

# Four New Species of *Agave* (Agavaceae) of the *Marmoratae* Group

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**Abstract**—We present a re-evaluation of the taxonomic status of *Agave gypsophila*, for which a narrower circumscription is proposed, and four new species from western Mexico are described and illustrated: *Agave abisaii*, *A. andreae*, *A. kristenii* and *A. pablocarrilloi*. All four species are narrow endemics occurring on a variety of limestone outcrops and belong to the subgenus *Agave* and to the *Marmoratae* species group sensu Berger. They are morphologically related to *A. gypsophila* s. s. from Guerrero, Mexico, but clearly differ from it in various qualitative and quantitative morphological and ecological characteristics.

**Resumen**—Se presenta una re-evaluación del estatus taxonómico de *AGAVE GYPSOPHILA* en la cual se propone una circunscripción más estrecha, y se describen e ilustran cuatro especies nuevas del occidente de México: *Agave abisaii*, *A. andreae*, *A. kristenii* y *A. pablocarrilloi*. Las cuatro especies son endémicas restringidas y se presentan en diferentes afloramientos de roca calcárea, pertenecen al subgénero *Agave* y al grupo de especies *Marmoratae* sensu Berger. Todas tienen relación morfológica con *A. gypsophila* s. s. de Guerrero, México, pero difieren claramente de ésta en características morfológicas y ecológicas, tanto cualitativas como cuantitativas.

**Keywords**—Maguey de peña, maguey de piedra, *Agave abisaii*, *Agave andreae*, *Agave gypsophila*, *Agave kristenii*, *Agave pablocarrilloi*, Western Mexico.

The *Marmoratae* species group (Berger 1915) displays a notable pattern of allopatric speciation, habitat specialization and narrow endemism. The group has heretofore included six species of *Agave*, all from Mexico: *A. zebra* Gentry, *A. nayaritensis* Gentry, *A. valenciana* Cházaro & A. Vázquez, *A. gypsophila* Gentry, *A. marmorata* Roezl and *A. grijalvensis* B. Ullrich (Gentry 1982; Ullrich 1990; Etter and Kristen 2002; Cházaro-Basáñez et al. 2005; Vázquez-García et al. 2007). Martin Kristen, an experienced botanical explorer and gardener of succulents based at Atotonilco El Alto, Jalisco, informed us about an *Agave* population growing on calcareous outcrops at Maruata, Michoacán, which may not correspond to *A. gypsophila*. A close examination of available herbarium specimens, living individuals and descriptions traditionally referred to *A. gypsophila* (e.g. Gentry 1982; McVaugh 1989), unveiled a species complex with a great deal of overlooked and poorly understood morphological variability.

We here refer to this species complex as the *Gypsophila* complex and investigate the question of what the true circumscription of *A. gypsophila* is. Additional field work in the states of Colima, Guerrero, Jalisco, and Michoacán supplied

morphological and ecological data to support a narrower circumscription for *A. gypsophila* while providing evidence to propose four new species which are formally described below. As a result of this addition, the *Marmoratae* species group now includes ten species (Fig. 1). However, the position of *Agave grijalvensis* B. Ullrich (syn. *A. kewensis* Jacobi) remains uncertain, since Gentry (1982) considered it as member of the *Sisalanae* group, whereas Ullrich (1990) proposed this species as a part of the *Marmoratae* group. [F1]

## TAXONOMIC TREATMENT

The *Marmoratae* Group circumscription (Berger 1915), as a result of the addition of these four new species, needs to be broadened to include: a) the surculose habit present in *A. abisaii*, *A. kristenii*, and *A. pablocarrilloi*; b) the numerous leaves feature found in *A. andreae*; c) the smooth texture of leaves represented by *A. abisaii*, *A. andreae* and *A. gypsophila* s. s.; d) the orange colored flowers typical of *A. abisaii*, *A. kristenii* and *A. pablocarrilloi*; and e) its more commonly calcareous habitat, now represented in six out of the ten *Marmoratae* species.

## KEY TO THE SPECIES OF THE *MARMORATAE* GROUP

1. Larger mature rosettes usually 1.8–4.1 m in diameter ..... 2
2. Leaves broadly lanceolate, 20–60 cm wide, rigid, undulate, evidently cross-zoned, teeth 6–12 mm long ..... 3
3. Rosettes 1.7–2.2 × 2.7–3.3 (–4.1) m; leaves 7–15, 150–230 × 37–46 (–53) cm, dark green; flowers 50–60 (–70) mm long; on volcanic substrate with tropical dry forest or oak woodland ecotones, 900–1250 m; Jalisco ..... *A. valenciana*
3. Rosettes 1.2–1.3 × 2 m; leaves 30–50, 100–135 × 20–30 cm, light green; flowers 40–48 mm long; on limestone with xerophytic scrub or oak woodlands, 1550–1900 m; Puebla and Oaxaca ..... *A. marmorata*
2. Leaves narrowly lanceolate to lanceolate, 12–15 cm wide, brittle-flexible, straight to slightly undulate, not evidently cross-zoned, teeth 3–4 mm long ..... 4
4. Spine 30–45 mm long; flowers 60–74 mm long, ovary 30–40 mm long, anthers at anthesis 26–27 mm long, tepals 18–20 mm long, tube 12–15 mm long; on limestone with tropical dry forest, 400–1,000 m; Chiapas ..... *A. grijalvensis*

4. Spine 9–26 mm long; flowers 34–45 mm long, ovary 18–25 mm long, anthers at anthesis 14–16 mm, tepals 11–17 mm long, tube 4–6 mm long; on limestone or volcanic substrate with mixed or tropical dry forest, 585–1,400 m; Nayarit or Michoacán ..... 5
5. Spine 9–15 (–20) mm long; marginal teeth 10–20 mm apart at mid leaf, interstitial margin straight; panicle including the peduncle 1–4 m tall; flowers 40–45 mm long, bright yellow; capsules 16–28 mm long; on volcanic substrate with mixed tropical forest, 585–679 m; Nayarit ..... *A. nayaritensis*
5. Spine 15–26 mm long; marginal teeth 30–38 mm apart at mid leaf, interstitial margin curved; panicle including the peduncle 5–7.3 m tall; flowers 34–40 mm long, orange; capsules 32–45 mm long; on limestone with tropical dry forests, 1,400 m; Michoacán ..... *A. andreae*
1. Larger mature rosettes usually less than 1.8 m in diameter ..... 6
6. Plants not surculose; leaves lanceolate, 8–19 cm wide, spine 9–75 mm long; panicle, including the peduncle 5–8 m tall; flowers yellow ..... 7
7. Rosettes 0.8–1 m tall, leaves 10–11, firm but brittle and smooth, not evidently cross-zoned, spine 9–11 mm long, teeth 1–2 mm long; flowers 31–34 mm long; on limestone with tropical dry forest, 600–900 m; Guerrero ..... *A. gypsophila*
7. Rosettes 0.4–0.6 m tall, leaves ca. 30, rigid and scabrous, evidently cross-zoned, spine 35–75 mm long, teeth 10–20 mm long; flowers 40–55 mm long; on limestone with desert scrub, 600–900 m; Sonora ..... *A. zebra*
6. Plants surculose; leaves narrowly lanceolate to narrowly triangular or linear, 5–13 cm wide, spine 4–5.5 mm long; panicle, including the peduncle 2.3–4 m tall; flowers orange ..... 8
8. Rosettes 0.4–0.5 × 1.4 m; leaves thick throughout, narrowly triangular, rarely narrowly lanceolate, straight to slightly undulate, evidently cross-zoned; flowers 46–51 mm long; on limestone with thorn forest, 50–130 m; Michoacán ..... *A. kristenii*
8. Rosettes 0.8–1 × 1.5–1.8 m; leaves thin at margins, narrowly lanceolate, undulate, not evidently cross-zoned; flowers 28–36 mm long ..... 9
9. Leaves light to dark green, abaxially glaucous at the base, thick at the base, firm but brittle, smooth, tepals 14–16 mm long, bulbils present; on limestone with tropical dry forest, 640–792 m; Jalisco ..... *A. abisaii*
9. Leaves glaucous gray, rigid and scabrous, sheath clasping; tepals 10–13 mm long, bulbils absent; on limestone with succulent woodland, 300–610 m; Colima ..... *A. pablocarrilloi*

1. ***Agave abisaii*** A.Vázquez & Nieves, sp. nov.—TYPE: MEXICO. Jalisco: Mun. Pihuamo, A 5 km sobre la brecha La Estrella–Los Trojes, km 41 de la carr. Colima–

Pihuamo 19°10.447' N, 103°25.111' W, 792 m, 19 feb 1997 (fl. and fr.), *A. García-Mendoza et al.* 6414 (holotype: MEXU; isotype: IBUG).

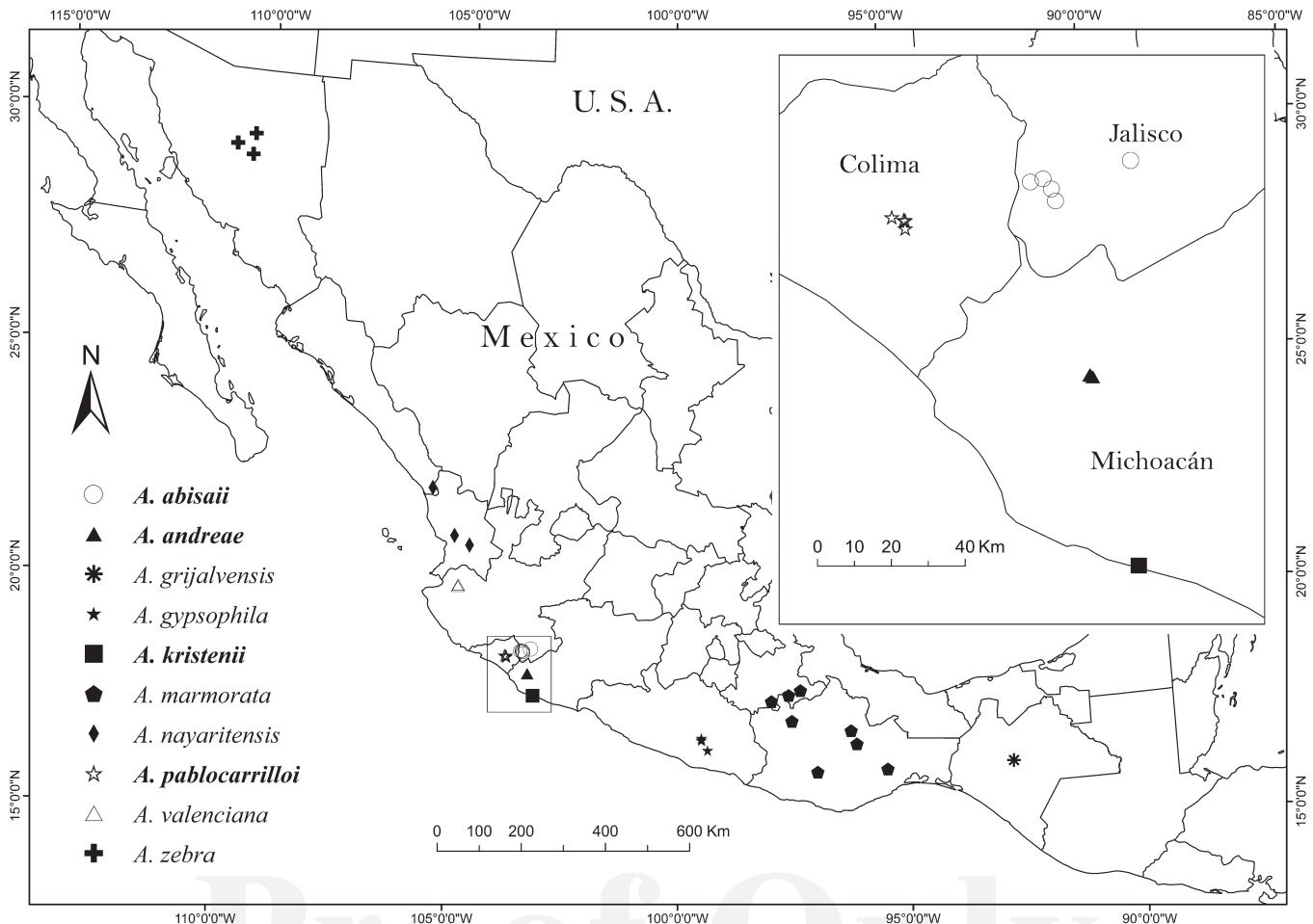


FIG. 1. Distribution in Mexico of *Agave abisaii*, *A. andreae*, *A. kristenii*, *A. pablocarrilloi*, and the other species in the *Marmoratae* group (Gentry 1982; Etter & Kristen 2002; Cházaro-Bazáñez et al. 2005; this study).

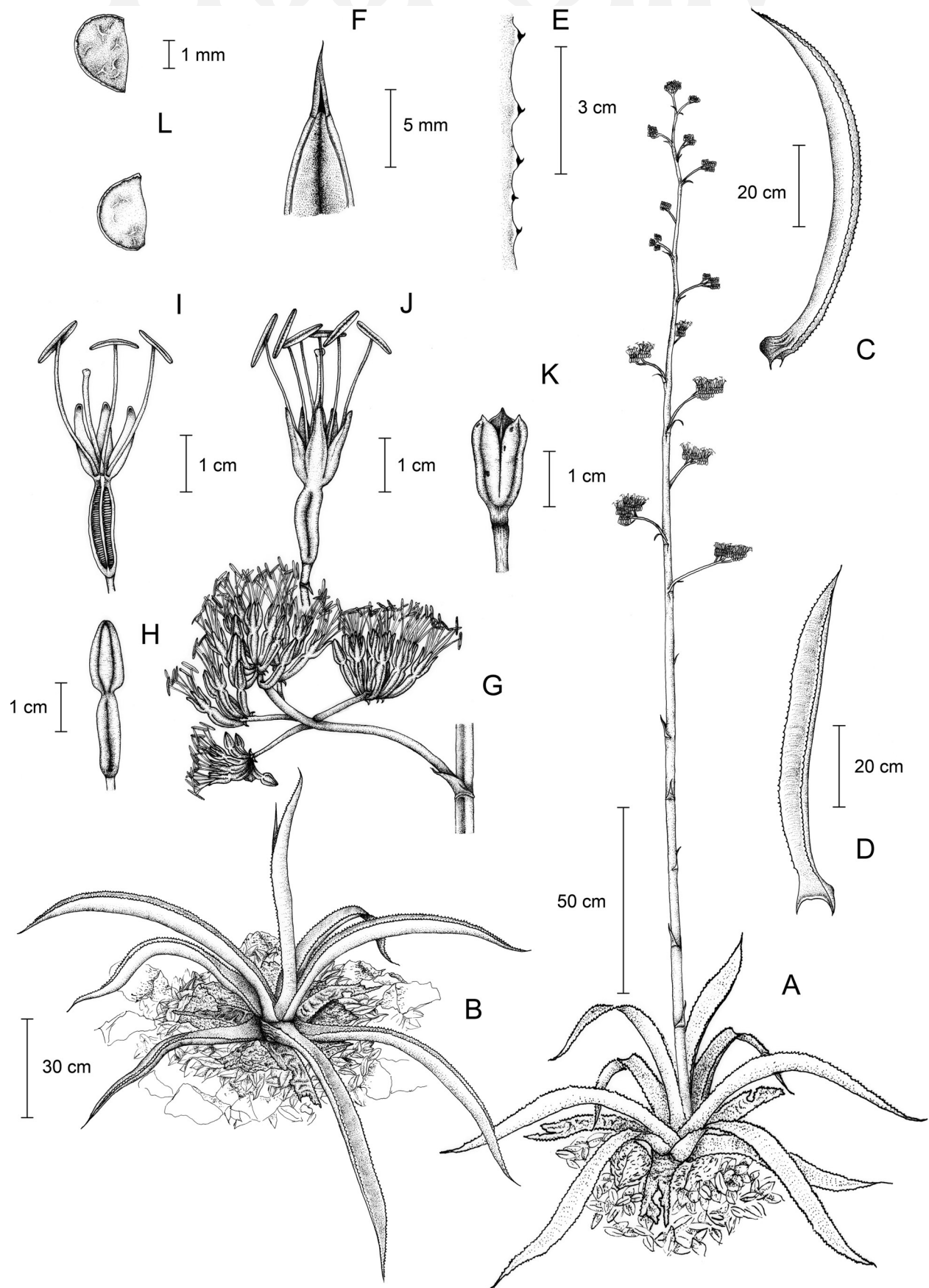


FIG. 2. *Agave abisaii* A.Vázquez & Nieves. A. Habit with panicle. B. Habit. C and D. Leaves. E. Leaf teeth. F. Spine. G. Flowers on a branch. H. Flower bud. I. Longitudinal section of a flower at anthesis. J. Flower at anthesis. K. Capsules. L. Seeds. From García-Mendoza et al. 6414 (specimen in photographs).



*Agave gypsophila* aemulans, differt rosulis surculosis, dentibus foliorum aequidistantibus, floribus aurantiacis (vs floribus flavis vel armeniatis vel aurantiacis), inflorescentiis brevioribus, bulbis rubris, capsulis brevioribus.

**Rosettes** multiannual, surculose, 9–11 leaved, 0.95–1 × 1.5 m; **mature leaves** 80–90 × 9–13 cm, to 7 cm wide at base, to 3.5 cm thick at base, linear to narrowly lanceolate to obtrullate, concave adaxially, convex abaxially, weak, wider above the base, abaxially with a transversal or longitudinal wrinkle at the base, firm but brittle, generally arched, smooth, light to dark green, not evidently cross-zoned, abaxially glaucous at the base; **margins** closely dentate with regularly spaced teeth, the sides involute, undulate, with mammae 3–4 × 2.5–3 mm; teeth firm, 1–3 mm long, 6–17 mm apart at mid leaf, the cups from broad bases 2–5 mm wide, mostly curved, dark brown, with few interstitial denticles, interstitial margin curved; **spine** 4–5 mm long, short and conic, firm, dark brown, nondecurent; **panicles**, including the peduncles, 2.5–3 m tall, oblong, occasionally with numerous red bulbils; shaft 2.5–3 cm in diameter at base, with 13 primary flowering branches in the upper third of the shaft; bracts triangular, the basal ones to 7.5 cm long, acute at the apex, spirally arranged, smooth, 15–18 cm apart; **flowers** 30–38 per branch, 28.5–35.5 mm long, orange, protandrous; ovary 12–16 × 2–3 mm, tube 2.5–3.5 × 6–8 mm (upper part of tube), funnelform, green; tepals 14–16 × 2.5–4 mm, triangular, erect, fleshy, the apex galeate, orange; filaments 18–25 mm, inserted 1 mm above the base of tube; anthers at anthesis 8–10 mm long, centric, yellow; **capsules** oblongoid, 22 × 10 mm, slender, short stipitate, apiculate, thin walled; carpels acute, 22 × 7 mm, curving outward; **seeds** 3–4 × 2–3 mm, lunular, thin, flat, membranous, black. Figure 2.

[F2]

*Agave abisaii* resembles *A. gypsophila* in having few-leaved rosettes with smooth green leaves. However, it differs from the latter in having suckering rosettes, linear to narrowly obtrullate leaves, transversal or longitudinal wrinkles at the abaxial base of leaves, glaucous leaf base, regularly spaced marginal teeth at mid leaf, orange flowers rather than mostly yellow, red bulbils on the inflorescence, smaller inflorescence with fewer (ca. half) flowering branches, and smaller capsules (Table 1).

[T1]

**Distribution and Ecology**—*Agave abisaii* is endemic to southern Jalisco state, on limestone outcrops of both Encino (Late Aptian, 118–112 mya) & Vallecitos formations (Early Albian, 112–106 mya) (Pantoja-Alor & Estrada-Barraza 1986) in tropical dry forest, with *Bursera* spp., *Cochlospermum vitifolium* (Willd.) Spreng., *Pseudobombax* spp., *Stenocereus* spp., *Opuntia* spp., *Ursulaea mcvaughii* (L. B. Sm.) Read & Baensch., *Philodendron warcewiczii* K. Koch & C.D. Bouché, *Bromelia* sp., and *Tillandsia* spp.; at 640–792 m (Table 1).

**Phenology**—Flowering and fruiting from February to March.

**Etymology**—The specific epithet honors Abisai García-Mendoza, a renowned researcher of the Agaves of Mexico.

**Ethnobotany and Conservation Status**—Due to the attributed anti-inflammatory medicinal properties of the roasted leaves, it has been heavily extirpated from large areas in the vicinity of Fátima, Pihuamo, in the State of Jalisco. This use should be investigated and regulated to make it compatible with species survival.

**Additional Specimens Examined**—MEXICO. Jalisco, Mun. Pihuamo, ca. 25 mi NE of Colima, 640 m, 8 Feb 1975, H.S. Gentry 23532 (DES, MEXU—not found, MICH!); Mun. Pihuamo, Hw Pihuamo to the Encino

mine, just Before Puente de Fátima, G. Hernández-Vera et al. 37–1 (19°07'90" N, 103°24'46" W, 590 m), 37–2 (19°07'91" N, 103°24'45" W, 601 m), 15 Dec 2002 (IBUG—not found); Mun. Pihuamo, 600 m East of km 2.5 on road from La Estrella to Fátima, km 41 carr. Colima–Pihuamo, 786 m, 28 Mar 2011 (sterile) J.A. Vázquez-García 9078, 9078b (IBUG!, GUADA!); Municipio de Pihuamo, Las Trojes–Puente de Fátima, km 5.5 km, 100 m al lado E del camino, 19°10'43.93" N, 103°25'09.19" W, 16 mar 2012 (fl bud), J. Antonio Vázquez-García & Jesús Padilla-Lepe 9334 (IBUG, MEXU); Municipio de Tecalitlán, Sierra del Halo, 10 km al E de Alotitlán, 1610 m, 19°16'16.18" N, 103°14'40" W, 12 mar 2012 (fl), Arturo Castro et al. 2950 (IBUG, IEB, ENCB, MEXU, XAL, ZEA).

2. **Agave andreae** Sahagún & A.Vázquez, sp. nov.—**TYPE:** MEXICO. Michoacán: Mun. Chinicuila, Sierra de Coalcomán, Risquera de Tehuantepec, Predio de Ángela Ortega, 18°41'53.6" N, 103°18'5.2" W, 1386 m, 14 Apr 2011 (fl), M. A. Muñiz-Castro & J. Padilla-Lepe 862 (holotype: IBUG; isotypes: IEB, GUADA, MEXU, MICH, MO, WIS).

Species magnitudine rosularum exsurculosarum, colore foliorum et altitude inflorescentiarum (4–5(–6) m) cum *Agave gypsophila* Gentry optime congruens, sed differt numero foliorum (20–40 vs 10–11) et floribus longioribus.

**Rosettes** multiannual, solitary, not suckering (rarely surculose), 0.8–2.3 × 1.5–3.6 m, with 20–40 leaves; **mature leaves** 90–150 (–210) × 12–14 (–23) cm, to 11.5–15 cm wide at base, to 4–5.5 cm thick at base, 14–23 cm at the base of the sheath, narrowly lanceolate, firm but brittle, concave to channeled with the sides almost perpendicular, light green and slightly darker above, glaucous underneath at the base, smooth on both the abaxial and the adaxial surfaces, not evidently cross-zoned on both sides; **margins** slightly undulate, distinctly crenate in the middle to closely dentate basally and apically, with mammae 3–4 × 4–5 mm; teeth mostly 3–5 mm long, 30–38 mm apart at mid leaf, 5–11 mm apart at base, flattened, the cups from broad bases 3–4 mm wide, mostly ascending and curved, dark brown, interstitial margin curved with teeth few or none; **spine** 15–26 mm long, usually short and conic, firm, nondecurent, dark brown; **panicles**, including the peduncles, 5–7.3 m high, shaft 5–8 cm in diameter at base, with 27–36 compact flowering branches in the upper two thirds of the shaft; bracts triangular, the basal ones to 15 cm long, acute at the apex, transversally ridged at base, variable in size along the shaft, spirally arranged, smooth, 7–13 cm toward the base; **flowers** 190–219 per branch, 34–40 mm long, orange, protandrous; ovary 18–21 × 1.7–2.1 mm, the neck 3–4 × 5.5 mm, constricted, green; tube 5–6 × 11–12 mm wide, somewhat funnelform; tepals 11–13 × 5–7 mm, triangular, fleshy, erect, the apex galeate, orange at the apex, yellow at base; filaments 32–36 mm long, inserted at 2–3 mm above the tube base, firm, orange; anthers at anthesis 14–15 mm long, centric, yellow; **capsules** oblongoid 32–39 (–45) × 18–19 mm, stipitate, apiculate, thin-walled; carpels acute, 33–43 × 14–15 mm, curving outward for dehiscence; **seeds** 5–6 × 4 mm, lunular, 334 (207 black, 127 white-frequently sterile), but curved on one side, flat, membranous, black. Figure 3.

[F3]

*A. andreae* is related to *A. gypsophila* Gentry s.s. in having non suckering rosettes comparable in size, smooth green leaves, not evidently cross-zoned, and a tall inflorescence 4–5 (–7) m, including the peduncle; however, it differs from the latter in having many more ascending leaves, more robust inflorescence, larger flowers (Table 1), and growing at a much higher elevation.

TABLE 1. Morphological and eco-geographical differences among species in the *Gypsophila* complex.

Characters	<i>A. abisaii</i>	<i>A. andreae</i>	<i>A. gypsophila</i>	<i>A. kristenii</i>	<i>A. pablocarrilloi</i>
Rosette height & diameter	0.95–1 × 1.5 m	0.8–2.3 × 1.5–3.6 m	0.8–1 × 1.4–2 m	0.4–0.5 × 1.4 m	0.8 × 1.8 m
Bulbils	Present	Absent	Absent	Absent	Absent
Habit	Surculose	Solitary	Solitary	Surculose	Surculose
No. of leaves	9–11	20–40	10–11	7–10	10–15
Leaf size	80–90 × 9–13 cm	90–150 (–210) × 12–14 (–23) cm	[70–100 (–125)] × 8–19 cm	30–79 × 5–6.2 cm	50–70 (–100) × 7–8.5 cm
Leaf shape	Linear to narrowly lanceolate to obrullate	Narrowly lanceolate	Narrowly lanceolate to obrullate	Linear to narrowly triangular or narrowly lanceolate	Narrowly lanceolate, clasping sheath
Blade strength	Firm but brittle	Firm but brittle	Firm but brittle	Firm, rigid	Firm, rigid
Leaf texture	Smooth	Smooth	Smooth	Rough	Rough
Leaf margin	Undulate	Slightly undulate	Undulate	Straight to slightly undulate	Undulate
Mammæ size	3–4 × 2.5–3 mm	3–4 × 4–5 mm	2–4 × 4–6 mm	4–5 × 4.5 mm	4–5 × 5.6 mm
Interstitial margin	Curved	Curved	Curved	Straight	Curved
Leaf color	Light to dark green, abaxially glaucous base	Light to dark green, abaxially glaucous base	Light to dark green	Green to gray, or reddish brown	Glaucous gray
Leaf cross-zoning	No evidently cross-zoned	No evidently cross-zoned	No evidently cross-zoned	Evidently cross-zoned	No evidently cross-zoned
Spine length	4–5 mm	15–26 mm	5–11 mm	5–6 mm	4–5 mm
Teeth length	1–3 mm	3–5 mm	1–2 mm	1–2.9 mm	2–3.5 mm
Teeth distance at mid leaf	6–17 mm	30–38 mm	5–16 (25) mm apart	15–30 mm apart	9–25 mm
Height of Panicle	2.5–3 m	5–7.3 m	5–6 m	3–3.6 m	2.3–4 m
Flower color	Tepals orange	Tepals orange	Tepals yellow	Tepals orange	Tepals orange-yellow
Ovary size	12–16 × 2–3 mm	18–21 × 1.7–2.1 mm	18–20 × 3.5–4 mm	14–20 × 4–5 mm	14–18 × 3.5–4 mm
Tube size	2.5–3.5 × 6–8 mm	5–6 × 11–12 mm	4–5 × 9 mm	3–4 × 7–10 mm	4–5 × 6–8 mm
Tepal size	14–16 × 2.5–4 mm	11–13 × 5–7 mm	10–11 × 3–4 mm	12–14 × 4–5 mm	10–13 × 3 mm
Filament insertion height above base of tube	1 mm	2–3 mm	1–2 mm	1–1.5 mm	1 mm
Filament length	18–25 mm	32–36 mm	20–23 mm	21–29 mm	7–24 mm
Anther length at anthesis	8–10 mm	14–15 mm	11–12 mm	6–10 mm	8–9 mm
Capsule size	22 × 10 mm	32–39 (–45) × 18–19 mm	28–30 × 17–20 mm	30–32 × 14–15 mm	21–28 × 13–16 mm
Seed size	3–4 × 2–3 mm	5–6 × 4 mm	3–3.7 × 1.7–2.4 mm	4–4.5 × 3–4.5 mm	4–6 × 3–4 mm
Vegetation	Tropical dry forest	Tropical dry forest	Tropical dry forest	Thorn forest	Succ. wood., thorn trop. dry for.
Common genera	<i>Stenocereus</i> , <i>Opuntia</i> , <i>Bursera</i> , <i>Pseudobombax</i> , <i>Ursulaea</i> , <i>Philodendron</i>	<i>Opuntia</i> , <i>Lysiloma</i> , <i>Bursera</i> , <i>Pittocaulon</i>	<i>Bursera</i> , <i>Ficus</i> , <i>Acacia cornigera</i> , <i>Cephalocereus</i> , <i>Pseudobombax</i> , <i>Lippia</i> , <i>Opuntia</i>	<i>Cephalocereus</i> , <i>Opuntia</i> , <i>Agave colimana</i>	<i>Pedilanthus</i> , <i>Bursera</i> , <i>Ipomoea</i> , <i>Jatropha</i> , <i>Pachycereus</i> , <i>Neobuxbaumia</i>
Distribution	Jalisco, Mex.	Michoacán, Mex.	Guerrero, Mex.	Michoacán, Mex.	Colima, Mex.
Elevation	640–792 m	1400–1435 m	600–900 m	50–130 m	300–610 m
Mean annual T	22–26°C	20–24°C	22–26°C	26–28°C	24–26°C
Mean annual rainfall mm	1000–1200	1000–1200	1500–2000	800–1200	800–1000

**Distribution and Ecology**—So far, *Agave andreae* is endemic to Sierra de Coalcomán, Michoacán, at 1400–1435 m. *Agave andreae* is found on limestone outcrops of Tecalitlán (Late Aptian, 118–112 mya) and Tepalcatepec (Early Albian 112–99.6 mya & Cenomanian 99.6–93.5 mya) formations (Corona-Esquivel & Alencáster 1995) at higher elevations of the Sierra de Coalcomán, in tropical dry forest, with *Opuntia* spp., *Lysiloma acapulcense* Benth., *Bursera* spp., *Pittocaulon hintonii* H. Rob. & Brettell and *Pedilanthus coalcomanensis* Croizat (Table 1).

**Phenology**—Flowering from January to March; fruits dehiscing from March to April.

**Etymology**—The specific epithet is named after Andrea Sahagún-Romo, daughter of the senior authority of this species.

**Ethnobotany and Conservation Status**—“Maguey de piedra” is traditionally used to treat internal contusions

although this property needs to be scientifically validated. *Agave andreae* is locally abundant but regionally rare.

**Potential Use and Economic Value**—*Agave andreae* is the largest within the *Gypsophila* complex, worthy of cultivation as an ornamental because of its very robust habit and spectacular inflorescence with brilliant orange-yellow flowers.

**Additional Specimens Examined**—MEXICO. Michoacán: Mun. Chinicuila, Hw Aquila–Coalcomán, 2 km NE of road to Tehuantepec, 18°42′06″ N, 103°18′26″ W, 1435 m, 19 Mar 2000 (fl), Sahagún-Godínez 1608 w/Lomeli-Senci6n (GUADA); Mun. Chinicuila, Hw Aquila–Coalcomán, 2 km of road to Tehuantepec, 1400 m, 4 Feb 2002 (fl), Cházaro-Basáñez et al. 8170 (IBUG, IEB); Mun. Chinicuila, Sierra de Coalcomán, parcel of Ángela Ortega, 18°41′53.6″ N 103°18′5.2″ W, 1386 m, 14 Apr 2011 (fl, fr), Muñiz-Castro 856, 857, 858, 859, 860, 861 (IBUG, MEXU, MO, WIS); Mun. Chinicuila, carretera Aquila–Coalcomán, 3 km al NE del cruce de Tehuantepec, frente a una fonda, 1400 m, 15 mar 2012 (fl bud), J. Antonio Vázquez-García & Jesús Padilla-Lepe 9333 (IBUG, MEXU).

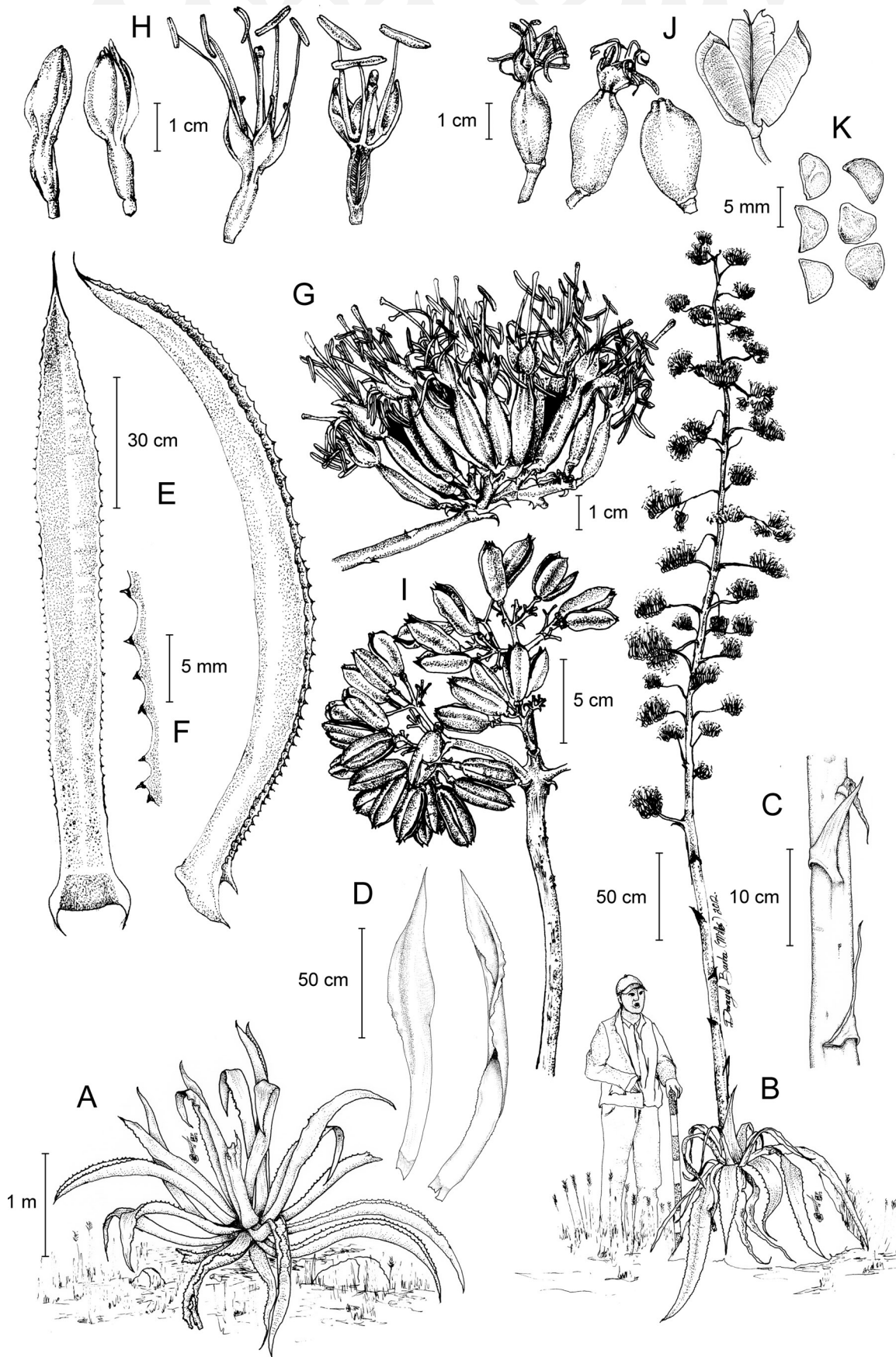


FIG. 3. *Agave andreae* Sahagún & A. Vázquez. A. Habit. B. Habit with panicle, including peduncle. C. Scales on the shaft. D and E. Leaves. F. Leaf margin and teeth. G. Flowers on a branch. H. Flower stages and longitudinal section at anthesis. I. Capsules on a branch. J. Capsules. K. Seeds. From Muñiz-Castro & Padilla-Lepe 862 and photographs (MAMC).



3. *AGAVE GYPSOPHILA* Gentry, *Agaves of Continental North America*, p. 510. 1982—Type: MEXICO. Guerrero: Mun. Acahuizotla, 4 miles SE of Acahuizotla, along highway to Acapulco, 3000 feet, 14 Jun 1954 (fl), H.A. Floyed & C.L. Ryan 103 (holotype: MICH).

Diagnostic characters for a new and narrower circumscription for *Agave gypsophila* include: leaves that are narrowly lanceolate to obtrullate, smooth, flexible, green, and not evidently cross-zoned (Table 1). Specimens from Guerrero: Moore & Valiente 6193 (BH, MEXU); and Muñiz-Castro 845, 846, 847 (IBUG) should be regarded as authentic material representative of *A. gypsophila* Gentry s.s., although some specimens are unusual. For example, Flores-Sánchez 216 (MEXU), from Rancho Viejo, Gro. may likely represent a mixed collection, since a loose larger flower (55 mm long) does not match the size of any of the remaining flowers (40 mm long) of the specimen. Furthermore, the leaves on this specimen are unusual in that the upper third leaf is exceedingly narrow. Perhaps this is due to the immaturity of leaves at the time they were pressed. We tried to replicate this scenario by pressing immature sheathing leaves that we removed from the central axis of a living plant, and our leaves also had the unusually narrow apical section. In addition, the leaves on a duplicate of Flores-Sánchez 216 (MEXU), showed mature leaves that did not have the unusually narrow apical part. Thus, without the extraneous material, this specimen fits well within *A. gypsophila* s.s.

**Distribution and Ecology**—*Agave gypsophila* thrives on the limestone outcrops of the Morelos Formation (Cretaceous: Albian to Cenomanian, 112–93 mya) (Consejo de Recursos Minerales, ERCT-UAG 1997), in thorn and tropical dry forest with *Bursera* spp., *Ficus* spp., *Acacia cornigera* (L.) Willd., *Guazuma ulmifolia* Lam., *Pseudobombax* sp., *Lippia* sp., *Opuntia* spp. and *Cephalocereus* spp. and is occasionally found near the ecotone with pine oak forest; from 600–900 m (Table 1).

**Phenology**—Flowering from February to June; fruiting from March to July.

**Etymology**—The specific epithet refers to the rocky calcareous habitat where it grows.

**Ethnobotany and Conservation Status**—“Maguey de ixtli”, “quite” or “calegual”, which refers to the shaft that is often used for construction of rural houses (Illsley-Granich et al. 2004; Pureco-Ornelas et al. 2001). The species is locally abundant but its overall distribution is narrow.

**Additional Specimens Examined**—MEXICO. Guerrero: Highway between Chilpancingo and Acapulco, near km 335, 3 Jan 1951 (sterile), Ogden 5104 (MEXU!, US—not seen); Km 338 on road to Acapulco, ca. 3 km beyond Acahuizotla, 960 m, 28 Mar 1952 (fl), Moore & Valiente 6193 (BH—not seen; MEXU!); Mun. Chilpancingo, Rincón de La Vía, 17°17'15" N; 99°28'55" W, 900 m, 28 Feb 1960 (fl), Kruse 190 (MEXU!), 4 May 1964, Kruse 1399 (MEXU), 950 m, 7 Mar 1966 (fl), Kruse 1046 (MEXU!); 29 km S Chilpancingo, 13 Mar 1980 (fl), Leuenberger & Schiers 2730 (MEXU!); Acahuizotla, Rancho Viejo, toward Río Apetlanca, Mun. Chilpancingo, 600 m, 27–28 Feb 1988 (fl), Flores-Sánchez 216 (MEXU!); 7–8 km S of Acahuizotla (along highway to Acapulco), Mun. Chilpancingo, 17°17'43.5" N, 99°28'23.4" W, 900 m, 12 Mar 2011 (sterile), Muñiz-Castro 845, 846, 847 (IBUG!).

4. *Agave kristenii* A.Vázquez & M.Cházaro, sp. nov.—TYPE: MEXICO. Michoacán: Mun. Aguila, Maruata, km113 Carretera Lázaro Cárdenas–Tecomán, 18°13'10.86" N, 103°10'27.72" W, 130 m, 5 Mar 2011 (fl & fr), J.A. Vázquez-García 9076 (holotype: IBUG; isotypes: MEXU, MICH, MO, WIS).

Habitu exiguo, inflorescentiae axe relative subtili, distributione (habitat ad rupes gypseas), et usu medicinali *A. gypsophila* et affinibus similis et nullo dubio his speciebus proxima, praecipue differt rosulis brevioribus et rosulis surcolosis praesentibus, foliis anguste obtrullatis rigidis crassioribus et scabris, dentibus longioribus et remissioribus, inflorescentia axibus brevioribus et mollioribus.

**Rosettes** multiannual, surculose, 0.4–0.5 × 1.4 m, with 7–10 leaves; **mature leaves** 30–79 × 5–6.2 cm, to 5.5 cm wide at base, to 5.1 cm thick at base, linear to narrowly triangular or narrowly lanceolate, wider at base, convex below, concave above, the margin involute, generally arched and weavy, firm, rigid, rough, green to gray, or reddish-brown, glaucous cross-zoned on both sides; **margins** straight to slightly undulate, closely dentate basally and apically, with mammae 4–5 × 4–5 mm; interstitial margin straight; the teeth firm, mostly 1–2.9 mm long, 15–30 mm apart, flattened, the cups from narrow bases 1–2 mm wide, mostly curved toward the base, dark brown, interstitial denticles few or none; **spine** 5–6 mm long, usually short and conic, firm, dark brown, nondecurent; **panicles**, including the peduncles, 3–3.6 m tall, shaft 3–3.5 cm in diameter at base, the lateral branches 15–18 in the upper two thirds of the shaft; bracts triangular, the basal ones to 14 cm long, acute at the apex, spirally arranged, scabrous, 13–27 cm apart; **flowers** 80–87 per branch, 32–36 mm long, protandrous, orange; ovary 14–20 × 4–5 mm, green, the neck 2.5–5 mm long and constricted; tube 3–4 × 7–10 mm, somewhat funnelform; tepals 10–14 × 4–5 mm, triangular, fleshy, erect, the apex galeate, orange; filaments 21–29 mm long, inserted at 1–1.5 mm above base of tube, firm, orange; anthers at anthesis 6–10 mm long, centric, yellow at anthesis; **capsules** 30–32 × 14–15 mm, oblongoid, slender stipitate, apiculate, thin-walled; carpels acute, 25–28 × 13–14 mm, curving outward for dehiscence; **seeds** 4–4.5 × 3–4.5 mm, lunular, but curved on one side, flat, membranous, black. Figure 4. [F4]

Except for its surculose habit and orange rather than bright yellow flowers, *Agave kristenii* shares most of the distinctive characters of the *Marmoratae* species group (Berger 1915), such as crenate margins, small spines, small flowers with small tubes ¼ to ½ as long as the tepals and leaves cross-zoned on both sides (Table 1). *A. kristenii* is related to *A. gypsophila* from Guerrero, with which it shares brittle leaves with little fiber, restriction to limestone outcrops and similarly attributed medicinal properties. However, it differs from the latter in having a much smaller and suckering rosette, with linear to narrowly triangular or narrowly lanceolate, boat shaped, firm, thicker and rough leaves, which are not wider above mid leaf as in *A. gypsophila*. Additionally, its marginal teeth and mammillae at mid leaf are larger and more widely spaced. *A. kristenii* also has an even smaller and more delicate shaft with smaller inflorescence branches, and grows at a much lower elevation (130 m) on seaward-facing slopes of Michoacán, in thorn forest (Table 1) (Gentry 1982; McVaugh 1989; Cházaro-Bazáñez et al. 2005; Vázquez-García et al. 2007). Photographs M2, M9 and M10 (Plate M, pp. xxxvi, xxxvii) taken at southeastern Maruata, in Michoacán by J. Etter and M. Kristen, which were referred to *A. gypsophila* by Vázquez-García et al. (2007), actually correspond to *A. kristenii*.

**Distribution and Ecology**—*Agave kristenii* appears to be endemic to the seaward facing slopes southeast of Maruata, Michoacán, at 50–130 m. This species is reported to inhabit

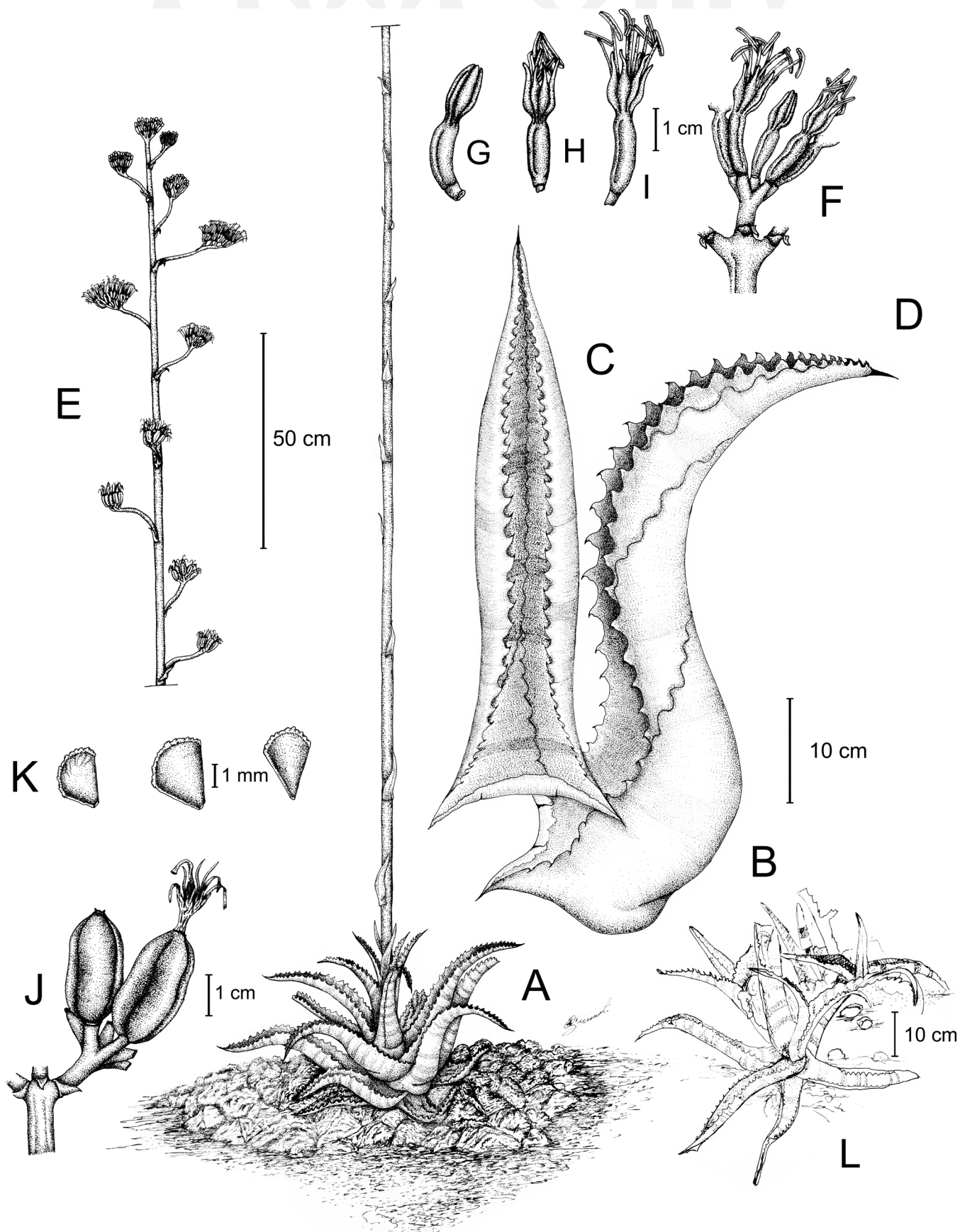


FIG. 4. *Agave kristenii* A. Vázquez & M. Cházaro. A. Habit. B. Leaf. C. Leaf teeth. D. Spine. E. Panicle, including peduncle. F. Flowers on a branch. G. Flower bud. H. Flower before anthesis. I. Flower at anthesis. J. Capsules. K. Seeds. L. Surculose habit. From Etter & Kristen s. n. (IBUG-cult.).



although without supporting collections, the vicinity of Arenas Blancas and Chocoala, Michoacán (Eleazar Garibo Cisneros, pers. comm. Playa Azul, Mar, 2010). It thrives on the limestone outcrops of the Tepalcatepec Formation (Early Albian, 112–99.6 mya & Cenomanian, 99.6–93.5 mya) (Corona-Esquivel & Henríquez 2004), in thorn forest with *A. colimana* Gentry, *Opuntia* spp., and *Cephalocereus* spp. (Table 1).

**Phenology**—Flowering from February to March; fruits dehiscing from March to April.

**Etymology**—The specific epithet honors Martin Kristen, an outstanding botanical globetrotter and photographer, whose work led to the discovery of this new species.

**Ethnobotany and Conservation Status**—*Agave kristenii* is locally known as “Maguey de piedra,” traditionally used as an anti-inflammatory, and applied to relieve internal contusions, tumors and cancer (Longinos Dimas Alvarado, pers. comm., March 5, 2011). However, these properties are yet to be scientifically validated. It is locally abundant and produces suckers, however, individuals or even entire colonies are extirpated for medicinal purposes. Its rhizome is easily extracted completely, due to its weak roots on shallow soils, sometimes growing barely over the surface of limestone rocks. Thus, its abundance is decreasing due to over collecting.

**Potential Use and Economic Value**—*Agave kristenii* is a remarkable addition to the succulent flora of western Mexico and is worthy of cultivation as an ornamental because of its wavy Aloe-like rosette, arched cross-zoned leaves, showy prominent mammillate teeth, and delicate shaft with bright orange flowers.

**Additional Specimens Examined**—MEXICO. Michoacán: Mun. Aquila, Maruata, km 113, on road from Lázaro Cárdenas to Tecmán, 18°13′10.86″ N, 103°10′27.72″ W, 130 m, Mar 2009, Etter & Kristen s.n. (cult. spec.) (IBUG); Mun. Aquila, km 113, on road from Lázaro Cárdenas to Tecmán, 130 m, 12 Mar 2011 (fl, fr), Vázquez-García 9076b (cult. spec.) (IBUG).

**5. *Agave pablocarrilloi*** A. Vázquez, M.A. Muñoz & Padilla-Lepe, sp. nov.—TYPE: MEXICO. Colima: Mun. Coquimatlán, Barranca Las Agujas, 1.5 km al oeste de Calera de Moisés, 450–500 m, 19 Apr 2011 (fr), J. A. Vázquez-García & J. Padilla-Lepe 9090 (Holotype: IBUG, isotypes: MEXU, MO).

*A. pablocarrilloi*, qouad rosularum magnitudem, folia fragilia et undulata ad marginem, et distributionem (habitat ad rupes gypseas) ad *A. gypsophilam* accredit, praeterea ab ea distat habitu surculoso, foliis glaucis scabris et complanatis apicem versus, dentibus rigidis et approximatis, paniculis brevioribus, et dimidia panicularum ramis principalibus.

**Rosettes** multiannual, sparsely to densely surculose, 0.80 × 1.8 m, with 10–15 leaves; **mature leaves** 50–70 (–100) × 7–8.5 cm, with a semi-amplexicaul sheath; narrowly lanceolate, wider at base and above mid leaf, concave on the lower third, occasionally flat on the distal half, undulate, firm, rigid, rough, not evidently cross-zoned, bluish glaucous-gray on both sides; **margins** undulate, distinctly crenate in the middle (9–25 mm apart), closely dentate basally (5–10 mm apart), with mammae 4–5 × 5–6 mm; teeth 2–3.5 mm long, firm, flattened, the cups from broad bases 2–3 mm wide, usually ascending, frequently curved, dark brown, interstitial margin curved with denticles more frequent at mid leaf; **spine** 4–5 mm long, short and conic, firm, dark brown, nondecurent; **panicles**, including the peduncles, small, 2.3–4 m, shaft 3–4 cm in diameter at base, with few, 8–15 (–19) branches in the upper half of

the shaft, bracts triangular, the basal ones 12 × 5 cm, acute at the apex, rough, 6.5–8 cm apart; **flowers** ca. 50 per branch, 28–36 mm long, orange-yellow; ovary 14–18 × 3.5–4 mm; tube 4–5 × 6–8 mm, somewhat funnelform; tepals 10–13 × 3 mm, triangular, fleshy, galeate, orange-yellow, filaments 7–24 mm, firm, inserted 1 mm above the base of tube; anthers at anthesis 8–9 mm, centric, yellow; **capsules** 21–28 × 13–16 mm, oblongoid, stipitate, apiculate, thin walled; carpels 2–2.5 × 10–11 mm, obovate, apiculate; **seeds** 4–6 × 3–4 mm, sub triangular or semi-circular thin, black. Figure 5.

[F5]

Populations previously cited from the State of Colima as *Agave gypsophila* (Gentry 1982; McVaugh 1989; Vázquez-García et al. 2007) actually correspond to *A. pablocarrilloi* (i.e. Carrillo-Reyes 1783, 1744, 1744b (GUADA, IBUG); Pérez de la Rosa 619 (IBUG); Lott & Solís 915 (MO); Gentry 18328 (MICH); Gentry 19563, 22193, 23533 (ARIZ; DES, MICH, US)). This species is similar to *A. gypsophila* in its medium sized rosettes, brittle leaves with undulate margin, rarely cross-zoned patterning, and calciphilous habitat. It differs from *A. gypsophila* in its suckering habit, rough, bluish glaucous-grayish leaves that are flat on the lower half, close firm teeth, smaller panicles with only 8–15 (19) lateral branches (vs. 28–30 in *A. gypsophila*) and being confined to lower elevations.

**Distribution and Ecology**—*Agave pablocarrilloi* is endemic to the State of Colima. It is found on limestone outcrops of the Madrid Formation (Albian, 105–100 mya) (Corona-Esquivel & Henríquez 2004), at 300–610 m, in succulent woodland, thorn forest and tropical dry forest with *Cordia* sp., *Pachycereus* sp., *Pedilanthus* sp., and *Neobuxbaumia* sp. (Table 1).

**Phenology**—Flowering from February to April; fruiting from April to May.

**Etymology**—The specific epithet is named after Pablo Carrillo-Reyes, a promising botanist and outstanding explorer of the succulent flora of western Mexico.

**Ethnobotany and Conservation Status**—*A. pablocarrilloi* is locally known as “Maguey de piedra”, it is locally abundant but a narrow endemic to Coquimatlán, Ixtlahuacán, and Colima municipalities.

**Additional Specimens Examined**—MEXICO. Colima: Mun. Colima: West of Cd. Colima, on Manzanillo road, 2000 ft, 610 m, 1955, C. Miegs s. n., grown at Desert Botanical Garden, Phoenix, 33°27′33″ N, 111°56′35″ W, 1200 ft., 366 m, accession number 1955 5144, 14 Apr 2005 (fl), Hodgson & Damrel 19341 (DES); Mun. Colima/Ixtlahuacán, seaward facing slopes, 18–24 km S of Colima, Gentry 18328 (ARIZ—not seen); 400 m, 5 Dec 1959, Gentry 19563 (DES, MEXU, MICH, US—not seen); Mun. Colima: Ca. 17 km SSW of Colima, on road to Manzanillo, 23 Mar 1982 (fl), 400–500 m, Lott & Solís-Magallanes 915 (DES!, MEXU!, MO!); Mun. Colima, West of Km 18, on road from Colima to Manzanillo, 300 m, 11 Mar 1984 (fl), Pérez de la Rosa 619 (IBUG); Mun. Coquimatlán, 1 km S of Ejido El Alcomún (Luis Echeverría Álvarez), on road to La Brasileira and La Antena, 5 km ENE of Madrid, 29 Apr 2001 (sterile), Carrillo-Reyes 1744 (GUADA-cult!), 1744b (IBUG-cult!); Mun. Coquimatlán, E of Barranca Las Agujas, 1.5 km W of Calera de Moisés, 450–500 m, 19 Apr 2011 (fr), Vázquez-García 9091 (IBUG). Mun. Coquimatlán, Barranca Las Agujas, 2 km W of Calera de Moisés, 500–600 m, 30 Apr 2001 (fl), Carrillo-Reyes 1783 (IBUG!). Mun. Ixtlahuacán, 13 miles S of Cd. Colima, crossroad along road to Manzanillo, 22 Nov 1966 (old fr), Gentry 22193 (ARIZ!, DES!, MEXU!, MICH, US—not seen); Mun. Ixtlahuacán, 13–14 miles SW of Cd. Colima, near Rn. La Salada, 9 Feb 1975 (sterile, fl buds), 1500 feet, Gentry & Gentry 23533 (ARIZ!, DES!, MEXU!, MICH—not seen, US—not seen); Mun. Ixtlahuacán, 550 m NE of Rancho La Salada, Km 4, on road from Ixtlahuacán to Colima, 450 m, 19 Apr 2011 (st), Vázquez-García 9086, 9087, 9088, 9089 (IBUG-cult).

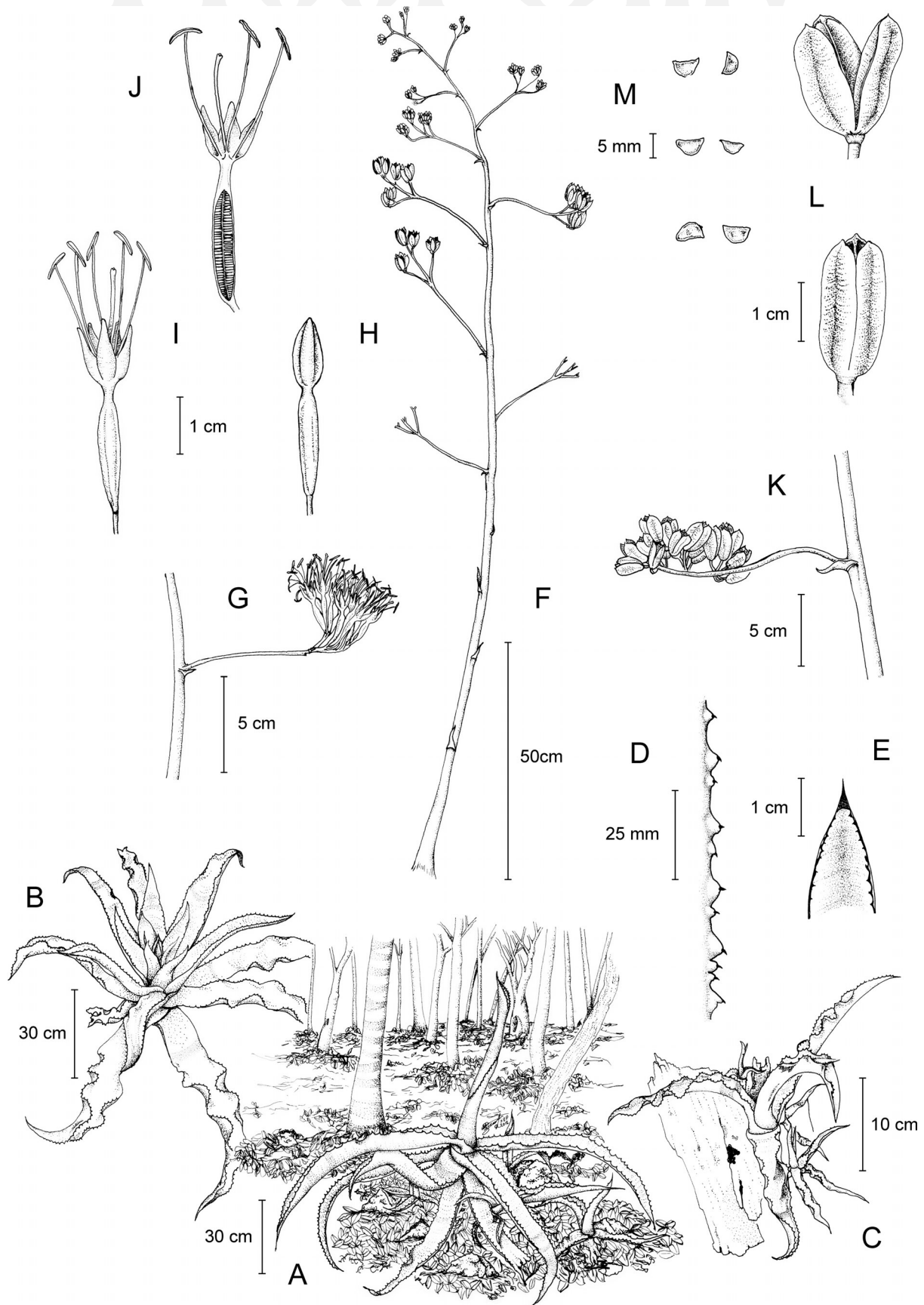


FIG. 5. *Agave pablocarrilloi* A. Vázquez, M. A. Muñiz & Padilla-Lepe. A. Habit. B. Cultivated and well watered habit. C. Juvenile and surculose habit. D. Leaf margin and teeth. E. Spine. F. Panicle, including peduncle, with remaining capsules. G. Flowers on a branch. H. Flower bud. I. Mature flower. J. Longitudinal section of a mature flower. K. Capsules on a branch. L. Capsules. M. Seeds. Adult habit from Vázquez-García & Padilla-Lepe 9090, juvenile habit from Carrillo-Reyes 1744, flowers from Perez de la Rosa 619.

## DISCUSSION

The *Marmoratae* species group sensu Berger (1915), with its new additions, now includes 10 species of *Agave*, all from Mexico (Fig. 1): The four new species, *A. abisaii*, *A. andreae*, *A. kristenii*, and *A. pablocarrilloi*, grow in thorn forest or tropical dry forest on rather dry hills and cliffs, and are largely confined to Albian to Cenomanian Cretaceous limestone formations in southeastern Jalisco, southwestern Michoacán, central coast of Michoacán, and south of Colima, respectively, at non overlapping segments within a 1,500 m elevational gradient. *Agave gypsophila* s. s., grows in thorn or tropical dry forest near the ecotone with oak forest and is restricted to Albian to Cenomanian Cretaceous limestones of the Morelos Formation in the state of Guerrero, not from the states of Jalisco, Colima or Michoacán as cited by Gentry (1982), McVaugh (1989), Vázquez-García et al. (1995), and Vázquez-García et al. (2007). In particular, specimens from Guerrero (*Floyd & Ryan 103* (Holotype-MICH); *Muñiz-Castro 845, 846, 847* (IBUG); *Ogden 5104* (MEXU, US); and *Moore &*

*Valiente 6193* (BH, MEXU) should be regarded as representative of *A. gypsophila* s.s. *Agave grijalvensis*, *A. nayaritensis*, and *A. valenciana* are largely restricted to tropical dry forest habitats, in humid canyons and cliffs of Depresión Central de Chiapas, Nayarit–Sinaloa and western Jalisco, respectively (Gentry 1982; Ullrich 1990; Etter and Kristen 2002; Cházaro-Bazáñez et al. 2005; Vázquez-García et al. 2007). *Agave nayaritensis* and *A. valenciana* grow on volcanic, not calcareous rocks, while *A. grijalvensis* is confined to calcareous rocks. Finally, *A. marmorata* and *A. zebra* inhabit semiarid to arid scrub xerophytic vegetation in the Oaxaca–Puebla and Sonoran Deserts, respectively (Gentry 1982).

The species in the *Gypsophila* complex display relevant patterns of niche differentiation at various elevation belts. *Agave gypsophila*, the only species overlapping with others in elevation is both clearly separated by latitude and the most distant geographically. Since no geographic overlap has been documented, the isolated distribution may have resulted in allopatric speciation in the *Gypsophila* complex. Nevertheless, other speciation processes such as hybridization cannot

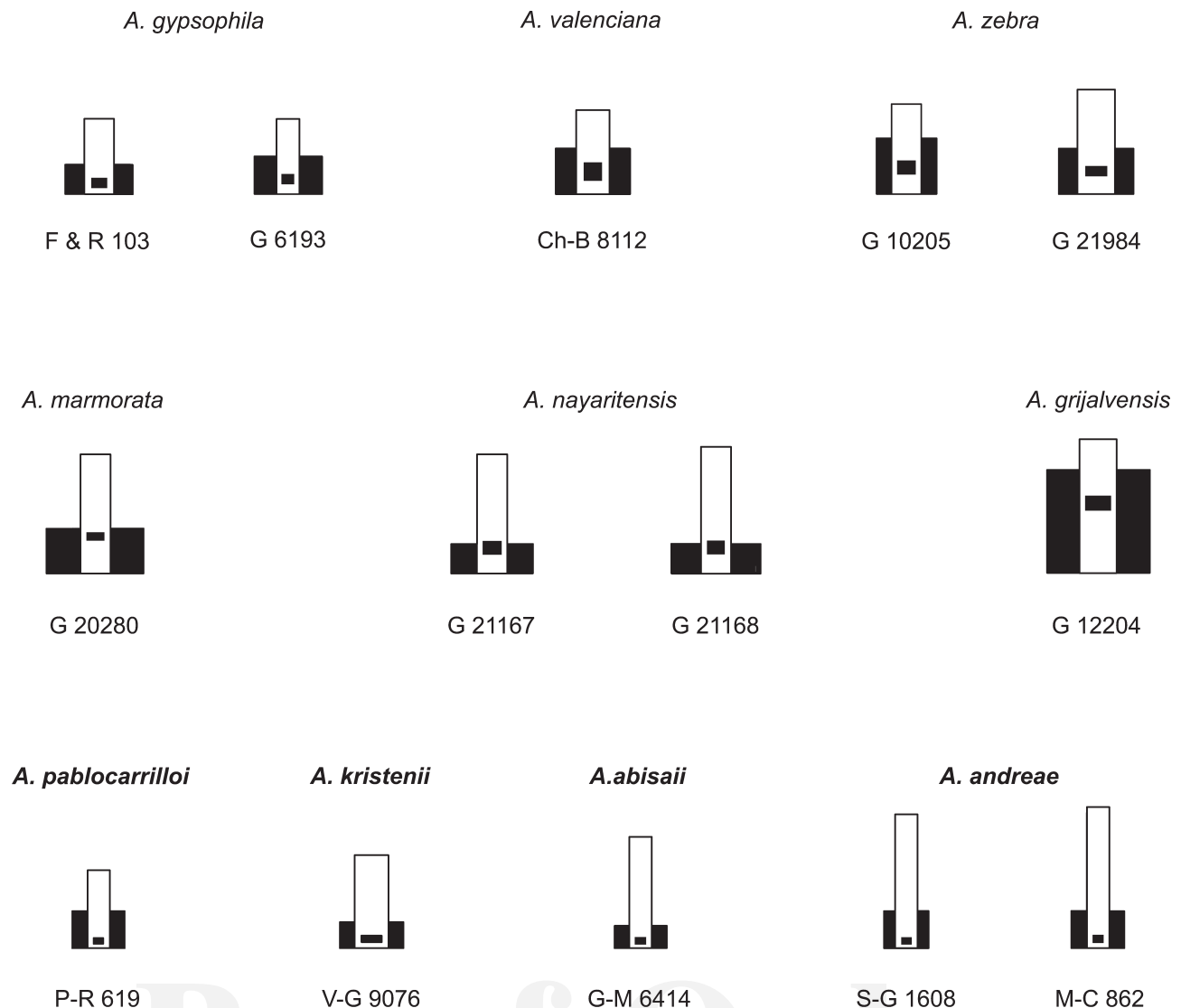


FIG. 6. Flower ideographs for the species in the *Marmoratae* group. Black bars represent average height and width of tube, white bars represent the average height and width of tepals, and height of black rectangles inside the white bars represents the distance of filament insertion to the bottom of the tube (Gentry 1982).



immediately be ruled out because the plants involved in possible past hybrid events may have long disappeared from areas straddling current populations. Research on chromosome numbers and ploidy level is needed to shed light on this interesting topic.

The size of flowering parts in ideographs of the *Marmoratae* group display a great extent of continuous morphological variation, except for *A. grijalvensis* which stands as an outlier (Fig. 6). This species has a flowering morphology more related to the *Sisalanae* group, as was suggested by Gentry (1982), contrary to its placement within the *Marmoratae* group by Ullrich (1990). The species of the *Gypsophila* complex may be characterized by having filament insertion points closer to the flower base than any other species within the *Marmoratae* group, but this observation requires further examination of additional fresh flowering material, since some flowers never regain full size after rehydration (Gentry 1982). All four new taxa differ in terms of flowering morphology from *A. gypsophila*. *Agave abisaii*, *A. andreae* and *A. pablocarrilloi*, have narrower tepals and tubes, while *A. kristenii*, has slightly wider tepals and shorter tubes (Fig. 6). The presence of bulbils in the inflorescences is not widespread and in fact is a rare occurrence in the *Marmoratae* group. *Agave abisaii* commonly produces bulbils in situ but *A. andreae*, *A. kristenii*, and *A. pablocarrilloi* do not. However, a photograph of a plant with bulbils taken from a plant collected at Maruata that apparently corresponds to *A. kristenii* was published by Ullrich (1991). Nevertheless, that plant flowered nearly after a decade under cultivation in Germany. Thus, we have to conclude that the prolonged stress of the unusual environmental conditions under which the plant had been cultivated was the reason for the presence of the bulbils and cannot, with the evidence at hand, be considered typical for that species. The presence of bulbils in *A. kristenii* in Ullrich (1991) contradicts the observations of the authors of this paper, none of which have ever observed bulbils on plants of this species either growing in the wild or cultivated in Mexico.

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