

Notes on *Agave palmeri* Engelm. (Agavaceae) and its allies in the Ditepalae

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Summary: The Ditepalae, an informal taxonomic grouping recognized in the genus *Agave* L., currently consists of 12 species, most of which geographically straddle the border between the southern USA and Mexico. All of these species were used as sources of food, fibre and beverage, with some likely being transported to new habitats by migrating indigenous peoples. Of the 12 species of Ditepalae, *Agave palmeri* Engelm., appears to be of central biocultural importance as it has the widest distribution range. The taxonomy and affinities of this native of Arizona and New Mexico in the USA and Sonora and Chihuahua in Mexico, are discussed; an amplified description and illustrations of its vegetative and reproductive morphological characters are included. The other members of the Ditepalae are discussed and a key is provided to all members of the group.

Zusammenfassung: Die Ditepalae sind eine informelle taxonomische Gruppierung innerhalb der Gattung *Agave* L.; sie umfasst derzeit 12 Arten, die mehrheitlich im Grenzgebiet der südlichen USA und Mexiko vorkommen. Alle diese Arten wurden von nomadisierenden einheimischen Ethnien als Lieferanten von Nahrung, Fasern, und Getränken genutzt, und einige wurden wahrscheinlich auch entlang der Wanderrouen in neue Habitate transportiert. Von den 12 Arten der Ditepalae scheint *Agave palmeri* Engelm. von zentraler biokultureller

Wichtigkeit zu sein, denn sie hat das grösste Verbreitungsgebiet. Die Taxonomie und die Verwandtschaftsbeziehungen dieser in den USA in Arizona und New Mexico und in Mexiko in Sonora und Chihuahua heimischen Art werden diskutiert, gefolgt von einer erweiterten Beschreibung sowie Abbildungen der vegetativen und reproduktiven morphologischen Merkmale. Weitere Arten der Ditepalae werden diskutiert, und es wird ein Schlüssel zu allen Angehörigen der Gruppe gegeben.

Introduction

The genus *Agave* L. has an exclusively New World geographical distribution range, where it stretches in a broad band from California across to Florida in the southern United States, thence southwards to the Caribbean Islands and into Mexico, central America, and tropical northern South America (García-Mendoza, 1998; Smith, 2006; Reveal & Hodgson, 2009). The highest concentration of species is located in Mexico (Gentry, 1982). Of the 41 native US taxa, which include species, infraspecific taxa and natural hybrids, 17 are endemic to the country. Arizona is the state with the highest diversity of species, with 23 taxa, or just over 50% of those recorded for the USA. Five of these are included in the Ditepalae. (The authors were informed by an anonymous referee that two new taxa from the Ditepalae group are currently being described, namely the Page Springs agave and Sacred



Figure 1. Upper portion of the inflorescence of *A. palmeri* showing the comparatively small, open panicles. The flowers are carried on short, lateral side-branches. Photo: Gideon Smith. **Figure 2.** Close-up of the leaves of *A. palmeri* showing bud imprints and short, recurved, marginal spines. Photo: Gideon Smith. **Figure 3.** *A. applanata* showing the compact rosette of stiff, ensiform leaves. Photo: Brian Kemble.

Mountain agave, both occurring in central Arizona.)

Although now in some respects out of date, the most comprehensive taxonomic treatise on *Agave* remains Gentry (1982). In this work he recognized several informal groups to which no formal rank has subsequently been assigned. In so doing his approach approximated that of Reynolds (1966), who partly reflected the classification of the tropical African, and all the Madagascan aloes, in informal groups. The Ditepalae, in which Gentry (1982) included 10 species (12 taxa), is one of the informal groups that he recognized in *Agave* subg. *Agave*.

Several representatives of the Ditepalae are important economically. For example *Agave palmeri* Engelm., commonly known in north-eastern Sonora as lechuguilla, is known for the use of its processed core as food, for the production of fibres from its leaves, and to produce a type of mescal (Gentry, 1982; Hodgson, 2001b). The danger of wild representatives of the species

being over-collected for the bootleg mescal industry in northern Mexico has been noted (Plant Sciences Center of Sierra Vista, 2009). The plant parts of most Ditepalae are low in sapogenin and being relatively sweet are acceptable as a source of foodstuffs and beverages (Gentry, 1972; 1982). Leaf fibres are used in hunting nets, baskets, rope and sandals (Plant Sciences Center of Sierra Vista, 2009). In addition, the species has had many other uses by Native Americans, such as for the production of candies, dried and substitution foods, sewing material, decorations, paint, tools and weapons (Buskirk, 1986). Its use as an edible plant by Native Americans has been recorded since 1888 (Hedrick, 1972). This is one of a handful of agaves whose geographical distribution range probably reflects synanthropic dispersal, the plants having been cultivated and traded by pre-Columbian farmers (Hodgson, 1999, 2004; Reveal & Hodgson, 2002).

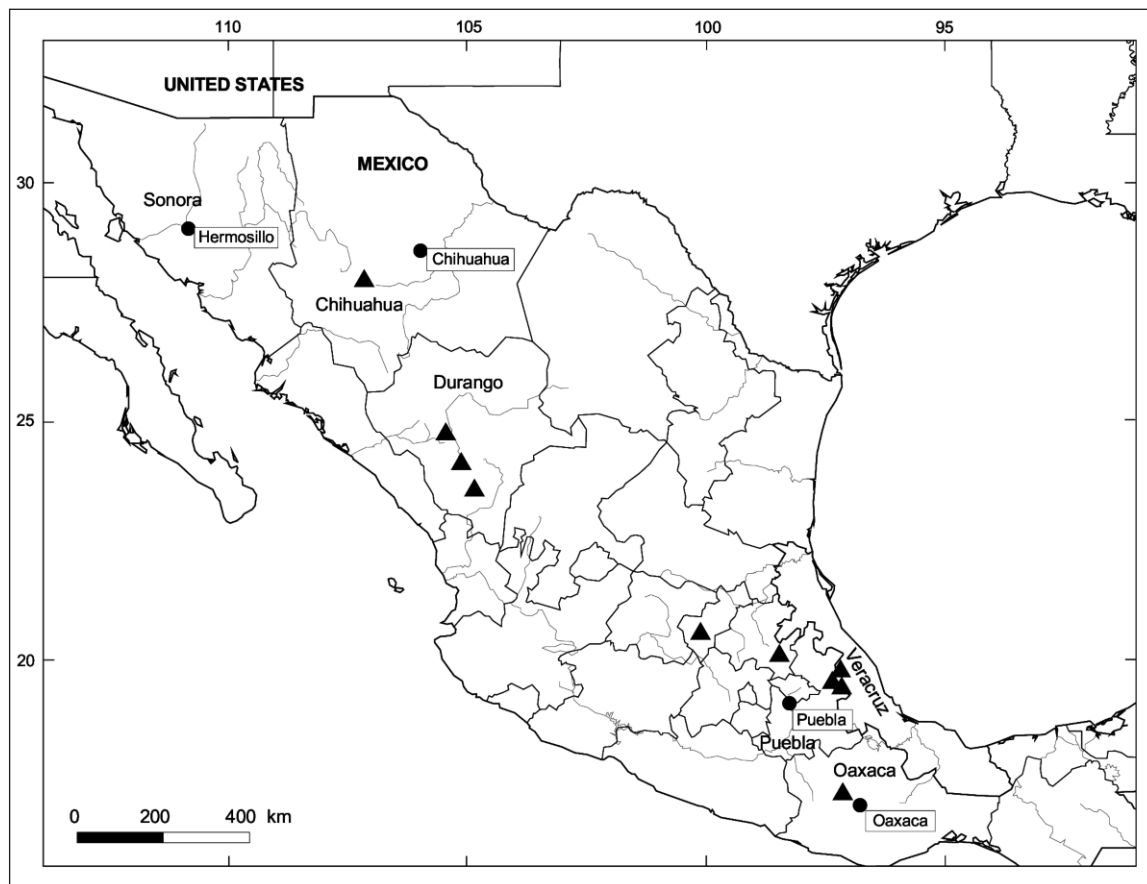


Figure 4. Geographical distribution range of *A. applanata* based on Gentry (1982).



Figure 5. Portion of the inflorescence of *A. chrysantha* showing the congested umbels and small, golden-yellow flowers with shallow tubes and proportionately long tepals. **Figure 6.** *A. chrysantha* showing the linear lanceolate leaves with remote marginal teeth on a frequently undulate to repand margin. Photos: Brian Kemble.

Given the economic importance of representatives of the Ditepalae, this group is here enumerated and briefly discussed and described. Since several of the species can be confused, a key is provided to assist identification. For one of the species of Ditepalae, *A. palmeri*, which appears to be geographically central in this group, an amplified description is provided.

Affinities of representatives of the Ditepalae

The Ditepalae are defined by flowers that have long tubes, tepals that are short, leathery, persistently erect and unequal, and have the filaments inserted at two ranks (Gentry, 1982). This last characteristic was later questioned as defining

for the group due to the inclusion in it of further species with stamens inserted in one rank only (Hodgson, 2001a). Although not strict diagnostic characters, comparatively small and slender, open panicles (Figure 1), as well as a predominant bluish grey leaf colour (Figure 2) are common in the Ditepalae.

Of the 14 taxa now recognized in Ditepalae (Hodgson & Slauson, 1995; Hodgson, 2001a), *A. palmeri* can be reasonably confused with several close relatives. It can generally be distinguished by its long-lanceolate leaves, with close-set, slender teeth and the perianth tube that about equals the reddish tepal lobes in length (Gentry, 1982).

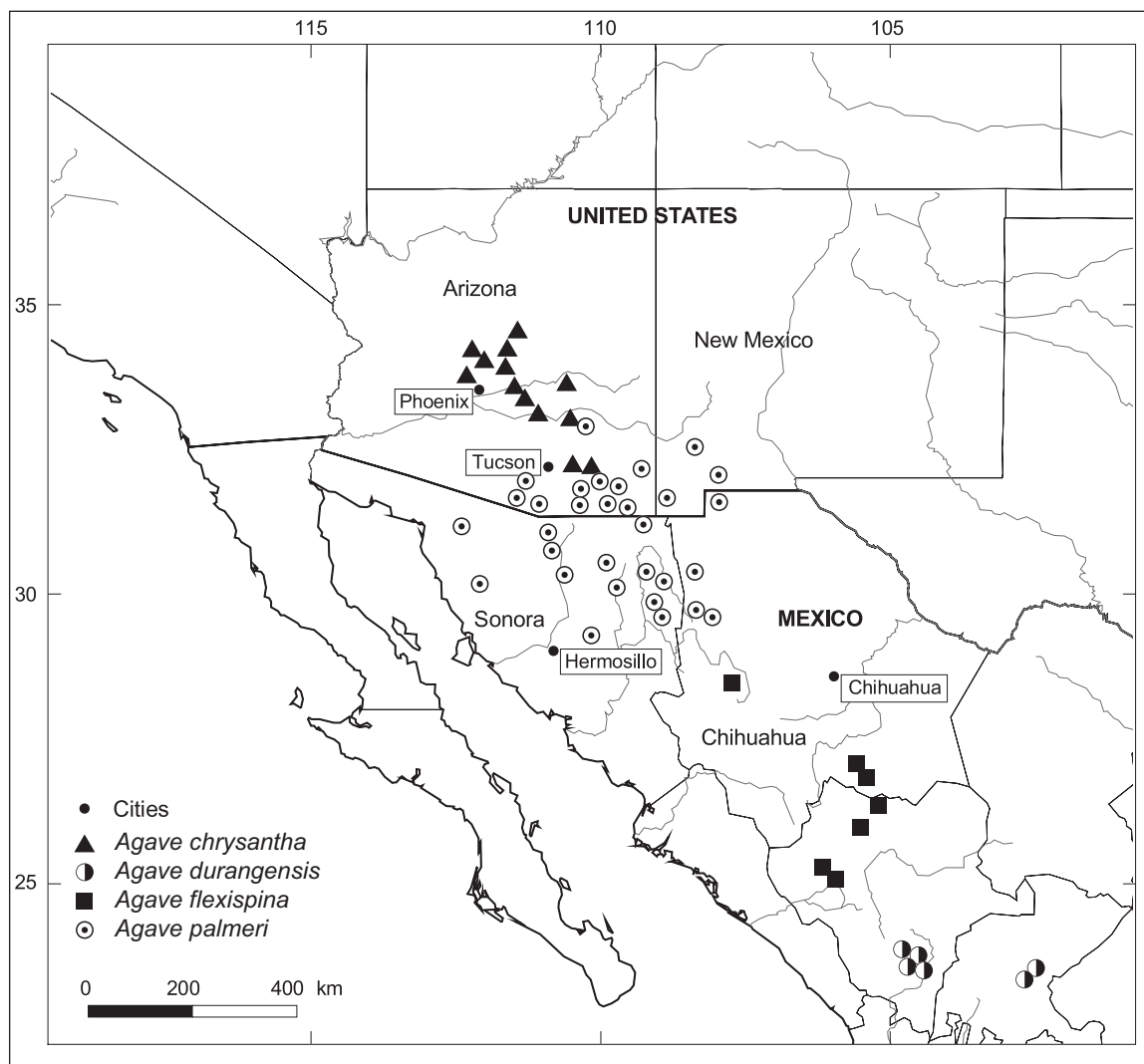


Figure 7. Geographical distribution ranges of *A. chrysantha*, *A. durangensis*, *A. flexispina* and *A. palmeri* based on Gentry (1982).



Figure 8. *A. colorata* showing the characteristic broad, cross-zoned leaves with deeply crenate to undulate margins. **Figure 9.** The dense panicles with short, wide-tubed flowers of *A. colorata*. **Figure 11.** The rosettes of *A. flexispina* are the smallest in the group. Photos: Brian Kemble.

Other members of Ditepalae can be distinguished by the following characters:

1. *Agave applanata* Lem. ex Jacobi has short, stiff leaves that are compact in juvenile and middle stages, but long-ensiform on mature plants, with a slightly asperous texture and very strong fibres (Figure 3). It is endemic to the highlands of Veracruz and adjacent Puebla, Mexico and is also widely naturalised over the Mexican plateau from central Chihuahua to Oaxaca (Figure 4). It grows on weathering lava; 2,300 m and above (Gentry, 1982).

2. *Agave chrysantha* Peebles has small flowers with a shallow tube and proportionately

long tepals, which are a golden-yellow (Figure 5). The umbels are congested and the panicles short and ascending. Further distinguishing characters are its linear lanceolate leaves measuring $25\text{--}60 \times 12\text{--}18$ cm, with remote marginal teeth on a frequently undulate to repand margin (Figure 6). This highly variable agave is endemic to central Arizona in the USA (Figure 7) and grows on granitic and volcanic mountain slopes; 900–1,800 m (Gentry, 1982).

3. *Agave colorata* Gentry is characterised by its broad, cross-zoned leaves, which are reddish or pink alternating with light grey, with a slightly asperous texture and deeply crenate to

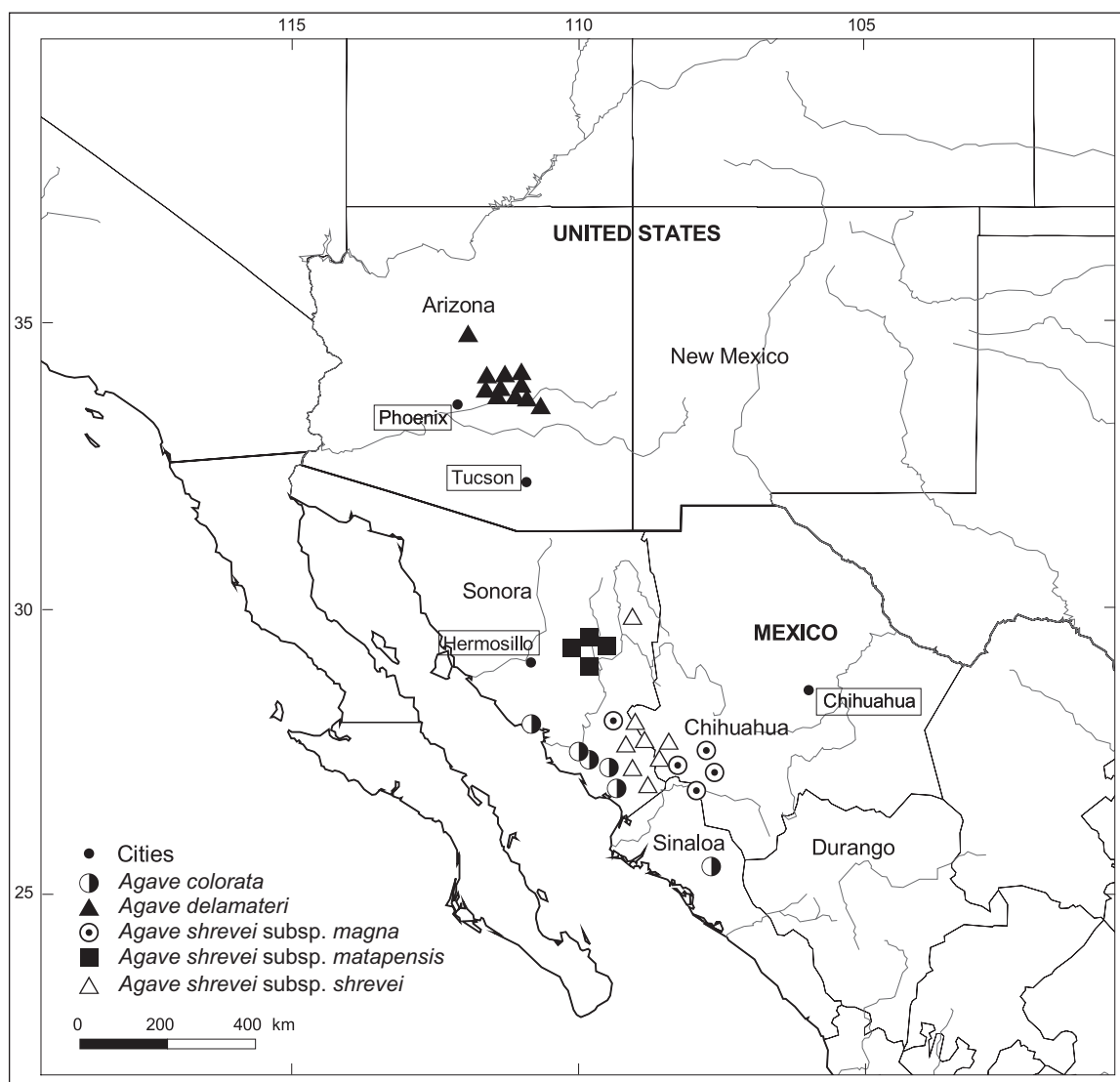


Figure 10. Geographical distribution ranges of *A. colorata*, *A. delamateri* and *A. shrevei* based on Gentry (1982) and Hodgson & Slauson (1995).



undulate margins (Figure 8). It has dense panicles with short, wide-tubed flowers (Figure 9). It occurs in Mexico in low-lying areas of western Sonora and Sinaloa (Figure 10) and grows in Thorn Forest on open rocky sites in foothills and coastal areas (Gentry, 1982).

4. *Agave delamateri* W.C. Hodgson & Slauson forms numerous rhizomatous offsets. Its leaves are easily cut, broadly lanceolate, apically incurved and glaucous with a purple tinge. Its tepals are long, with a wide perianth tube and greenish ochroleucous with rusty-maroon tips, while the slightly flattened, maroon filaments are 1-seriate. It occurs in central Arizona in the USA (Figure 10) and grows on open, level to moderately steep slopes of alluvial fans or old dissected terraces; 725–1,554 m (Hodgson & Slauson, 1995). This species has been seldomly encountered.

5. *Agave durangensis* Gentry has large, rigid, broadly lanceolate leaves, with an asperous texture, which is heavily armed with flexuous teeth on a deeply crenate margin. The panicle is large and open with a flexuous or zig-zag shaft. It



Figure 12. The small panicles of *A. flexispina*. **Figure 14.** *A. shrevei* subsp. *shrevei* showing the broad, light glaucous grey leaves with well-developed brown teeth. **Figure 15.** The panicles of *A. shrevei* subsp. *shrevei* showing the flowers with deep tubes and short, erect tepal lobes. Photos: Brian Kemble.

occurs in Mexico in southern Durango and Zacatecas (Figure 7) where it grows in grassland on rocky slopes and gravelly bajadas; 1,700–2,600 m (Gentry, 1982).

6. *Agave flexispina* Trel. has the smallest rosettes (0.25–0.35 × 0.5–0.7 m) (Figure 11) and inflorescences (2.5–3.5 m tall) in the group (Figure 12). The filaments are also inserted on a single level in the perianth tube, rather than on two levels. It occurs in Mexico on the Sierra Madre Occidental from southern Chihuahua south through the Durango Highlands (Figure 7) and grows in grassland and oak woodland; 1,300–2,300 m (Gentry, 1982).

7. *Agave fortiflora* Gentry is distinguished by its light grey glaucous leaves with a finely tuberculate rugose texture. It has large, long-lasting flowers with a short perianth tube that is broad and bulging at the place of attachment of the filaments (Gentry, 1982). It occurs in northwestern Sonora, Mexico (Figure 13) where it grows on small, isolated mountain ranges (Hodgson & Slauson, 1995). This species is extremely rare and has not been observed since Gentry's initial discovery.

8. *Agave murpheyi* F. Gibson is characterised by its prolifically bulbiferous, short and compact inflorescence with flowers ± 70 mm long. It has

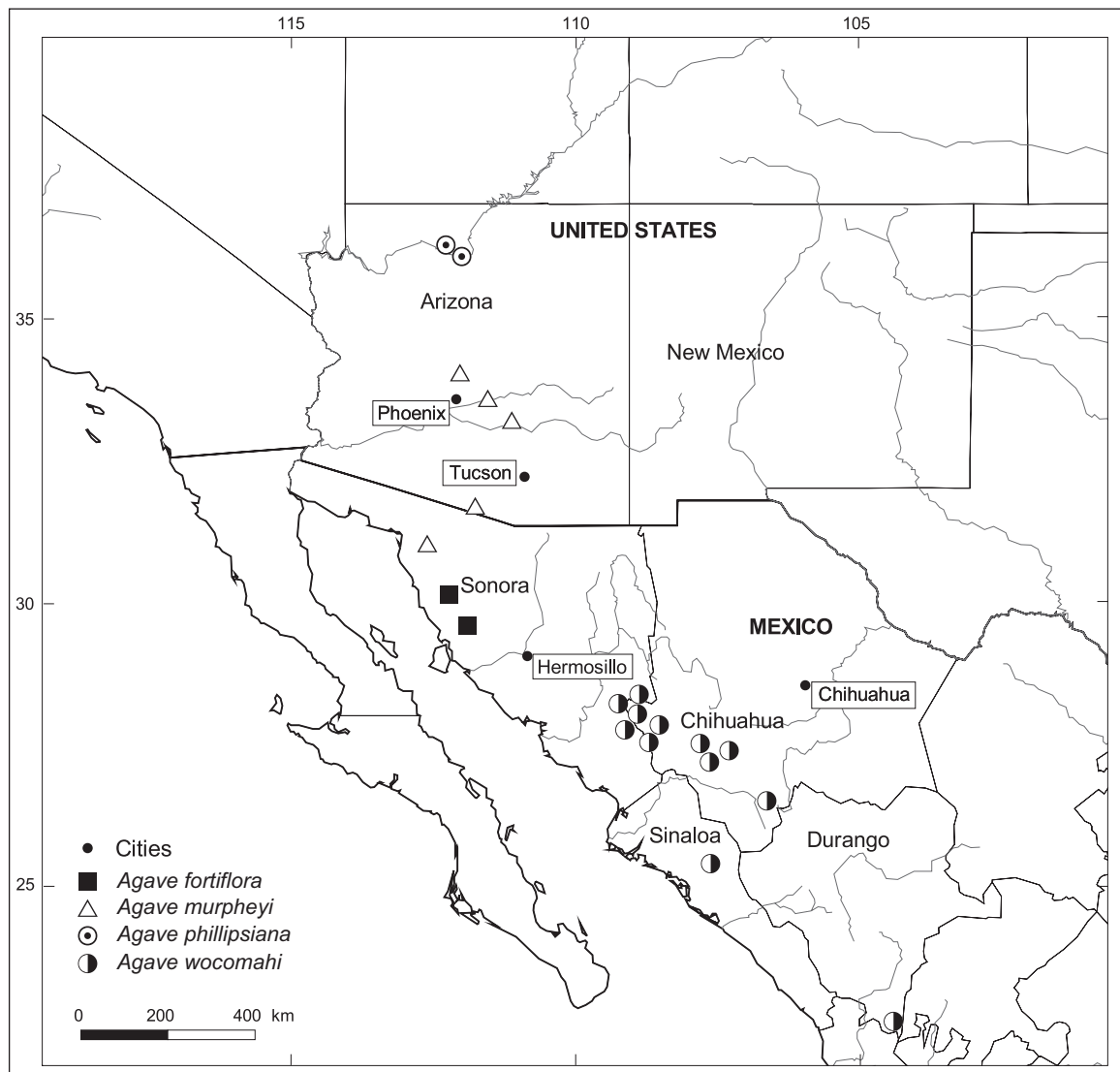


Figure 13. Geographical distribution ranges of *A. fortiflora*, *A. murpheyi*, *A. phillipsiana* and *A. wocomahi* based on Gentry (1982) and specimens listed in Hodgson (2001a).

linear leaves with a short terminal spine of up to 20 mm long. It occurs as 'wild' populations from the lower slopes of the Tonto Rim to southwestern Arizona in the USA; in adjacent Sonora in Mexico, it occurs near contemporary habitation sites (Figure 13). It grows on mountainous slopes or bajadas in the 'arborescent desert'; 460–930 m (Gentry, 1982). This species has been seldomly encountered.

9. *Agave phillipsiana* W.C. Hodgson is distinguished by its open rosette, with large glaucous leaves and narrowed paniculate inflorescence with large flowers (68–86 mm long). It is endemic to Arizona and is known only from a few populations in Grand Canyon National Park and central Arizona, USA (Figure 13), where it grows on terraces along permanent waterways; 700–1,140 m (Hodgson, 2001a). This species has been seldomly encountered.

10a. *Agave shrevei* Gentry subsp. *shrevei* has broad, light glaucous grey leaves, with a slightly asperous texture and well-developed brown teeth (Figure 14). The leathery perianth forms a deep tube, with short, persistent, erect tepal lobes that are much shorter than the perianth tube (Figure 15). It occurs in Mexico from middle Sonora southward to both sides of the Chihuahua–Sonora border (Figure 10) and grows in oak woodland and oak-pine forests on open, rocky limestone slopes; 900–1,850 m (Gentry, 1982).

10b. *Agave shrevei* subsp. *magna* Gentry is distinguished by its large leaves that arch outwards, giving the rosette a flat-topped, open crown appearance. The leaves have a slightly asperous texture. The filaments are very long, up to 70 mm. It occurs in Mexico in southeastern Sonora and southwestern Chihuahua near the Chihuahua–Sinaloa border (Figure 10) where it grows in oak woodland on rocky slopes (Gentry, 1982).

10c. *Agave shrevei* subsp. *matapensis* Gentry has leaves with deflexed teeth and a slightly asperous texture. The flowers are small with the tepal lobes longer than the short perianth tube. It occurs in Mexico north of Matapé, Sonora (Figure 10) and grows in oak woodlands on granitic and deformed limestone; 620–930 m (Gentry, 1982).

11. *Agave wocomahi* Gentry is characterised by its distinctive dark green leaves with a smooth texture and widely spaced teeth. It occurs in Mexico from southeastern Sonora and adjacent Chihuahua to southern Durango (Figure 13). It grows in oak woodlands on open, rocky, limestone mountain slopes; 1,400–2,500 m (Gentry, 1982).

Nomenclature of *Agave palmeri*

Agave palmeri Engelm. in *Trans. Acad. Sci. St Louis* 3: 319–320 (1875). Berger: 149–150 (1915); Breitung: 104 (1968); Bailey & Bailey: 38 (1976); Gentry: 101–105 (1972); Gentry: 443–447 (1982); Irish & Irish: 144–145 (2000); Thiede: 53 (2001); Reveal & Hodgson: 460 (2002); Reveal & Hodgson (2009).

Type: Syntypes: USA, Arizona, 1855, A. C. V. Schott; southern Arizona, 1869, E. Palmer s.n. (MO(3)); 1874, J. Rothrock. (*vide* Espejo Serna & López-Ferrari: 21 (1993)).

Type locality: In the mountains of southern Arizona (*vide* Engelmann, 1875).

Amplified description of *Agave palmeri* (Figure 16)

Medium-sized, stemless, herbaceous, succulent, monocarpic multi-annual; rosettes single, often later suckering freely through rhizomatous offsets, in time forming clumps of a few large and numerous smaller rather open rosettes with many leaves, 0.4–1.3 m tall, 0.6–1.3 m in diameter. Leaves numerous, straight, rigidly spreading, linear-lanceolate, acuminate, fleshy throughout, more so near base, narrowed in lower $\frac{1}{4}$, broadest in middle, lower $\frac{1}{4}$ flat above, upper $\frac{3}{4}$ concave to flat adaxially, convex abaxially, not vallecuate, 350–920 mm long, 25–190 mm wide in middle, cymbiform in transverse section, dull light green to light glaucous green, remaining so once flowering starts; upper and lower surfaces smooth with darker green bud impressions, these equally pronounced adaxially and abaxially; leaf bases enlarged, overlapping, stem-clasping, thickening the stem; margins \pm straight to slightly undulate, not filiferous, marginal teeth reddish to dark brown, not fading in colour with age, apically slightly to distinctly curved towards leaf base, rarely straight or curved towards leaf apex, regularly spaced, 5–20 mm distant, small, but conspicuous, 2–6 mm long, inserted on small teat-like protuberances, smaller and more distant lower down; terminal spine shortly grooved adaxially, dark to reddish brown, becoming dull greyish white, very pungent, 25–60 mm long. Inflorescence paniculate, erect, (1.7–)2.5–5.0(–7.2) m tall, side-branches laxly clustered in upper quarter to third, not bulbiferous after flowering; peduncle laxly sterile bracteate, 30–50 mm in diameter near base; bracts linear-lanceolate, tapering to a very sharp needle-like point, diagonally curved

Key to the Ditepalae (adapted from Gentry (1982), with incorporation of species since described)

1. Leaves of mature plants linear to long-lanceolate, 5 to 12 times longer than wide; widest part at or below the middle, margin straight or nearly so.....2
- 1'. Leaves of mature plants ovate to lanceolate, 2 to 6 times longer than wide; widest part at or above middle, margin undulate or prominently teated.....8
2. Leaves with marginal teeth remotely spaced, \pm 40–60 mm apart*A. applanata*
- 2'. Leaves with marginal teeth more closely set, up to 30 mm apart3
3. Terminal spines of leaf short, up to 20 mm long; panicle regularly bulbiferous*A. murpheyi*
- 3'. Terminal spine of leaf acicular, longer than 25 mm; panicle normally not bulbiferous4
4. Perianth tube much shorter than tepal lobes.....*A. fortiflora*
- 4'. Perianth tube equal to or slightly shorter than tepal lobes.....5
5. Leaf margin with large, widely spaced teeth, 5–10 mm long, mostly 10–30 mm apart; tepals golden-yellow*A. chrysantha*
- 5'. Leaf margin with small, closely set teeth, mostly up to 6 mm long, 1–20 mm apart; tepals conspicuously tipped with red or reddish brown.....6
6. Rosettes single, rarely suckering; leaves with marginal teeth 5–20 mm apart, terminal spine 30–60 mm long*A. palmeri*
- 6'. Rosettes suckering to form groups; leaves with marginal teeth up to 11 mm apart, terminal spine up to 40 mm long7
7. Leaves 50–63 cm long; flowers 47–70 mm long; perianth tube 11–16 mm long, lobe limbs 14–18 mm long*A. delamateri*
- 7'. Leaves 76–78 cm long; flowers 68–86 mm long; perianth tube 15.5–20 mm long, lobe limbs 20–21.5 mm long*A. phillipsiana*
8. Rosettes medium to large, generally not suckering; panicles large, mostly taller than 5 m, usually with more than 15 umbels.....9
- 8'. Rosettes small to medium, usually suckering; panicle smaller, up to 5 m tall, with 8 to 20 umbels.....11
9. Leaves dark green to light green, texture smooth; margins straight to undulate; perianth tube more or less equal to tepal lobes in length*A. wocomahi*
- 9'. Leaves glaucous grey, texture finely asperous; margins crenate; perianth tube longer than tepal lobes....10
10. Rosettes 1.4–1.7 m tall, 2.5 m diameter; leaves 120–150 cm long, flexible; marginal teeth 6–10 mm long, 30–50 mm apart*A. shrevei* subsp. *magna*
- 10'. Rosettes 0.8–1.2 m tall, 1.2–1.8 m diameter; leaves 40–90 cm long, rigid; marginal teeth 10–20 mm long, 10–20 mm apart.....*A. durangensis*
11. Rosettes small, 0.25–0.35 m tall; leaves 16–30 cm long; panicle 2–3 m tall with 6–12 few-flowered umbels; filaments not conspicuously 2-ranked in insertion*A. flexispina*
- 11'. Rosettes larger, mostly 0.4–0.7 m tall; leaves usually longer than 30 cm; panicles more than 3.5 m tall, or, if shorter, with 15 to 20 densely flowered umbels; filaments inserted at two distinct levels in tube12
12. Leaves conspicuously cross-zoned and sometimes tinged with red; panicle 2–3 m tall, relatively dense, with 15–20 umbels*A. colorata*
- 12'. Leaves uniformly grey; panicle taller than 3 m, open, with 8–16 umbels.....13
13. Leaves 30–45 cm long; marginal teeth deflexed; perianth tube 15–20 \times 11–14 mm, tepal lobes 11–16 mm long; filaments yellow or red; rosettes suckering sparingly*A. shrevei* subsp. *matapensis*
- 13'. Leaves up to 60 cm long; marginal teeth straight or flexed; perianth tube 18–23 \times 10–12 mm, tepal lobes 10–12 mm long; filaments green to pink; rosettes closely suckering*A. shrevei* subsp. *shrevei*

away from peduncle to fully recurved and hugging the peduncle low down, drying quickly, stem-clasping, not bulbiferous, 10–50 mm long, 6–12 mm broad at base; lateral side branches subtended by single, dark purplish brown, triangular, sharp-tipped bract, 25–30 mm long, purple above, light green below, ramified, horizontally spreading, densely flowered with numerous

tightly balled, multi-flower clusters, 100 mm long when flowers open, decreasing in length higher up. Flowers sessile in groups of 3–5(–16), subtended by a minute bract-like structure, strongly fruit salad-scented, distinctly constricted above ovary, copiously nectariferous, distinctly protandrous, tricoloured with basal (ovary) part and lower parts of free portions of

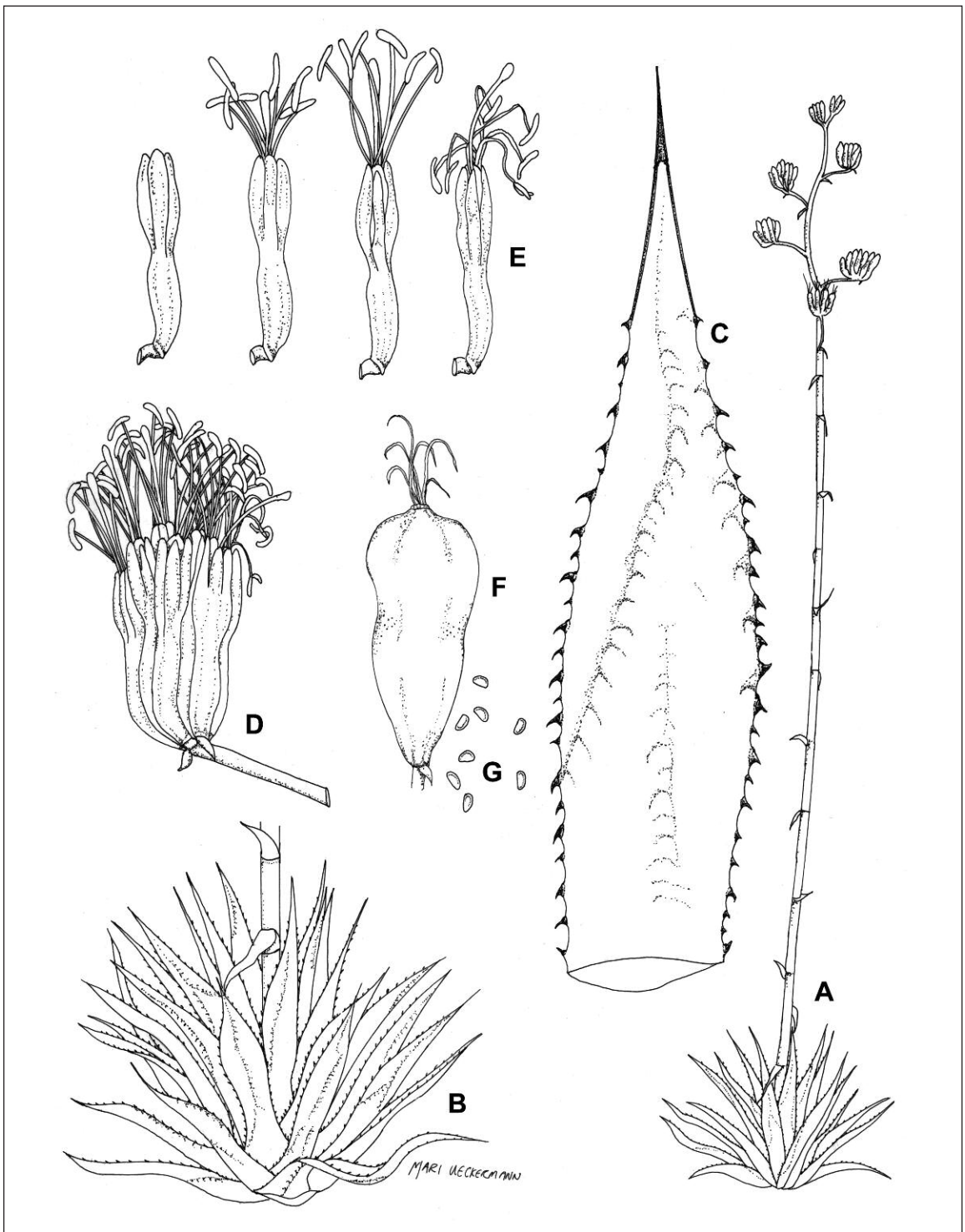


Figure 16. *A. palmeri* Engelm. A: habit of plant 0.6 m tall, with inflorescence of 2.5 m ($\times 0.06$). B: rosette with basal portion of peduncle ($\times 0.1$). C: adaxial view of leaf showing bud imprints ($\times 0.45$). D: cluster of flowers in male phase ($\times 1$). E: floral series from bud (left) through to female phase (right) ($\times 1$). F: ripe fruit ($\times 1$). G: seed at dispersal stage ($\times 1$). Artist: Marië Ueckermann.

tepals dull light green, free segments light pinkish, tips of tepals reddish brown; flower groups subtended by a single, small, triangular, dry, greyish brown bract tapering to a blunt tip, up to 4 mm long; flowers rapidly and completely abscising after anthesis. Perianth 3 + 3; tepals free, united below to form a tube, petaloid, unequal in length with outer ones over-topping inner ones, tepals of outer whorl 24 mm long, tepals of inner whorl 21 mm long, slightly succulent, distinctly spatulate, 5–7 mm broad at base; tepals of inner whorl with two distinct lengthwise grooves abaxially yielding raised ridge between tepals of outer whorl, tips markedly incurved throughout exposing reddish brown tips; wilting tepals remaining closely adpressed and turning uniformly dull light yellowish green after flower reaches female phase, reddish brown colour of tips extending down floral tube as flower matures and dries out; perianth tube succulent, 4 mm deep, 10–12 mm wide at level of filament insertion in female phase flower. Stamens 6, exerted 35–45 mm beyond free segments in male-phase flower, widely divergent and flared out beyond mouth of flower; filaments uniformly light, shiny reddish purple, stout, tapered towards apex, inserted more or less in two series in throat of perianth tube above base of tube, (40–)60–65 mm long, collapsing and becoming thread-like during female phase of flower; anthers (11–)20(–25) mm long, linear to banana-shaped, dorsifixed, versatile, bright yellow, attached in middle to apex of filament; pollen bright yellow contrasting with purple filaments. Ovary terete, tapering apically into a distinct neck, not grooved lengthwise, (18–)25–30(–36) mm long, 8–9 mm in diameter; style stout, terete, 70–75 mm long in female-phase flower, light shiny purple, capitate, stigma white, wet. Fruit a trilocular, club-shaped capsule, light shiny green and fleshy at first, becoming woody, rough, chartaceous, very hard, dark brown when dry, with irregular creamy to light brown surface spots; 35–60 mm long, 15–18 mm in diameter at widest point, distinctly beaked apically, thick-walled, dried flower remains often remaining attached to beak. Seeds many, D-shaped, flat to irregularly angled, black, (3–)7 × 5(–2) mm, interspaced with flat, creamy white, seed-like structures. Plants weakly self-fertile. Chromosome number $2n = 60$ fide Thiede (2001). Voucher specimen: *G.F. Smith & E. Figueiredo* 3 (PRE).

Distinguishing characters: Long-lanceolate leaves, with close-set, slender teeth. Perianth tube about equalling the reddish tepal lobes (Gentry, 1982).

Icones: Breitung: Figures 258, 259 & 260 (1968); Gentry: Figure 35 (1972); Gentry: Figures 16.1, 16.4, 16.5, 16.10, 16.24, 16.25, 16.26 (1982); Irish & Irish: Plate 29 (2000).

Distribution: USA: southeastern Arizona and southeastern New Mexico. Mexico: Sonora and Chihuahua (Figure 7). Occurs in sandy to gravelly places on limestone in oak woodlands and grassy plains; 900–2,000 m (Reveal & Hodgson, 2009).

Common names: Lechuguilla (which is also applicable to other agaves), Maguey de tlalcoyote, Palmer agave, Palmer century plant, Palmer's century plant (Integrated Taxonomic Information System, 2009).

Eponymy: The species was named for Dr Edward Palmer (1831–1911), plant explorer who contributed to knowledge of the flora of the Sonoran Desert.

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