



Fog and coffee: a new species of *Tridimeris* (Annonaceae) endemic to the mountain cloud forest of Mexico

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Abstract

Tridimeris is the only genus of Annonaceae endemic to Mexico. Despite this, the genus has been largely ignored and very little is known about it; specifically its diversity and distribution in Mexico are not well studied. Here a new species of *Tridimeris*, *T. huatuscoana*, is described and illustrated. The most general characteristics of the new species confirm that dimerous flowers (two sepals and four petals) and the large, and fleshy fruits are the most obvious synapomorphies for the Mexican genus *Tridimeris*. With respect to the other two species described so far (*Tridimeris hahniana* and *T. chiapensis*), the new species can be easily distinguished by the unique combination of 2-flowered inflorescences, large petals pubescent outside, food bodies present at the base of its inner petals, setose leaf domatia, and fruits shortly pedunculate and stipitate. The new species expands the richness of the genus to three species, all endemic to Mexico and restricted to montane cloud forests.

Keywords: dimerous flowers, Huatusco, Miliuseae, morphology, Neotropical

Introduction

Tridimeris Baillon (1869: 219) is the only genus of Annonaceae endemic to Mexico. Despite this, very little is known about its morphology, diversity, distribution and evolutionary history. So far two species have been described, *Tridimeris hahniana* Baill. (1869: 219) distributed in the mountain system of eastern Mexico, and *T. chiapensis* M.A. Escobar & Ortiz-Rodr. (in Ortiz-Rodríguez *et al.* 2016a: 86), endemic to southern Mexico. Both species share axillary, dimerous flowers (two sepals and four petals), a reduced number of carpels per flower (1-5), and large, fleshy fruits, these being distinctive characteristics of the genus *Tridimeris* (Ortiz-Rodríguez *et al.* 2016a). Phylogenetic studies show that this genus is monophyletic (its two species are closely related) and that they form part of an early divergent clade (Miocene: between 23 and 12 Ma) within the subtribe Sapranthinae (Ortiz-Rodríguez *et al.* 2016b, Ortiz-Rodríguez *et al.*, 2018). The genus *Tridimeris* is sister to the Neotropical genus *Sapranthus* Seemann (1866: 369). The characteristics of the seed (smooth coat, with lamellate ruminations), large and fleshy fruits with numerous seeds, and usually eucamptodrome leaf venation pattern, support the relationship between both genera (Schatz *et al.* 2018). However, both lineages differ markedly in their flower characteristics (e.g., trimerous vs. dimerous flowers) and in their ecological preferences (*Sapranthus* occurs in dry forests vs. *Tridimeris* in montane moist forests).

Many lowland plant lineages in Mexico are considered tolerant to drier and colder forests (Toledo, 1976), which during past periods of climate change facilitated their survival and invasion of other types of vegetation such as the mountain cloud forest. Thus, the evolutionary history of the montane cloud forest in Mexico and its relationship with past climate change (Ramírez-Barahona and Eguiarte 2013) is probably involved in the most recent evolution of the genus *Tridimeris*, a hypothesis that has not been tested yet.

As a result of recent botanical explorations in the coffee growing region of Huatusco, Veracruz, in Mexico, a species of *Tridimeris* with an interesting combination of morphological characteristics, was collected. The very large flowers of this species, its inflorescences composed of more than one flower, its setose leaf domatia, and the food bodies

present at the base of its inner petals, allowed us to propose that this species was new to science. The new species is described and illustrated here, and its phylogenetic relationships, morphological similarities and conservation status are discussed.

Material and methods

Species differentiation:—the putative new species of *Tridimeris* was recognized using the unique combination of features criteria (Donoghue, 1985) through comparisons with morphologically similar species and literature review. We visited and reviewed the specimens of *Tridimeris* deposited in the XAL and MEXU herbaria (Thiers, 2022).

Conservation status:—Based on the known distribution for the new species, we assessed its conservation status by calculating its extent of occurrence (EOO) and its area of occupancy (AOO) using the GeoCAT tool (Bachman *et al.*, 2011) and applying the IUCN Red List Categories and criteria (IUCN, 2022).

Taxonomic treatment

Tridimeris huatuscoana Marinero-Sobal & Ortiz-Rodr. *sp. nov.* (Figs. 1–3, Table 1).

Type:—MEXICO. Veracruz, Huatusco, Río seco, road between Ixpila and Huatusco on the way to Tenejapa, approximately 3 km south of Huatusco, 19.127376° N, 96.981851° W, 1283 m, montane cloud forest, tree 7 m tall, cream-white flowers, in riparian vegetation within the montane cloud forest, 2 January 2022, *E. J. Marinero-Sobal 425* (holotype MEXU!, isotypes CIB!, MO!).

Similar to *Tridimeris chiapensis* in its glabrous fruit surface and flowers with food bodies at the base of the inner petals, but differing from this species by its setose leaf domatia, longer and pubescent cream-white petals, greater number of flowers per inflorescence, fewer carpels per flower, and by its shorter pedicels.

TABLE 1. Comparison of diagnostic morphological characters of *Tridimeris chiapensis*, *Tridimeris hahniana*, and *Tridimeris huatuscoana*.

Characters	<i>Tridimeris chiapensis</i>	<i>Tridimeris hahniana</i>	<i>Tridimeris huatuscoana</i>
Leaf domatia	Glabrous	Glabrous	Setose
Flowers per inflorescences	1	1	2
Pedicels surface	Glabrous	Pubescent	Pubescent
Flower pedicels	10–17 mm	5–10 mm	1–3 mm
Food bodies	Present	Absent	Present
Petals length	8–14 mm	10–12 mm	10–25 mm
Petals color	Green	Green	Whitish or beige
Carpels	2 to 5	1 or 2	2 or 3
Monocarps	Glabrous	Velvety	Glabrous

Tree 5–7 m tall and 3–14 cm in diameter; young branches slightly pubescent, trichomes appressed and golden-brown in color, very soon glabrous. Leaves membranaceous to chartaceous, alternate, phyllotaxy distichous, 7–17 cm long to 2.5–5.5 wide, narrowly elliptic to obovate, apex acute to long acuminate, base acute to obtuse, sometimes slightly asymmetrical; upper and lower surface glabrous; venation eucamptodromous to weakly brochidodromous, 6–9 secondary veins per side, pocket domatia in the axils of the main veins, setaceous; midrib impressed above and slightly canaliculate toward the base, lateral veins impressed above; midrib and lateral veins prominently elevated below and with very sparsely and appressed light-brown hairs, lateral veins decurrent at midrib insertion; petiole swollen and blackish when dry, 0.3–0.6 cm long, canaliculate, with sparsely and appressed light-brown hairs. Inflorescences axillary, 2-flowered short shoots (rhipidia), flowers develop in succession, sympodial axis minute, 0.1–0.2 cm long, densely

golden-brown tomentose. Flowers almost sessile, pedicels 0.1–0.3 cm long (up to 0.5 cm in fruit), densely covered by appressed golden-brown trichomes and bearing 2–3 minute, densely golden tomentose and broadly ovate basal bracts. Sepals 2, connate, 0.2–0.3 cm long \times 0.2–0.3 cm wide, decurrent along the pedicel, broadly ovate to orbicular, rounded at apex, sparsely to densely covered by appressed golden-brown trichomes outside, glabrous inside, margins ciliate. Petals 4, free, in two subequal whorls, 10–25 mm long \times 3–5 mm wide, linear lanceolate to linear-triangular, whitish or beige, rarely yellowish green when immature, sparsely to densely pubescent outside, glabrous inside, acute at apex, base truncate and cusped around the stamens; outer petals, more or less thin, with faint venation, reflexed at anthesis; inner petals thicker, \sim 1 mm, and fleshier and not reflexed with a shallow, more or less triangular white patch near the base inside. Stamens, 40–45, 1–1.5 mm long, extrorse, filament very short, apical part of connective expanded over the thecae, shield-shaped, ellipsoid to angulate, glabrous. Carpels, 2–3 per flower, to 2 mm long; stigma more or less globose, to 0.5 mm diam., and essentially glabrous; style absent; ovaries ellipsoid and more or less curved, like a small banana with densely light-brown hairs; ovules 10–13, lateral, in two rows. Monocarps, 1–3 per fruit (frequently 2), large and fleshy, 5–7 cm long \times 3–4 cm wide, ellipsoid, apex and base rounded, glabrous, shortly stipitate, stipes to 1 mm long or absent; young monocarps green, yellow to light brown when ripe with a peach-like sweet odor; seeds lunate to wedge-shaped, 1.7–2 cm long with lamellate ruminations.



FIGURE 1. *Tridimeris huatuscoana*. A) Habit. B) Branchlet with inflorescences. C) Dimerous flower, note the white triangular patch at base of inner petals (food bodies). D) Monocarps. (Photographs by Esteban Marinero-Sobal).

Habitat and ecology:—The type locality of *Tridimeris huatuscoana* is located within one of the most important regions for coffee cultivation in Mexico, which is mostly covered by montane cloud forest. Interestingly, *Tridimeris huatuscoana* forms part of the riverine vegetation on limestone karst soils, along with *Platanus mexicana* Moricand (1837: 39), *Cojoba arborea* (L.) Britton & Rose (1928:29), *Oreopanax xalapensis* (Kunth) Decaisne & Planchon (1854:108), *Siparuna thecaphora* (Poepp. & Endl.) Candolle (1868: 657), *Ardisia compressa* Kunth (in Humboldt *et al.* 1819: 245), *Bunchosia biocellata* Schlechtendal (1836: 241), *Trichilia martiana* de Candolle (1878: 205), *Spathacanthus magdalenae* Castillo-Campos (in Castillo-Campos *et al.* 2013: 449), *Cnidioscolus multilobus* (Pax) Johnston (1923: 86), and *Cornutia pyramidata* Linnaeus (1753: 628), as well as with some representative elements of

the forest edge zones, such as *Moussonia deppeana* (Schltdl. & Cham.) Hanstein (1865: 284). Individuals of *Tridimeris huatuscoana* are always present on the banks of the river, are scattered distributed, separated from each other by a few tens of meters.

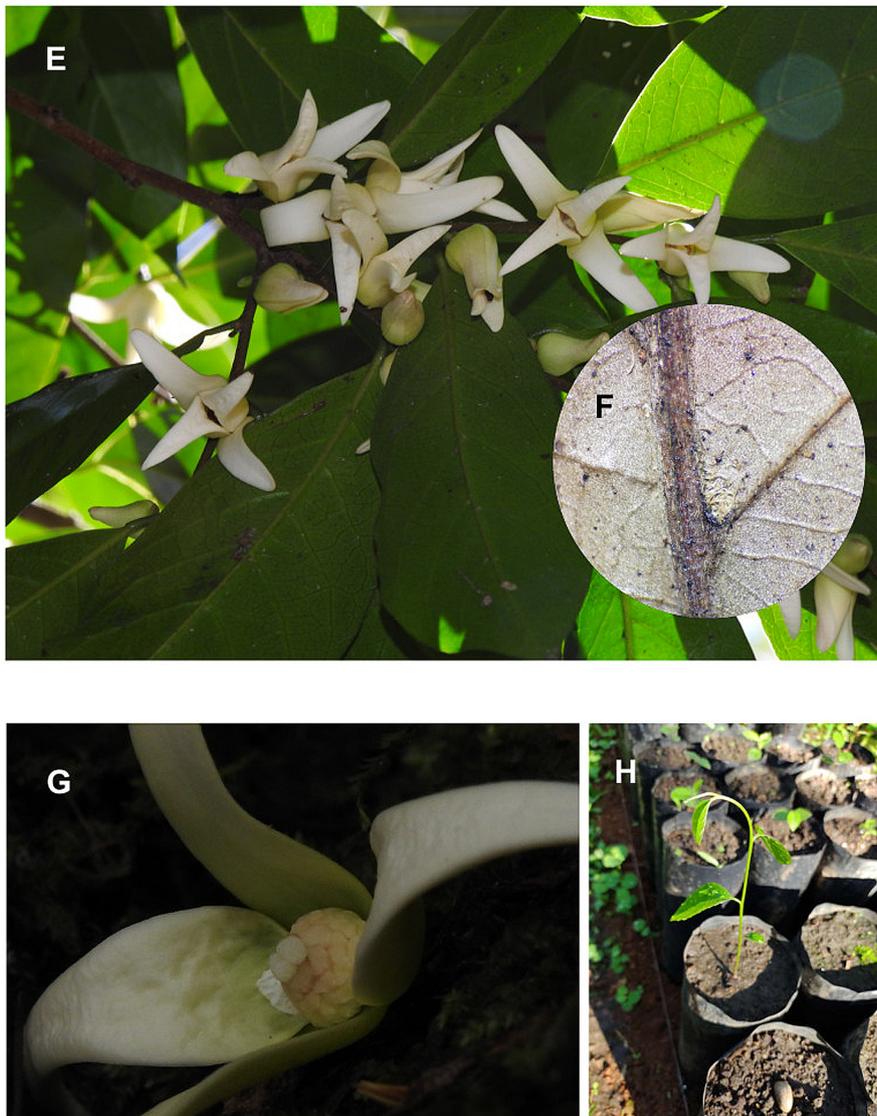


FIGURE 2. *Tridimeris huatuscoana*. E) Branchlet with inflorescences, note the color of the flowers and the pollination chamber. F) Setose pocket domatia. G) Close-up of the flower, note the two carpels surrounded by numerous stamens. H) Small plant of *Tridimeris huatuscoana*. (Photographs by Esteban Marinero-Sobal).

The flowers of *Tridimeris huatuscoana* form a pollination chamber during anthesis, which is when the internal petals get closer to each other in such a way that the reproductive organs of the flower are covered (Fig. 2E). In this way, floral visitors are filtered so that only those that meet a certain body size could have contact with the carpels, thus carrying out pollination. In addition, the flowers have a white triangular patch at the base of the inner petals (Fig. 1C), a structure that signals a greater thickening of the petals and considered a reward for pollinators (food bodies, *sensu* Schatz *et al.* 2018). We did not observe floral visitors on *T. huatuscoana* but daytime pollination chamber observations might suggest that pollination of this species is diurnal.

Phenology:—The species has two flowering peaks, at the end of the year between October and December, where fruits can also be observed, and then at the beginning of the year between March and May, where fruiting is rather absent.

Seed germination:—We collected nine seeds of the new species and submerged them for 24 hours in water followed by sowing in bags with local enriched soil (30% black soil, 30% vermicompost, 20% tepezil and 20% coffee and sheep pulp fertilizer). The bags were kept constantly humidified (40%) for three months. Shortly after this (three months and two weeks) all seeds germinated and after six months they reach sizes of up to 10 cm (Fig. 2H).

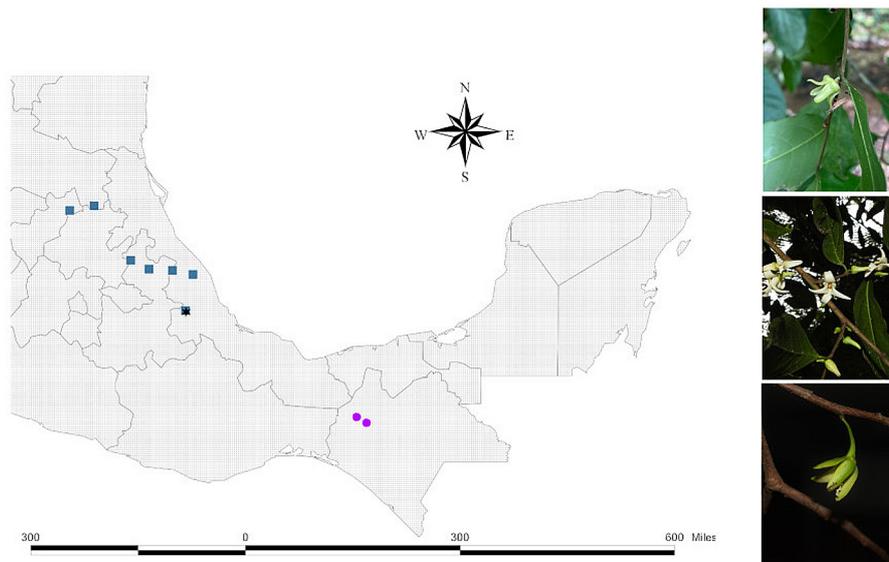


FIGURE 3. Distribution range of *Tridimeris huatuscoana* (black star), *Tridimeris hahniana* (blue squares) and *Tridimeris chiapensis* (purple dots). To the right and from top to bottom, flowers of *Tridimeris hahniana*, *Tridimeris huatuscoana*, and *Tridimeris chiapensis*.

Etymology:—The specific epithet is in honor of the municipality of Huatusco, in Veracruz, Mexico, one of the most important regions for coffee production, full of history and culture, and an obligatory path for many botanical explorers.

Conservation status:—*Tridimeris huatuscoana* is known only from the type locality in Huatusco, Veracruz (Fig. 3). According to the criteria established by the IUCN, it is possible to tentatively determine that the species is Critically Endangered [CR B1ab (iii)]. The Area of occupancy (AOO) of *T. huatuscoana* is 4.0 km² and the Extent of occurrence (EOO) is 0.0 km², suggesting a very restricted overall distribution. Although the only known population of the species is located within a large fragment of montane cloud forest (Fig. 4), the species appears restricted to the banks of a river where it is really scarce (less than 10 individuals in one hectare). In addition, the forests around the type locality are threatened by non-sustainable activities (logging, fires, illegal settlements and land use change) and at more local scales the forest is evidently fragmented characterized by many small isolated patches which are surrounded by roads, croplands and cattle pastures (Fig. 4).

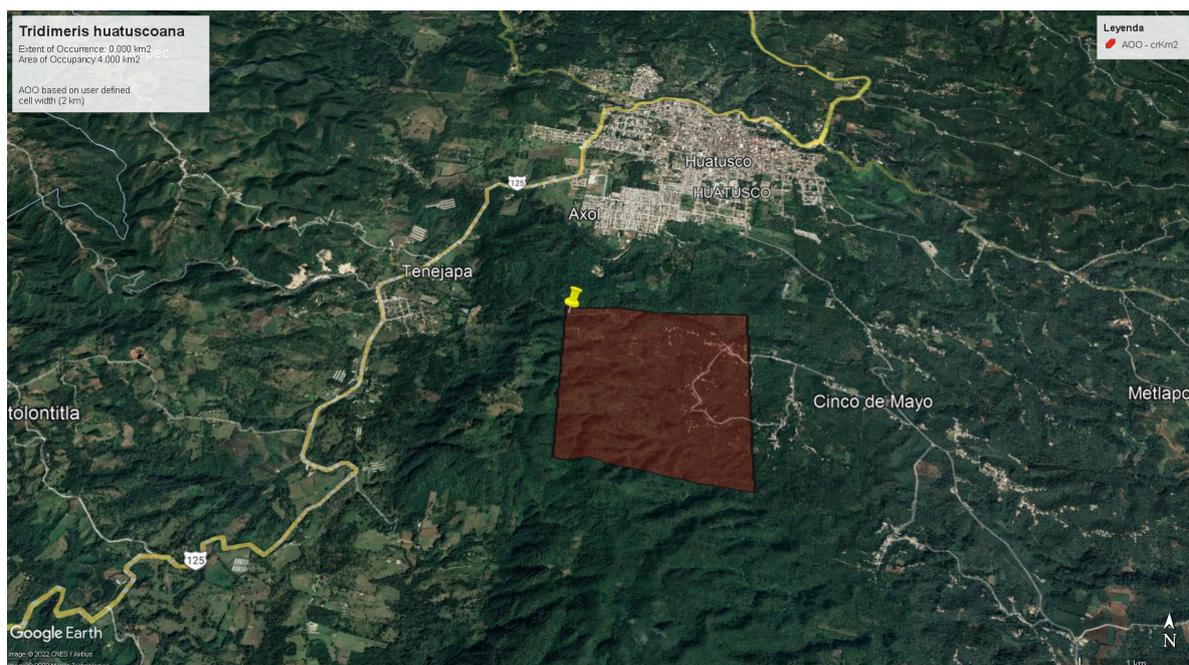


FIGURE 4. The type locality of *Tridimeris huatuscoana*. The red box represents the Area of occupancy (AOO) accordingly to its conservation status assessment using the GeoCAT tool.

Additional specimens examined:—MEXICO. Veracruz: From the type locality, 4 September 2021, *E. J. Marinero-Sobal* 426, 427, 428 (MEXU).

General discussion

The most general characteristics of *Tridimeris huatuscoana* confirm that dimerous flowers (two sepals and four petals), a reduced number of carpels per flower, and the large, and fleshy fruits are the most obvious synapomorphies for the Mexican genus *Tridimeris* (Fig. 1). The presence of leaf pocket domatia is a character shared among the three species of *Tridimeris* but not exclusive to this genus (Fig. 2F). Some individuals of *Sapranthus microcarpus* (Donn. Sm.) R.E. Fr. (1900: 12) have been observed with leaf pocket domatia (according to Schatz *et al.* 2018). Also, the food bodies on the adaxial surface of the inner petals are a character shared among two species of *Tridimeris* and all species of *Sapranthus* (Schatz *et al.* 2018). Interestingly, in most *Sapranthus* that structure appear as a verrucose or corrugated region inside the inner petals, whilst in *Tridimeris*, the small triangular patch at the base of the inner petals is considered a vestige (Schatz 1998). The notable differences between the flower characteristics of *Sapranthus* and *Tridimeris* support their current circumscription and monophyly, in parallel the divergence times estimates proposed so far (Ortiz-Rodríguez *et al.* 2018) suggest that flower differences among sister genera were acquired in a very short period of time.

Within the genus *Tridimeris*, *T. huatuscoana* is morphologically more similar to *T. hahniana* (Table 1). Both species are sympatric at the type locality of *Tridimeris huatuscoana* (Fig. 3) and share the general pubescence of the flowers and inflorescences (Table 1). However, *T. hahniana* has glabrous leaf domatia; solitary, longer pedicellate flowers, with smaller green petals and without food bodies at the base of the inner ones; and fruit surface rugose and densely covered by golden brown hairs (velvety). This marked differences in reproductive characteristics could facilitate their sympatric distribution (Table 1), something observed for other species of Annonaceae (Lau *et al.* 2016). The glabrous fruits and the presence of food bodies at the base of inner petals are characteristics that *T. huatuscoana* shares with *T. chiapensis* (Table 1). However, both species differ markedly in flower size, number of flowers per inflorescence, pubescence of petals, peduncle length, and pubescence of leaf domatia (Table 1). Furthermore, both species are allopatrically distributed (Fig. 3). In addition to the above, *T. huatuscoana* is the only species with almost sessile flowers, white or beige long petals, and inflorescences composed of two flowers in succession.

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