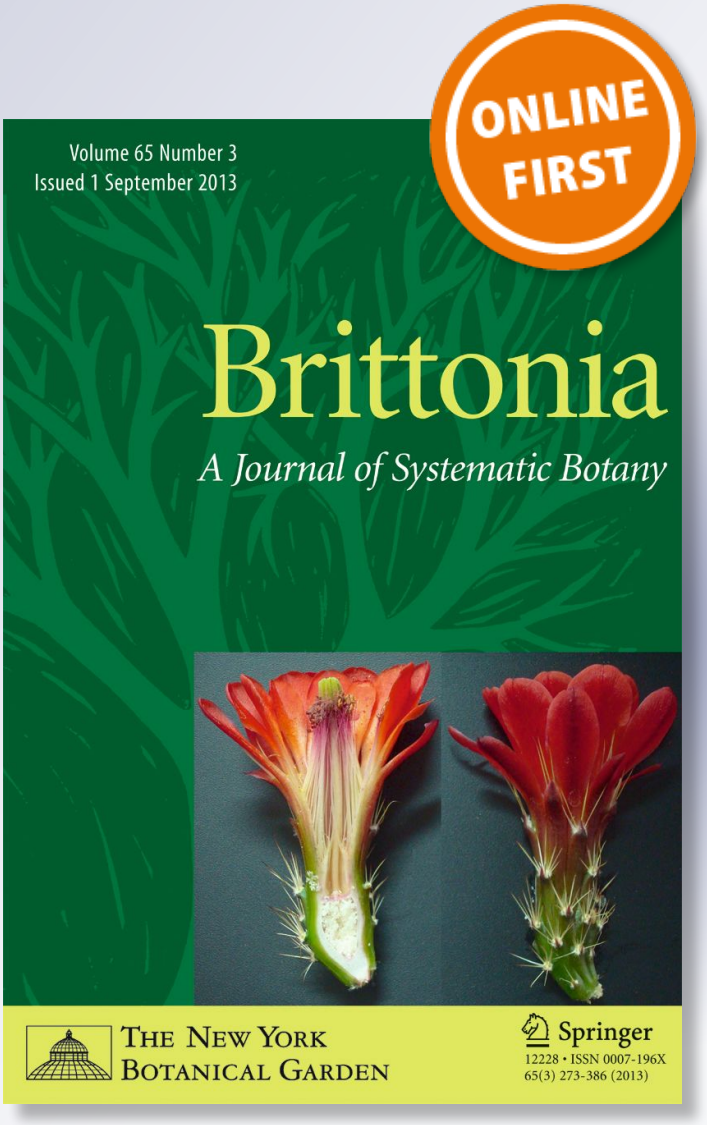
Acer binzayedii *(Sapindaceae), a new maple species from Mexico*

Yalma L. Vargas-Rodriguez, Lowell E. Urbatsch, Vesna Karaman-Castro & Blanca L. Figueroa-Rangel

Brittonia

ISSN 0007-196X

Brittonia
DOI 10.1007/s12228-017-9465-5



Springer

Acer binzayedii (Sapindaceae), a new maple species from Mexico

Yalma L. Vargas-Rodriguez[1,2], Lowell E. Urbatsch[1], Vesna Karaman-Castro[1], and Blanca L. Figueroa-Rangel[3]

[1] Department of Biological Sciences, Louisiana State University, 202 Life Sciences Building, Baton Rouge, LA 70803, USA; e-mail: ylvargasro@conacyt.mx
[2] National Council of Science and Technology, Av. Insurgentes Sur 1582, Col. Crédito Constructor, Ciudad de México, 03940 D.F., México
[3] Department of Ecology and Natural Resources, Centro Universitario de la Costa Sur, Universidad de Guadalajara, Av. Independencia Nacional 151, 48900, Autlán de Navarro, Jalisco, México

Abstract. **Acer binzayedii**, a new species of Sapindaceae from cloud and high elevation forests in Jalisco State, Mexico, is described and illustrated. *Acer binzayedii* is characterized by deeply sagittate anther bases bearing scattered trichomes, the wing sulcus covering more than half of the nutlet, sparsely distributed coalescent and anastomose veins of the wings with reticulate veinlets sometimes present, trichomes on the abaxial leaf surfaces with short nodulations of reduced prominence, conical buds, and grey bark with long vertical ridges. The new species is compared to putative relatives *A. skutchii, A. floridanum, A. saccharum, A. grandidentatum,* and *A. nigrum*.

Keywords: *Acer saccharum*, *Acer skutchii*, North America, sugar maple.

Resumen. **Acer binzayedii**, especie nueva de Sapindaceae de los bosques nubosos en elevaciones altas en el estado de Jalisco, México, se describe e ilustra. *Acer binzayedii* se caracteriza por la antera pronunciadamente sagitada en la base con tricomas esparcidos, el surco del ala cubre más de la mitad del fruto, las venas coalescentes y anastomosas del ala están espaciadamente distribuídas con venas secundarias reticuladas algunas veces presentes, los tricomas en el lado abaxial de la hoja con nódulos cortos de prominencia reducida, yemas cónicas, corteza gris con costillas largas verticales. La especie nueva se compara con los parientes más cercanos *A. skutchii, A. floridanum, A. saccharum, A. grandidentatum,* y *A. nigrum*.

The name *Acer skutchii* Rehder (Sapindaceae; cloud forest sugar maple) has traditionally been applied to maples distributed in Guatemala —from where it was originally described (Rehder, 1936) — and northeastern (Tamaulipas), southeastern (Chiapas), and western (Jalisco, Guerrero) Mexico (Murray, 1975; Breedlove, 1986; Jardel et al., 1996; Vázquez et al., 2000; Vargas-Rodriguez, 2011). It is typically found in cloud forests where it coexists with other temperate tree genera, e.g., *Cornus* L., *Carpinus* L., *Quercus* L. (Vargas-Rodriguez & Platt, 2012). According to Rehder (1936), *A. skutchii* is closely related to the North American *A. saccharum* Marshall (1785) sugar maple, and *A. nigrum* Michaux (1812) black sugar maple, and can be distinguished from these two species by its much larger fruits. Collectivly known as "sugar maples," these trees belong to section *Acer*, series *Saccharodendron* (Rafinesque) Murray, and are characterized by apetalous flowers and a connate perianth (van Gelderen et al., 1994). The series is exclusive to North and Central America and contains about six species; in addition to *A. skutchii*, the only other species with a southernmost distribution is *A. grandidentatum* Nutt., which occurs in northern Mexico.

The sugar maples have a complicated taxonomic history. In the case of *A. skutchii*, it was subsequently lowered to a subspecies –*Acer saccharum* subsp. *skutchii* (Rehder) A. E. Murray (Murray, 1975, 1980) – following Desmarais's

Brittonia, DOI 10.1007/s12228-017-9465-5
ISSN: 0007-196X (print) ISSN: 1938-436X (electronic)

Published online: 22 February 2017

(1952) earlier treatment of *A. saccharum* as one species with six subspecies: typical subsp. *saccharum*, in addition to subsp. *floridanum* (Chapm.) Desmarais, subsp. *grandidentatum* (Nutt.) Desmarais, subsp. *leucoderme* (Small) Sudw., subsp. *nigrum* (F. Michx.) Desmarais, and subsp. *schneckii* (Rehder) Desmarais. However, Desmarais's (1952) treatment was based only on leaf characters (which are extremely variable even within a single individual), without consideration of other morphological features such as flowers and fruits. Taking into account the differences with *A. saccharum* s.l. in terms of anther ornamentation, perianth and anther length, size and shape of fruits, length of the wing and its sulcus, and leaf trichome ornamentation, we accept the species status of *A. skutchii* as distinct from *A. saccharum*, as established by Rehder (1936). In addition, a number of DNA insertions and deletions in noncoding regions of the chloroplast genome distinguish *A. skutchii* from *A. saccharum*, possibly suggesting different evolutionary processes acting in *A. skutchii* (Vargas-Rodriguez, unpublished data).

During the development of a taxonomic treatment of Mesoamerican maples by the first author, it was possible to discern two different entities previously identified as *A. skutchii*. When describing *A. skutchii,* Rehder (1936) did not observe the flowers, nor did he evaluate many qualitative and quantitative differences. Later, other populations of *Acer* were discovered in northeastern, western, and southeastern Mexico, but the morphological variation among these new populations were not carefully examined or contrasted, and they were often identified using only the size and shape of the leaves, and were thus assumed to be the same as *A. skutchii* from Guatemala. As field observations and collections of fertile material were gathered and analyzed, it was possible to note new diagnostic characters, thus recognizing the populations in western Mexico as a different entity. Herein, we include bark, bud, leaf, flower, and fruit characters that distinguish *A. skutchii* from the new species.

Materials and methods

Herbarium specimens of *Acer* were studied at the following Mexican and international herbaria: AGUAT, BIGU, BM, EAP, F, GH, IBUG, IEB, LL-TEX, MEXU, MICH, MO, NY, TENN, US, UVAL, WIS, XAL, ZEA (Thiers, continuously updated). Morphological characters were measured and characterized as follows: wing measurements followed terminology by Wolfe and Tanai (1987); parts of the leaves were recorded according to Anderson and Hubricht (1938); trichome ornamentation followed Krause (1982). Observations were performed using an Olympus SZX12 dissecting stereo microscope (Tokyo, Japan). Flowers of dried herbarium specimens were rehydrated using Aerosol OT following the protocol described by Ayensu (1967). Flowers and buds were dissected and prepared under the Olympus SZX12 dissecting stereo microscope (Tokyo, Japan). Dried pollen and leaf material was coated with gold:palladium (60:40) in an Edwards S-150 sputter coater (Edwards High Vacuum Co. International, Wilmingotn, MA, USA) and observed using a Cambridge S-260 scanning electron microscope. Estimates of pollen age were obtained using linear interpolation; the model was run with CLAM 2.2, using interCal 13.

Taxonomy

Acer binzayedii Vargas-Rodriguez, **sp. nov.** Type: Mexico. Jalisco: Autlán de Navarro municipio: cloud forest, Cañada La Moza, 19°36′ N, 104°17′ W, 1850 m, 19 June 2003, *Y. L. Vargas-Rodriguez & F. Vargas-Aguilar 373* (holotype: LSU; isotypes: GH, MO, NY, US, ZEA) (Figs. 1–2).

Acer binzayedii is most similar to *A. skutchii* (in which it was previously included), but it differs from that species by its grey bark with long vertical ridges; conical buds; trichomes on the abaxial leaf surface with short nodulations of reduced prominence; elliptic wings, sometimes with reticulate veinlets; the sulcus of the wing more than half the width of the nutlet; the perianth 2.5–3.6 mm wide; mucronate anthers with long trichomes and a deeply sagittate base; and the filaments of the stamens 3.5–5.8 mm long. Moreover, *A. skutchii* is distributed in northeastern and southeastern Mexico and Guatemala, whereas *A. binzayedii* is restricted to the state of Jalisco in western Mexico.

Tree 20–30 m tall, deciduous, 60–90 cm in diameter; bark grey with long vertical ridges. *Petioles* tomentose to sparsely villose or glabrous, auburn; buds conical, 2–3 × 1–2 mm, scale pairs 3 or 4, basal scale prickle is inconspicuous or absent. *Leaves* with 5 lobes, leaf base cordate, minor lobes sometimes present, teeth projections around the margin 6–14, acute or lobed; lamina 6.4–19.2 × 6.1–19.4 cm, radius 4.6–10.3 cm, midvein 5.8–17.2 cm, primary side vein 5.2–16.5 cm, intersinus 3–6.9 cm, horizontal vein 3.4–9.1 cm, abaxial side

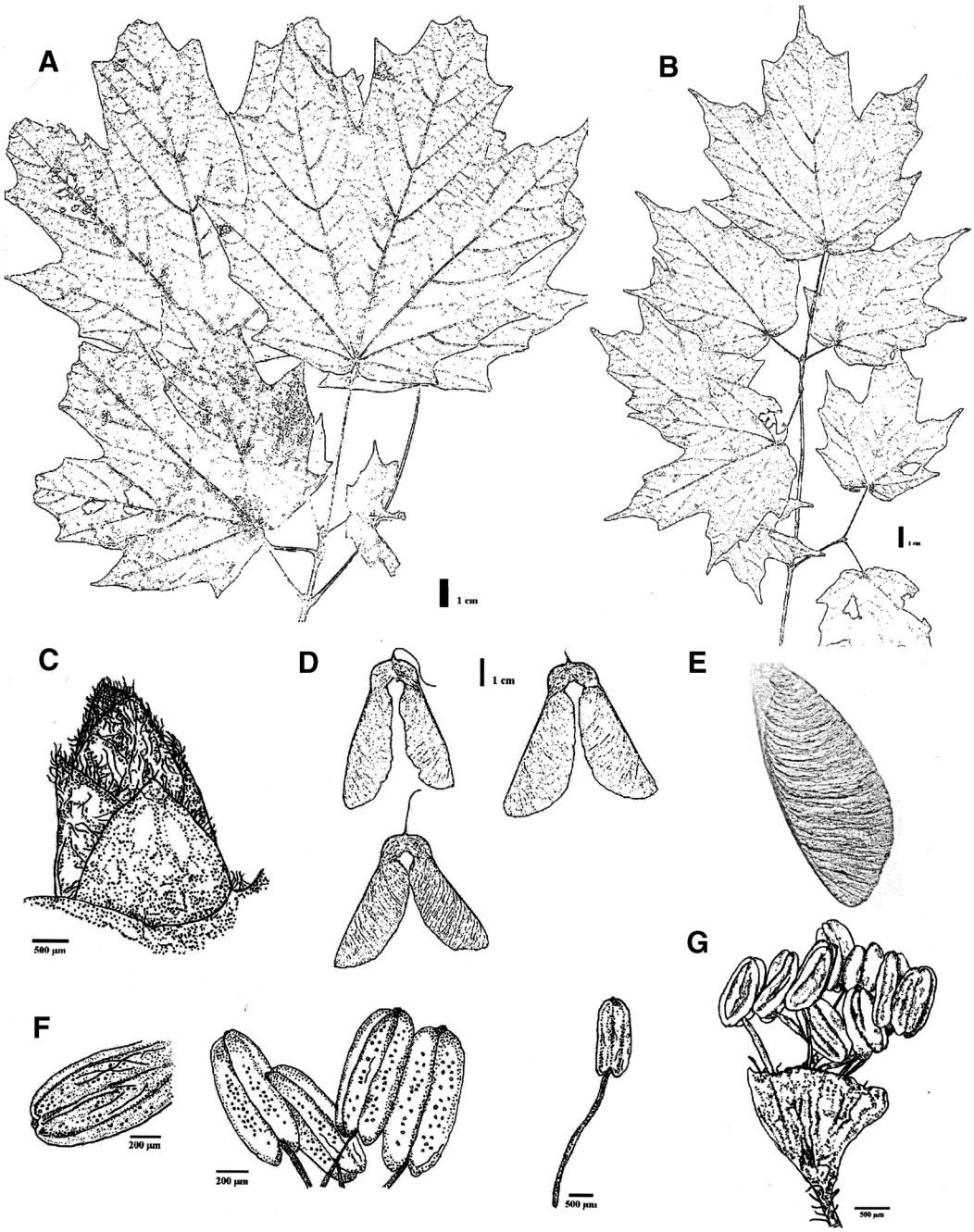


Fig. 1. *Acer binzayedii.* **A, B.** Variation in leaf shape and size within the same individual. **A.** Larger leaves growing under shade environment, in lower branches. **B.** Branchlet in open conditions. **C.** Conical buds. **D.** Shape variation of fruits, wing sulcus covering more than half of the nutlets. **E.** Sparsely distributed coalescent and anastomose veins of the wings with reticulate veinlets sometimes present. **F.** Anther with scattered trichomes (left), subbasifixed anthers, mucronate, with sagittate base and sometimes with a distal connective protrusion. **G.** Flower with perianth connate. Drawn from the holotype.

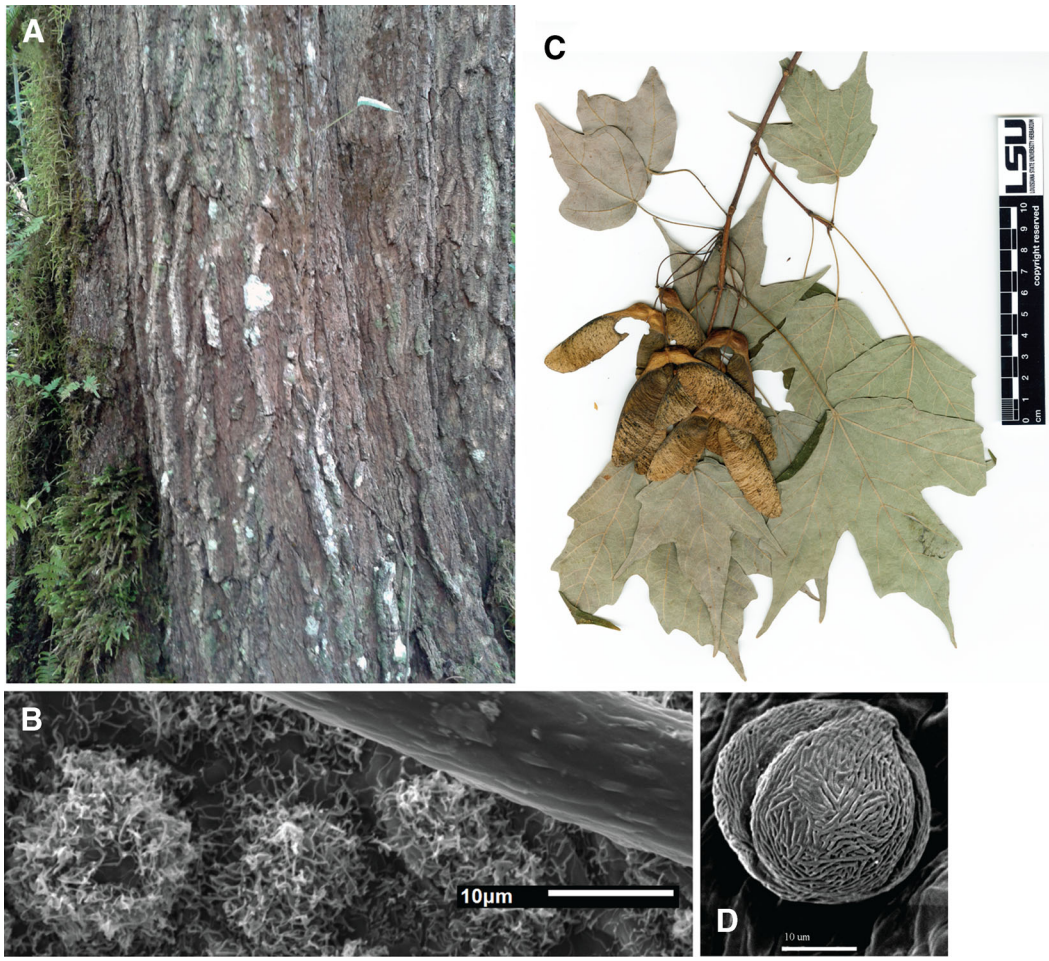


Fig. 2. *Acer binzayedii.* **A.** Trunk with grey bark and long vertical ridges. **B.** Leaf with trichomes on the abaxial leaf surfaces with short nodulations of reduced prominence. **C.** Branch with infructescence, wings elliptic. **D.** Pollen tricolpate, exine striate-reticulate, with coarse reticulum, grain sub-oblate spheroid. Photos from the type.

villous-tomentose, abaxial trichomes with short nodulations of reduced prominence. *Flowers* in corymbs, light yellow, apetalous. *Perianth* connate, sparsely villous along the edge and at the base; perianth 2.7–3.5 × 2.5–3.6 mm. *Stamens* 6–9, filaments length 3.5–5.8 mm, the anthers oblong, base deeply sagittate, attachment subbasifixed, with scattered trichomes, papillate, distal connective protrusion sometimes present with mucronate shape, anthers 1.7–2.6 × 0.8–1.2 mm; pollen tricolpate, 3 furrows, exine striate-reticulate, with coarse reticulum, grain sub-oblate spheroid, polar axis 20.8–39.4 µm, equatorial diameter 23–30.5 µm. *Pistil* with style 0.5 mm, nectary disc 0.3–0.5 mm in height, stigma 3–4 mm; male flowers with abortive pistil densely villose, and stigma 0.6–0.9 mm. *Nutlet* elliptic, sparsely villous, hair yellowish, veins present, sometimes rugose,extremely inflated; 0.8–1.1 × 0.8–1.1 cm; distal keel present, proximal keel protruding, nutlet contact scar 0.8–1 cm; *seed* spheroid 0.5–0.7 cm; *wings* elliptic, wing divergence angle 20.4–63°; coalescent proximal veins and anastomoses sparsely distributed, reticulate veinlets sometimes present; wings 3.7–5.6 × 1.4–2.5 cm, wing sulcus 0.6–1.1 cm wide.

Distribution and ecology.—In western Mexico, Jalisco state: Cañada de la Moza (Sierra de Manantlán), Ojo de Agua del Cuervo (Sierra de Cacoma), from 1790–1880 m elevation. Mean annual temperature is 18.5°C, mean annual precipitation is 1257.6–1294.6 mm. Substrates in the area

are intermediate extrusive rocks and Cambisol soils.

Acer binzayedii is found in remnant ravine cloud forests, were it co-occurs with *Carpinus caroliniana* Walter, *Cornus disciflora* Moc. & Sessé ex DC., *Dendropanax arboreus* (L.) Decne. & Planch., *Ostrya virginiana* K. Koch., and *Quercus salicifolia* Née, among others (Vargas-Rodriguez, 2005). The currently known area of forest patches containing the species is less than 2 ha, and these patches are surrounded by *Pinus-Quercus* forests. Fossil pollen grains were retrieved in a forest hollow, revealing the presence of the species and an ancient cloud forest dated approximately 931 AD in the Cañada de la Moza (Figueroa-Rangel et al., 2011).

Estimates of basal area and density of maples ≥ 1 cm dbh in the two populations are 18 m^2 ha^{-1} and 327 tree/ha, respectively. Diameters of adult trees range from 60–90 cm dbh, with the largest individual measured occuring in the Ojo de Agua del Cuervo population. Maple juveniles and saplings abundance is 558 in 0.3 ha at the Ojo de Agua del Cuervo locality and 916 in 0.1 ha at Cañada de la Moza (Vargas-Rodriguez & Platt, 2012). Diameter, height, and seedlings and saplings structure of *A. binzayedii* suggest that the population can be considered an old growth stand (Vázquez et al., 2000; Vargas-Rodriguez & Platt, 2012). The estimate of tree species richness at Ojo de Agua del Cuervo forest is 43, with 12 species (in 0.3 ha) under legal protection for conservation purposes, while at Cañada de la Moza there are 19 tree species of which 6 species (in 0.1 ha) have conservation status (Vargas-Rodriguez & Platt, 2012).

Phenology.—Leaves appear in January and turn red in October. Flowering occurs from December to January. Fruits form in March and reach maturity in August.

Etymology.—The specific epithet honors a philanthropist committed to the protection of the environment and the preservation of species, His Highness Sheikh Mohammed bin Zayed Al Nahyan, Crown Prince of Abu Dhabi and Deputy Supreme Commander of the United Arab Emirates Armed Forces. Through his philanthropic endowment, the first author was able to conduct phylogeographic and taxonomic studies of *Acer* in tropical America; this research led to the discovery and recognition of this new species.

Local names.—Algodoncillo.

Conservation status.— *Acer binzayedii* is evaluted as Endangered EN B1ab(i,ii,iii,iv,v) under the IUCN Red List guidelines (IUCN, 2010). One population is located inside a Biosphere Reserve. The number of observed adult trees is less than 90. Abundance of seedlings and saplings is low. Logging, forest fires, and sporadic cattle grazing are common in areas surrounding *Acer* populations. Genetic diversity is low in both populations in Jalisco (Lara-Gomez et al., 2005; Vargas-Rodriguez et al., 2015).

Discussion

A number of qualitative and quantitative characters separate *A. binzayedii* from *A. skutchii*. The perianth and stamen filaments in *A. binzayedii* are up to twice as long as those in *A. skutchii*, and the anthers are subbasifixed and mucronate with a deeply sagittate base, sometimes with a distal connective protrusion, and have long trichomes, whereas the anthers of *A. skutchii* have a cordate base, lacking the distal protrusion and the trichomes. A distal keel is present in the nutlet of *A. binzayedii*, and the proximal keel is protruding, elliptic in shape, sparsely villous, with veins, and is sometimes rugose. However, in *A. skutchii* the distal keel –if present– is often inconspicuous, and the proximal keel is only sometimes protruding, with a square-like shape, glabrous or sparsely villous, and the smooth surface is only sometimes veined. The nutlets are larger in *A. binzayedii*, with the width of the wing sulcus more than half the width of the nutlet, but half or less than half the width of the nutlet in *A. skutchii*. The wings of *A. binzayedii* are elliptic in shape with coalescent proximal veins and anastomoses sparsely distributed, sometimes with reticulate veinlets, whereas the wings of *A. skutchii* are with straight (sometimes curved), with abundant anastomosing veins that are bifurcating toward the distal part and with abundant reticulate veinlets. Wings are larger and the divergence angle is wider in *A. binzayedii* compared to those in *A. skutchii*. Contrastingly, leaf teeth projections and leaf intersinus are smaller in *A. binzayedii* compared to those in *A. skutchii*. Trichomes on the abaxial leaf surface are with short nodulations of reduced prominence and unlike those in *A. skutchii*, which have long nodulations. *Acer binzayedii* displays conical buds and grey bark with long vertical ridges, whereas *A. skutchii* displays ovate buds and gray to whitish or auburn-reddish bark that is smooth or with scaly, thin plates that peel in old trees (Table 1). Although the bark morphology changes during tree growth,

Table 1 Diagnostic differences between *Acer binzayedii* and *Acer skutchii*.

Character	*Acer binzayedii*	*Acer skutchii*
Bark	grey, long vertical ridges	smooth gray to whitish or auburn-reddish, scaly thin plates that peel in old trees
Buds	conical, 2–3 × 1–2 mm, scale pairs 3 or 4, basal scale prickle is inconspicuous or absent	ovate, 3–4 × 2-3 cm, scale pairs 3–5, appressed silky white hair along scale edge, basal scale with prickle 0.1–0.7 mm
Leaf intersinus	3–6.9 cm	2.7–8.2 cm
Leaf teeth projections	6–14, acute or lobed	1–22, acute or lobed
Trichomes in the abaxial leaf side	with short nodulations of reduced prominence	with long nodulations
Flower, perianth size	2.7–3.5 × 2.5–3.6 mm	1.9–3 × 1.3–2.9 mm
Filament length	3.5–5.8 mm,	1.4–3.5 mm
Stigma	3–4 mm	2.3–5.5 mm
Style	0.5 mm	0.8–2 mm
Anther	oblong, base deeply sagittate, attachment subbasifixed, scattered trichomes, papillate, distal connective protrusion sometimes present, mucronate in shape, 1.7–2.6 × 0.8–1.2 mm	oblong, base cordate, trichomes absent, distal connective protrusion absent, 1.5–1.7 × 0.6–0.7 mm
Nutlet	0.8–1.1 × 0.8–1.1 cm	0.7–1.1 × 0.6–1.1 cm
Wing	elliptic, 3.7–5.6 × 1.4–2.5 cm	proximal side straight, sometimes slightly curved, 2.1–4 × 0.8–1.6 cm
Wing sulcus	0.6–1.1 cm	0.3–0.6 cm
Divergence angle	20.4–63°	6–47°
Wing veins	coalescent proximal veins and anastomoses sparsely distributed, reticulate veinlets sometimes present	anastomoses veins abundant and bifurcating towards distal part, reticulate veinlets abundant
Nutlet contact scar	0.8–1 cm	0.6–0.75 cm
Nutlet	distal keel present, proximal keel protruding, sparsely villous, elliptic shape, with veins, sometimes rugose, extremely inflated	distal keel often inconspicuous, proximal keel sometimes protruding, glabrous or sparsely villous, square-like shape, smooth surface sometimes veined, extremely inflated

the first author has not observed long vertical ridges in adult individuals of *A. skutchii* both in cultivation and in their natural habitat.

Acer binzayedii is also distinguished using molecular data. Chloroplast DNA as well as nuclear microsatellites indicate that the populations are highly differentiated from those of *A. skutchii,* pointing to a strong barrier to gene flow between the two species. In addition, the Jalisco populations have different haplotypes. Using Bayesian inference in connection with a relaxed molecular clock with a coalescent approach, the age of the most recent common ancestor of the two species was dated to ca. 5.4 mya (95% HPD: 4.1–7.3 mya), suggesting that the lineage diverged from its relatives around the beginning of the Pliocene or late Miocene. The uplift of a mountain barrier (Trans-Mexico Volcanic Belt) and subsequent volcanic activity could have isolated the cloud forest sugar maple populations in Jalisco, facilitating their eventual divergence (Vargas-Rodriguez et al., 2015).

Acer skutchii and *A. binzayedii* differ from their close relatives as follows: 1) *A. floridanum* (Chapm.) Pax (1886) has wider but shorter perianths, as well as a prominent anther distal connective protrusion; 2) *A. saccharum* has an anther with a distal mucronate-type connective protrusion, abortive pistils lacking pubescence, and smaller globose nutlets (0.6 × 0.8 cm). In addition, *A. saccharum* presents abaxial leaf trichomes with recessed or elongated nodulations; 3) *A. nigrum* has perianth lobes, perianth two times as broad, abaxial leaf trichomes with oval nodulations, and leaf stipules often present; 4) *A. grandidentatum*

has a basifixed anther attachment and lacks a distal connective protrusion, the nutlet keel is absent, and it has smaller wings and smaller leaf intersinus lengths (1.3–2.9 cm).

Additional specimens examined. MEXICO. JALISCO: Municipio Autlán de Navarro: Arroyo La Moza, ejido de Ahuacapán, 19°37′ N, 104°18′ W, 1850 m, *A. Santiago 4* (WIS); 3.5 km al NW de la ECLJ, Cañada La Moza, 19°36′ 50″ N, 104°18′07″ W, 1850 m, 30 March 1991, *E. Jardel et al. 195, 196* (WIS, ZEA), 4 April 1991, *E. Jardel et al. 321, 322* (WIS, ZEA), 4 August 1991, *E. Jardel et al. 323* (WIS, ZEA), 4 November 1991, *E. Jardel 324* (MICH, WIS, ZEA); cañada La Moza, 2.5 km al NE de El Zarzamoro, 1800 m, 8 June 1991, *R. Cuevas & E. Jardel 4157, 4158* (ZEA); 1.3 km by road due SE of Corralitos toward Las Joyas, 19°36′32″ N, 104°17′51″ W, 1840 m, 19 June 1991, *T. Cochrane & A. Vázquez 12612* (IBUG, F, MICH, WIS, ZEA,); cañada de La Moza, 3.5 km al NE de Las Joyas, 19°36′50″ N, 104°18′07″ W, 1850 m, 4 April 1992, *E. Jardel & A. Santiago 325, 326, 327, 328, 329, 330* (IEB, MICH, WIS, ZEA); La Moza, just down-slope from road W of Las Joyas on road to Ahuacapán, ca 2 km SE of Corralitos (Ejido Ahuacapán), 19°36′10″ N, 104°17′45″ W, 1880 m, 8 March 1992, *H. Iltis et al. 30960* (MICH, WIS, ZEA); cañada La Moza, Estación Científica Las Joyas, 7 September 1994, *R. Cuevas & L. Guzmán 4620* (ZEA); cañada La Moza, 19°36′ N, 104°17′ W, 1850 m, 19-20 June 2003, *Y. L. Vargas-Rodriguez & F. Vargas-Aguilar 371, 372* (LSU, ZEA), 20 August 2008, *Y. L. Vargas-Rodriguez & F. Vargas-Aguilar 851–875* (LSU). Municipio Talpa de Allende: Ojo de Agua del Cuervo, 20°12′ N, 104°45′ W, 1798 m, 12 July 2003, *Y. L. Vargas-Rodriguez 389* (LSU), 24 June 2005, *Y. L. Vargas-Rodriguez 798–809* (LSU), 19 August 2008, *Y. L. Vargas-Rodriguez 810–850* (LSU).

Acknowledgements

The Mohamed bin Zayed Species Conservation Fund provided financial support. Collection permits were granted by SEMARNAT, Mexico. The curators of all cited herbaria are thanked for making specimens available. Two anonymous reviewers provided valuable comments on the manuscript.

Literature cited

Anderson, E. & L. Hubricht. 1938. The American sugar maples. I. Phylogenetic relationships, as deduced from a study of leaf variation. Botanical Gazette 100: 312–323.

Ayensu, E. S. 1967. Aerosol OT solution–an effective softener of herbarium specimens for anatomical study. Stain Technology 42: 155–156.

Breedlove, D. E. 1986. Listados florísticos de México: IV Flora de Chiapas. Instituto de Biología, Universidad Nacional Autónoma de México, México D.F., **246 pp**.

Desmarais, Y. 1952. Dynamics of leaf variation in the sugar maples. Brittonia 7: 347–387.

Figueroa-Rangel, B. L., M. Olvera-Vargas & K. J. Willis. 2011. Late Holocene successional dynamics in a transitional forest of west-central, Mexico. The Holocene 22: 143–153.

Jardel, E., R. Cuevas, A. Santiago, E. Muñoz & J. Aragón. 1996. Nueva localidad y características de la población de *Acer skutchii* Rehder en la Sierra de Manantlán, Jalisco, México. Acta Botánica Mexicana 35: 13–24.

Krause, C. R. 1982. Differentiation of black and sugar maple cultivars with scanning electron microscopy. Journal of the American Society for Horticultural Science 107: 186–188.

Lara-Gomez, G., O. Gailing & R. Finkeldey. 2005. Genetic variation in isolated Mexican populations of the endemic maple *Acer skutchii* Rehd. Allgemeine Forst und Jagdzeitung 176: 97–103.

Marshall, H. 1785. *Acer saccharum* Marsh. Arbustrum Americanum 1–4.

Michaux, F. A. 1812. *Acer nigrum*, the black sugar tree. Pp. 238–241. *In*: Historie des arbres forestiers de L´Amérique Septentrionale. Tome II. Paris.

Murray, A. E. 1975. North American maples. Kalmia 7: 1–20.

———. 1980. Mexican maples (arces mexicanos). Kalmia 10: 5–8.

Pax, F. A. 1886. Monographie der Gattung *Acer*. Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie. Leipzing 7: 243–244.

Rehder, A. 1936. A new species of *Acer* from Guatemala. Journal of the Arnold Arboretum 17: 350–351.

IUCN [=International Union for Conservation of Nature and Natural Resources] 2010. Guidelines for application of IUCN Red List criteria at regional and national level. Version 4.0. International Union for Conservation of Nature and Natural Resources, Species Survival Commission. IUCN, Gland, Switzerland and Cambridge, UK.

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/.

van Gelderen, D. M., P. C. de Jong & H. J. Oterdoom. 1994. Maples of the world. Timber Press, Portland, Oregon.

Vargas-Rodriguez, Y. L. 2005. Ecology of disjunct cloud forest sugar maple populations (*Acer saccharum* subsp. *skutchii*) in North and Central America. M.Sc. thesis, Louisiana State University, Baton Rouge, Louisiana.

———. 2011. Una población relicta de *Acer saccharum* subsp. *skutchii* (Aceroideae) en el estado de Guerrero, México. Acta Botánica Mexicana 95: 11–28.

——— & W. J. Platt. 2012. Remnant sugar maple (*Acer saccharum* subsp. *skutchii*) populations at their range edge: Characteristics, environmental constraints and conservation implications in tropical America. Biological Conservation 150: 111–120.

———, ———, L. E. Urbatsch & D. W. Foltz. 2015. Large scale patterns of genetic variation and differentiation in sugar maple from tropical Central America to temperate North America. BMC Evolutionary Biology 15: 257. doi:10.1186/s12862-015-0518-7.

Vázquez, J. A., Y. L. Vargas-Rodriguez & F. Aragón. 2000. Descubrimiento de un bosque de *Acer-Podocarpus-Abies* en el municipio de Talpa de Allende, Jalisco, México. Boletín del Instituto de Botánica 7: 159–183.

Wolfe, J. A. & T. Tanai. 1987. Systematics, phylogeny, and distribution of *Acer* (maples) in the Cenozoic of western North America. Journal of the Faculty of Science, Hokkaido University 22: 1–247.