, with androecium and connate, adnate petal bases not removable, as irregular ring at base above lobed receptacle. —F. Petal, abaxial, missing base drawn in. —G. Pistil. —H. Capsule halved, interior view, showing extent of corneous endocarp from apex to lower broken line. —I. Seed, lateral view. —J. Seed, apical view. Based on the holotype, *Dwyer & Liesner 12292* (MO); B–J drawn by camera lucida by Saunders; A drawn and A–J inked by Francisco Rojas.

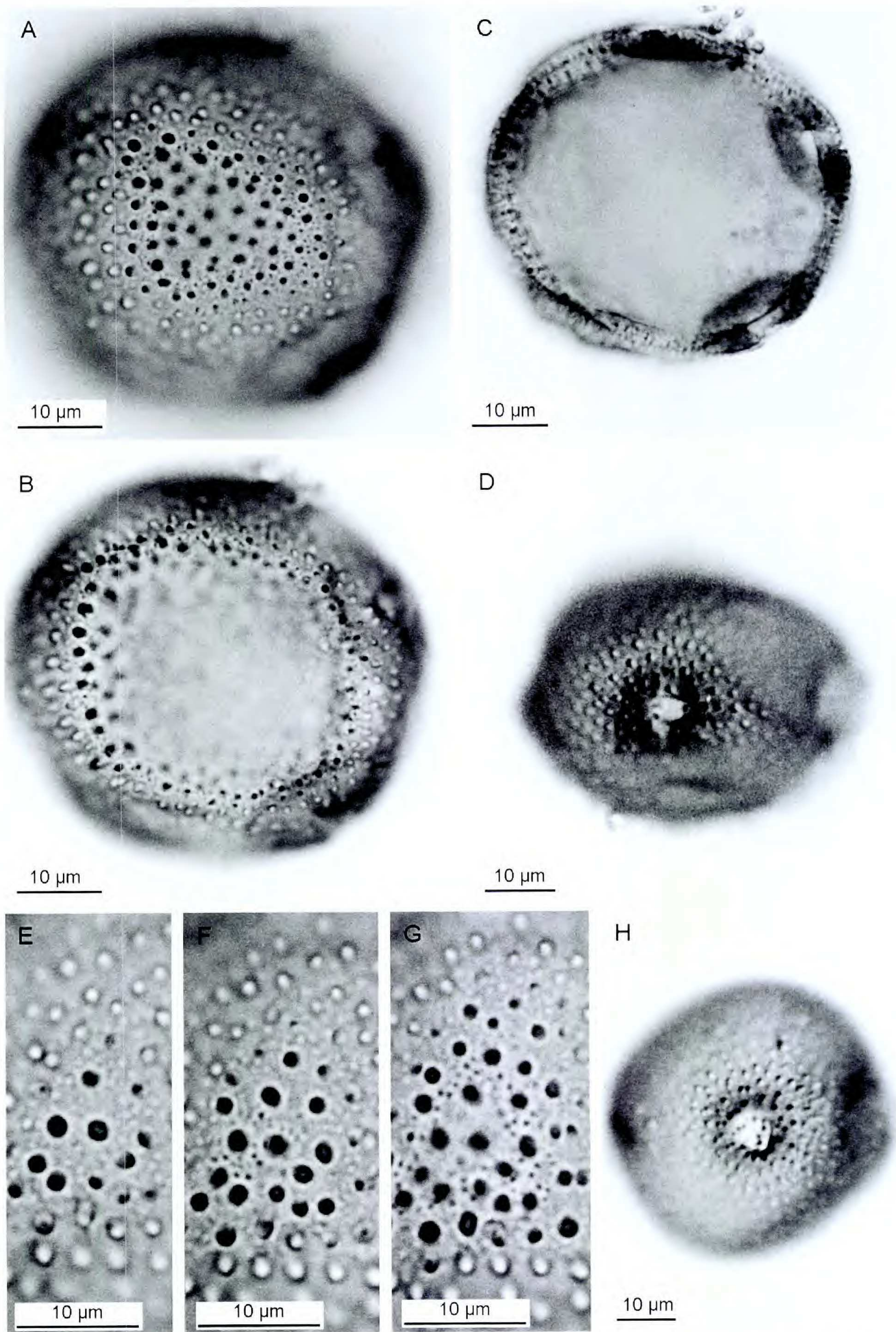


Figure 2. Thrum-like pollen morphology of *Waltheria belizensis* J. G. Saunders compared to thrum pollen aperture morphology of *W. petiolata* K. Schumann. A–G. *Waltheria belizensis* J. G. Saunders, from *Dwyer & Liesner 12292* (holotype, MO). —A–C. Lux obscuritas (LO) pattern of pollen grain in polar view. —D. Equatorial view of pollen grain with ectoaperture in Nomarsky focus. —E–G. LO pattern of pollen wall in polar view showing large dark spinules and smaller baculae. —H. *Waltheria petiolata* from *Saunders & Peixoto 3197* (SI), equatorial view of pollen grain with ectoaperture in Nomarsky focus.

glossy, finely anastomose, tuberculate from trichome stalks. Leaves with 2/5 phyllotaxy; leaf blades narrowly ovate to ovate-lanceolate, sublanceolate,  $2-7 \times 0.9-3.6$  cm (L:W ratio 1.9-3.3:1), the bases rounded and entire, the apices widely acute-apiculate from an extended apical tooth, lateral margins crenate-mucronate, all of tooth margin revolute, the adaxial surfaces darker, grayish olive, pinkish brown-tinged when dry, slightly rugose, a little convex between lateral veins, more rugose and plicate marginally, the trichome overlayer sparse, subsessile, the trichome underlayer densely diminutively stellate-tomentulose, obscuring surface, the trichome radii fine, appressed, mostly 0.1(0.2) mm long, the abaxial surfaces gray-olive, minutely tomentose, obscuring surface, the trichome radii 0.3-0.4 mm, finer, whiter, more spreading compared to those above; veins 8 to 11(13) lateral pairs, 2 to 3 of these at base, 1 subcostal, first through third order veins impressed adaxially, raised abaxially; petioles (0.3)0.6-1.5(1.7) cm  $\times$  0.8-1 mm, woody, at base semi-terete, oblate at midlength, adaxially shallowly tapering-sulcate up to 1/4 twist at apex, the apex flattened above, slightly ridged on sides, the dorsal ridge very prominent, the cortex and vestiture as stem; stipules 3-5  $\times$  0.3-0.6 mm, linear-lanceolate, adaxially short-pubescent with mostly simple and few-branched trichomes, with uniseriate filiform glandular trichomes at apex. Inflorescences pedunculate, axillary, compressed-deltoid, 1.5-5 cm diam., by Schumann's (1886: 52, 62) terms "decompositae, corymbiform-disposed cymes from cincinni brought together by many short, free naked branchlets"; peduncles 0.3-2 cm  $\times$  0.6-0.8 mm. Primary cyme sympodial; flower pairs subtended by 4 bracts; nodes between flower pairs bearing 3 bracteoles, apparently consisting of 2 stipules and a central teretely based bradytelic leaf with filiform glandular hairs; bracts subequal, 5-7.5  $\times$  0.5-0.8 mm, lanceolate to linear, stellate-setulose abaxially and on margins, the margins subserrulate, the adaxial surface stellate-tomentulose. Flowers potentially distylous, only thrum-like flowers seen. Thrum-like flowers pedicellate; pedicels 0.4-1  $\times$  0.2-0.3 mm, longest in fruit, tuberculate; calyx persistent, turbinate, 5-6  $\times$  3-5 mm, divided halfway; laciniae lanceolate-acuminate, longitudinally inflexed and concave adaxially along midvein, 2.7-3.8  $\times$  1-1.2 mm, with lateral veins subcostal, with midvein not prominent, the areoles obscure, puberulent within above base with simple and bifurcate straight acropetal hairs to 0.4 mm, short-villose with flagellate hairs at apices; calyx tube inside faintly veined between non-prominent lateral veins and midvein, the lateral veins not adjoined 0.3 mm below sinuses, subglabrous, a few simple trichomes above

nectaries; nectary 0.8 mm; corolla yellow, the base gamopetalous and tubular for 0.4 mm with claw dissecting away only above connate portion adnate to staminal tube (Fig. 1E); petals maturing last, opposite stamens in early stages, becoming subopposite by growth of stamen tube, 4.7-6  $\times$  1.2-1.5 mm; lamina narrowly obovate, obovate-oblong, the base usually gradually attenuate, the apex rounded and retuse, where a few minute hairs (simple, V-shaped, 0.2 mm) occur, hirsute within for 2/3 length above claw, a few hairs above, hairs to 0.4 mm, outer surface with minute appressed-stellate hairs scattered over veins (radii 10 to 20, 0.2 mm long), primary to secondary veins a little thick except near margins; claw ca. 1.2  $\times$  0.6 mm, alate, undulate at apex, adnate for 0.4 mm basally to stamen tube, vein strap-like, cuneate; thrum-like stamens 5.5 mm long; stamen tube 1.7 mm (1/3 length), slightly imparipinnate, semitransparent with filaments thickened mid-length to apex; free filaments 3.3 mm, thick, darker-colored, glabrous; anthers oblong, 0.8-1 mm, the apex incised, connective dark; pistil 4 mm; ovary apex velutinous, with hairs to 1 mm; style filiform (oblate in transection), densely hirsute to apex; stigma penicillate, hemi-globose, 1.2  $\times$  1.8 mm, with ca. 30 branches 0.8-1 mm, the column 0.4 mm. Capsule loculicidal, inclined-turbinate, the apex curved and apiculate (near style), apex tomentose; endocarp thinly corneous almost to base (Fig. 1H), only membranous at base and laterally at sutures; seed in lateral view obovoid-rhomboid, 1.8-1.9  $\times$  1.2-1.3 mm, apex lacking apical ridge, undulations, or sulci, in apical view contour subpentagonal with each 1 of the 3 anterior lobe faces obtuse-rounded, similar, the posterior face truncate; strophiole calyptrate, red, 0.1  $\times$  0.4 mm, very shallowly triangular; cuticle pusticulate and ochre apically, brown and striate-foveolate below to base; testa castaneous, shiny.

Pollen of thrum-like flowers (N = 15 except as noted): exine spinulose, apertures 5 to 6 (average 5.2, N = 113), zonocolporate, colpus index (polar axis/colpus length) = 3.9, 49.3  $\times$  51.8  $\mu$ m, polar diameter/equatorial diameter (P/E) ratio = 0.95, oblate-spheroidal, colpi 12.6  $\times$  2.5  $\mu$ m, baculae ca. 0.8  $\mu$ m, spinulae ca. 1  $\mu$ m, ora lalongate, 4  $\times$  12.8  $\mu$ m (N = 10). Figure 2A-G.

*Distribution and habitat.* From extensive museum material examined without any other examples of *Waltheria belizensis* seen, it appears to be a restricted endemic to the Mountain Pine Ridge (MPR) National Forest Reserve situated along the northern drier slopes of the Maya Mountains in the Cayo District of Belize. The single locality known, 4.5 km south of Blancaneaux Lodge, occurs at or near the Douglas

D'Silva Forest Station (16°58'0N, 88°58'60W), situated at 495 m elevation, with an annual rainfall of 1550 mm and seasonally dry February through May (Falling Rain Genomics, 2006; Casado Internet Group, 2006). The Douglas D'Silva Forest Station, which was previously called the Augustine Forest Station, borders savanna vegetation class 17: Pine forest, savanna class 19: Transitional pine, grass, and palmettos, and savanna class 20: Open grass (Penn et al., 2004: 37–39; associated species given there) in a zone characterized by Balick et al. (2000: 2) as “highly weathered, nutrient-poor soils of igneous and metamorphic origin.”

*Other MPR plant endemics.* The MPR Reserve is of interest for its physical and historical geology, isolated grass and pine savanna (Penn et al., 2004; Casado Internet Group, 2006), and potential for endemism (Balick et al., 2000), raising the question of whether the savanna there has been long maintained (see Cole, 1982). Because estimates for the number of plant endemics present within and limited to the park were not given in the literature, a list was compiled. Updating distributions (W3TROPICOS, 2006) for the 41 plant species of listed country endemics provided by Balick et al. (2000), combined with other data in Balick and Johnson (1994), Penn et al. (2004), and the new data for *Waltheria belizensis*, provides data that nine of the 38 Belizean flora endemic species considered here (nearly 24%) are present within the reserve, and that four of them (10% of Belizean plant endemics) are restricted to the MPR reserve, which has an area of nearly 200 square miles (among 18,000 square miles in Belize) and an elevation ranging from 394 to 3336 m (Balick et al., 2000; Casado Internet Group, 2006). Three species (ca. 8% of the country endemics) appear to be limited to the Douglas D'Silva Forest Station–Blancaneaux Lodge zone: (1) *Waltheria belizensis* is calculated to belong to class 19 at 100 m (cf. the electronic version of the Penn et al. (2004) vegetation map (Lone Aagesen, pers. comm., 2006)), (2) *Mimosa pinetorum* Standley (W3TROPICOS, 2006), and (3) *Syngonanthus bartlettii* Moldenke (W3TROPICOS, 2006) is cited as endemic to class 20 (Penn et al., 2004) and its present country endemic status is confirmed (N. Hensold, pers. comm., 2006). *Koanophyllon sorensenii* R. M. King & H. Robinson is also contained within the reserve limits, but *Axonopus ciliatifolius* Swallen, primarily from the Douglas D'Silva Forest Station–Blancaneaux Lodge zone, shows one collection in another district. Other country endemics are broadly present within the reserve, but not limited to it: *Anemia bartlettii* Mickel, *Schippia concolor* Burret, *Zinowiewia pallida* Lundell, and *Telanthophora bartlettii* H. Robinson & Brettell. This

apparent high endemism for the MPR reserve needs assessment.

Several species at the MPR reserve are here considered excluded from country endemic status: *Galactia anomala* Lundell (W3TROPICOS, 2006; Pérez et al., 2005: 94), *Calyptanthes bartlettii* Standley, and *Metastelma stenomeres* (Standley & Steyermark) W. D. Stevens. Another species that has not been found at the MPR reserve is also excluded: *Piper schippianum* Trelease & Standley (W3TROPICOS, 2006).

#### KEY TO THE SPECIES OF *WALTHERIA* IN BELIZE

- 1a. Inflorescences to 4.5 cm diam., in age decomposite from many naked branchlets becoming diffuse at base with their cincinni brought closely together forming a compressed-deltoid, flat-topped, corymbiform cluster; leaves with surfaces obscured on both sides, pale gray-olive, tomentulose above with minute appressed-stellate trichomes 0.1–0.2 mm long, tomentose below, with 8 to 13 pairs of lateral veins; flowers thrum-like, possibly pin-like, pedicellate (0.4–1 mm long); calyx divided halfway, the laciniae 2.7–3.8 mm long, lanceolate-acuminate  
..... *W. belizensis*
- 1b. Inflorescences to 1.5–2.5 cm diam., composite, condensed, not naked, usually sympodial from base to tip, rarely a little lax at base; leaves with adaxial or both surfaces visible, pubescent to tomentose and brown (dried) above, tomentose below, both sides with stellate, rarely simple, trichomes 0.5–1 mm long, with 3 to 8(9) pairs of lateral veins; flowers homostylous, sessile; calyx lobed less than halfway, the lobes 1–3 mm long, triangular. . . . .  
..... *W. indica* s.l.

*Relationships.* This new species is placed within *Waltheria* sect. *Waltheria* as formerly circumscribed (Schumann, 1886) within the *W. cinerescens* A. St.-Hilaire species alliance (Saunders, 1995) by its penicillate stigma (termed fan-plumose in Saunders, 1993) and capsule with mostly complete corneous endocarp. It resembles *W. petiolata* in its decomposite inflorescence, its calyx laciniae in every aspect, its indented apical petal margins, and especially by its seed shape that is subpentagonal in apical view and subrhomboidal in lateral view. For the characters that distinguish the two species, see Table 1. *Waltheria petiolata* is a thicket-forming, apparently rare species occurring on morros or restinga in or near Rio de Janeiro city, Brazil (Saunders, 1995). Important differentiating characters are given below.

#### KEY BETWEEN RELATED SPECIES

- 1a. Stems becoming tomentulose, with all trichome rays 0.2–0.5 mm long, in the underlayer stout, appressed, almost straight, hyaline-ferruginous; leaf teeth margins revolute; leaf lateral vein pairs 8 to 13; inflorescence corymbiform-decomposite; flowers pedicellate; petal apical margins retuse

Table 1. Distinguishing characters between *Waltheria belizensis* and *W. petiolata*.

Character	<i>W. belizensis</i>	<i>W. petiolata</i>
Stem		
Vestiture	tomentulose	tomentulose
Trichomes	rays 0.1–0.3(–0.5) mm, ferruginous-tinged, brown contents at base, straight, a little curved at times	rays 0.5–1 mm, hyaline, twisted apically
Leaves	concolorous, slightly darker above	discolorous, much darker above
Adaxial surface	dark gray-olive; surface obscured	bright green (fresh), red-brown (dried); surface visible
Abaxial surface	densely puberulent, pale gray-olive; surface obscured	soft tomentose-velutinous, white; surface visible
Teeth	revolute entire margin	flat
Lateral veins	8 to 13 pairs	6 to 8 pairs
Inflorescence	decompositae-corymbiform	decompositae-umbelliform
Flower pedicels	present	absent
Petal apical margins	retuse, scant pubescent, a few simple and V-shaped thin hairs 0.2 mm at center	emarginate, short-bearded longer, to 0.3 mm, across 3/4 of margin
Stamen free filaments	glabrous	scant hirsute
Capsule apicula	oblong	narrowly triangular
Seed (apical view)	all anterior lobes obtuse-rounded, similar	anterior 3 lobes pronounced, middle one obtuse-angled
Cuticle pusticula	minute, crowded at very apex	prominent, scattered on upper 1/3 and at raphe

with a few central thin hairs 0.2 mm; capsule apicula oblong and recurved 15°; seed obscurely lobed laterally in apical view; cuticle slightly pusticulate. . . . . *W. belizensis*

1b. Stems tomentulose, with trichome rays 0.5–1 mm long, fine, spreading, twisted, hyaline to white; leaf teeth margins flat; leaf lateral vein pairs 6 to 8; inflorescence umbelliform-decompositae; flowers sessile; petal apical margins emarginate with similar hairs but more widely distributed across apex, the hairs to 0.3 mm; capsule apicula narrowly triangular and recurved 45°; seed markedly lobed anteriorly and laterally in apical view; cuticle pusticulate. . . . . *W. petiolata*

*Relationships pertinent to breeding system status and biogeography.* Except for *Waltheria rotundifolia* Schrank, disjunct from Brazil to southern North America, and *W. glabra* Poir., from the Antilles, which both appear to be more derived by their pollen (Köhler, 1971, 1976), the *W. cinerescens* alliance (= *W. cinerescens* clade, Saunders, unpublished phylogenetic analysis) is composed of species narrowly endemic within Brazil. The portion of the clade containing *W. petiolata* includes *W. ackermanniana* K. Schumann, which is sister to *W. erioclada* DC.; *W. erioclada*, which is sister to *W. glazioviana* K. Schumann; and *W. glazioviana*, which is sister to *W. petiolata*. *Waltheria ackermanniana*, *W. erioclada*, and *W. glazioviana* are all from Brazil. All of these phyletic neighbors are distylous except for *W. erioclada*; *W. erioclada* is potentially distylous but as yet is too poorly known. Those four species share the character combination of serrulate linear bracts,

truncate pin stamen tubes, and darkened anther connective (Saunders, 1993, 1995, unpublished phylogenetic analysis). However, although it is suggested by phylogeny, by the number of distylous species in *Waltheria* (ca. 84%) (Saunders, 1993, 1995) and its putative sister genus *Melochia* L. (approximately 74%, Goldberg, 1967), and by its spinulose pollen found to be perfectly correlated thus far with thrums of distylous species within the genus, fieldwork is necessary to determine whether only thrum-like plants of *W. belizensis* are present or if pin plants are also present at the type locality in isoplethic or anisoplethic proportions. If only thrum-like plants occur, the breeding system of the new species would be considered to be derived monomorphic thrum rather than distylous, which is encountered less frequently than derived monomorphic pins (Ganders, 1979: 629).

*Discussion of isotypes and Waltheria glomerata in Belize.* Two duplicate specimens of *Waltheria belizensis*, now unmarked isotypes, were first identified and distributed to unrecorded locations not yet apparent, and the collection Dwyer & Liesner 12292 was cited (Dwyer & Spellman, 1981) as the only occurrence of *W. glomerata* C. Presl in Belize. Balick et al. (2000) excluded *W. glomerata* from the Belize checklist. Other results concur that *W. glomerata* lacks collections known from Belize (Saunders, 1993, 1995, unpublished data). That species is distant by its clavate-fimbriate stigma and capsule lacking hardened endocarp (Saunders, 1993).

*Pollen of Waltheria belizensis and W. petiolata.* Köhler's (1971, 1973, 1976) pollen studies of the genus have established the most understanding of evolution within the genus. All spinulose pollen encountered within the palynologically well-studied genus belongs only to thrum floral morphs; all thrums have spinulose pollen. Pin morphs, homostylous morphs, or homostylous species have pollen with reticulate exines, different grain shapes, smaller grain size, and fewer average apertures with longer colpi (Köhler, 1971, 1973, 1976; Saunders, 1993, 1995). Interspecific pollen comparisons are made by morph type. Pollen of a *W. petiolata* thrum collection was newly studied for comparison to *W. belizensis* thrum-like pollen because the previous report (Köhler, 1971) was based upon a misidentified collection (Macedo 3199, S, specimen seen but species identity still uncertain). Thrum pollen of *W. petiolata* is spinulose, apertures 5 to 6(7) (average 5.9 for N = 50), zonocolporate, grains  $49.3 \times 52 \mu\text{m}$ , P/E ratio = 0.94, oblate-spheroidal, colpi  $9.5 \times 2 \mu\text{m}$  (N = 10), endexine at pores  $2.9 \mu\text{m}$ , ca.  $1.2 \mu\text{m}$  otherwise, bacula ca.  $0.6 \mu\text{m}$ , spinulae  $1.2 \mu\text{m}$  long  $\times$   $1.3 \mu\text{m}$  diam., ora  $4.4 \times 11.2 \mu\text{m}$  wide (Saunders & Peixoto 3197 thrum SI, N = 10).

Thrum-like pollen of *Waltheria belizensis* (Fig. 2A–G) primarily differs from thrum pollen of *W. petiolata* (Fig. 2H) by an average aperture number of 5.2 versus 5.9; a colpus index of 3.9 versus 5.2; colpus length of  $12.6 \mu\text{m}$  versus  $9.5 \mu\text{m}$ ; and a colpus width of  $2.5 \mu\text{m}$  versus  $2.0 \mu\text{m}$ , with colpi less reduced, longer, and a little more extended beyond the pore, and the annulus less thickened and less protruding internally around the pore. Köhler (1976) discovered and illustrated the trend toward increased number of pollen apertures and shortening of ectoaperture size and colpus length, with a thickening of the endoaperture pore borders operating within both morphs among species of the genus. For the new species, we follow Köhler's (1976: 153) interpretations for the same trends of aperture evolution in the genus in concluding that the thrum-like pollen of *W. belizensis* is more plesiomorphic with respect to its lower average aperture number and longer colpus length of apertures compared with thrum pollen of *W. petiolata*.

If distyly is confirmed in *Waltheria belizensis*, this important character suggests that the shared ancestor of *W. belizensis* and *W. petiolata* had a broader American distribution and either that the South American species evolved faster or that incremental past migration was from North America to South America but not vice versa in recent times, even though its clade of mostly restricted endemics is now concentrated in central and eastern Brazil (Saunders, 1995). If *W. belizensis* is distylous, its reproductive

biology favors either of the first two hypotheses, but not long-distance dispersal from South America to North America. This is because in distylous *Waltheria* widely disjunct populations are found only rarely, because they do not become established readily after long-distance dispersal unless both morphs are dispersed or self-incompatibility is lost or weakened (Saunders, 1993, 1995, 2005; Cristóbal et al., 2005), which is not indicated by the spinulose pollen in *W. belizensis*. For most distylous *Waltheria* sampled, isoplethic ratios of pin and thrum morphs, signaling strong self-incompatibility, were usually present (Saunders, unpublished data). In addition, *W. belizensis* and its close relatives lack long setae on the exterior calyx that might function as the exozoochoric mechanism for its long-distance dispersal; these setae are present in the few disjunct species of *Waltheria*. Consequently, it is Saunders's hypothesis, based upon her present understanding of the genus, that *W. belizensis* might be a relictual species.

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