

# Agaves of Oaxaca: part one

Two recently described species: *Agave megalodonta* and *Agave quiotepecensis*

## Introduction

The most recent comprehensive monograph covering the genus *Agave* was that of Howard Scott Gentry (1982) in which he covered all the known species found in Continental North America. He built on work of preceding *Agave* monographers such as Baker (1877), Berger (1915), and Trelease (1920), and grouped the species together based on common characteristics whether floral or vegetative. Because of this arrangement, his monograph has been the starting point for modern taxonomic work. Gentry spent several decades traveling throughout the United States, Mexico, and Central America, collecting and observing plants in habitat. However, access to many parts of Mexico was very limited in his time and as new roads open, more territory becomes accessible. This accessibility has resulted in 54 taxa either being described as new, or names placed in synonymy being reevaluated and sometimes being considered as valid species. Of those 54, ten are in section *Heteracanthae* (the section in which the subjects of this paper belong), and of those ten, five occur in Oaxaca. Oaxaca is a botanically rich and diverse state, and the genus *Agave* is well represented but a comprehensive review of all species within the state is lacking; I hope the first installment of such a review of the species of *Agave* in Oaxaca helps mitigate that lack.

## *Agave megalodonta*

*Agave megalodonta* (Figs. 1 & 2) was described by García-Mendoza et al. (2019) from the Rio Balsas in far western Oaxaca, eastern Guerrero, and southwestern Puebla (Map 1). The name was derived from the Greek *megalo-* meaning large and the Greek *donta-* for teeth, an appropriate reference to the large teeth seen on the leaves of this species. García-Mendoza et al. (2019) placed this species in Gentry's (1982) group *Marginatae*, which has been changed to section *Heteracanthae* (Thiede et al. 2019), and stated that it is morphologically closest to *A. xylonacantha*. However, *Agave megalodonta* can be differentiated by the former

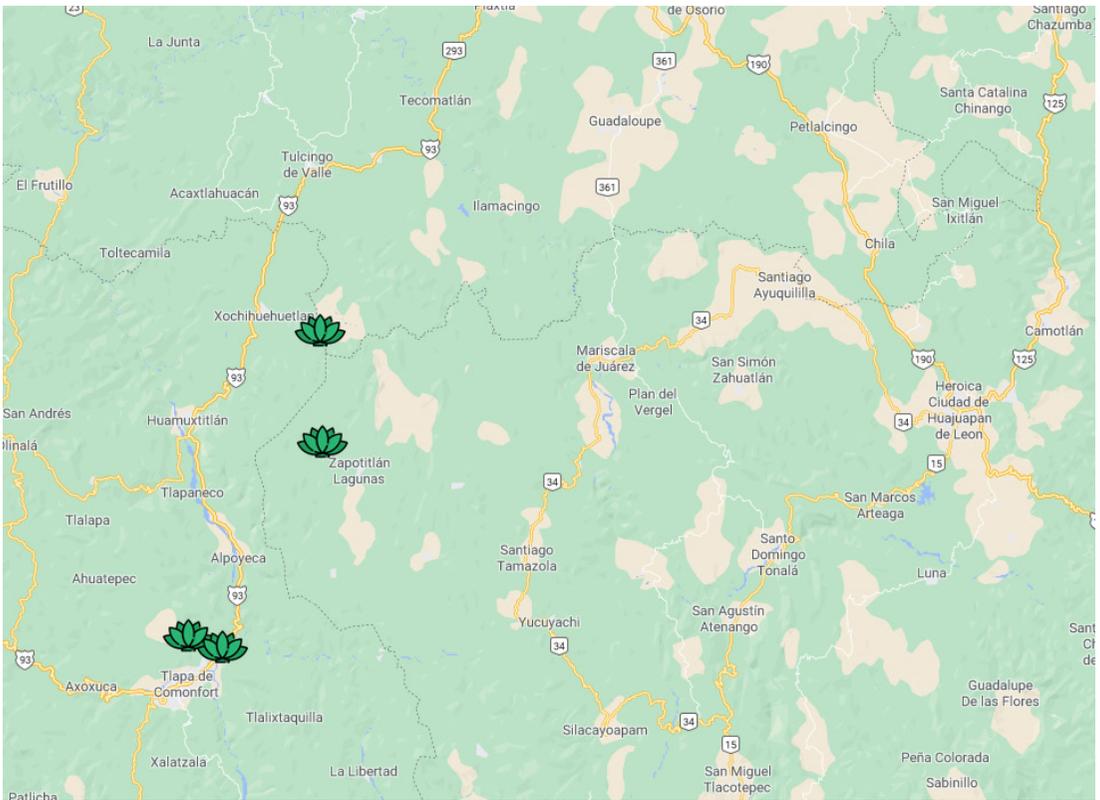


1. A handsome specimen of *Agave megalodonta* seen at the type locality.



2. Young or old, *Agave megalodonta* plants are impressive.

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**Map 1.** Distribution of *Agave megalodonta*.

having longer and wider leaves, a straighter leaf margin with larger teeth, and a longer terminal spine García-Mendoza et al. (2019). I read the description of *Agave megalodonta* shortly after it was published and was intrigued by the drawing and the photographs accompanying the description. The plant pictured was not strikingly impressive, but the marginal teeth looked quite wicked and gnarly. As part of my ongoing research and understanding of the section *Heteracantha*, I wanted to see this species and compare it to others in the same section. The opportunity to visit two of the localities, including the type, presented itself in October 2020. Having gone stir crazy due to the Covid-19 pandemic, I enlisted fellow agavephile, Tristan Davis, to brave the world and travel to Oaxaca, Chiapas, Puebla, and Guerrero on an agave-fishing expedition. I readied a list of the known localities for *Agave megalodonta* (Map 1) in the hopes we would be able to visit each of them. The type locality is always the first place to start when you want to get a baseline understanding of the concept of a particular species, so we made that locality a priority. For *Agave megalacantha*, the type locality is off the beaten path along a not so well-traveled road; but first, we would be driving by another population prior to encountering the



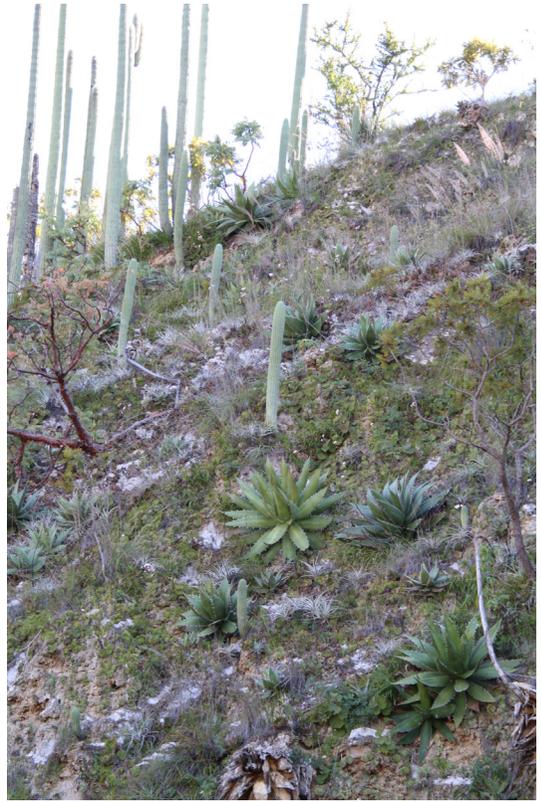
**3.** Dark green leaves are a nice contrast to the gray teeth of *Agave megalodonta*.



4. *Agave megalodonta* plants inhabit steep slopes of calcareous origin.

population at the type. We left the town of Tepelmeme, Oaxaca early in the morning with our goal being the two stops for *Agave megalodonta*. Upon arriving at the first population about mid-afternoon, the first order of business was to race up the hill, check out the plants and take some photos (Figs. 4–7). At our first stop, the plants were found on an open west-facing slope derived from limestone and growing with a variety of subtropical vegetation including *Agave cupreata*, *Bursera* species, *Cephalocereus mezcalaensis*, *Coryphantha* species, *Fouquieria ochoteranae*, *Hechtia* species, and *Mammillaria albilanata*.

As we arrived at the type locality for *Agave megalodonta*, the sun was getting low in the sky and the hill loaded with agaves was cast in shade, which rendered photography a bit of a challenge. The plants here were magnificent, and I realized the drawing and photo in the original description did not do the plant justice (Figs. 6 & 7). Climbing around on the slope was a bit challenging as the gypsum-based soil was loose and crumbly. Fortunately, there were enough spots to catch purchase and I was able to spend some time examining the plants. None of the agaves were in flower, but they were clearly unlike any other described species. I found the large variously curved marginal teeth (Figs.



5. *Agave megalodonta* growing with *Cephalocereus mezcalaensis*.

8–11) most captivating and silently congratulated the authors on a well-chosen species name.

## Description

The following description is adapted from García-Mendoza et al. (2019) and augmented with my observations. Plants are solitary rosettes growing to 3–4 feet tall by 4–5 feet across (0.9–1.2 m by 1.2–1.5 m); rarely do the plants get larger. Leaves are yellowish green to dark green leaves, smooth to the touch, ensiform oblong-lanceolate, ovate-lanceolate, or ovate, 2–3 feet long by 3–5 inches wide (60–90 cm by 7.5–13 cm) at the widest point and long acuminate at the apex. Large chocolate brown to gray or white marginal teeth are variously curved, hooked, or flexed, rarely bi-cuspid at the tip, and create noticeable bud prints on the leaves. The large stout chocolate brown to gray or white terminal spine is 2–3 inches long (5–7.6 cm). The tall spike-like flower stalk can reach 15–20 feet tall (4.5–6 m) with flowers in the upper half. Flowers are pale yellow to greenish yellow about 1.5–2 inches long (3–5 cm) and appear in December and January.



6. A large *Agave megalodonta* at the type locality showing off its awesome teeth.



7. A young *Agave megalodonta* at the type locality.



8. Wickedly curved teeth are the hallmark of *Agave megalodonta*.

### Taxonomic Affinities

With its spiciform inflorescence, leaves with continuous corneous margins, flowers with short tubes and long tepals that clasp the filaments at anthesis, *Agave megalodonta* belongs in the subgenus *Littaea* (Gentry 1982) and in section *Heteracanthae* (Thiede et al. 2019) along with several other southern Mexican species from Oaxaca and Puebla. Flower characteristics in section *Heteracanthae* are generally quite uniform so *Agave* taxonomists rely heavily on vegetative characteristics to distinguish species rather than the traditional method of the use of flower characteristics.

García-Mendoza et al. (2019) suggested that *Agave megalodonta* was closest to *Agave xylonacantha* based on vegetative characteristics. However, using the key provided by Gentry (1982; pp. 128–129), *Agave megalodonta* would be intermediate between *Agave xylonacantha* and *Agave ghiesbreghtii*. The leaf shape was described as ensiform (sword-shaped) oblong-lanceolate and 6–10 times longer than wide for *Agave megalodonta*. However, I also saw plants with broader leaves that would be best described as ovate to ovate-lanceolate. *Agave xylonacantha* has a leaf shape being ensiform-lanceolate and 5–10 times longer than wide, and



**9.** Young *Agave megalodonta* leaves have teeth that are mostly chocolate brown with a hint of gray.



**10.** The large, variously curved teeth of *Agave megalodonta* create quite the bud prints on leaf surfaces.



**11.** Looking at these teeth one can see *Agave megalodonta* is appropriately named.



**12.** *Agave oteroi* has large teeth reminiscent of those on *Agave megalodonta*.



**13.** Note the exceptionally wide margin on *Agave oteroi*, one feature of several that can be used to separate this species from *Agave megalodonta*.



**14.** A specimen of *Agave quiotepecensis* showing teeth similar to those on *Agave megalodonta*.



**15.** A specimen of *Agave titanota* showing teeth similar to those on *Agave megalodonta*.



**16.** *Agave xylonacantha* with bicuspid teeth perched on prominent teats.

*Agave ghiesbreghtii* has a leaf shape broadly lanceolate, ovate, or deltoid and about 4 times longer than wide. *Agave megalodonta* has leaves that tend to be narrowed near the base, broadest near mid-blade, and

short-attenuate at the tip, while those of *Agave xylonacantha* tend to be similar width from base to well above mid-blade and longer attenuate to the tip. Also, the leaf margins on *Agave megalodonta* are straight



**17.** An attractive specimen of *Agave xylonacantha* showing large teeth like those on *A. megalodonta*.

or slightly undulate without large prominent teeth while *Agave xylonacantha* leaves have teeth perched on prominent teeth (Fig. 16). Even though leaf shape of *Agave megalodonta* and *Agave ghiesbreghtii* is similar, the two can be distinguished by teeth characteristics and leaf thickness and rigidity. *Agave megalodonta* has larger teeth and thick stiff leaves compared to the smaller teeth and thinner more flexible leaves of *Agave ghiesbreghtii*.

Additionally, the teeth seen on *Agave megalodonta* (Figs. 8–11) are more like those seen on *Agave oteroi* (Figs. 12 & 13), *Agave quiotepecensis* (Fig. 14), *Agave titanota* (Fig. 15), and *Agave xylonacantha* (Figs. 16 & 17).

### *Agave quiotepecensis*

*Agave quiotepecensis* (Figs 18 & 19) was described by García-Mendoza et al. (2019) from near the village of Santiago Quiotepec south to San Juan Coyula in Oaxaca (Map 2). This species was also placed in Gentry's (1982) group Marginatae, now section Heteracanthae (Thiede et al. 2019), and was considered most closely related to *Agave titanota* as defined by Gentry. However, *Agave quiotepecensis* has lanceolate leaves with a long acuminate apex which separate it from *Agave titanota* with linear-ovate leaves and short acuminate apex García-Mendoza et al. (2019).

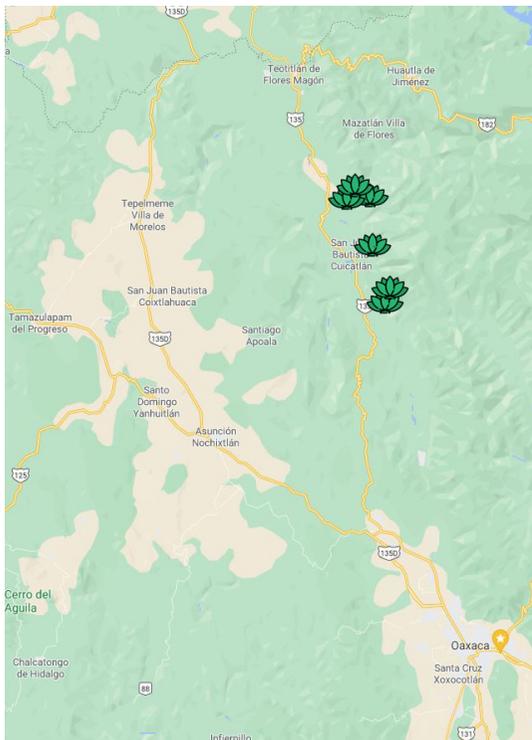
I first became aware of the plants that would eventually be described as *Agave quiotepecensis* from a paper on the Agavaceae for the Flora del Valle de Tehuacán-Cuicatlán (García-Mendoza 2011). At the time, the plants seen near Santiago Quiotepec were identified as *Agave titanota*; however, García-Mendoza apparently had never visited the type locality of *A. titanota* because he did not list any of his own specimens from that locality (Rancho Tambor). My first opportunity



**18.** *Agave quiotepecensis* growing near the trail that leads to *Echeveria laui*.



**19.** An exceptional example of *Agave quiotepecensis* found near Santiago Quiotepec.



**Map 2.** Distribution of *Agave quioitepecensis*.

to search for these plants came in February 2015 while on a botanical expedition with Jeff Chemnick leading a small group of plant enthusiasts through much of central and eastern Oaxaca including parts of the Tehuacán-Cuicatlán Valley. We were scheduled to visit Santiago Quiotepec where we would hire a guide to take the group to see *Echeveria laui*. García-Mendoza listed a locality for *Agave titanota* along Mexico Highway 135 that was 2 km south of the turnoff to Santiago Quiotepec, so we were on the lookout for it while in the area. Upon reaching an area about 2 km from the turnoff, we parked in a pullout wide enough to safely accommodate the van and scoured the roadcuts and cliffside looking for agaves. We spotted a few growing high up on the rocky cliffs above the road with one nearing the end of flowering (Fig. 20). Satisfied, we continued into Santiago Quiotepec, and hired a guide to lead the group to see *Echeveria laui* (Figs 21). There were more of the same agave growing out of crevices in the rock on the slopes both above and below the trail (Figs. 22 & 23).

Two months after my trip with Jeff, ethnobotanist David Yetman sent me photos of an agave growing on the archaeological site of Cerro Quiotepec. These had also been identified by García-Mendoza as *Agave titanota* and appeared to be the same species encountered just south of the turnoff to Santiago Quiotepec



**20.** The flowering stalk of *Agave quioitepecensis* near the end of its prime.

and along the trail to *Echeveria laui*, so plans were made to visit the archaeological site and study the agaves growing there. I made two visits, the first in February 2016 and the second in February 2017. Both times the agaves were in peak bloom, and I immediately made note of the deep fertile portion that comprised 85–100 percent of the flower stalk (Fig. 24). To access the archaeological site, it is necessary to obtain permission from the town of Santiago Quiotepec commission and to hire a guide to accompany you to the sensitive site. The site sits across the Rio Grande and crossing can be a challenge. My first visit, I crossed on foot and for the second visit I was on horseback which was much easier and the recommended method. The plants from near Santiago Quiotepec south to San Jose finally received a proper name when they were described as *Agave quioitepecensis* (García-Mendoza et al., 2019).

### Description

The following description is adapted from García-Mendoza et al. (2019). Plants are solitary acaulescent rosettes and described as being 4.5–5 feet tall by 6.5–8 feet wide (1.4–1.5 m by 2–2.5 m); however, my



21. *Echeveria laui* perched on a rock shelf above head height.



22. A handsome specimen of *Agave qurotepecensis* from near the village of Santiago Quiotepec.



23. *Agave qurotepecensis* growing on the rocky slopes near Santiago Quiotepec.



**24.** The deeply spiciform inflorescence of *Agave quio-tepecensis* is readily apparent.

observations and measurements of plants growing at two localities show them to be substantially smaller, reaching 2–3.75 feet tall by 3.75–5.25 feet across (0.6–1.1 m by 1.1–1.6 m). There are 20–50 leaves per rosette (rarely more). Leaf shape is long lanceolate to ovate-lanceolate, and each measures 1.5–3 feet long by 4–7 inches wide (45–90 cm by 10–17 cm) at the widest point just above mid-blade. They are smooth to asperous to the touch along the ventral side, light yellowish green to dark green or occasionally dull glaucous-green during the wet season, flushing red or purplish during the dry season and usually with a conspicuous light yellow or greenish yellow central stripe (Figs. 25–27). The continuous woody margin is straight, lightly undulate, irregularly wavy, or deeply crenate with small to

large variously curved teeth that are dark chocolate brown on new leaves turning white on older leaves even on young plants (Fig. 28). The stout terminal spine is about 2 inches long dark chocolate brown on new leaves and aging to white or gray on older leaves. The dense spike-like flower stalk grows to 10–16 feet (3–4.8 m) tall with a deep fertile section comprising 85–100 percent of the distal end of the stalk (Fig. 24). This deep fertile section is an unusual and distinctive characteristic also seen in *Agave calciphila* (Starr 2020a, 2020b). Greenish yellow flowers are about 2 inches long and stamens are yellow or sometimes flushed with red. Blooming is during the dry season from December to March with seed maturing in March to June just in time for the rainy season.



26. *Agave quiotepecensis* during the dry season with the central stripe being prominent.



27. *Agave quiotepecensis* flushing purplish red during the dry season showing the conspicuous central stripe.



25. A green plant of *Agave quiotepecensis* after the rainy season showing the central stripe.



28. A young *Agave quiotepecensis* growing on the rocks in the dry season showing off its purplish color.

## Taxonomic Affinities

*Agave quiotepecensis* has a thick and dense spiciform inflorescence, a continuous corneous leaf margin, and flowers with a short tube and long tepals, and clearly fits in the subgenus *Littaea* and section *Heteracanthae* (Thiede 2019). García-Mendoza et al. (2019) stated that *Agave quiotepecensis* is morphologically like *Agave titanota* but differs from Gentry's (1982) description of that species by the leaves, terminal spine, and flower measurements. *Agave quiotepecensis* leaves are lanceolate, 5–7 times longer than wide, and long acuminate at the apex. In comparison, the leaves of *Agave titanota* are ovate or spatulate, 3–4.5 times longer than wide, and acute at the apex.

Using the key in Gentry (1982) and the description provided by García-Mendoza et al. (2019), *Agave quiotepecensis*, with its long, lanceolate, green leaves that are 5–7 times longer than wide, nestles in most closely to *Agave ghiesbreghtii* and not *Agave titanota*. However, my observations of plants regarded as *Agave ghiesbreghtii* show a much different plant with a very different inflorescence than seen on *Agave quiotepecensis*. Regardless of the murkiness of affiliation, *Agave quiotepecensis* is an attractive plant worthy of inclusion in any collection.

## Discussion

Both *Agave megalodonta* and *Agave quiotepecensis* are in subgenus *Littaea* and section *Heteracanthae*, a section in which species relationships are not always clear because floral morphology is often very similar among species. García-Mendoza et al. (2019) concluded that *Agave megalodonta* was most like *Agave xylonacantha* based on teeth characteristics, but my observations indicate the leaves and teeth are more like *Agave oteroi*, *Agave quiotepecensis*, and *Agave titanota* than *Agave xylonacantha*. That *Agave megalodonta* went undescribed until 2019 is a mystery because one of the localities is along the well-traveled Mexico Highway 93 in eastern Guerrero.

Further complicating the affinities of *Agave quiotepecensis* was the initial misidentification as *Agave titanota* by García-Mendoza (2011). At the time, he misunderstood the concept of *Agave titanota* and

included plants that were later described as *Agave oteroi* (Starr and Davis 2019). Based on distribution, *Agave quiotepecensis* would be closest to *Agave convallis* and *Agave kerchovei*, but the inflorescence characteristics are very different. The flower stalks for both *Agave convallis* and *Agave kerchovei* are very tall, 10–20 feet (3–6 m) with the fertile section comprising about 50 percent of the stalk, while the flower stalk for *Agave quiotepecensis* is 13–16 feet (4–5 m). My own measurements show the flower stalk to be 10–13 feet (3–4 m) tall with the fertile section comprising 85–100 percent of the stalk.

Having studied section *Heteracanthae* in the field throughout its range, I find it fascinating that species relationships are not always easily established, especially in southern Mexico where the number of species is quite high and morphological diversity is very extensive. The genus *Agave* in general, and section *Heteracanthae* specifically, needs a complete phylogenetic study. Unfortunately, none of the species in *Heteracanthae* are of great economic importance, pushing any comprehensive study far down the list for potential investors and leaving it in the hands of researchers whose interests are in the systematics and phylogenetics of the genus *Agave*.

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