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A New Species of *Mortoniodendron* (Malvaceae *sens. lat.*) from the Rain Forests of the Isthmus of Tehuantepec, Mexico

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Abstract: The taxonomic history, defining characters, and relationships of the genus *Mortoniodendron* are briefly sketched. Characters that define *M. pentagonum,* a species known from a limited area in Guatemala, are elaborated. A closely related but distinct species from Veracruz, Mexico, **M. uxpanapense** Dorr & T. Wendt, is described and illustrated. The new species is considered to be Critically Endangered (CR) under the IUCN red list classification.

Resumen: Se presenta un bosquejo breve de la historia taxonómica, los caracteres genéricos, y las afinidades del género *Mortoniodendron.* Se presentan datos sobre *M. pentagonum,* una especie restringida a un área de distribución muy limitada en Guatemala. Se describe **M. uxpanapense** Dorr & T. Wendt como especie nueva para la ciencia, estrechamente relacionada a *M. pentagonum,* y se incluyen ilustraciones de la misma. La especie nueva se considera en la categoría de "en peligro crítico" (CR) según los criterios de la UICN.

Keywords: Flora of Mexico, flora of Veracruz, Malvaceae, *Mortoniodendron,* Tiliaceae, Uxpanapa, *Westphalina.*

In 1938, the genus *Mortoniodendron* Standl. and Steyerm. was described in the Tiliaceae (Steyermark, 1938). It was based on *Mortoniodendron anisophyllum* (Standl.) Standl. and Steyerm., a southern Central American tree species originally described from Panama in 1929 and placed at that time in the large tropical genus *Sloanea* L. (Elaeocarpaceae). Two years later, the genus *Orthandra* Burret was described in the Tiliaceae (Burret, 1940), also based on *Sloanea anisophylla* Standl. and thus a superfluous renaming of *Mortoniodendron.* By 1968, another nine species had been added to *Mortoniodendron.* These species were from throughout Central America and southeastern Mexico, some rather widespread and moderately common. This rather rapid growth in the number of known species, uncommon for a tree genus so recently described, was remarked upon by several authors (e.g., Miranda, 1965). Only one of the species (apart from the type) had been previously described in another genus, again in *Sloanea*: *Mortoniodendron pentagonum* (Donn. Sm.) Miranda, based on the 1893 name *Sloanea pentagona* Donn. Sm. and thus bearing the oldest specific epithet in *Mortoniodendron* (Miranda, 1965). Since 1968, no further species have been described, but Alexánder Rodríguez G. of INB (Rodríguez, in press) is in the process of describing at least five new species from Costa Rica and is working on several others, while one of us (LJD) is working on at least one more from Panama. A lack of specimens has generally hindered the study of the genus, and it may be that some of the published names represent variants of widespread variable species. A best guess at present would thus make this a genus of

perhaps 18 species, strongly Central American and Mexican in distribution (but reaching western Colombia), and growing in lowland to mid-montane wet forests. *Mortoniodendron* appears to have been in the region since at least the Middle Miocene, with Graham (1979) referring palynomorphs from the Upper Miocene of Mexico and from the Middle Miocene and Pleistocene of Panama to the genus.

The genus *Mortoniodendron* is characterized by: tree or shrub habit; alternate, entire leaves; very small, caducous stipules; free sepals; stamens often more or less connate basally into five groups opposite the petals (when petals are present); 3–5-locular ovaries with (2)4–many biseriate ovules per locule; woody to fibrous capsular fruits; and seeds each developing an orange aril (Steyermark, 1938; Miranda, 1956; Bayer and Kubitzki, 2003; A. Rodríguez, pers. comm.) As in many Malvaceae *sens. lat.*, abundant mucilage is produced in the twigs, bark, portions of the flowers and fruits, and other parts (Miranda, 1956). Miranda (1956) and Dorr (2001) both noted that the connation of the stamens is quite variable between species and is thus probably not a strong generic character. The relationships of the genus never have been clear. In describing the new genus, Standley and Steyermark placed it in Tiliaceae "only after long and careful consideration," noting a similarity also to Sterculiaceae (Steyermark, 1938). Burret (1940) allied *Orthandra* (i.e., *Mortoniodendron*) with *Luehea* Willd., but Miranda (1956) argued that the characters Burret (1926) used to subdivide the Tiliaceae would ally *Mortoniodendron* with the Tilioideae and not Grewioideae where *Luehea* is placed. Miranda (1956) further noted that the presence of an aril makes *Mortoniodendron* unique within Tiliaceae. He was impressed sufficiently with the multiovulate locules and the arillate seeds that he proposed the new monotypic tribe Mortoniodendreae Miranda[1], which he compared to the Tilieae that Burret (1926) had characterized as two ovulate. Within an expanded Malvaceae, in which both Tiliaceae and Sterculiaceae have been subsumed, Bayer and Kubitzki (2003) likewise treated the genus as anomalous, including it as one of very few genera *incertae sedis* and noting that its relationships may be with either Tilioideae or Brownlowioideae. Limited molecular data for *Mortoniodendron* (2 chloroplast genes, 1 species) place it closest to, but not within, the mostly paleotropical Brownlowioideae (Bayer et al., 1999). While there is agreement with respect to the tilioid pollen, *Mortoniodendron* nonetheless differs from Brownlowioideae with respect to its anthers (elongate versus basally dilated), sepals (free versus fused), and seeds (arillate versus exarillate).

A species of tree collected by the second author from the Uxpanapa region of extreme southern Veracruz, Mexico, is similar in many respects to *Mortoniodendron pentagonum* and led us to investigate that species more fully. *Mortoniodendron pentagonum* is a well differentiated species in a genus in which species delimitation is often not clear. It is the only species with the combination of the presence of petals and leaves with obvious translucent dots (these latter representing mucilage cells, according to Lislie Solis [pers. comm.]; although such cells are present in the leaves of all species of *Mortoniodendron,* they are large and obvious only in a few species). It further displays a series of other characters that, taken together, are likewise unique in the genus:

[1] Miranda (1956: 334) wrote that he was adding this new tribe to the "sección Tiliinae" of Burret (1926). Miranda's use of the word section ("sección") is confusing in this context since a section is a subdivision of a genus (see Greuter et al., 2000). He may, however, have been forced into this semantic muddle by the fact that Burret (1926) created a classification of the Tiliaceae that included a rank between subfamily and tribe, and for which he used the ending (i.e., "-inae") normally reserved to denote subtribe. Miranda's confusion as to what Burret meant by "Tiliinae" is therefore understandable.

relatively large (typically 15–30 cm long) thickish leaves with strongly scalariform tertiary venation, equilateral to only slightly oblique leaf bases, and domatia or tufts of hairs lacking in the axils of primary and secondary veins; pedicels not articulate; flowers large for the genus, carnose sepals ca. 15 mm long; filaments only short-connate to essentially free; numerous ovules per locule; fruits large (discussed below); and an aril nearly completely covering the seed.

The type (*H. von Türckheim 1411,* holotype US!) was collected at Pansamalá in Alta Verapaz, Guatemala, at 4000 feet elevation. In 1977, Bamps and Robyns described the monotypic genus *Westphalina* A. Robyns & Bamps in the Tiliaceae, based on the new species *W. macrocarpa* A. Robyns & Bamps; the type (*I. Kunkel s.n.,* holotype BR!, isotype F!) and all paratypes are from the same west-central part of Alta Verapaz as the type of *M. pentagonum.* Dorr (2001) showed that *W. macrocarpa* is synonymous with *M. pentagonum,* the genus *Westphalina* thus also falling into synonymy with *Mortoniodendron* as presently circumscribed. However, since *M. pentagonum* was otherwise known only from its type, the more abundant material of "*Westphalina*" housed at BR (type and paratypes, plus numerous other mostly sterile collections made by I. Kunkel and examined by the present authors) allows a better understanding of the morphology and variation of *M. pentagonum.* In addition, since the BR material was collected as part of an ecological study (Kunkel-Westphal and Kunkel, 1979), a clearer picture of the habitat of *M. pentagonum* emerges. The species grows at 1000–1300 m elevation; at the type locality of *Westphalina macrocarpa,* it is a common mid-story (15–20 m) tree in wet forests on limestone substrate (Kunkel-Westphal and Kunkel, 1979). These forests are strongly lowland-neotropical in the composition of their flora, with such species as *Terminalia amazonia* (J. F. Gmel.) Exell, *Calophyllum brasiliense* Cambess., and *Vochysia guatemalensis* J. D. Smith (as *V. hondurensis* Sprague) cited among the codominant trees, but the forests also have a significant holoarctic element (e.g., *Quercus* L., *Juglans* L., *Magnolia* L., *Prunus* L., *Billia* Peyr.) and in some cases (e.g., *Quercus*) the holarctic genera are among the codominants (Kunkel-Westphal and Kunkel, 1979). The forests are, essentially, transitional in their composition between lowland rain forest and montane temperate forest.

The previously mentioned *Mortoniodendron* from southern Veracruz shares with *M. pentagonum* all of the characters outlined in the previous paragraph (with the exception of the occasional presence of weakly developed tufts of hairs in the axils of the lateral veins of the leaves). However, it differs in several characters, the two most notable being vegetative vestiture and fruit size. The twigs and petioles of the Uxpanapa material are covered by an extremely dense and persistent vestiture of minute, flat, stellate hairs (Fig. 1A, C, D). Although *M. pentagonum,* like the Uxpanapa material, has a dense indumentum of slightly larger stellate hairs on many parts of the inflorescences and flowers, the young vegetative structures of *M. pentagonum* are only very sparsely beset with stellate hairs (Fig. 1B) that quickly fall, leaving the twigs, petioles and leaves soon uniformly glabrous. Large fruit size was emphasized by Bamps and Robyns (1977) in describing *Westphalina* (*M. pentagonum*); these fruits are 55–90 mm long, with walls 8–10 mm thick at midfruit. The Uxpanapa material, on the other hand, has mature fruits 25–30 mm long with walls 5 mm thick. The position of the small cymes appears to differ as well, those of the Uxpanapa material being either terminal or in the upper 1–3 leaf axils, while in *M. pentagonum* there is a strong tendency for these to be borne in the axils of older leaves or even at leafless nodes along the branchlets. In addition, in the Uxpanapa material each carpel bears 10–12 ovules, as opposed to the 18–20 reported for *M. pentagonum* (Bamps and Robyns, 1977), al-

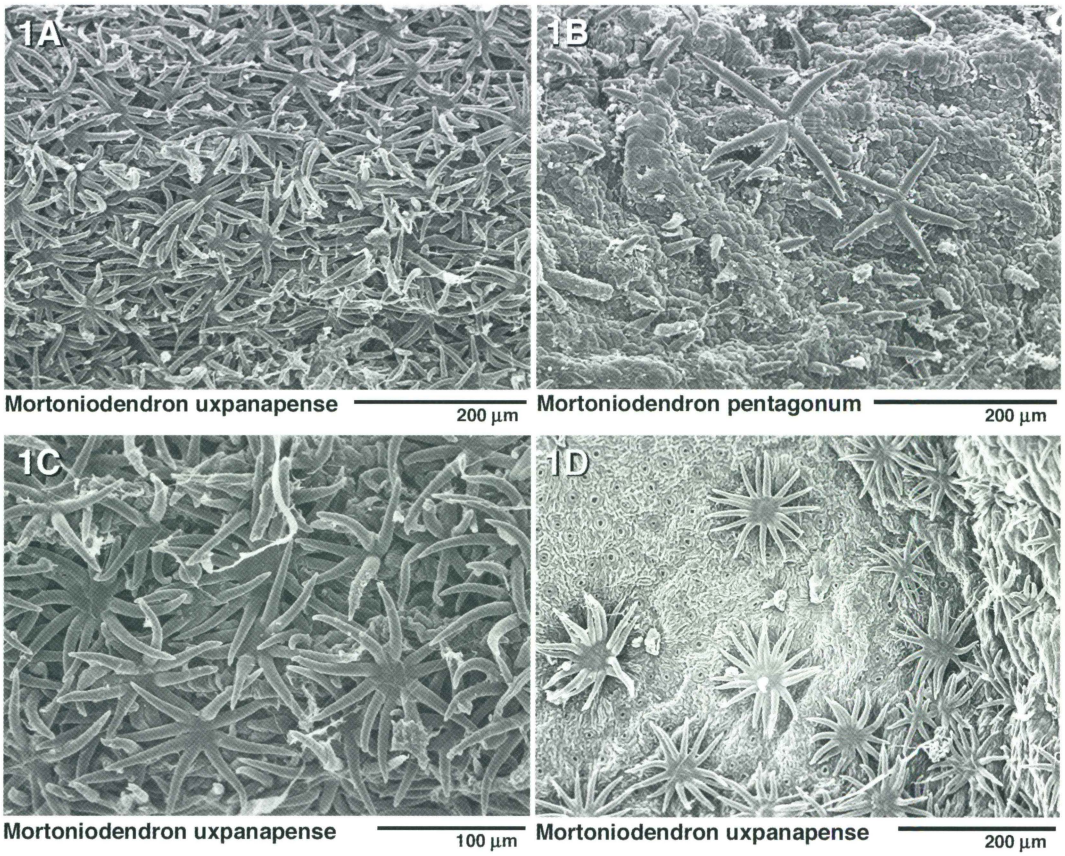

FIG. 1. Vegetative vestiture of *Mortoniodendron uxpanapense* and *M. pentagonum.* A. *M. uxpanapense,* petiole. B. *M. pentagonum,* petiole at same scale as previous. C. *M. uxpanapense,* petiole at higher magnification than A. D. *M. uxpanapense,* detail of scattered stellate trichomes from abaxial extreme base of leaf blade by midrib. A, C, D from *T. Wendt et al. 2819* (CHAPA); B from *I. Kunkel 506* (BR). All scanning electron digital micrographs taken by John Mendenhall, Institute for Cell and Molecular Biology, University of Texas, using a Philips SEM 515; material sputter-coated with 60/40 gold/palladium.

though more floral material of both is necessary before accepting this as a meaningful or consistent difference. As already noted, *M. pentagonum* is a species of limestone mountains at 1000–1300 m elevation, in wet forests floristically transitional between lowland rain forest and montane temperate forest. The Uxpanapa tree, while also inhabiting limestone hills, grows at lower elevations (200–250 m) in lowland rain forest, although at least one associated codominant species (*Terminalia amazonia*) is the same. While clearly related to *M. pentagonum,* the Uxpanapa tree nevertheless cannot be referred to that species, or to any of the new species to be described by Rodríguez (in press). We therefore propose the following new species:

Mortoniodendron uxpanapense Dorr & T. Wendt, sp. nov. (Figs. 1–3)

TYPE: **MEXICO.** VERACRUZ: Mpio. Minatitlán [now Mpio. Uxpanapa]. Lomas al S del Poblado 11, ± 27 km al E de La Laguna, arroyo (cascada) empinado pedregoso en cañón, 17°14′N, 94°17′W, 200 m, 3 Jun 1981 (fl, fr), *T. Wendt, A. Villalobos,*

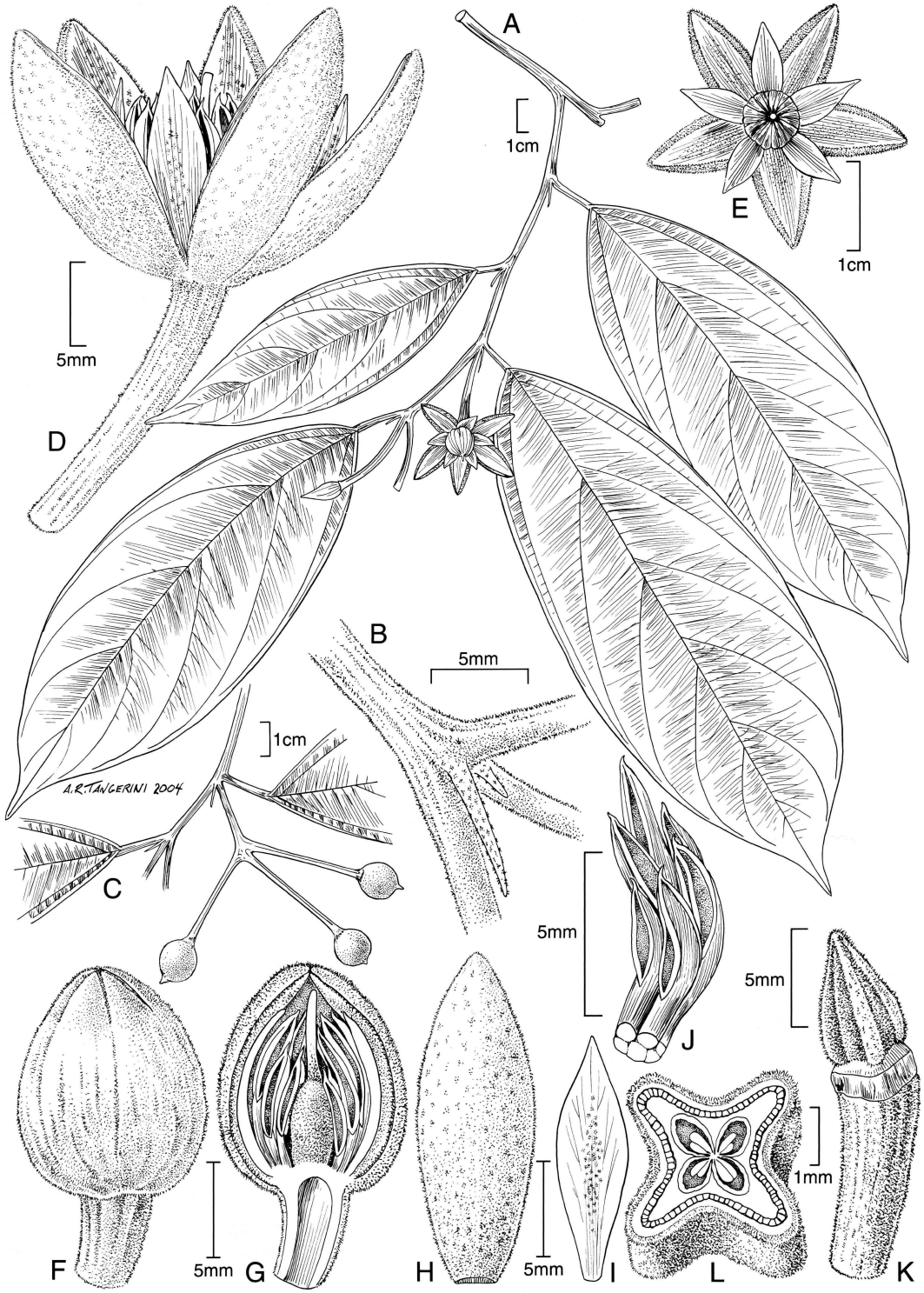

FIG. 2. *Mortoniodendron uxpanapense.* A. Fertile branchlet. B. Branchlet node with stipule. C. Inflorescence showing branching (3-flowered cyme in axil of leaf). D. Flower (from rehydrated material and thus appearing partially closed), lateral view. E. Flower, apical view with anthers

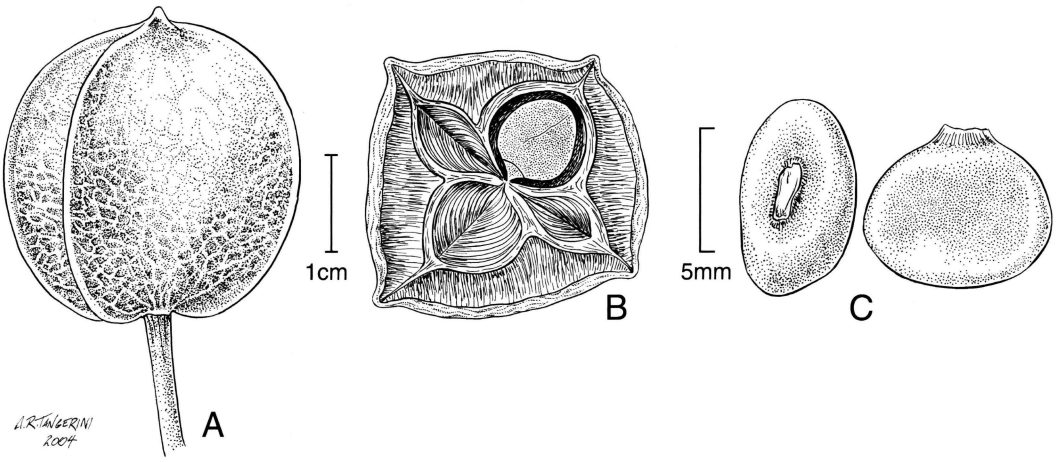

FIG. 3. *Mortoniodendron uxpanapense.* A. Fruit, showing entire capsule before dehiscence. B. Fruit (cross-section) showing 4 locules and arillate seed. C. Seeds, arils removed and hilum visible. A–C from *T. Wendt et al. 2819* (US) (drawn by Alice Tangerini).

J. García, I. Navarrete y J. Anguiano 3402 (HOLOTYPE: CHAPA!; ISOTYPES: US(2)!)

Mortoniodendro pentagono affinis sed ramulis et petiolis trichomatibus minutis stellatis planis dense obsitis, fructibus parvioribus 25–30 mm longis (in *M. pentagonum* 55–90 mm longis) notabilis.

TREE to 10–12 m tall, spreading, low-branched. TRUNK to 40–45 cm diam. near base (below branching); BARK ashy-brown to dull reddish-brown, general aspect ± smooth, fine aspect irregularly finely undulate to asperous, with scattered to crowded lenticellar warts; SLASH of bark with no prominent odor, the very thin outer layer reddish-brown, the rest light yellowish-brown, the sapwood cream-colored to almost white. Ultimate BRANCHLETS 2–3 mm thick, completely covered by a dense layer of flat stellate trichomes mostly 0.07–0.15 mm in diam. (with or without quite scattered larger trichomes of similar form), this indumentum so fine, uniform, and appressed that branchlets may appear glabrous without sufficient magnification, each trichome with ca. 8–20 rays all spreading and ± parallel to surface, the rays ± fused irregularly near bases. LEAF BLADES thick but not coriaceous, elliptic to slightly obovate, mostly 15–24 cm long by 5.3–9.2 cm wide when mature, 2.4–3.4 times as long as wide, finely but distinctly pellucid-punctate due to mostly circular to oblong internal mucilage cells variable in size, the blade apex gradually to abruptly acuminate, the acumen ca. 1–2 cm long, the base broadly acute to rounded, very slightly oblique; VENATION actinodromous in lower portion, ± brochidodromous distally, with 5–8 lateral veins per side, the lowest pair arising

←

coherent. F. Floral bud, anthesis just beginning. G. Floral bud (longitudinal section) showing from exterior to interior sepals, petals, stamens, gynoecium. H. Sepal, abaxial view. I. Petal, abaxial view showing hairs. J. Group of anthers (from bud), lightly coherent (but not connate). K. Very immature capsule, with calyx, sepals, and anthers removed. L. Immature, 4-carpeled fruit (cross-section) showing 4 locules and superposed ovules. A, B, D, F, G, from *T. Wendt et al. 3402* (US); C, K, and L from *T. Wendt et al. 3402* (CHAPA); E from a photograph by Wm. Wayt Thomas; and H–J from *T. Wendt et al. 4837* (CHAPA) (all drawn by Alice Tangerini).

1–3 mm above the blade base and most often at a narrower angle (25–40°) to the midrib than the distal ones (45–65° in distal half blade), this near-basal lateral pair giving a slightly triplinerved aspect to many leaves but these veins the same size as the other laterals and not obviously further spaced than the others, a smaller pair of thinner lateral veins (tertiary venation size) arising with or just below the near-basal pair and paralleling the basal portion of the blade margin, the tertiary venation strongly scalariform, the finer venation subscalariform to coarsely reticulate, the midvein slightly sunken to plane above, all other veins finely raised above, all veins raised beneath, the midvein and laterals prominently so; VESTITURE of blade adaxially lacking or essentially so, abaxially the midvein sparsely to moderately beset, especially toward the base, with minute stellate hairs like those of stem, such hairs otherwise very scattered on finer venation and leaf surface, the axils of the lateral veins each usually with an extremely inconspicuous concentration of minute appressed stellate hairs like those of rest of blade, the rays of these only occasionally elongated (to 0.5 mm) and erect to form a still rather inconspicuous axillary tuft. PETIOLES of mature leaves 11–22 mm long, slightly thickened-pulvinate distally, with dense stellate indumentum like stem. STIPULES linear, dark (at least when dry), ca. 4–8 mm long, fugaceous, with scattered stellate hairs. CYMES mostly 1–4 flowered, solitary in upper 1–3 leaf axils and/or terminal and then sometimes paired, to 8 cm long, the branches and pedicels divergent, the axes and pedicels with indumentum like that of the branchlets but also with abundant larger (0.2–0.3 mm diam.), less appressed and more reddish stellate hairs mixed in; PEDUNCLE 2–20 mm long; BRACTS ca. 1–1.5 mm long, fugaceous; PEDICELS 19–40 mm long, distally thickened, not articulate. FLOWERS ± nutant; SEPALS 5 (or 6, *fide* A. Rodríguez), spreading, very thick, white, each one ovate, with sharply acute apex, 11–18 mm long, 4–6 mm wide, eventually caducous, abaxially densely stellate-tomentose like the pedicels, adaxially with much less dense covering of tiny unkempt weak-rayed stellate hairs, this very dense near tip; PETALS 5 (or 6, *fide* A. Rodríguez), spreading, thin, white (apparently becoming purplish after anthesis, dark brown when dry), each one ± narrowly rhombic or somewhat clawed with a trullate blade, 7–12 mm long, 2.5–3 mm wide, with a long narrowly acute apex, quickly caducous after anthesis, abaxially rather densely beset with minute stellate hairs in center, adaxially only distally and very lightly so; STAMENS ca. 72, some seemingly short-connate at filament bases but definitely not forming a set number of distinct fascicles of connate stamens, all lightly coherent and inflexed around style at anthesis (Fig. 2E), the outer stamens much longer than the inner ones due mostly to longer filaments, the filaments white, broad, those of the outer stamens to 6 mm long and 0.6–0.9 mm broad, those of the inner stamens as short as 2 mm, the anthers orange-brown, linear-lanceolate, the same width as the filaments, 4–6 mm long, narrowly acute, each with a terminal narrowly conical appendage 0.2–0.5 mm long; OVARY ca. 5–6 mm long, ovoid, 4–5-angled, externally densely stellate-tomentulose, the locules 4–5, glabrous within, with ca. 10–12 ovules/locule, these biseriate, the style ca. 4 mm long, tomentulose in basal one-fifth to three-fourths, distally glabrous. FRUIT a loculicidally dehiscent woody capsule, subglobose with 3–5 flattened sides in cross-section and slightly ribbed along sutures, ca. 25–30 mm long, ca. 25–35 mm wide (before dehiscence), externally very finely and densely stellate-tomentose, greenish brown, the outer walls thick, woody, ca. 5 mm thick at mid-fruit; FERTILE LOCULES 3–5, glabrous within, each with 1–3 seeds. SEEDS brown, subglobose to ellipsoid (often irregularly so by compression), ca. 8–10 mm long; TESTA smooth to minutely verruculate, the hilum conspicuous, 2.0–2.5 mm long; ARIL thin, orange, ± completely covering seed.

PHENOLOGY: Collected with flower in April and June, and with fruit in June and October.

DISTRIBUTION AND HABITAT: Known only from one small drainage in the south-central part of the Uxpanapa region of Veracruz, near the Oaxaca border in the Isthmus of Tehuantepec, where a small population occurs at 200–250 m along a steep, somewhat rocky limestone drainage in otherwise mostly deep-soil hills that rise to about 500 m. The new species occurs directly along the edge of parts of the seasonal stream that become rushing cascades and waterfalls in the rainy season. Characteristic canopy trees of the hill forest of the nearby slopes include *Dialium guianense* (Aubl.) Sandwith, *Terminalia amazonia, Guatteria anomala* R. E. Fr., *Poulsenia armata* (Miq.) Standl., and *Pouteria sapota* (Jacq.) H. E. Moore & Stearn. Average annual rainfall at this site is ca. 4000 mm, according to unpublished short-term data from the now-defunct federal Comisión del Papaloapan.

CONSERVATION ASSESSMENT: Following the IUCN (The World Conservation Union) Red List guidelines (IUCN, 2001), it is clear that, based on present knowledge, *Mortoniodendron uxpanapense* meets the criteria for a Critically Endangered (CR) species [CR A3c;B1ab(i,ii)+2ab(i,ii);D], although certainly there are many unknowns concerning its population parameters. The species is known from only one small population where only a few individuals were noted (although searching for additional individuals of the species was not done at the time). The known Extent of Occurrence (EO) and Area of Occupancy (AO) are both thus much less than 1 km^2, although the species may occur in other canyons of the same hills. This entire area is under continual threat of deliberate deforestation and burning; a single such event could easily kill all known individuals (if it has not in fact already done so). The limestone hills in which it occurs are on the north edge of the major and poorly known mountainous area of the Sierra de Tres Picos; however, that range is largely igneous in origin and thus is not likely suitable habitat. Areas immediately to the north have either been deforested or have rain forest on limestone karst with minor hills; locally intensive collecting in that area has not uncovered the species. Possible suitable habitat for the species occurs to the east, in the eastern end of the Uxpanapa region, in and around the limestone Sierra del Espinazo del Diablo in the area where the states of Veracruz, Oaxaca, and Chiapas converge. Several localized plant species known from the Uxpanapa region are also found yet further eastward in extreme northern Chiapas and adjacent Tabasco, in the "crescent area" (*area del arco*) of Wendt (1989). In the present case, however, related material of *Mortoniodendron* known from that area appears to represent an undescribed species, a common tree of certain forest types in the Selva del Ocote of northwestern Chiapas that differs from *M. uxpanapense* in features of the vestiture and other characters. The taxonomic placement of these populations is currently being studied by Mario Ishiki, Lislie Solís, and Nelson Rendón at the Colegio de la Frontera Sur (ECOSUR) in Chiapas.

ADDITIONAL SPECIMENS EXAMINED: **MEXICO. VERACRUZ. Mpio. Minatitlán [now Mpio. Uxpanapa]:** Type locality, 250 m, 2 Oct 1980 (fr), *T. Wendt et al. 2819* (CHAPA!, US(2)!), 200 m, 26 Apr 1985 (fl), *T. Wendt et al. 4837* (CAS, CHAPA!, MEXU!, TEX!).

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Robbrecht (BR), for permission to remove material of loaned *M. pentagonum* for SEM studies; Alice Tangerini (US) for the fine illustrations; John Mendenhall (Institute for Cell and Molecular Biology, University of Texas) for the SEM work; Gwen Gage (School of Biological Sciences, University of Texas) for formatting Fig. 1; James Henrickson for his very helpful review; and the curators of BR, CHAPA, F, MO, and WIS for the loan of material. The second author (TW) undertook field work in the Uxpanapa region while working at the Centro de Botánica, Colegio de Postgraduados, Chapingo (now Montecillos), Mexico. He thanks all who participated in the field trips on which *M. uxpanapense* was collected (Agustín Villalobos, José García, Isidro Navarrete, Juan Anguiano, Wayt Thomas, Jim Grimes, Emily Lott, and Rubén Lara), as well as the now-defunct Comisión del Papaloapan, S.A.R.H., for its financial and logistical support of same.

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