

A review of *Agave ellemeetiana* K.Koch (Asparagaceae/Agavaceae)

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Summary: A broad overview of the history, publication, author, introduction, rediscovery, distribution, habitats, typification, and relationships of *Agave ellemeetiana* K.Koch is given. The species was first published by K.Koch in 1865 from cultivated plants of unknown origin and was rediscovered in habitat only in the last couple of years in Central Veracruz (Sierra de Zongolica), northern Oaxaca (Sierra Mazateca and near San Bartolomé Ayautla), and in western Oaxaca (Putla/Tlaxiaco region). Plants from western Oaxaca differ consistently in their finely denticulate leaf margins and are distinguished as *Agave ellemeetiana* subsp. *subdentata* (Trelease) Thiede comb. nov. from the plants in Veracruz and northern Oaxaca with entire, smooth leaf margins (= *Agave ellemeetiana* subsp. *ellemeetiana*).

Zusammenfassung: Es wird eine breitgefaßte Übersicht über die Geschichte, Veröffentlichung, Autorschaft, Einführung, Wiederentdeckung, Verbreitung, Standorte, Typifikation und Verwandtschaft von *Agave ellemeetiana* K.Koch gegeben. Die Art wurde zuerst von K.Koch 1865 nach kultivierten Pflanzen unbekannter Herkunft veröffentlicht und erst in den letzten Jahren an Naturstandorten in Zentral-Veracruz (Sierra de Zongolica), in Nord-Oaxaca (Sierra Mazateca und bei San Bartolomé Ayautla) und in West-Oaxaca (in der Region Putla/Tlaxiaco) wieder entdeckt. Pflanzen aus West-Oaxaca unterscheiden sich konstant durch ihren fein gezähnelten Blattrand und werden als *Agave ellemeetiana* subsp. *subdentata* (Trelease) Thiede comb. nov. von den Pflanzen in Veracruz und Nord-Oaxaca mit ganzrandigem, ungezähneltem Blattrand (= *Agave ellemeetiana* subsp. *ellemeetiana*) unterschieden.

Introduction

The systematics of the genus *Agave* L. are in a continuous flux and receive attention by many authors: since the taxonomic synopsis by Thiede in 2001, some 30 new species were published, including the most remarkable *Agave albopilosa* I. Cabral, Villarreal & A.E. Estrada (2007). How-

ever, besides the discovery of novelties, several long-known species of unknown origin in the wild were rediscovered in habitat such as *A. albomarginata* Gentry (Magallán & Hernández, 2000) and *A. warelliana* Baker (Lott & Garcia-Mendoza, 1994; Cházaro *et al.*, 2008). The most notable among the rediscovered species is certainly *A. ellemeetiana* K.Koch, a species of subg. *Littaea* with nearly stemless rosettes of rather few, broad, flat, soft and unarmed shiny green leaves with a soft terminal spine (Figures 1–4, 6–14). Since its publication in 1865, *A. ellemeetiana* was known from cultivated plants of unknown origin in the wild and was not rediscovered in habitat until the last couple of years (Köhres, 2008; Cházaro *et al.*, 2012). Albeit published nearly 150 years ago, the history, publication, author and typification of the species and its introduction, rediscovery, distribution, habitats and relationships remained incompletely known. This paper aims to fill these gaps of knowledge.

1. History and publication

The history of *Agave ellemeetiana* is connected with three people: Professor Karl Heinrich Emil Koch (1809-1879; see Anon., 1879; Wimmer, 2004), horticultural botanist at the Botanical Garden Berlin and author of nearly 2100 new plant names including some 20 new names in *Agave*, the Prussian general Georg Albano von Jacobi (1805–1874, see Gutte, 2006), renowned author of an 11-volume treatise on European field artillery, owner of a large agave-collection, and author of about 110 new names in *Agave*, and the eponym of the species, Jonkheer Willem Cornelis Mary de Jonge van Ellemeet (1811-1888, see Koch, 1864b; Alsemgeest, 2004), a Dutch landowner, mayor and keeper of an important succulent collection on his estate “Overduin” near Oostkapelle (The Netherlands) which in 1856 comprised 200 cactus names with emphasis on *Mammillaria* Haw. (Janse, 1977), but later Ellemeet specialized on *Agave* and its relatives.

The first appearance of *A. ellemeetiana* in printed matter as a mere name without descrip-



Figure 1. *Agave elmeetiana* (subsp. *elmeetiana*). Part-coloured lithograph from Saunders' *Refugium Botanicum* (plate 163, Baker 1869) from a plant flowering in the greenhouse of W.W. Saunders, with an inflorescence 4.25m (14 ft.) in height. This plate represents the first illustration of a flowering *Agave elmeetiana* and is reproduced here in colour for the first time (courtesy of G.D. Rowley). Photograph by Jonathan Clark



Figure 2. *Agave ellemeetiana* (subsp. *ellemeetiana*). Hand-coloured copper-enchaving from *Curtis's Botanical Magazine* (plate 7027, Baker 1888b) from a plant flowering at Kew Gardens.

(courtesy of The Biodiversity Heritage Fund).

tion was in October 1862 when Koch (1862) reported on a plant exhibition in June 1862 in Middelburg (The Netherlands) close to Ellemeet's estate where the latter exhibited his plants, including "his" *A. ellemeetiana*. During that occasion, Koch also visited Ellemeet's collection with a specimen of the "absolutely rare *A. ellemeetiana*" (Koch, 1864b).

Jacobi (1865) mentioned that *A. ellemeetiana* received its name in Paris and lists the 'author name' "Hort. Paris" for it. In 1873 (reproduced in Alsemgeest, 2004), Ellemeet mentioned that Koch and Jacobi found the rare agave named after him in Paris. Koch made his first visit to Paris not until August to September 1864 (Wimmer, 2004), but his reports in the journal which he edited ("*Wochenschrift des Vereines zur Beförderung des Gartenbaues in den Königlich Preussischen Staaten für Gärtnerei und Pflanzenkunde*"; abbreviated as "*Wochenschrift*" in the following and

as "*Wochenschr.*" in the references) do not mention any *Agave*. Thus, Koch may have seen the plant in Paris in 1864 together with Jacobi, but the first appearance of the name *A. ellemeetiana* in print was two years earlier in October 1862 by Koch, as mentioned above.

During the 27th to 29th April 1864, the collection of the Belgian agave-collector van der Vinnen was auctioned in Brussels, Belgium (Vermeulen, 1864; Koch, 1864a), and Ellemeet purchased an especially large specimen of *A. ellemeetiana*. Shortly thereafter, Ellemeet donated the plant to the Botanical Garden Berlin for further study where it was kept from no later than 29th May 1864 onwards (Koch, 1864c). Based on the van der Vinnen plant at Berlin, Koch (1865a) validly published *A. ellemeetiana* as a new species on 1st April 1865 in his "*Wochenschrift*".

Just one week later, from 7th to 12th April 1865, Koch attended the "Exposition Universelle d'Horticulture" at Amsterdam (NL) where he, as his report shows (Koch, 1865b), had intensive contacts with Ellemeet. Most certainly, Koch presented a reprint of his publication of *A. ellemeetiana* to Ellemeet, albeit no written record could be found. Eduard August von Regel (1815-1892), botanist and later director of the Imperial Botanical Garden of St. Petersburg (Russia), also attended the Amsterdam exposition and mentioned in his report (Regel, 1865) that Ellemeet received an award for his agaves. The specimen of *A. ellemeetiana* exhibited at Amsterdam was most probably Ellemeet's plant, but doubtless not the specimen from the van der Vinnen auction which was kept in Berlin from no later than 29th May 1864 onwards (Koch, 1864c, see above). M. Witte (1865), chief gardener at BG Leiden (The Netherlands) published a report on a visit to Ellemeet's estate where he saw an "admirable plant" of *A. ellemeetiana* with a diameter of 2m (!) and a leaf size of 90 × 20cm "throning in the centre" of Ellemeet's agave collection.

Six month after Koch's publication, Jacobi (1865) independently published *A. ellemeetiana* based on the same specimen in Berlin in the October-issue of the "*Hamburger Garten- und Blumenzeitung*" with the 'author name' "Hort. Paris" and without the additive 'Nob.' (nobis, Latin = us) which he used for the species he intended to describe as new (Thiede, 2014: 296). Albeit Koch already noted in 1871 that his publication in "*Wochenschr.* 7: 103, 1865" antedates that of Jacobi, most later works wrongly cited Jacobi as author (e.g. Baker, 1888a; Berger, 1915; Gentry, 1982; Thiede, 2001; Govaerts, 2014); only a few works correctly cited Koch (e.g., IPNI, 2014). Regel (1865), in his report on the Amsterdam ex-



Figure 3. *Agave ellemeetiana* (subsp. *ellemeetiana*) flowering in cultivation at Kew, showing an inflorescence about 4.50m high and with about 3150 flowers (from Anonymous 1910; courtesy of The Biodiversity Heritage Fund).

position, provided a short description of *A. ellemeetiana* (“Grosse, hellgrüne, länglich-ovale, ganzrandige Blätter, die in einen Krautstachel ausgehen”) which must be considered to represent a further, albeit unintended, publication of that name unrecognized by previous authors. Regel’s publication appeared in the August issue of the *Gartenflora* 1865, thus antedating Jacobi’s publication from October 1865.

In 1871, Ellemeet’s agave collection comprised 137 different “names”, including 4 rather large specimens of “his” *A. ellemeetiana* measuring up to 1.55m in diameter (Ellemeet, 1871; reproduced by Morren, 1871; André, 1872). However, many of these species names are now placed in the synonymy of long-known variable species such as *A. mitis* Mart., *A. americana* L., *A. salmiana* L., *A. angustifolia* Haw. and *A. lophantha* Schiede ex Kunth (Alsemgeest, 2004). About two years later, Ellemeet’s whole collection of 323 specimens was auctioned on his estate on 22nd. September 1873



Figure 4. *Agave ellemeetiana* (subsp. *ellemeetiana*) flowering in cultivation at Rotterdam Zoo in 1922, with an inflorescence more than 4m in height (from van den Houten 1930).

(Anon., 1873a, 1873b; Alsemgeest, 2004). The auction was completely unsuccessful, and Ellemeet presented his whole collection to the Zoological Gardens at Rotterdam (The Netherlands) in 1874 and 1875 (Krelage, 1885). In 1885, Ellemeet’s agaves at Rotterdam still represented the best agave collection in the Netherlands (Krelage, 1885). Several plants at Rotterdam Zoo possibly going back to Ellemeet were depicted by van den Houten in 1930, and some agaves going back to Ellemeet were still in cultivation in 2004 (Alsemgeest, 2004), 130 years after Ellemeet’s collection was disintegrated. In 2011, no plant from Ellemeet was still present at Rotterdam, but a few were still kept at Amsterdam (Alsemgeest, *pers. comm.* 2011).

2. Introduction into cultivation Europe.

Agave ellemeetiana has most certainly been continuously in cultivation in Europe from not later than 1862 onwards, albeit it was (and still is) uncommon. The first record from the UK dates from 1865 when Jacobi (1867) saw a living plant in the collection of the British insurance broker, entomologist and botanist William Wilson Saunders (1809-1879); the plant came into flower two

years later (see below). The British agave collector W. B. Kellock of Stamford Hill exhibited a specimen in May 1872 (Anon., 1872). At Kew Gardens, nine plants came into flower between 1874 and 1949 (see below; Figure 2 & 3). The species was seen at Kew by Howard S. Gentry (1903-1993, see Ullrich 1993), the intrepid explorer and monographer of the genus in Continental North America, in 1969 (Gentry, 1982: 96) and in 1975 by Janse (1977) and is still in cultivation there (Royal Botanic Gardens Kew, 2014), possibly unintentionally from not later than 1874 onwards.

At Hanbury Gardens in La Mòrtola (Italy; see Russo, 2001; Smith & Figueiredo, 2014a), *A. ellemeetiana* was cultivated no later than 1889 (Cronmeyer, 1889) and was still seen there in 1993 (M. Greulich, *pers. comm.*). John Gilbert Baker (1834-1920), botanist at Kew, keeper of the herbarium, and monographer of agave and other monocotyledons, studied a plant at Hanbury in 1891 (Baker, 1892). Alwin Berger (1871-1931, see Schröder, 2011), curator at Hanbury from 1897 to 1914, listed *A. ellemeetiana* in his "*Hortus Mortolensis*" (Berger, 1912: 11) and depicted a flowering plant at Hanbury in his agave monograph (Berger, 1915: 125). Gentry (1982: 97) did not find *A. ellemeetiana* at Hanbury during his visit in 1955. At the Jardin Botanique "Les Cèdres" at St. Jean-Cap-Ferrat (France), the species was cultivated from no later than 1961 (Breitung, 1961, see below) and was still present in 1990 (Kolendo, 1990). According to SYSTAX (2014), the species is at present cultivated in Germany in the botanical gardens at Kiel and Ulm, but it was also seen by the author at BG Bochum in 2012.

USA.

The earliest record for the cultivation of *A. ellemeetiana* in the USA is found in a letter from ca. February 1885 by James Gurney (1831-1920), head gardener at Missouri Botanical Garden (St. Louis) since 1867 (Knotts & Pagels, 2014). Gurney (1885) lists the agaves cultivated at Missouri, among them *A. ellemeetiana*. In 1912, *A. ellemeetiana* was still kept at Missouri, as is indicated by a herbarium specimen made in spring 1912 by Charles Henry Thompson (1870-1931), Assistant Botanist and keeper of the succulent collection (Tropicos, 2014). The US Department of Agriculture imported *A. ellemeetiana* seeds from the nursery Vilmorin-Andrieux & Co. (Paris, France) in 1923 (USDA, 1925) and in 1930 (USDA, 1930). In 1931, *A. ellemeetiana* was commercially offered by the nursery of Edward O. Orpet at Santa Barbara, California (Manning, 1931), and in 1933 it was cultivated at Balboa Park in San Diego (Greer, 1933). The US agave collector August J.

Breitung (1961) obtained plants from the Jardin Botanique "Les Cèdres" (France), wrongly stating that this appeared to be a new introduction to the Southwestern USA. All these records invalidate Gentry's (1982: 97) statement "that there is no record of *A. ellemeetiana* in North American gardens". At present, *A. ellemeetiana* is rare in cultivation and is kept mainly in specialist collections and botanical gardens in the USA and Europe; seeds or plants are commercially offered by several nurseries.

Asia.

Agave ellemeetiana is (or was) cultivated at Bogor (Indonesia; Raja, 1963) and on the Philippines (Madulid, 1995).

3. Flowering specimens, plates and photographs

The first flowering specimen: In June 1867, Jacobi when just in the field on a military campaign, received a message from W. W. Saunders that the latter's *A. ellemeetiana* was in flower with an inflorescence of nearly 4m (13 ft.) in height and the upper 2.75m (9 ft.) densely beset with flowers (Jacobi, 1867). Jacobi saw that plant himself in autumn 1865 and received pressed flowers from Saunders and from which he provided the first, very detailed description of the flowers of *A. ellemeetiana* (Jacobi, 1867). Saunders had received the plant from the Royal Horticultural Society (RHS) at Chiswick. Baker (1869) published a partly coloured plate of the same plant in Saunders' "*Refugium Botanicum*" showing the inflorescence of 4.25m (14 ft.) in height. This plate, reproduced here as Figure 1, represents the very first illustration of a flowering specimen of *A. ellemeetiana*. Eight years later, Baker (1877) provided the first complete description of *A. ellemeetiana* including the inflorescence and flowers accompanied by a black and white woodcut of a non-flowering plant (the plate was reproduced by Alsemgeest, 2004).

Kew Gardens: At Kew, *A. ellemeetiana* flowered in May 1874 (Anon. 1874), in February to March 1877 (Anon., 1877a, 1877b) and in June 1883 (Anon., 1883a, 1883b). From the specimen flowering in 1877, four herbarium sheets were prepared, three of which were much later selected as neotype by Gentry (1982: 96; see below). A further plant came into flower in 1888 at Kew and was illustrated with a fine hand-colored copper engraving in "*Curtis' Botanical Magazine*" (reproduced here as Figure 2; Baker, 1888b), noting that the species was introduced about 1864. This date was repeated by later authors, but, as noted above, *A. ellemeetiana* is known for sure from no



Figure 5. Distribution of *Agave ellemeetiana* in the Mexican states of Veracruz and Oaxaca, and towns referred to in the text. Subsp. *ellemeetiana*: triangles, subsp. *subdentata*: circles; filled symbols = herbarium specimens, open symbols = literature and photographic records. Symbols may represent more than one record. (map: Wikimedia Commons 2014).

later than 1862. At Kew, *A. ellemeetiana* flowered again in 1910 (inflorescence about 4.5m high and with about 3150 flowers; Anon., 1910 with a black and white photograph reproduced here as Figure 3), in 1918 (with black and white photograph, Anon., 1918), in 1926 (with several lateral inflorescences below the lowest leaves which attained a height of nearly one meter and bore numerous perfect flowers; Wright, 1926), in 1927 (2 plants, Anon., 1928), and in 1949 (Anon., 1950).

Other gardens: A plant from Ellemeet's collection flowered at Rotterdam Zoo (The Netherlands) in 1875 (Krelage, 1885). At Hanbury (Italy), *A. ellemeetiana* flowered repeatedly before 1915, and in 1913, even with 3 specimens (Berger, 1915: 125, with black and white photograph), at the Palmengarten Frankfurt (D) in 1918 (Krauss, 1918, with black and white photograph), the Botanical Garden, Berlin in 1918 or 1919, as is indicated by the distribution of seeds via the *Index Seminum* in 1919 and 1920 (Anon., 1919, 1920), Rotterdam Zoo in 1921 (van den Houten, 1922), and the Botanical Garden, Berlin in 2002 (Alseemgeest, 2004; with the first colour photographs of a flowering plant by I. Richter which are also reproduced in Richter, 2011: 62). The plant flowering at Rotterdam in 1921 possibly goes back to Ellemeet and was depicted with a black and white photograph by van den Houten (1930; reproduced here as Figure 4). The illustrations of the plants



Figure 6. *Agave ellemeetiana* subsp. *ellemeetiana* in habitat on calcareous rock faces in the Sierra de Zongolica near Totomachapa (central Veracruz). The larger rosettes with pendent dried leaves appear to be the bromeliad *Tillandsia grandis* which co-occurs with *Agave ellemeetiana* in the Sierra de Zongolica (Wrinkle 2011) and also at Ayautla (Figure 10) 15th January 2013, photo: Michael Greulich.

flowering at Kew (Figure 3) and at Rotterdam (Figure 4) both represent the most impressive photographs of *A. ellemeetiana* thus far published.

4. Rediscovery, distribution and habitats

All early agave authors (Koch, Jacobi, Baker, Trelease) up to modern monographers (Berger, Gentry) knew *A. ellemeetiana* from cultivated plants which may all only go back to the first introduction no later than 1862. During the last couple of years, localities in central Veracruz and in three different areas in Oaxaca became known (see the map in Figure 5):

Central Veracruz. William Trelease (1857-1945), botanist, director of Missouri Botanical Garden, eminent researcher on the Agavaceae, and the most prolific author of names in *Agave* (192; Smith & Figueiredo 2014b), was the first to mention a possible wild locality for *A. ellemeetiana* from around Xalapa (Jalapa) in central Veracruz (Trelease, 1920). The source of this information was not given, but the record was repeated by many later authors (e.g., Meyrán García, 1987; Sosa & Gómez-Pompa, 1994). Castillo-Campos *et al.* (2005) and Espejo-Serna (2012) list *A. ellemeetiana* as endemic to Veracruz and known from one herbarium specimen only (Castillo-Campos *et al.*, 2005).

Cházaro *et al.* (2012) provide the first printed habitat report of *A. ellemeetiana* from Veracruz: They show photographs of flowering plants in habitat, cite two specimens from Totomochapa in Mpio. de Tequila and from Joya Chica in Mpio. de Zongolica (listed below), and list further sight

records from near Naranjal, Córdoba, Tlilapan, Orizaba, and near Texhuacán. Surprisingly, *A. ellemeetiana* is rather abundant on the slopes and limestone cliffs in the mountain regions of the Sierra de Zongolica between San Andrés Tenejapa and the town of Zongolica, but it remained unnoticed by botanists for a long time (Cházaro *et al.*, 2012). An *A. ellemeetiana* habitat near Totomachapa (between Naranjal and the town of Zongolica) was also visited by the German agave specialist Michael Greulich in January 2013 (Figures 6–8). In the “Reserva del Bicentenario”, a private nature reserve in the Sierra de Zongolica, *A. ellemeetiana* occurs on rocks in cloud forest (Reserva del Bicentenario, 2014). The US nurseryman Guy Wrinkle (2011) offered young plants of an “*Agave* species Zongolica” which apparently represent young *A. ellemeetiana* plants originating from the Sierra de Zongolica where the plant is “growing on vertical cliffs along with [the bromeliad] *Tillandsia grandis* Schltdl”.

Specimen data: Veracruz, Mpio. de Tequila, Totomochapa, cantil rocoso “El Popocatl”, Y. A. Gheno H. 100, 14.02.2011 (flowering). CORU, XAL (Cházaro *et al.*, 2012).

Veracruz, Mpio. de Zongolica, paraje Joya Chica, junto al Instituto Tecnológico Superior de Zongolica, 5 kilómetros al oeste de la ciudad de Zongolica, 1300m, M. Cházaro B. & L. Escandon 9805, 27.04.2010 (flowering). CORU (Cházaro *et al.*, 2012).

Northern Oaxaca – Sierra Mazateca. The Mexican botanist and Agavaceae specialist A. García-Mendoza (2002) briefly mentioned the rediscovery of *A. ellemeetiana* in Oaxaca, but without indicating a locality. Two years later, García-Mendoza (2004) mentioned *A. ellemeetiana* to occur between 400–1200m in the distritos Teotitlán and Tuxtepec, i.e., roughly in the Sierra de Mazateca (= Sierra de Huautla) in Northern Oaxaca and just southeast of the Sierra de Zongolica (Figure 5). The records by García-Mendoza were most probably based on three *A. ellemeetiana* specimens in the National Herbarium of Mexico (MEXU) which were collected in 2001 in the course of a floristic study of the montane cloud forests in the Sierra Mazateca (Lorea & Munn, 2005).

Specimen data: Oaxaca, Mpio. de Eloxochitlán de Flores Magón, brecha de San Antonio Eloxochitlán a San José Buenavista, adelante del segundo puente, 1320m, D. X. Munn Estrada & F. Mendoza 1442, 1.10.2001. Bosque de niebla. Creciendo sobre roca en una ladera del cerro. Infructescencia de 1.30m de alto, frutos secos. Abundante. MEXU (AGA1108894), XAL. (Instituto de Biología, 2010a; Cházaro *et al.*, 2012).

Oaxaca, Mpio. de Huautla de Jiménez, vereda de Agua de Fierro, (3.5km del Puente de Fierro, por la terracería a Sta. María Chilchotla), a la terracería de Sta. Cruz-Aguacatitla, 1460m, D. X. Munn Estrada & F. Mendoza 1387A, 26.09.2001. 18°10'11"N 096°50'37"W. Ladera con exposición W. Vegetación secundaria derivada de Bosque Mesófilo de Montaña. Peñas de roca en la ladera del cerro. Infructescencia de 1.90m de alto; frutos secos. Abundante. MEXU (AGA1108992), MO. (Instituto de Biología, 2010b; Tropicos, 2014).

Oaxaca, Mpio. de Huautla de Jiménez, aprox. 1.5km de Aguacatitla, por la terracería de Aguacatitla a Sta. Cruz de Juárez, 1589m, D. X. Munn Estrada & T. Kasey 1181, 12.05.2002. 18°09'54"N 096°50'43"W. Paredes de roca expuesta, a la orilla de la terracería. Inflorescencia de 80cm; flor blanca(!). Abundante. MEXU (AGA1109024), MO. (Instituto de Biología, 2010c; Tropicos, 2014).

One of the two latter specimens was apparently used for the molecular study by Gil-Vega *et al.* (2007; see below).

Northern Oaxaca – San Bartolomé Ayautla.

The first who verifiably rediscovered *Agave ellemeetiana* in habitat was the plant explorer Alfred Bernhard Lau (1928–2007, see Staples, 2007). In 1987, Lau (1993a, 1993b) travelled along the new road MEX 182 winding from San Felipe Jalapa de Díaz up to Huautla de Jiménez along the Rio Santo Domingo gorge (Figure 9). Lau stopped in between at San Bartolomé Ayautla to see the local endemic cycad *Dioon rzedowskii* De Luca, A. Moretti, Sabato & Vázquez Torres (1980) (Figure 12). On the almost vertical karstic cliffs of Cerro Rabón above Ayautla, Lau discovered an especially large species of butterwort published as *Pinguicula gigantea* Luhrs (1995) growing together with a “large population of a form of *Agave attenuata* Salm-Dyck in an area of 3000mm rainfall annually” (Lau, 1993a, 1993b, 1998). The accompanying photographs show *Pinguicula gigantea* and agave leaf tips (Lau, 1993a, 1993b). Ullrich (2007: Figure 6 & p. 28) reproduces a photograph made by Lau in Oaxaca most probably at Cerro Rabón (Ullrich l.c.: “near Jalapa de Díaz” which is ca. 10 road km E of Ayautla) and comments that the plant cannot be determined with certainty, but may be *A. ellemeetiana*. Partrat (2014) reproduces Lau’s habitat photograph from Cerro Rabón showing *Pinguicula gigantea* and agave leaf tips, and Rivadavia (2014) provides additional photographs of both species which make the agave clearly identifiable as the stemless, green-leaved and toothless *A. ellemeetiana*. Lau’s misidentification of *A. ellemeetiana* with the similar *A. attenuata* ssp. *dentata* (J. Verschaaff.) B. Ullrich (= *A. pedunculifera* Trel.) whose eastern-most



Figure 7. Plants of *Agave ellemeetiana* subsp. *ellemeetiana* on calcareous rock faces in the Sierra de Zongolica near Totomachapa (central Veracruz)

15th January 2013, photo: Michael Greulich.



Figure 9. Mountains with cloud forest/tropical rainforest near San Bartolomé Ayautla (Northern Oaxaca), habitat region of *Agave ellemeetiana* subsp. *ellemeetiana*. San Bartolomé Ayautla is situated at the Rio Santo Domingo which is visible just in the midst behind the right banana plant.

October 2008, photo: Art Vogel.

localities lie about 300km westwards (Ullrich, 2007: 25) precluded the report of its rediscovery. The Dutch horticulturist Art Vogel (*pers. comm.*) observed *A. ellemeetiana* growing on near vertical calcareous rock faces along MEX 182 in the Ayautla area (Figures 9–12). Vogel even found one plant growing epiphytically on the stem of a cycad (most probably *Dioon rzedowskii*, Figure 12); his photograph is the first record of *A. ellemeetiana* growing as an epiphyte.

Western Oaxaca – Putla/Tlaxiaco region. In May 2008, the German nurseryman Gerhard Köhres (2008) reported *A. ellemeetiana* from volcanic rocks at about 2300m northeast of Putla near Santiago Nuyoó in Western Oaxaca. Köhres (2008) published habitat photographs of *A. ellemeetiana*, also including an inflorescence, and pro-



Figure 8. Rosette of *Agave ellemeetiana* subsp. *ellemeetiana* on a vertical calcareous rock face in the Sierra de Zongolica near Totomachapa (central Veracruz). The insert shows the entire leaf margin without denticles.

15th January 2013, photos: Michael Greulich.



Figure 10. Vertical calcareous rock cliff in cloud forest/tropical semideciduous forest near San Bartolomé Ayautla (Northern Oaxaca) with *Agave ellemeetiana* subsp. *ellemeetiana* and the bromeliad *Tillandsia grandis* (rosettes with pendent old leaves), the largest species in its genus occurring largely lithophytic.

October 2008, photo: Art Vogel.



Figure 11. *Agave ellemeetiana* subsp. *ellemeetiana* on vertical calcareous rock cliffs in cloud forest/tropical semideciduous forest near San Bartolomé Ayautla (Northern Oaxaca).

October 2008; photo: Art Vogel.

vided the first record of the species from the Sierra Madre del Sur, i.e., the southern mountain chain exposed to the Pacific Ocean (Figure 5). The UK garden designer Paul Spracklin found *A. ellemeetiana* in March 2010 and depicts it from about 20km east of Putla (which is roughly around Santiago Nuyoó) where it occurs around 2600m along with a large population of *A. atrovirens* Karw. ex Salm-Dyck on a rock face (Spracklin, 2010; Figures 15 & 16). The US nurseryman Jeremy Spath and Kelly Griffin (2011) found *A. ellemeetiana* a couple of years before and depict the species from between Putla and Tlaxiaco at about 2440m (8000 ft.; Griffin, 2011). The Köhres locality was re-visited by the Dutch agave specialists Bertus Spee and Wim Alsemgeest in January 2014 (Figures 17 & 18). Plants of the Köhres' collection are cultivated in Germany (Figure 19), and plants of the Spath & Griffin collection were offered commercially (Figure 20).

Most interestingly, Thomas (Tom) Baillie Mac-



Figure 12. As a rare exception, *Agave ellemeetiana* subsp. *ellemeetiana* grows as epiphyte on the stem of a cycad, most probably the local endemic *Dioon rzedowskii* in cloud forest/tropical semideciduous forest near San Bartolomé Ayautla (Northern Oaxaca).

October 2008, photo: Art Vogel.

Dougall (1895-1973), intrepid botanist-explorer who spent 42 winters until his death collecting plants and animals in Oaxaca and Chiapas (Phillips, 2006), mentioned in his field notes that on 19.11.1949 he saw “a large *Agave* sp. - magüey pelon -, the leaf margins are spineless”. The agave was observed on an abandoned ranch at Zarzamora in Tlaxiaco Mpio. (MacDougall, 1971), which is west of Tlaxiaco and south of San Andrés Chicahuaxtla and thus just within the area mentioned above where *A. ellemeetiana* is now known to occur. Since no other spineless agave is known from that area (cf. Lott & Garcia-Mendoza, 1994), MacDougall most probably already rediscovered *A. ellemeetiana* back in 1949(!), but without noting the importance of his find.

5. Habitats and cultivation

In Oaxaca, *A. ellemeetiana* subsp. *ellemeetiana* occurs between 400 and 1460m on rocks in mon-



Figure 13. Old cultivated plant of *Agave ellemeeitiana* subsp. *ellemeeitiana* as it is known in cultivation in Europe for nearly 150 years. Berkenhof Tropical Zoo, Kwadendamme, The Netherlands. 8th September 2009; photo: Bertus Spee.

tane cloud forests (bosque mesófilo de montaña) and tropical semideciduous forests (bosque tropical subperennifolio; Garcia-Mendoza, 2004), i.e., on edaphically arid microsites within humid habitats with fog during most of the year. García-Mendoza (2002) mentions four *Agave* species that occur in cloud forests: *A. ellemeeitiana* as well as *A. atrovirens*, *A. attenuata*, and *A. warelliana*. *Agave gomezpompae* Cházaro & Jimeno-Sevilla (Cházaro *et al.*, 2010), *A. graciellae* Galván & Zamudio (2013) and *A. mitis* (Gentry, 1982: 222; Alcántara & Luna, 2001; Cartujano *et al.*, 2002; all as *A. celsii* Hook.) which occur, among other vegetation types, also in cloud forests can be added, as well as as five species of the former genus *Manfreda* Salisb. and two species of the former genus *Polianthes* L., both now placed in *Agave* subg. *Manfreda* (Salisbury) Baker (Thiede, 2001): *Agave debilis* A. Berger (as *Manfreda pringlei* Rose), *A. pubescens* Regel & Ortgies [as *Manfreda pubescens* (Regel & Ortgies) Espejo & López-Ferrari], *A. scabra* Ortega (as *Manfreda scabra* (Ortega) McVaugh; all three in Castillejos Cruz 2009), *A. justosierrana* (García-Mendoza) Thiede (as *Manfreda justosierrana* García-Mendoza (2011)), and *A. umbrophila* (García-Mendoza) Thiede (as *Manfreda umbrophila* García-Mendoza (2011)), as well as *A. coetocapnia* (M. Roemer) Govaerts & Thiede (López-Pérez & al. 2011; as *Polianthes geminiflora* (Lexarza) Rose)), and the recently published *Polianthes alboaustralis* Solano & Ríos-Gómez (2014) for which a binomial in *Agave* is yet wanting. Thus, with fourteen species, agaves are much more common in cloud forests than previously thought.

The habitats give a clue on the cultivation requirements: *A. ellemeeitiana* should tolerate a higher air and soil humidity and would do better



Figure 14. *Agave ellemeeitiana* subsp. *ellemeeitiana*. Pure green leaf of a cultivated plant showing the entire leaf margin and the soft-herbaceous terminal spine.

14th May 2014; photo: Michael Greulich.

in a greenhouse for bromeliads or orchids which are frequent companions on its habitats, than in a hot desert greenhouse. *Agave ellemeeitiana* can rapidly grow into large specimens and does not necessarily need a pronounced resting period in winter; with sufficient light, it can grow almost continuously.

6. Structure of the leaf margin

Early authors (Koch, 1865a; Jacobi, 1865; Baker, 1869, 1877, 1888a, 1888b) described the leaf margin of *A. ellemeeitiana* as white, parchmenty and completely toothless. Later authors (Berger, 1915; Gentry, 1982; Cházaro *et al.*, 2012) added that the margin may sometimes be reddish and finely serrulate towards the leaf apex. Cultivated plants (Figure 14) as well as plants in habitat in Veracruz (Figure 8) and Northern Oaxaca match this description, but since the plants from both areas cannot be distinguished, it is not possible to prove that Ellemeet's original plants came from Veracruz as (indirectly) stated by Trelease (1920).



Figure 15. *Agave ellemeetiana* subsp. *subdentata* on a rock face in temporarily dry semideciduous forest 20km east of Putla (Western Oaxaca), around 2600m. The leaves of old plants are glaucous. 5th March 2010, photo: Paul Spracklin.



Figure 17. *Agave ellemeetiana* subsp. *subdentata* on volcanic rocks northeast of Putla (Western Oaxaca); one specimen showing an inflorescence with wilted flowers. 28th January 2014, photo: Bertus Spee.

28th January 2014, photo: Bertus Spee.



Figure 16. *Agave ellemeetiana* subsp. *subdentata* in habitat 20km east of Putla (Western Oaxaca); a young plant with pure green leaves. The insert shows the margin of the plants densely beset with small denticles.

5. March 2010, photos: Paul Spracklin.



Figure 18. *Agave ellemeetiana* subsp. *subdentata* on rocks northeast of Putla (Western Oaxaca); old plant with glaucous leaves. The inserts show the leaf margins of adult leaves (left) and of young, in-folded leaves (right), both densely beset with small denticles.

28th January 2014, photos: Bertus Spee.

Plants from Western Oaxaca differ in having whitish to reddish leaf margins which are finely denticulate throughout (Köhres, 2008; Spracklin, 2010; Figures 16, 18, 19 & 20). For the latter, the name *Agave ellemeetiana* var. *subdentata* Trelease in L.H.Bailey with "leaves very minutely denticulate" (Trelease, 1914: 236) is re-established here at subspecific rank.

7. Nomenclature, typification and synonymy

Agave ellemeetiana K.Koch, *Wochenschr.* 8: 103, 1.April 1865. **Holotype**: sterile plant cultivated at BG Berlin (not known to be preserved). – **Neotype** (designated here): "*Hort. Kew.* March 10, 1877, sheet 1, 2, 3" (= K000524804,

K000524803, K000524802, *teste* N.E.Brown; K digital images!) = *Agave ellemeetiana* K.Koch, *Wochenschr.* 7: 164, 28. May 1864, *nomen*.

= *Agave ellemeetiana* Regel, *Gartenflora* 14: 266, Aug. 1865 (*nom. illeg.* Art. 53.1). Type: not indicated. **Syn. nov.**

= *Agave ellemeetiana* Jacobi, *Hamburger Garten- & Blumenzeitung* 21: 457, Oct. 1865 (*nom. illeg.* Art. 53.1). Holotype: sterile plant cultivated at BG Berlin (not known to be preserved). – Neotype (designated by Gentry, 1982: 96): “*Hort. Kew.* March 10, 1877, sheet 1, 2, 3” (= K000524804, K000524803, K000524802, *teste* N.E.Brown; K digital images!). **Syn. nov.**

Typification: Since no original material was known to be preserved, Gentry (1982: 96) designated three sheets (1, 2, 3) at Kew (K) as neotype for *A. ellemeetiana* Jacobi (Gentry omitted sheet 4). All three sheets bear the same handwritten label by N. E. Brown and belong to the same specimen since “the parts are clearly labelled as being part of that same specimen” (ICN Art. 8.3, McNeill *et al.*, 2012). The same sheets are designated here as neotype for *A. ellemeetiana* K.Koch which was based on the same cultivated plant as *A. ellemeetiana* Jacobi, as exemplified above.

Etymology: Named after Jonkheer Willem Cornelis Mary de Jonge van Ellemeet (1811-1888, see Koch, 1864b; Alsemgeest, 2004), a Dutch landowner, mayor and keeper of an important agave collection on his estate “Overduin” near Oostkapelle (The Netherlands).

Characters: For more detailed morphological descriptions, see Jacobi (1865), Baker (1869), Baker (1877), Baker (1888b), Berger (1915: 125–126), Gentry (1982: 94, 96), Irish & Irish (2000: 118–119), Thiede (2001: 30), and Cházaro *et al.* (2012).

Distribution (Figure 5): Mexico: Veracruz (Sierra de Zongolica; Figures 6–8), Oaxaca (Sierra Mazateca; near San Bartolomé Ayautla, Figures 9–12; Putla/Tlaxiaco region, Figures 15–18).

Key to the subspecies of *Agave ellemeetiana*:

- Leaf margin mostly without denticles, sometimes finely denticulate towards the apex, whitish, sometimes reddishsubsp. *ellemeetiana*
- Leaf margin with denticles throughout, whitish or reddishsubsp. *subdentata*

Agave ellemeetiana K.Koch subsp. *ellemeetiana*

Diagnostic characters: Leaf margin parchmenty and mostly completely toothless, sometimes finely serrulate towards the apex, white,

sometimes reddish (Figures 8 & 14).

Distribution & habitats (Figure 5): Mexico: Central Veracruz (Sierra Madre Oriental: Sierra de Zongolica; Figures 6–8), Northern Oaxaca (Sierra Madre Oriental: Sierra Mazateca and near San Bartolomé Ayautla; Figures 9–12); on often near-vertical cliffs and rock-faces, in cloud or tropical semideciduous forests, in the cloud belt, 400–1460m; flowers February to May.

Illustrations: (hab. = habitat, inf. = inflorescence, bwpl. = black & white plate, colpl. = colour plate, bwph. = black & white photograph, colph. = colour photograph):

Baker (1869, inf. colpl. [reproduced as Figure 1]); Baker (1877, bwpl.); Baker (1888b, inf. colpl. [reproduced as Figure 2]); Berger (1915: 125–126, inf. bwph.); Anonymous (1910, inf. bwph. [reproduced as Figure 3]); Anonymous (1918, inf. bwph.); Krauss (1918, inf. bwph.); van den Houten (1930: 3, inf. bwph. [reproduced as Figure 4]); Breitung (1961: 22, bwph.); Janse (1977, bwph.); Gentry (1982: 94–97, bwph.); Kolendo (1990, bwph.); Lau (1993a, hab. colph.); Lau (1993b, hab. colph.; both as *A. attenuata*); Alsemgeest (2004, inf. colph.); Heller (2006: 82–83, colph.); Ullrich (2006, hab. colph.; as *A. attenuata* (?)); Richter (2011: 62, inf. colph.); Cházaro *et al.* (2012, hab. inf. colph.); Rivadavia (2014, hab. colph.); Reserva del Bicentenario (2014, hab. colph.).

Material studied: Ex cult., Anonymus *s.n.*, March 10, 1877 (sheets 1, 2, 3, 4 [= K000524804, K000524803, K000524802] K digital images!) (1, 2, 3 = neotype); living plant at BG Bochum.

Agave ellemeetiana* K.Koch subsp. *subdentata (Trelease) Thiede, **comb. nov.**

= *Agave ellemeetiana* var. *subdentata* Trelease in L.H.Bailey, *Stand. Cycl. Hort.* 1: 236 (1914).

Type: (not indicated). **Neotype** (designated here): ex cult., *J. Thiede* *s.n.*, 8th October 2014; from living plant raised from seed collected in Mexico, Oaxaca, between Putla and Tlaxiaco, ca. 2400m; *J. Spath & K. Griffin* *s.n.* (ZSS!) (Figure 20)

Taxonomic rank: The morphologically as well as geographically discrete populations from the Putla/Tlaxiaco region are classified as subspecies which necessitates a new combination based on var. *subdentata* Trelease.

Typification: In his short protologue (“With lvs. [= leaves] very minutely denticulate it becomes var. *subdentata*, the distinction of which from *A. pruinosa* [= *A. attenuata* ssp. *dentata* (Roehl) B. Ullrich (2007)] is not clear.”), Trelease (1914: 236) did not indicate a type. In an assessment of Trelease’s online type material, Smith & Figueiredo (2014b) did not designate a type for the name. Here, a neotype is designated from culti-



Figure 19. *Agave ellemeetiana* subsp. *subdentata*. A cultivated plant raised from seed from the Köhres collection near Santiago Nuyoó. The insert shows the leaf margin of young leaves densely beset with small denticles.

15th June 2014, photos: Michael Greulich.

vated material of the Spath & Griffin collection (Figure 20).

Diagnostic characters: Leaf margin whitish or reddish, finely, but clearly denticulate throughout (Figures 16, 18, 19 & 20). Leaves of adult plants have a distinct wax bloom (Figures 15 & 18) absent from subsp. *ellemeetiana* (Figures 7, 8 & 11) and appear to be at least sometimes broader (cf. Figure 15 with Figures 8, 11 & 13), but measurements are not available.

Distribution & habitats (Figure 5): Mexico: Western Oaxaca (Sierra Madre del Sur: Putla/Tlaxiaco region (Figures 15–18); on volcanic rocks in cloud or tropical semideciduous forests, 2300–2600m; flowers in January.

Illustrations: Köhres (2008, hab. inf. colph.); Spracklin (2010, hab. colph.); Griffin (2011, hab. colph.); Pilbeam (2013: 78 hab. colph.); all as *A. ellemeetiana*.

Material studied: Living plants raised from seed collected between Putla and Tlaxiaco (Mexico); *J. Spath & K. Griffin* s.n. (= neotype collection; Figure 20).

8. Placement and relationships – morphological data

Early agave authors (Koch, 1865a; Jacobi, 1865; Baker, 1877, 1888a, 1888b) stressed the similarity in habit and leaf structure between *A. ellemeetiana* and *A. attenuata* and placed both species as close relatives, partly together with further unarmed and soft-leaved species such as *A. sartorii* K.Koch (= *A. pendula* Schnittsp.) or even with species of *Agave* subg. *Manfreda* (Salisb.) Baker. Jacobi (1867), when studying pressed flowers of *A. ellemeetiana* he obtained from W.W.



Figure 20. Commercially offered young plant of *Agave ellemeetiana* subsp. *subdentata*, from seed collected in the Putla/Tlaxiaco region (Spath & Griffin s.n., = neotype collection). The insert shows the leaf margin of young, infolded leaves densely beset with small denticles.

22nd August 2012, photos: Joachim Thiede.

Saunders (mentioned above), noted that its nearly tubeless flowers differ much from those of *A. attenuata* with a clearly developed tube, and concluded that both species cannot be placed together. Nevertheless, one year later, Jacobi (1868) continued to place *A. ellemeetiana* closest to *A. attenuata*, together with *A. pruinosa* Lem. ex Jacobi and *A. debaryana* Jacobi (both synonyms of *A. attenuata* subsp. *dentata*; formerly known as *A. pedunculifera*; Ullrich 2007).

Berger (1915) combined floral features with leaf characters and established a section *Anoplagave* A.Berger for species with short or lacking tube and soft leaves subdivided into two subsections: *Dracontagave* A.Berger for the stem-forming, short-tubed *A. attenuata* and taxa now placed in its synonymy, and *Leptagave* A.Berger with the tubeless and stemless species *A. ellemeetiana* and *A. bracteosa* S.Watson ex Engelm. Gentry (1982)

followed a similar concept and established an informal Group *Choritepalae* for species with tubeless flowers which includes *A. ellemeetiana*, *A. bracteosa* and *A. guiengola* Gentry. I.e., over the time, agave classifications based largely or exclusively on leaf-characters (Jacobi, Baker) were replaced by systems combining floral features with leaf characters (Berger, 1915; Gentry, 1982).

The German agave specialist Bernd Ullrich (1991) suggested that *A. ellemeetiana* might represent a "garden clone" of *A. pedunculifera* (= *A. attenuata* subsp. *dentata*) only, an assumption clearly rebutted by the rediscovery of the former in habitat. Ullrich (1991) placed both species in a re-established Group *Attenuatae* Baker, together with *A. attenuata*, *A. vilmoriniana* A.Berger, *A. chrysoglossa* I.M.Johnst. and *A. ocahui* Gentry.

Data from leaf anatomy (Blunden *et al.*, 1973) and phytochemistry (steroidal saponinins; Blunden *et al.*, 1978) are inconsistent with regard to the relationships of *Agave ellemeetiana*.

9. Placement and relationships – molecular data

Gil-Vega *et al.* (2007) provide a broad assessment of relationships in agave based on molecular AFLP data for 85 accessions, including a specimen of *A. ellemeetiana* (subsp. *ellemeetiana*) from Huautla, Oaxaca, most probably representing one of the two collections cited above, as well as a specimen named "A. aff. *pedunculifera* JE s/n. Putla, Oaxaca", which most probably represents *A. ellemeetiana* subsp. *subdentata* which occurs in just that area (see above). In the resulting dendrogram, the three species of Group *Choritepalae* sensu Gentry, 1982 (*A. bracteosa*, *A. guiengola* and *A. ellemeetiana*) are placed separate from each other. *Agave ellemeetiana* subsp. *ellemeetiana* and *A. ellemeetiana* subsp. *subdentata* are placed separate, but not far from each other, between members of Group *Amolae* (*A. attenuata*, *A. nizandensis* Cutak, *A. pedunculifera* (= *A. attenuata* subsp. *dentata*), *A. vilmoriniana*, and *A. yuccaefolia* Redouté (= *A. spicata* Cav.) as well as *A. filifera* Salm-Dyck (Group *Striatae*) and *A. garciae-mendozae* Galván & L.Hern. (Group *Marginatae*). The cladogram of Gil-Vega *et al.* (2007) provides the first molecular evidence that Gentry's Group *Choritepalae* is artificial and that *A. ellemeetiana* might best be grouped together with other soft- and few-leaved species of Group *Amolae*, as suggested by Ullrich (1991).

The finding that the two accessions of *A. ellemeetiana* (i.e., subsp. *ellemeetiana* and subsp. *subdentata*) studied by Gil-Vega *et al.* (2007) are placed somewhat separated from each other might indicate that subsp. *subdentata* could possibly even merit separate specific rank. In any case, the pop-

ulations of *A. ellemeetiana* from the Sierra Madre del Sur in Western Oaxaca designated as subsp. *subdentata* here need further study of their characteristics, variability and differences from subsp. *ellemeetiana*.

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