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# MAHONIA SAGRANA, A NEW SPECIES FROM CUBA, AND LECTOTYPIFICATION OF MAHONIA TENUIFOLIA AND BERBERIS FRAXINIFOLIA FROM MEXICO

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The only *Mahonia* species found in Cuba is investigated. Although known since the nineteenth century, it has previously been identified as *Mahonia tenuifolia* (or its synonym *Berberis fraxinifolia*), otherwise found in Mexico. The Cuban species is shown to differ *inter alia* from the Mexican species by its leaf shape and texture, shorter racemes and pedicels, and greater number of ovules. The habitat and distribution of the species are described. *Mahonia tenuifolia* and *Berberis fraxinifolia* are also lectotypified.

Keywords. Berberidaceae, Flora of Cuba, Ramón de la Sagra.

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#### Introduction

Mahonia Nuttall (Berberidaceae) (Nuttall, 1818), as recently recircumscribed by Yu & Chung (2017) and reconfirmed by Hsieh *et al.* (2022), consists of about 80 species occurring disjunctly in East and Southeast Asia and in western North America and Central America (Ahrendt, 1961; Ying & Boufford, 2011; Boufford, 2013).

Since its publication, *Mahonia* has been successively maintained as a separate genus or merged with *Berberis* L., the most species-rich genus in Berberidaceae. For the most important participants in this debate, see the references in Adhikari *et al.* (2015), Yu & Chung (2017) and Colin *et al.* (2021). In this paper, we have accepted the arguments in Yu & Chung (2017) and Hsieh *et al.* (2022) that *Mahonia* and *Berberis* are separate genera.

## Taxonomic history of Mahonia in Cuba

The first recorded collection of the new species was made by the Spaniard Ramón de la Sagra, who resided in Cuba intermittently in the 1820s and 1830s. A specimen was sent to Achille Richard in France, but Berberidaceae did not appear in Richard's *Histoire Physique*, *Politique et Naturelle de L'Île de Cuba: Botanique. Plantes Vasculaires* (1845), and the specimen in Richard's personal herbarium (subsequently transferred to the Paris herbarium) remained unnamed until 1960.

Between 1860 and 1864, the American Charles Wright collected various specimens of the new species in Cuba, all numbered '1855' by Asa Gray of Harvard University and widely distributed by him (confusingly, Gray also gave the same number, '1855', to what became

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the type of *Hyperbaena crebriflora* Miers [Menispermaceae]). *Wright* 1855 was identified by Grisebach (1866) as *Berberis fraxinifolia* Hook.f., the type of which is from Xalapa in Veracruz State, Mexico. This identification was accepted by Wright (1868), Sauvalle (1873) and Gómez de la Maza (1889, 1890, 1897). Further collections of the new Cuban species were not made until some 60 years after Wright's initial collection.

When Fedde (1901) transferred all pinnate-leaved species of *Berberis* to *Mahonia*, he treated *B. fraxinifolia* as a probable synonym of *M. tenuifolia* (Lindl.) Loudon (a later homonym of *M. tenuifolia* (Lindl.) Czerw. & Warsz., 1864), the basionym of which was *B. tenuifolia*, published by Lindley (1838) on the basis of material collected by Karl Hartweg in Zaquapam, also in Veracruz State.

In synonymising *Berberis fraxinifolia*, Fedde (1901) cited no Mexican specimens but one of Wright's 1855 Cuban ones in G-DC (barcode G00405991), questioning whether in Cuba it was native. His synonymy of *Berberis fraxinifolia* was also accepted as probable by Ahrendt (1961) and as certain by Roig y Mesa (1953) and Marroquín (1972, 1993), although these latter authors treated it as *Berberis* rather than *Mahonia*. In 1960 Alain annotated the de la Sagra specimen (P, barcode P02327264) as *Berberis tenuifolia*, but later (1969), citing Ahrendt, he treated the Cuban species as *Mahonia* rather than *Berberis*, although adding that "Some authors do not accept this change of genus".

In recent inventories of the Cuban flora, the new species has been considered as *Berberis tenuifolia* (Acevedo-Rodríguez & Strong, 2012) or *Mahonia tenuifolia* (Greuter & Rankin Rodríguez, 2022). Surprisingly the former authors describe it as an exotic, the latter as not indigenous but possibly naturalised ("No indígena pero posiblemente naturalizado"), their unevidenced claims possibly having their origin in Fedde's (1901) questioning of its genesis.

What is particularly interesting is that at no point was there any published investigation of our new species or any detailed description of it (nor indeed in most cases any description of it at all). In proposing his synonymy, Fedde (1901) simply noted it was "probably a broadleaved form of *M. tenuifolia*, since the two plants otherwise have the same characteristics". In the longest subsequent account, Roig y Mesa (1953) simply noted the following: "Shrub up to 3 m; leaves compound-pinnate, commonly with 7 to 11 oblong-lanceolate leaflets 3–10 cm long; bright green with flowers in racemes as long or longer than the leaves".

Our investigation revealed that description to be not completely accurate and showed that our new species differs from the Mexican *Mahonia tenuifolia* in more ways than just the breadth of its leaves noted by Fedde (1901).

#### Materials and methods

Taxonomic decisions were based on the examination of 93 herbarium specimens of *Mahonia tenuifolia* and 65 herbarium specimens of the new species, the latter supplemented by plants observed in the field and in cultivation.

Ahrendt's (1961) and Marroquín's (1972) descriptions of the flower structure of *Mahonia tenuifolia* were amplified using dissections of the flowers of *Medina & Vasquez* 599 (XAL) by Sergio Avendaño and C. C. Yu and from drawings (presumed to be by Schneider) of the flowers from *Purpus* 13075 (S) and *Purpus* 13075B (C) from Zaquapam (herbarium acronyms follow Thiers, continuously updated).

Schneider's line drawings have been used, for as Harber (2020) noted, his immaculate drawings can be found attached to numerous *Berberis* specimens in A, BM, C, E, K, S and US. In cases where the first author was able to compare them with other specimens of the same species or with material from living plants, Schneider's drawing were always found to be accurate.

Seed characters of *Mahonia tenuifolia* were recorded from dissection of two specimens from Vera Cruz at CAS, *Ventura* 2553 and *Ventura* 2964, by Bruce Bartholomew (CAS).

Flower structure for the new species was investigated using flowers collected in Parc Codina by N. Arbelo in 2016 and preserved in spirit (specimens are now lost but some photographs are still extant), and a line drawing (clearly by Schneider) attached to *E.L.Ekman* 17623 (S), the accuracy of which was verified by a dissection of a flower by the first author when on loan to K.

Seed characteristics were recorded from dissection of fruits of *I. Arias* et al. *HFC-62947*, HAJB) by the first author and of a fruit of *Alain* 10944 (HAC) by the second author.

### Results

A comparison of key characters of *Mahonia tenuifolia* and the new species is shown in the **Table**. A full description of both species is to be found in the *Taxonomic treatment* section.

There is also a difference in habitat between the new species and *Mahonia tenuifolia* in that the former is found in karstic ecosystem known in Cuba as mogotes, whereas

Table. Comparison of characters of the new species and M. tenuirolla		
Character	sp. nov.	M. tenuifolia
Leaf length	16-29 cm	30-35 cm
No. of leaflets	2-4 pairs	3-6 pairs
Distance to first pair from base of petiole	2.7-4.5(-6) cm	(3-)5.5-8(-10) cm
Leaflet shape	Broadly ovate, elliptic-ovate or elliptic; margin entire; apex subacute, rarely obtuse or retuse	Ovate-lanceolate or lanceolate, rarely broadly ovate; margin entire; apex acute or acuminate, rarely obtuse
Leaflet length	6-8.5(-9.5) cm	5-8(-10) cm
Leaflet width	(2-)3.5-6(-7) cm	(1.5-)2.25-3.5(-4) cm
Leaf texture	Coriaceous	Papyraceous
Raceme length	To 17 cm	To 37 cm
Pedicel length	5–7 mm	4-15 mm
No. of ovules or seeds	(3-)4-5	2

Table. Comparison of characters of the new species and M. tenuifolia

according to Marroquín (1993), *M. tenuifolia* is found among secondary vegetation in deciduous and semi-evergreen forests including oaks. In Cuba, oaks are always associated with pine forest on very acid soils on quarzitic sand and slate schists in Pinar del Rio. The pine and oak forests may be adjacent to the mogotes but their floras are completely different (see Capote & Berazaín, 1984; Borhidi, 1991).

It should also be noted that although the new species grows up to c.3 m tall, herbarium specimens of *Mahonia tenuifolia* record its height as being up to 5 m. However, Marroquín (1993) reports 5–8 m and González-Espinosa et al. (2011) up to 13 m. The latter may be based on *R. M. Laughlin* 294 (F, barcode F1662803), Chiapas State, Venustiano Carranza, 670 m, 25 ii 1966, the only collection we have found from Chiapas, which is reported to be 40 ft (12.2 m) high and may be of another species.

#### A note on flower structure in Mahonia

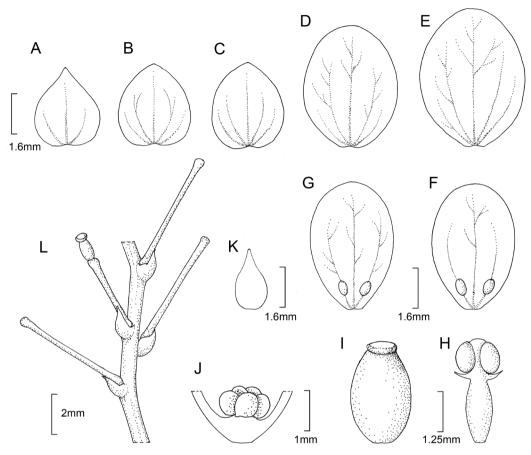
At this point, it is perhaps worth considering the question of flower structure in *Mahonia*. Takeda (1917) placed particular importance on this for species delineation and identification, as illustrated in his plates XXXIII–XXXVI. Interestingly, Schneider, in introductions to a series of articles (1916, 1939, 1942) progressively came to the same conclusion as Takeda as to the importance of flower structure in relation to *Berberis*, the only difference being that of the number of ovules, which Schneider regarded as crucial but which Takeda maintained "was not of much use in distinguishing closely allied species" because the number was not constant.

Our investigations suggest that the importance Schneider attached to the number of ovules in species delineation in *Berberis* also applies to *Mahonia*, thus bringing into question Takeda's doubts about their usefulness in distinguishing closely related species of the latter genus. Takeda's study was, of course, exclusively of Old World species, and he did not seem to have considered the possibility that ovules can vary within a species but within defined and ascertainable limits, which was Schneider's view of *Berberis*.

#### Taxonomic treatment

#### Mahonia sagrana Harber & Bécquer, sp. nov.

Differs morphologically from *Mahonia tenuifolia* by its fewer leaflets (2–4 pairs vs 3–6 pairs), shorter distance to first pair of leaflets from base of petiole (2.7–4.5(–6) cm vs (3–)5.5–8(–10) cm), leaf texture coriaceous (vs papyraceous), shorter racemes (to 17 cm long vs to 37 cm long), and greater number of ovules ((3–)4–5 (vs 2)). – Type: Cuba, Pinar del Río Province, Sierra de los Organos, grupo del Rosario at Río Taco-taco, 12 x 1923, *E.L. Ekman* 17623 (holotype S [S16-43280!]; isotypes G [G00405854] image!, HAC!). **Figures 1, 2, 3, 4**.



**Figure 1.** *Mahonia sagrana* Harber & Bécquer, sp. nov.: flower structure. A, Outer sepal; B and C, median sepals; D and E, inner sepals; F and G, petals; H, stamen; I, pistil; J, ovules; K, bract; L, pedicels. Drawn by Nicola Adams, based on a line drawing, by C. K. Schneider, attached to the sheet of holotype *E.L. Ekman* 17623 (S).

Shrubs, evergreen, c.3 m tall. *Leaves* imparipinnate, 16-29 cm long; leaflets 2-4 pairs, contiguous, lowest pair 2.7-4.5(-6) cm above base of petiole, abaxially and adaxially bright green, shiny, broadly ovate, elliptic-ovate or elliptic,  $6-8.5(-9.5) \times (2-)3.5-6(-7)$  cm, coriaceous; midvein raised abaxially, impressed adaxially, lateral veins inconspicuous on both surfaces, base attenuate; margin entire, slightly undulate; apex acute or acuminate. *Inflorescence* a single or 2-3(-5)-branched raceme to 17 cm, 25- to 40-flowered; pedicel 5-7 mm; floral bracts triangular ovate,  $1.5 \times 0.75$  mm, apex acuminate. *Flowers* bright yellow, c.5 mm in diameter; sepals in three whorls; outer sepals triangular ovate,  $1 \times 1$  mm; median sepals broadly ovate,  $2 \times 1.75$  mm; inner sepals broadly obovate to elliptic,  $4-4.5 \times 3-3.5$  mm. *Petals* ovate-elliptic to elliptic,  $4 \times 2.5$  mm, glands separate, apex obtuse.



**Figure 2**. *Mahonia sagrana* Harber & Bécquer, sp. nov.: pistil and stamen of a plant in Parc Codina, collected by N. Arbelo. No voucher material made.

Stamens dentate, with teeth pointing upwards or downwards, 3 mm; anther connective not extended, truncate. Ovary 2.5 mm; ovules (3-)4-5. Fruit berry black, ellipsoid or oblong  $6-12 \times 6-7$  mm, style persistent, short.

*Distribution*. Endemic to Cuba. Known from two separate mountainous areas: the Cordillera de Guaniguanico in the northwest and the Guamuhaya massif in the south centre of the island (Figure 5).

Habitat and ecology. Mahonia sagrana has been found in karstic dense woodlands at or near hill and mountain tops at 440–1000 m. It has been collected in flower from July and November and in fruit from August to February.

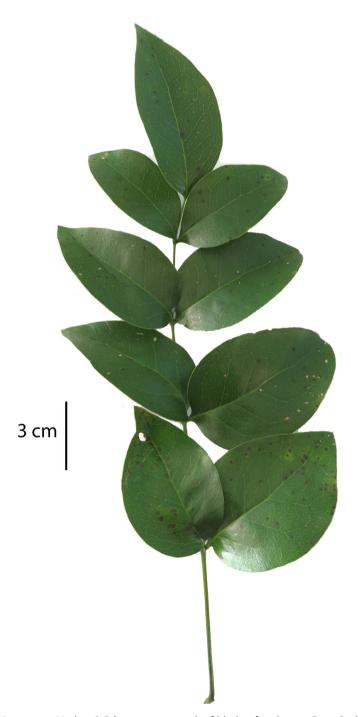
Etymology. Named after Ramón de la Sagra (1798–1871), who collected the first specimen of the species and who was one of the first to warn about the consequences of deforestation in Cuba (Funes Monzote, 2007).



**Figure 3**. *Mahonia sagrana* Harber & Bécquer, sp. nov.: in flower, Jardín Botánico National, Havana. No voucher material made. Photograph: Luis M. Leyva.

Proposed IUCN conservation category. Mahonia sagrana (as M. tenuifolia) was not assessed in the Red List of Cuban Flora (González Torres et al., 2016) but was recently considered Vulnerable (VU D2) by Bécquer & Rodríguez-Cala (2020). The assessment was based on its restricted geographical distribution (area of occupancy, 13 km²), but its habitat has a low history of anthropogenic impact and is mostly within protected areas (i.e. Ecological Reserve 'Lomas de Banao', Natural Protected Landscape 'Topes de Collantes' and Biosphere Reserve 'Sierra del Rosario'). However, several studies project that species of these mountains will be affected in the coming decades by climate change; therefore, Bécquer & Rodríguez-Cala considered this a plausible threat based on the Red List Criteria, version 3.1, of the IUCN (2012).

Notes. In Gómez de la Maza (1889) there is the entry "Berberis fraxinifolia, Hook.? (Mahonia cubensis Rich.)", this synonymy being repeated in Gómez de la Maza (1890, 1897), where "Rich." is expanded to "Richard", presumably referring to Achille Richard. No source was given for this "Mahonia cubensis". Richard's work (Richard, 1845) on the vascular plants of Cuba has no reference to any Berberidaceae, and the specimen sent to him by de la Sagra remained unidentified in his herbarium until 1960. Interestingly, neither Berberis nor Mahonia



**Figure 4**. *Mahonia sagrana* Harber & Bécquer, sp. nov.: leaf blade of a plant at Parc Codina, near Mirador, Trinidad, Santi Spiritus. No voucher material made. Photograph: Julian Harber.

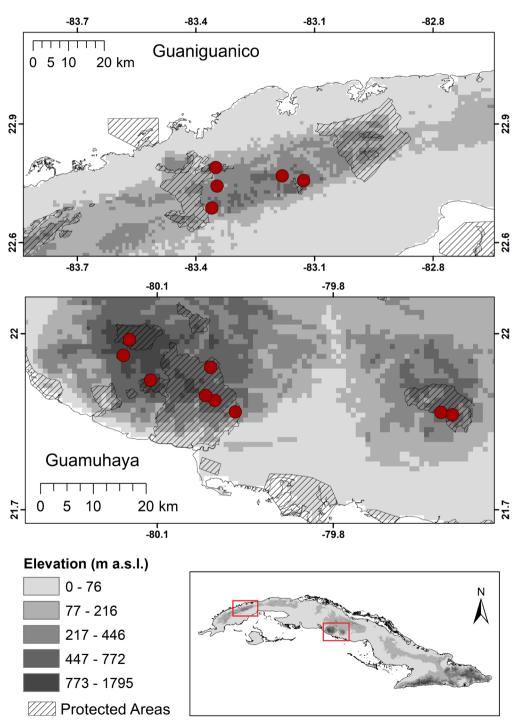


Figure 5. Distribution of Mahonia sagrana in Cuba. Map created by Ernesto Testé.

is listed in two earlier articles by Gómez de la Maza (1886a, 1886b), nor have we found any previous reference to a "Mahonia cubensis" by any other author. What prompted Gómez de la Maza in 1889 to refer to such a taxon thus remains unknown. Should any published description of a Mahonia cubensis from Cuba ever be found, then our M. sagrana would be a synonym. However, on current evidence such a discovery would seem quite unlikely.

Additional specimens examined. NB: collection numbers for specimens collected by Acuña, Bro. Leon, I. Arias et al., E. Bécquer et al., F. Felipe et al. and J. Natenson follow Gabancho et al. (2008).

CUBA. Cordillera de Guaniguanico: Sierra de los Órganos, Pinar del Río: Loma La Guira, ix 1935, *J. Natenson* SV-14323 (HAC). Sierra Rosario, Artemisa: San Cristobal, 7 xii 1915, *Roig* 1188 (HAC); San Cristobal, 8 xii 1915, *Roig* 8000 (HAC); Sierra de los Organos, in forest on top of Peña Blanca, 750 m, 30 iii 1923, *E. L. Ekman* 16379 (G G00405854, NY 0512012, S S16-43276); Sierra de los Organos, grupo del Rosario Sierra de Pendejeral, on top of the mountain, 750 m, 13 ix 1923, *E. L. Ekman* 17514 (S S16-43288); Sabicu, Rangel, Rosario Mts, 550 m, 1 vii 1926, *Bro. Leon* LS-12595 (GH 01154528, HAC, US 01078957); Rangel, Sierra del Rosario, on crest of Loma Sabicu, 440 m, viii 1926, *Bro. Leon* LS-12693 (GH 01154526, HAC, HAJB (3), NY 01512015-16, US 01078958); Pan de Guajaibón y Pendejeral, 26 xii 1936, *J. Acuña* SV-10944 (HAC); ibid., *J. Acuña* SV-11087 (HAC); Pan de Guajaibón, La Palma, *J. Acuña* SV-23337 (HAC); Rangel, Sierra del Rosario, viii 1941, *Bro. Leon* LS-20435 (HAC); Sobre el paredón de la Jutía, Rangel, 500 m, i 1953, *Bro. Alain* 2713 (GH 01154530, HAC, US 01078959); Bosques: Rangel, Sierra del Rosario, viii 1954, *Bro. Alain* 6085 (HAC); Rangel, Sierra del Rosario, viii 1954, *Bro. Alain* 6086 (GH 01154529, US 01078960); Municipio de Bahia Honda: Pan de Guajaibón, en el extremo oeste de la Sierra del Rosario, 22°47'23.6"N, 83°21'59.5"W, 699 m, 8 v 2004, *J. R. Abbott & E. Bécquer* 18893 (FLAS).

Guamuhaya massif: Sancti Spíritus: Edge of Río Tayaba, at San Juan de Letrán, 30 iii 1924, E. L. Ekman 18940 (S S16-43284); Trinidad Mts, Pico Sobrero, c.1000 m, 9 vii 1953, G. L. Webster et al. 232 (DAVH); Crest of Pico Potrerillo, Trinidad Mts, c.1000 m, 16 vii 1957, Bro. Alain 6364 (GH 01154525); Pico Potrerillo, 950 m, 21 vi 1970, A. Borhidi & O. Muñis s.n. (BP); San Juan, Cuabales, near summit on steep slope, 6 ii 1986, G. Yelenevsky & A. Yelenevskaya s.n. (MW MW0574605); Topes de Collantes, Mogote mi Retiro, 22.366667°N, 22°22'N, 79°50'W, 850 m, 2 vii 1993, P. Acevedo-Rdgz. et al. 5591 (US 00681647); Lomas del Garrote, A/P El Naranjal, Lomas del Banao, 700 m, 8 x 1995, E Bécquer 789 (Herbario Jardín Botánico, Sancti Spíritus); Base del farallón norte de Tetas de Juana, 21°51'46.8"N, 79°35'56.4"W, 600-650 m, 10-14 xii 2017, E. Bécquer et al. HFC-89693 (HAJB); Reserva Ecológica Lomas de Banao, cabezadas del río Tayabacoa, alturas cársicas entre Ioma La Ventana y Puerta de la lechuza, 21°51'53.7"N, 79°36'54"W, 700-740 m, 21-25 vi 2022, F. Felipe et al. HFC-90958 (HAJB). Cienfuegos: Vicinity of Soledad, viii 1941, R. A. Howard 6248 (GH 01154527); Cumanayagua, Lomas alrededor de Los Tornos, 4 xi 1987, I. Arias et al. HFC-62849 (HAJB (4)); Cumanayagua, Camino entre Los Tornos y El Sopapo, 6 xi, 1987, I. Arias et al. HFC-62931 (HAJB (4)); Cumanayagua, subida al Pico San Juan, 7 xi 1987, I. Arias et al. HFC-62947 (HAJB); Cumanayagua Lomas al sur del Pico San Juan, 9 xi 1987, I. Arias et al. HFC-63274 (HAJB (2)).

Without locality: s.d., R. de La Sagra 151 (P ex. Herb. Richard P02327264).

*C. Wright* 1855 specimens: *s.d.* (BP, BRU ex Herb. Bennett, BRU ex Herb. Olneyannum, K K001264493, P00752196, S S16-43286, US 01078961); 1860–1864 (BM BM001209248, G G00405936, G00405991, P P00752197, YU 244798); "Retiro Sept. 1... San Christobel" 1860–1864 (GH 01154524);

"Mogot de Mono" x 8, 1865 (NY 01512010); sine ano (NY 1512011); "Cultivated, but indigenous on the northern coast" 1863 (GOET GOET020003). "Cult but indigenous on the northern coast", v 27 sine ano (MO 1932676).

Cultivated specimens: Cienfuegos: Cienfuegos Botanical Garden, 17 ii 1933, J. G. Jack 8676 (NY 01512013); iv 1934, F. G. Walsingham s.n. (NY 01512014).

Living plants: Guamuhaya massif: Sancti Spíritus: Trinidad, Parc Codina, near mirador. Observed by Eldis Bécquer in ii 2015 and viii 2018 and Julian Harber in iv 2016. Two plants cultivated at the nurseries of National Botanical Garden, Havana (HAJB-201700057, from collection HFC-89693).

Mahonia tenuifolia (Lindl.) Czerw. & Warsz. Cat. Pl. Hort. Cracov 292 (1864). Basionym: Berberis tenuifolia Lindley, Edwards's Bot. Reg. 24 (Misc.): 64 (1838); Odostemon tenuifolius Standl., Contr. U.S. Natl. Herb. xxiii: 270 (1922). – Type: Mexico, [near Veracruz, Zacuapam, xii 1836], K. T. Hartweg s.n. [262] (lectotype BM designated by Ahrendt, 1961, missing or non-existent; new lectotype designated here (ICN Article 9.21: Turland et al., 2018) CGE 05241 ex Herb. Lindley!; isolectotypes K [K000994123!], LD [LD1420317] image!; probable isolectotype LE s.col., s.n., s.d., [01041505] image!).

Berberis fraxinifolia Hook. Icon. Pl. 4: t. 329 (1841). – Type: Mexico, Xalapa, 3000 m, i–x 1840, H. G. Galeotti s.n. [4640] (lectotype K ex. Herb Hook., designated here, K [K000407236!]; isolectotypes BR (3) [BR0000027930854, BR0000027930861, BR0000027930892] images!, G (2 sheets) [G00418680] images!, LE [01041505] image!, MEXU ex BR [1313357] image!, W not found; possible isolectotype E ex GL [E00318125!]).

Shrubs, evergreen, c.5 m tall. *Leaves* imparipinnate, 30-35 cm long; leaflets 3-6 pairs, contiguous, lowest pair (3-)5.5-8(-10) cm above base of petiole, abaxially palish yellow green, adaxially dark green, shiny, ovate-lanceolate or lanceolate, rarely broadly ovate; margin entire; apex acute or acuminate, rarely obtuse, papyraceous; midvein raised abaxially, impressed adaxially, lateral veins inconspicuous on both surfaces, base attenuate; margin entire, slightly undulate; apex acuminate. *Inflorescence* a single or 2(-5)-branched raceme to 37 cm, 25- to 45-flowered; pedicel 4-15 mm; floral bracts triangular ovate,  $1.5 \times 0.75-1$  mm, apex acuminate. *Flowers* yellow, c.4 mm in diameter; sepals in three whorls; outer sepals elliptic orbicular or triangular ovate,  $1 \times 1$  mm; median sepals elliptic,  $5 \times 5$  mm; inner sepals elliptic,  $5-6 \times 5$  mm. *Petals* elliptic,  $4-5 \times 2.5-3$  mm, glands separate, apex rounded. *Stamens* dentate, with teeth horizontal or pointing downwards, 2.5 mm; anther connective extended, rounded. *Ovary* 3 mm; ovules 2. *Fruit* berry black, obovoid  $7-8 \times 4-5$  mm, style persistent, conspicuous.

Distribution. Endemic to Mexico. Known from Veracruz and Oaxaca States.

Habitat and ecology. Found among secondary vegetation in deciduous and semi-evergreen forests including oaks, c.900–1020 m.

Proposed IUCN conservation category. Data deficient (DD).

Notes. Determining the type specimens of Mahonia tenuifolia was not completely straightforward. Lindley's protologue of Berberis tenuifolia stated that "seeds were sent by Mr Hartweg to the Royal Horticultural Society from the neighbourhood of Vera Cruz where it was found growing at a place called Zacuapam near the rancho of Mr Lavater". A specimen at GCE (barcode 05241 (CGE)) that is ex Herb Lindley is annotated "Mexico Hartweg" and "Berberis tenuifolia", with a later additional annotation stating "Berberis tenuifolia Bot Reg 1838".

Subsequent to Lindley's (1838) protologue, Bentham (1839), enumerating a small number of collections where there were insufficient specimens to distribute to all those who had subscribed to Hartweg's Mexican expedition, included *Hartweg* 262 from Zacuapam near Vera Cruz, collected in October 1836, identifying this as *Berberis tenuifolia* and citing Lindley's 1838 article.

Hartweg's expedition was a long one, lasting from 1836 to 1843, during which time he collected not just in Mexico but in Guatemala and elsewhere in Central America. The account he gave on his return (Hartweg, 1848) stated that he arrived in Mexico at Vera Cruz on 3 December 1836 (thus contradicting Bentham's dating) and immediately took advantage of an offer to stay with a Mr Laveter on his farm at Zacuapam, which he reached after a two-day ride. He described Zacuapam as being at about 3000 ft "on the eastern declivity of the snow-clad Orizaba". In this locality he recorded "Berberis tenuifolia forming a shrub 10 to 12 feet high". He left Zacuapam on 27 December, arriving at Jalapa [Xalapa] the following day. Although other species of *Berberis* (i.e. *Mahonia*) are recorded for later in his expedition, this is the only reference to *B. tenuifolia*.

There would appear to be no published reference regarding where any specimen of Hartweg's collection might have been until Ahrendt (1961) cited "Mexico; Vera Cruz State, below Mt Orizaba, near Zacuapam, 3000 ft, 1836, *Hartweg 262* (Type BM)". Given that Lindley did not cite any herbarium, this undoubtedly constituted a lectotypification (ICN Article 9.10: Turland et al., 2018). However, despite a thorough search, no such specimen has been found.

At Kew, however, there is an unnumbered specimen annotated as "Berberis tenuifolia Lindl. Bot Reg Misc 1838 p 64 Zacuapam nr Vera Cruz Hartweg 1839". The date, 1839, is clearly a mistake because in 1839 Hartweg was in Guatemala and elsewhere in Central America, but the Kew specimen is undoubtedly a type. However, the existence of this specimen raises a question as to whether there was ever a such specimen at BM, for Ahrendt was not always an accurate recorder and there is at least one instance of where he recorded a specimen at BM when it is actually at K. This is the type specimen of his *Berberis orthobotrys* var. *rupestris* from India (Ahrendt, 1961) – for further information, see Harber (2020).

The fact that the Kew specimen of *Mahonia tenuifolia* does not have the collection details found in Ahrendt's account is not necessarily important, in that it was sometimes Ahrendt's practice to give collection details from protologues and elsewhere that are not from the

specimen sheets he cites (see Harber, 2020). However, given the uncertainty as to whether or not the Kew specimen was actually the one Ahrendt was referring to, it would seem appropriate to designate the *GCE Hartweg* specimen that was originally in Lindley's personal herbarium as a new lectotype and the Kew specimen as an isolectotype. Should the type specimen eventually be found at BM, the selection of the GCE specimen would be void.

The label of a probable isolectotype at LE simply states "Bentham 1839" and "Berberis tenuifolia Zacuapam nr Veracruz", the latter being in the same hand as the text on the label of the specimen at K. There would seem no reason for citing Bentham unless it was in relation to Hartweg's collection.

Hooker's (1841) protologue of *Berberis fraxinifolia* was accompanied by a line drawing and a brief description and gave the collection details simply as "Xalapa, Mexico, Galeotti", without either date of collection or collector's number. Given that it was in a publication he edited subtitled "with Brief Descriptive Characters and Remarks of New or Rare Plants selected from the author's herbarium", it seems reasonable to assume that the Galeotti specimen at Kew that is stamped "Herbarium Hookerianum", and that has both a collector's number and a date, is at least one of the specimens the protologue was based on. Whether it was the only one cannot be proved. Therefore, it is designated here as a lectotype rather than recognised as the holotype.

The Galeotti specimen at E cited above as a possible isolectotype is unnumbered and has no collection details beyond "Jalapa". Fedde (1901) cited a specimen of *Galeotti* 4640 at W; its presence there is confirmed by an 1840 entry in their accessions register. However, the specimen cannot now be located. A large number of specimens of Berberidaceae were loaned by W to Schneider at B before the Second World War, and although most were returned, eleven sheets were not. It is probable that *Galeotti* 4640 was among these and therefore lost when the Berlin herbarium was destroyed (Christian Brauchler, personal communications, 23–25 August 2021).

Additional specimens examined. MEXICO. Veracruz State: Mirador, 1839, *J. Linden* 991 (FI [FI018235], G [G00426731, G00426733], GENT [GENT10163672], K ex Herb. Hooker [K000407234], LE [01041508]); Mirador, viii 1841 *F. M. Liebman* 254.(C (2), O [V:2132516]); Mirador, x 1841, *F. M. Liebman* s.n. (HBG [HBG-525597], M, NY [03091262]); Mirador, x 1841, *F. M. Liebman* 254 (C); Mirador ii 1842, *F. M. Liebman* s.n. (LD [1974465]); Mirador, vii 1843, *F. M. Liebman* s.n. (FI [FI018236], UPS [V-865713]); Mirador, 1841–1843, *F. M. Liebman* s.n. (H [1348030], L [L.1746580], O, UPS [V:2132515], VT [UVMVT139773]); Mexico, s.d., *F. E. Leibold* 18 (B [10 0743100]); Mexico, 1848, *A. Ghiesbreght* 157 (G [G00426734], LE [01041509]); Mirador, c.1000 m, ix 1906, *H. Ross* 640 (BP, M); Zacuapam, vii 1914, *C. A. Purpus* 7661 (GH (2), NY [03091267], UC [191111], US [00899927]); Zacuapam, 900 m, 22 iv 1922, *C. A. Purpus* 347 (HBG [HBG-525596], GH); Zacuapam, viii 1929, *C. A. Purpus* 12056 (GH, NY [03091261]); Near Zacuapam, ix 1929, *C. A. Purpus* 13075 (BM, CAS [0577428], K, S [S18-3175]); Zacuapam, ix 1930, *C. A. Purpus* 13076B (L [L.1746578-79], MICH [1550730]); Near Zacuapam, xi 1930, *C. A. Purpus* 13075B (C); Near San Martin Tlacotepec, xi 1932, *H. W. von Rozynski* 586 (F [V0083000], MICH [1550729], NY [03091260], US [00899926]); El Mirador, SE of Poblado, Mun. Totutla, 1000 m, 10

x 1970, F. Ventura 2553 (CAS [0577429], CR [48357], ENCB, MICH [15507280], MO, TEX); Mata Obscura, Mun. Totutla, 900 m. 9 xii 1970, F. Ventura 2964 (CAS [0577426], CR [48280], ENCB, MICH [1550727], MO, XAL [115376]); El Mirador Mun. Totutla, 1020 m, 8 x 1971, F. Ventura 4217 (CAS [0577427], ENCB, MICH [1550726], XAL); Mun. Totutla, Mata Obscura, 850 m, 10 i 1973, F. Ventura 7685 (CAS [0577430], ENCB, MEXU [260373], MO [6538501]); Xalapa, Potrero del Rancho La Palma, 1000 m, 10 iii 1973, M. Chazaro 41 (ENCB, MEXU [606205]); Totutla, El Mirador, 13 vii 1976, 1000 m, F. Ventura 12993, (MEXU [363516]); Totutla, Mirador, 900 m, 11 viii 1976, F. Ventura 13547 (MEXU [363515]); Mata Obscura, Mun. Totutla, 850 m, 26 vii 1977, F. Ventura 14314 (CAS [0577431], ENCB, IEB, MEXU [418658], XAL); Edo, Mun. Alto Lucero, camino del poblado Cruz Blanca a Sobrero, 19°45'N, 96°51'W, 1000 m, 9 ix 1979, J. I. Calzada 5691 (F [1875193], XAL); Totutla, El Encinal, 750 m, 8 ix 1980, F. Ventura 17811 (ENCB, MEXU [360454]); Edo, Mun. Totutla, 19°12'N, 96°51'W, 950-1000 m, 21 xi 1981, M. Nee & G. Cortés 23385 (F [1932649], K, NY [03091266]); Barranca 1 km S of Palmillas, 19°13'1.2"N, 96°46'1.2"W, 600 m, 23 v 1985, M. E. Medina & S. A. Contreras 134 (ENCB, MEXU [691569]); Barranca de Palmillas, 2 km. SE de dicha poblacion, Municipo Puente National, 19°13'N, 96°46'W, 450 m, 24 x 1985, M. E. Medina & E. F. Vazquez 599 (MEXU [771707], XAL [133759]); Totutla, Barranca 3 km SE of EL Mirador, 19°13'N, 96°52'W, 5 ii 1993, S. Avedaño & C. Durán 3052 (MEXU [723140], XAL), Oaxaca State: Tehuantepec, "El Ocotal", Cerro Guiengola, 16°21'N, 95°19'1.2"W, 950 m, 13 vi 1986, C. L Torres et al. 419 (MEXU [1208344]); Tehuantepec Entrando a "El Ocotal", lado derecho del arroyo por la ladera poniente Cerro Guiengola, 14 xi 1986, C. L Torres et al. 268 (MEXU [1208422]); Tehuantepec, "El Ocotal", Cerro Guiengola, 16°21'N, 95°19'1.2"W, 26 xi 1986, C. L Torres et al. 538 (MEXU [1208347-48]).

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## References

- Acevedo-Rodríguez P, Strong MT, editors. 2012. Catalogue of Seed Plants of the West Indies. Washington, DC: Smithsonian Institution. Smithsonian Contributions to Botany. 98. https://doi.org/10.5479/si.0081024X.98.1.
- Adhikari B, Milne R, Pennington RT, Sarkinen T, Pendry CA. 2015. Systematics and biogeography of *Berberis* s.l. inferred from nuclear ITS and chloroplast *ndhF* gene sequences. Taxon. 64(1):39–48. https://doi.org/10.12705/641.21.
- Ahrendt LWA. 1961. *Berberis* and *Mahonia*: a taxonomic revision. Journal of the Linnaean Society of Botany. 57(369):1–410. https://doi.org/10.1111/j.1095-8339.1961.tb00889.x.
- Alain H. 1969. Flora de Cuba. Suplemento. Caracas: Editorial Sucre.
- Bécquer ER, Rodríguez-Cala D. 2020. *Mahonia tenuifolia* Hoja de taxón. Bissea. 14(número especial 1):460–462. Spanish.
- Bentham G. 1839. Plantas Hartwegianas: imprimis mexicanas adjectis nonnullis Grahamianis enumerat novasque describit. London: G. Pamplin.
- Borhidi A. 1991. Phytogeography and Vegetation Ecology of Cuba. Budapest: Akadémiai Kiadó.
- Boufford DE. 2013. *Mahonia* (Berberidaceae) in Asia: typification, synonymy and notes. Memoirs of the New York Botanical Garden. 108:251–283.
- Capote RP, Berazaín R. 1984. Clasificación de las formaciones vegetales de Cuba [Classification of plant formations in Cuba]. Revista del Jardín Botánico Nacional. 5(2):27–75. Spanish.
- Colin O, Hinsinger DD, Strijk JS. 2021. *Mahonia lancasteri* (Berberidaceae), a new species originating from Sichuan (China) described from cultivation. Phytotaxa. 482(1):45–54. https://doi.org/10.11646/phytotaxa.482.1.5.
- Czerwiakowski IR, Warszewicz JR. 1864. *Mahonia tenuifolia*. Catalogus Plantarum quae in C. R. Horto Botanico Cracoviensi. Krakow: C. R. Universitatis Jagellonicae. p. 292.
- Fedde FKG. 1901. Versuch einer Monographie der Gattung Mahonia. Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie. 31:30–133. German.
- Funes Monzote R. 2008. From Rainforest to Cane Field in Cuba: An Environmental History Since 1492 [Revised English translation, by Alex Martin, of De bosque a sabana: Azucar, deforestación y medio ambiente en Cuba, 1492–1926, Coyoacán, Mexico, Siglo XXI]. Chapel Hill: University of North Carolina Press. https://doi.org/10.5149/9780807888865\_funes\_monzote.
- Gabancho LR, Rodríguez IV, Hernández RM. 2008 [2010]. Revisión histórica de los herbarios cubanos con énfasis en las series de especímenes. Revista del Jardín Botánico Nacional. 29:101–138. http://www.jstor.org/stable/42597272.
- Gómez de la Maza M. 1886a. D. M. Nombre moderno y clasificación familiar de las plantas representadas por A. Richard en la Fanerogamia de la Historia fisica, politica y natural de la Isla de Cuba por R. De la Sagra, El Progreso Médico [D. M. modern name and family classification of the plants represented by A. Richard in the *Phanerogamy of the Physical, Political and Natural History of the Island of Cuba* by R. De la Sagra, El Progreso Médico]. Revista Mensual de Medicina y Cirujia, Habana. 8(2):22–26; 8(3):39–42. Spanish.

- Gómez de la Maza M. 1886b. Catálogo de plantas Cubanas, El Progreso Médico [Cuban Plant Catalogue, El Progreso Médico]. Revista Mensual de Medicina y Cirujia, Habana. 8(5):70–73; 8(6):87–91; 8(8):113–118. Spanish.
- Gómez de la Maza M. 1889. Ensayo de farmacofitologia cubana. Habana: La Propaganda Literaria.
- Gómez de la Maza M. 1890. Catálogo Periantiadas Cubanas Espontáneas y Cultivadas. Anales de la Sociedad Española de Historia Natural. 19:213–278.
- Gómez de la Maza M. 1897. Flora Habanera: Fanerógamas. Havana: Librería, Imprenta y Fábrica de Sellos de Goma "La Moderna poesía".
- González-Espinosa M, Meave JA, Lorea-Hernadez FG, Ibarra-Manriquez G, editors. 2011. The Red List of Mexican Cloud Forest Trees. Cambridge: Flora & Fauna International.
- González Torres LR, Palmarola Bejerano A, González Oliva L, Bécquer ER, Testé E, Barrios Valdés D, Acosta Ramos Z, Alomá Moreno O, Álvarez Montes de Oca JC, Berazain Iturralde RC, et al., editors. 2016. Lista roja de la flora de Cuba [Red List of Cuban Flora]. Bissea. 10(número especial 1):1–352. http://repositorio.geotech.cu/jspui/handle/1234/1054. Spanish.
- Greuter W, Rankin Rodríguez R. 2022. Plantas Vasculares de Cuba Inventario. Tercera edición, actualizada, de Espermatófitos de Cuba. [Vascular Plants of Cuba. A Checklist. Third, updated edition of The Spermatophyta of Cuba]. Berlin: Botanischer Garten und Botanisches Museum Berlin, and Havana: Jardín Botánico Nacional, Universidad de La Habana. https://doi.org/10.3372/cubalist.2022.1.
- Grisebach A. 1866. Catalogus plantarum cubensium exhibens collectionem Wrightianam aliasque minores ex insula Cuba missas. Leipzig: W. Engelmann.
- Harber J. 2020. The *Berberis* of China and Vietnam a revision. Monographs in Systematic Botany from the Missouri Botanical Garden, vol. 136. St Louis, Missouri: Missouri Botanical Garden Press.
- Hartweg H. 1848. Notes of a visit to Mexico, Guatemala, and Equatorial America, during the years 1836 to 1843, in search of plants and seeds for the Horticultural Society of London. Transactions of the Horticultural Society of London, Series 2. 3:115–162.
- Hooker WJ. 1841. Icones Plantarum. Vol. 4. London: Longman, Rees, Orme, Brown, Green & Longman. t. 329.
- Hsieh CL, Yu CC, Huang YL, Chung KF. 2022. *Mahonia* vs. *Berberis* unloaded: generic delimitation and infrafamilial classification of Berberidaceae based on plastid phylogenomics. Plant Science. 12. https://doi.org/10.3389/fpls.2021.720171.
- IUCN. 2012. IUCN Red List Categories and Criteria, version 3.1, 2nd edition. IUCN Species Survival Commission. Gland, Switzerland, and Cambridge: International Union for Conservation of Nature. http://www.iucnredlist.org/technical-documents/categories-and-criteria.
- Lindley J. 1838. Edwards's Botanical Register. 24:64.
- Marroquín JS. 1972. A monographic study of the genus *Berberis* L. in Mexico. Unpublished thesis, Northeastern University, Boston.
- Marroquín JS. 1993. Berberidaceae. In: Sosa V, Gómez-Pompa, editors. Flora de Veracruz. Fasc. 57, México. Xalapa: Instituto de Ecología. pp. 1–15.

- Nuttall T. 1818. The Genera of North American Plants and a Catalogue of the Species to the Year 1817, Vol. 1. Philadelphia: D. Heartt.
- Richard A. 1845. Histoire Physique, Politique et Naturelle de L'Ile de Cuba: Botanique. Plantes Vasculaires. Paris: Arthus Bertrand.
- Roig y Mesa JT, Acuña Galé JB. 1953. Malpighiaceae. In: Alain H. Flora de Cuba III. Dicotiledóneas: Malpighiaceae a Myrtaceae. Contribuciones Ocasionales del Museo de Historia Natural del Colegio De La Salle. 13:9–28.
- Sauvalle FA. 1873. Flora cubana. Enumeratio nova plantarum cubensium. Havana: Imprenta 'La Antilla,' de Cacho-Negrete.
- Schneider CK. 1916. Weitere Beitrage zur Kenntnis der chinesischen Arten der Gattung *Berberis* (*Euberberis*) [Further contributions to the knowledge of the Chinese species of the genus *Berberis* (*Euberberis*)]. Oesterreichische Botanische Zeitschrift. 66:313–326. https://doi.org/10.1007/BF01634312. German.
- Schneider CK. 1939. Neue *Berberis* der Sect. *Wallichianae* [New *Berberis* of sect. *Wallichianae*]. Repertorium Specierum Novarum Regni Vegetabilis. 46:245–267. German.
- Schneider CK. 1942. Die *Berberis* der Section *Wallichianae* [The *Berberis* of section *Wallichianae*]. Mitteilungen der Deutschen Dendrologischen Gesellschaft. 55:1–60. German.
- Takeda H. 1917. Contribution to the knowledge of the Old World species of the genus *Mahonia*. Notes from the Royal Botanic Garden Edinburgh. 6:209–248, plates I–XXXVII.
- Thiers B. Continuously updated. Index Herbariorum: A Global Directory of Public Herbaria and Associated Staff. New York Botanical Garden's Virtual Herbarium. http://sweetgum.nybg.org/science/ih/.
- Turland NJ, Wiersema JH, Barrie FR, Greuter W, Hawksworth DL, Herendeen PS, Knapp S, Kusber WH, Li DZ, Marhold K, May TW, McNeill J, Monro AM, Prado J, Price MJ, Smith GF, editors. 2018. International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) Adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. Regnum Vegetabile 159. Glashütten: Koeltz Botanical Books. https://doi.org/10.12705/Code.2018.
- Ying TS, Boufford DE. 2011. *Mahonia*. In: Wu ZY, Raven PH, Hong DY. Flora of China. Vol. 19, Cucurbitaceae through Valerianaceae with Annonaceae and Berberidaceae). Beijing: Science Press, and St Louis: Missouri Botanical Garden Press. pp. 772–782.
- Yu CC, Chung KF. 2017. Why *Mahonia*? Recircumscribing *Berberis* s.l., with the description of two new genera, *Alloberberis* and *Moranthamnus*. Taxon 66(6):1371–1392. https://doi.org/10.12705/666.6.
- Wright C. 1868. *Berberis fraxinifolia* in Revisio Catologi Grisebachiana vel Index Plantarum Cubensium. Anales de la Real Academia de Ciencias Médicas, Físicas y Naturales de la Habana. 5:198.