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MONOGRAPH OF *HARRISIA* (CACTACEAE)

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ABSTRACT

The biology, taxonomy, and nomenclature are summarized for the 19 species of *Harrisia* recognized here. The genus consists of shrubs and trees native to South America, the West Indies, and Florida (USA). *Harrisia* produces large, nocturnal, ephemeral flowers and is further characterized by its distinctive seed and trichome morphology. The species of the Gran Chaco region and Brazil have the widest distributions, while the species of the Andes and Caribbean region are each confined to comparatively small areas. One species is known only from cultivation. An identification key to the 19 species and color photos, including habit and detail, are provided for all.

Harrisia comprises 19 species occurring in west-central and eastern South America, the Greater Antilles, the Bahamas, and Florida (USA), and one species is known only from cultivation (Table 1; Figs. 1–3). They are spiny, columnar cacti with elongate, indeterminate stems and large, nocturnal, ephemeral flowers. The genus is most easily characterized by its seed morphology with enlarged apical testa cells and a cavernous hilum-micropylar region (Fig. 4) as well as the scaly long trichomes on flowers and fruit areoles (Fig. 5). Within the Cactaceae, the genus is placed within subtribe Trichocereinae (sensu Nyffeler & Eggli 2010) of tribe Cereeae of subfamily Cactoideae. *Harrisia* likely originated in the east-central Andes some time around 3–7 Ma ago with the modern species forming ~0.2–1.5 Ma ago (Franck et al. 2013a, 2013b).

Two subgenera, four sections, and two series are recognized within *Harrisia* (Table 2). The southern range of *Harrisia* is represented by subg. *Eriocereus* (Fig. 1) and contains two sections. Sect. *Roseocereus* is endemic to Bolivia and contains one species, *H. tetracantha*. Sect. *Eriocereus* contains five closely related species in the Gran Chaco region (Argentina, Bolivia, Brazil, Paraguay, and Uruguay) and one known only from cultivation, *H. jusbertii*. The northern range of *Harrisia* is represented by subg. *Harrisia* and is divided into two sections. Sect. *Adscendentes* is endemic to northeast Brazil (Fig. 2) and contains one species, *H. adscendens*. Sect. *Harrisia* occurs in the West Indies (Fig. 3) and is further divided into two series. Ser. *Earlei* is monotypic containing only *H. earlei*, confined to western Cuba. Ser. *Harrisia* consists of 10 closely related species distributed in Florida and throughout the West Indies except the Lesser Antilles.

Even with the information presented here, much remains to be learned concerning *Harrisia*. Characterization of more flowers from various populations across the range of many species is needed. Some descriptions below are based on the observation of one or few flowers. Species relationships have not been fully elucidated and knowledge of them would benefit from intensive sampling for molecular analyses.

This monograph is intended to supersede and replace the draft monograph found in Chapter 4 of my dissertation (Franck 2012a). This present monograph has been extensively altered and revised from the draft in my dissertation, notably including additional information and discussions, updates, many corrected errors, and an abundance of color photographs. It should be noted that the prior dissertation (Franck 2012a) is not considered effective publication with respect to nomenclature (McNeill et al. 2012: Art. 30.8). When no person is named or no reference is given in the figure captions in this monograph, the figures and photos can be assumed to be the work of the author. Otherwise, the photographers and references are given in the captions for their respective photos and figures.

TAXONOMIC HISTORY

The earliest known references to species currently classified in *Harrisia* include those found in Sloane (1696: 197) and Trew (1751: 3, pl. 14), both as "Cereus altissimus gracilior" presumably referring to the Jamaican endemic *H. gracilis*, and the illustrations of Plumier from around the 1690s depicting *H. divaricata* (Mottram 2002). *Harrisia gracilis* was described by Philip Miller (1768, as *Cereus gracilis*) in England from specimens received in 1728 and put into the once broadly-defined genus *Cereus* Mill. s. lat." Lamarck (1785) later described *Cactus divaricatus* (=*H. divaricata*) from Plumier's plates (Burman 1758: pl. 193) illustrating a plant from Haiti. From 1837–1905, eight more names now classified in *Harrisia* were introduced: *Cereus eriophorus* Pfeiffer 1837 (=*H. eriophora*), *Ce. bonplandii* Pfeiffer 1837 (=*H. bonplandii*), *Ce. tortuosus* Otto & Dietrich 1838 (=*H. tortuosa*), *Ce. platygonus* Salm-Dyck 1849 (=*H. adscendens*), *Ce. martinii* Labouret 1854 (=*H. martinii*), *Ce. tetracanthus* Labouret 1855 (=*H. tetracantha*), *Ce. pomanensis* Weber 1897 (=*H. pomanensis*), and *Ce. guelichii* Spegazzini 1905 (=*H. pomanensis*).

Berger (1905) noted the value of the seed characters (Fig. 4) and was the first to provide the modern sense of the genus by uniting several species from the West Indies (ser. *Harrisia*) and South America (sect. *Eriocereus* and sect. *Roseocereus*) under *Cereus* subg. *Eriocereus*. Before Berger (1905), Labouret (1853), and Schumann (1899) had delimited the West Indian and South American species in unrelated infrageneric groups under *Cereus* s. lat.

Just as botanical nomenclature was beginning to be standardized in the 1900s (Nicolson 1991), the genus *Harrisia* was erected by Britton (1908), which at the time only accommodated the West Indian species (sect. *Harrisia*). Britton (1908) described five new species and made three new combinations. The earliest published species in the genus, *Cereus gracilis* (=*H. gracilis*), was selected as the type of the genus by Britton (1908). In the same year, *Cereus adscendens* (=*H. adscendens*) from the caatinga of Brazil was described (Gürke 1908). The South American species were reclassified under the genus *Eriocereus* by Riccobono (1909). In 1910, Weingart described *Cereus regelii* (=*H. regelii*) from South America. In their monograph of the Cactaceae, Britton & Rose (1920) then proceeded to unite the South American species previously placed under *Eriocereus* (Riccobono 1909) with the West Indian species of *Harrisia.* Britton & Rose (1920) also described three new species from Florida and one species from Cuba. W.T. Marshall described *Harrisia hurstii* (=*H. divaricata* or *H. portoricensis*) in 1941 and *H. nashii* var. *straminea* (=*H. divaricata*) in 1943 from the Dominican Republic. From the extreme western end of Cuba, Areces (1980) described *H. taetra*. The arborescent *H. tetracantha* from Bolivia was combined in the genus by Hunt & Taylor (1987), whereas Britton & Rose (1920: 136) had thought this species was closer to *Trichocereus macrogonus* (Salm-Dyck) Riccob. Hooten (1991, 1992) invalidly described *Harrisia donae-antoinae* (based on a specimen of *H. aboriginum*). Franck (2012b) described *H. caymanensis* from the Cayman Islands.

The systematics of sect. *Eriocereus* of the Gran Chaco region of South America were revised by Kiesling (1996) and Leuenberger (1995, 2000a, 2000b, 2001). A detailed synopsis of the one species in eastern Brazil, *Harrisia adscendens*, was provided by Taylor and Zappi (2004). Hunt et al. (2006) recognized only 1–2 species in the West Indies similar to Schumann (1899), whereas Anderson (2001) and regional floras (Areces 1980; Correll & Correll 1982; Liogier 1994; Wunderlin & Hansen 2011; Acevedo-Rodríguez & Strong 2012) used a narrower species circumscription (Table 2). Franck (2012b) revised the genus. The evolution and biogeography of *Harrisia* was studied by Franck et al. (2013a, 2013b), resulting in the recognition of infrageneric taxa (Table 1).

The recognition of *Harrisia* as a genus has been widely adopted (e.g. Small 1933; Kreuzinger 1935; Castellanos & Lelong 1938; Moscoso 1941; Leon & Alain 1953; Correll & Correll 1982; Proctor 1984; Liogier 1994; Kiesling 1996; Wunderlin 1998) and accepted by modern treatments (Anderson 2001; Hunt et al. 2006). Contrarily, Backeberg (1938; 1977) chose to recognize three genera, *Eriocereus* (= sect. *Eriocereus*), *Harrisia* (= subg. *Harrisia*), and *Roseocereus* (= sect. *Roseocereus*) while Berger (1929) and Marshall (1941) recognized only *Eriocereus* (=subg. *Eriocereus*) and *Harrisia* (= sect. *Harrisia*). Historically, *Cereus* s. lat. had been used to refer to nearly any cactus with elongate, cylindric, columnar stems and many species of *Harrisia* were once subsumed under *Cereus* s. lat. in various treatments (e.g. Urban 1910; Vaupel 1913; Fawcett & Rendle 1926; Werdemann 1931; Moscoso 1943; Little 1945; Benson 1969; Long & Lakela 1971; Wunderlin 1982). Several genera, such as *Harrisia*, have been segregated from *Cereus*, and *Cereus* s. str. now comprises ~30 species partly characterized by its radial symmetry of stamens, relatively elongate and slender hypanthium, relatively wide flower at the opening, and few widely-spaced glabrous areoles on the hypanthium and fruit (Kiesling 1975). *Estevesia* P.J. Braun had been erroneously synonymized with *Harrisia* (Nyffeler & Eggli 2010; Hernández-Ledesma et al. 2015), but *Estevesia* is likely more related to *Cereus* s. str. and *Monvillea* Britton & Rose. Like *H. martinii* or *H. tortuosa*, *Estevesia* seems to have spinose areoles on the pericarpel and hypanthium that resemble stem areoles. A total evidence analysis suggested a monophyletic *Trichocereus* (A. Berger) Riccob. requires inclusion of *Harrisia* (Albesiano & Terrazas 2012), but this concept of *Trichocereus* appears heterogeneous and polyphyletic (Schlumpberger & Renner 2012). It has also been argued that *Echinopsis* Zucc. should be expanded to include many other genera such as *Harrisia* (Anceschi & Magli 2013; Mottram 2014). Here it is opted to retain *Harrisia* as a genus, in favor of recognizing segregate genera for the revision of *Echinopsis* s. lat. (Schlumpberger 2012; Schlumpberger & Renner 2012).

The classification of *Harrisia* within subfamilial divisions of Cactaceae has changed frequently. Britton & Rose (1920) classified *Harrisia* into a broad subtribe Cereinae (as Cereanae). This classification was modified and further split, whence *Harrisia* was allied with groups containing *Nyctocereus* (A. Berger) Britton & Rose (= *Peniocereus* (A. Berger) Britton & Rose) due to their vegetative similarities (Berger 1929; Backeberg 1934, 1938; Buxbaum 1958; Backeberg 1977). Barthlott (1988) placed *Harrisia* in the tribe Echinocereeae (= Echinocereinae), apparently based on seed morphology. The genus was also once regarded as primitive in the Cactoideae subfamily (Mauseth et al. 1998; Terrazas & Arias 2003). Molecular work placed *Harrisia* in tribe Trichocereeae (Wallace 1995; Applequist & Wallace 2002), refined to subtribe Trichocereinae by Nyffeler & Eggli (2010).

CLASSIFICATION

Harrisia lies within the Cactaceae, a monophyletic family of ca. 130 genera and 1800 species. The family is part of the order Caryophyllales as demonstrated by the presence of betalains (Wohlpart & Mabry 1968) and sieve-element plastids with peripheral protein filaments (Behnke 1976, 1993). The axillary areoles, consisting of a cluster of spines, bristles, and/or hairs, are apomorphic for the Cactaceae. Most cacti stems are succulent, leafless when mature (though, the scales of the pericarpel and hypanthium are leaves, see Mauseth 2016), do not produce leaves within the areole (apart from the leaf that subtends the areole), are covered with stomata, and exhibit delayed bark formation to maintain a photosynthetic stem, with exceptions in some species of *Leuenbergeria* Lodé, *Pereskia* Mill., and *Maihuenia* (Phil. ex F.A.C. Weber) Phil. ex K. Schum. Some species of these three genera have precocious (not delayed) bark formation, lack stomata on the stems, and have persistent leaves (Leuenberger 1986; Edwards et al. 2005). Some species of *Leuenbergeria* and *Pereskia* have half-inferior ovaries and produce functional leaves within the areoles (Leuenberger 1986; Edwards et al. 2005). The flowers in cacti are considered long-shoots, as the ovary is surrouned by stem tissue (pericarpel) (Mauseth 2006b). The cactus flower typically has numerous intergrading scales (or leaves, see Mauseth 2016), “sepals”, and “petals”, as well as numerous stamens and ovules, the ovules then becoming the numerous seeds in the fruit.

With the exception of two taxa of tropical epiphytic *Rhipsalis* Gaertn. in the Old World, Cactaceae is endemic to the New World, originating ca. 35 Ma ago (Hershkovitz & Zimmer 1997; Arakaki et al. 2011), long after the Gondwanan continents South America and Africa separated from each other ca. 120 Ma ago. The succulent, photosynthetic stems of cacti are paralleled by other unrelated, cactiform species in the Old World, e.g., *Euphorbia* L., which do not exhibit areoles (Park & Jansen 2007). Cactaceae can be divided into five monophyletic subfamilies: Leuenbergerioideae, Pereskioideae, Maihuenioideae, Opuntioideae, and Cactoideae. The ribbed, columnar cacti with stem areoles subtended by a microscopic leaf (Mauseth 2007) represent subfamily Cactoideae, with approximately 1500 species in 110 genera (Nyffeler & Eggli 2010).

Cactoideae can be further divided into at least seven tribes (Korotkova et al. 2010; Nyffeler & Eggli 2010). The core Cactoideae (Hernández-Hernández et al. 2011) contains five tribes, excluding tribes Blossfeldieae and Cacteae. Blossfeldieae lacks a vascularized cortex unlike the rest of Cactoideae (Mauseth 2006a). The Cacteae seem to differ from the core Cactoideae by having flowers usually displaced from the areoles (Buxbaum 1950), often arising from between or at base of the short-shoot tubercles (or nearer to the areole in other Cacteae, e.g. *Ferocactus* Britton & Rose and *Leuchtenbergia* Hook.) and never having areoles on the flowers that resemble stem areoles. Compared to typical Cacteae, the flower shoots of core Cactoideae are shifted and arise directly from the apical portion of the areoles, similar to Opuntioideae.

The flower development (Zahra 1976) and phylogenetic position of *Calymmanthium* F. Ritter within core Cactoideae is intriguing and suggestive of two long-shoots being involved in core Cactoideae flowers. In *Calymmanthium*, a long-shoot resembling a stem elongates from the areole, apparently encasing a separate long-shoot flower bud developing within. As this stem long-shoot ceases elongating, the long-shoot flower then bursts through the stem long-shoot, and expands to expose its floral parts (e.g. stigma, anthers, “sepals,” and “petals”). If this flower development in *Calymmanthium* is homologous to flower devlepment in the rest of core Cactoideae, then it may be that one stem long-shoot tissue forms the initial outer flower bud and then becomes the elongate scaly, areolate flower tube (“hypanthium”) of core Cactoideae. Then, perhaps, a separate flower shoot with ovary, stamens, “sepals,” and “petals” develops within the stem long-shoot. These two shoots perhaps appear mostly fused in most of core Cactoideae. This development may then allow for elongate flowers with ovaries and nectaries deeply entrenched in the pericarpel, as found in many taxa of core Cactoideae. Perhaps this hypothetical specialized development of the flower requiring one shoot encased in another shoot in core Cactoideae prevents additional flowers from proliferating from the areoles of the flowers, as is sometimes found in taxa outside of Cactoideae. This, of course, is all speculative.

Within the core Cactoideae, tribe Cereeae contains globose to columnar cacti, and includes subtribe Trichocereinae (sensu Nyffeler & Eggli 2010) with ca. 250 species in 20 genera, characterized by pilose flower areoles with acute scale tips and a pericarpel and hypanthium having numerous areoles. With the exception of *Harrisia* in the West Indies and Florida, Trichocereinae is confined to South America.

SPECIES CONCEPT

A utilitarian approach (Levin 1979; Gilmour 1989) is here employed to lend taxonomic recognition to groups of individuals that share unique morphological characters, with the supposition that morphology reflects recent common ancestry. Although sampling in previous molecular analyses (Franck et al. 2013a, 2013b) was not adequate to ascertain clear relationships among many species, the relationships recovered were used to guide the taxonomic treatment. Additionally, since the possibility of paraphyly and polyphyly in traditional species concepts is considerable (Riesberg & Brouillet 1994), molecular monophyly should not be requisite for taxonomic recognition at or below the species level (Nixon & Wheeler 1990; Riesberg & Brouillet 1994), especially since phylogenetic context often relies on relatively few characters (e.g. DNA loci representing < 0.001% of the genome) taken from relatively few individuals. The polyphasic taxonomy approach (Colwell 1970) promoted in microorganisms (Vandamme et al. 1996; Samson & Varga 2009) is ideal for all organisms, including large eukaryotes, by analyzing several types of evidence to produce a classification with a minimum number of contradictions.

MATERIALS AND METHODS

Approximately 400 herbarium specimens (A, B, BRI, FLAS, FTG, G, GH, HAC, HAJB, HNT, IJ, JBSD, K, LPB, MAPR, MO, NCU, NY, P, PRE, PTBG, RSA, S, SI, US, USC, USF, UWI, ZSS) were examined to prepare the taxonomic treatment. Numerous historical illustrations were studied. Live plant photos (from G. Ardisson, K.A. Bradley, J.A. de Siqueira Fihlo, E.Y. Guerrero, P. Hughes, C. Hunter, B. Jestrow, R. Kiesling, D.A. Kolterman, J. Lodé, J. Menzel, J. Moore, M. Nee, L.J. Oakely, E. Oberg, Z. Rigerski, B. Ruthzats, K. Setzer, J. Tann, N. Taylor, A. Urquiola, R. Verdecia, M.A. Vincent, S. Woodmansee, J.P. Zegarra, S. Zona) in situ and ex situ with known provenance were also examined. Field studies in the Cayman Islands, Dominican Republic, Jamaica, and Florida were also conducted. Many taxa were cultivated in Lake Sarasota, Sarasota Co., Florida for further study.

MORPHOLOGY

Habit. Only one species forms large trees, the Bolivian *Harrisia tetracantha* (sect. *Roseocereus*). The Caribbean ser. *Harrisia* are generally erect shrubs though species can range from reclining shrubs to single-trunked small trees. The Brazilian *H. adscendens* (sect. *Adscendentes*) and sect. *Eriocereus* of the Gran Chaco region grow as reclining shrubs or scrambling thickets. A semi-epiphytic habit has been reported from the Pantanal of Brazil as *H. bonplandii* (Braun & Hofacker 2006), although the identity of the specimen is not consistent with *H. bonplandii*. The Cuban endemic *H. earlei* (ser. *Earlei*) grows as a decumbent, prostrate to pendent shrub.

Stems. The green photosynthetic stems of *Harrisia* are indeterminate long-shoots which contain numerous short-shoots. A cactus short-shoot is referred to as an areole, where the cluster of spines and trichomes arise (Figs. 6–7). The photosynthetic region surrounding and containing the areole is the tubercle, an undifferentiated combination of a modified leaf base and stem (Buxbaum 1950; Gibson & Nobel 1986). The term “stem” in cactus nomenclature thus may technically include leaf bases. Tubercles may be somewhat distinct on young stems but become amorphous on mature stems. The tubercles are vertically connected to form ribs. The number of ribs on a stem ranges from 3 to 14. The young stems of all species are generally erect to ascending but may begin to turn downwards due to the tenuous support of the stem. Stems of *H. adscendens* and sect. *Eriocereus* are often flexible and may become curvaceous. Stems of *H. tetracantha* are stout and rigidly erect and stems of sect. *Harrisia* are intermediate in rigidity and flexibility.

The surfaces of the photosynthetic stems are densely and evenly covered with stomata. The cuticle is fairly thin, 1–6 μm (Gibson & Horak 1978; Mauseth et al. 1998), and may be slightly rough (Gibson & Horak 1978). Under the cuticle is a thin epidermis (Mauseth et al. 1998; Arruda et al. 2005) with an outer surface that may be roughened (Mauseth et al. 1998). The epidermal cells of *H. adscendens* have straight anticlinal walls and parallelocytic stomata (Arruda et al. 2005). The collenchymatous hypodermis may be one cell thick in *H. martinii* (Gibson & Horak 1978) or 3–5 cells thick in other species (Mauseth et al. 1998; Arruda et al. 2005). Neither the epidermis nor the hypodermis contains crystals (Mauseth et al. 1998; Arruda et al. 2005). The palisade cortex (Fig. 8) is at least 1.5 mm thick in mature stems (Mauseth et al. 1998). Both the cortex and pith may be mucilaginous (Mauseth et al. 1998). The cortex of *H. pomanensis* is reported to be non-mucilaginous with calcium oxalate dihydrate (Hartl et al. 2007) crystal aggregates concentrated in the ribs (Gibson & Horak 1978). Mucilaginous cells and an absence of amyloplasts were observed in *H. adscendens* (Arruda et al. 2005).

In addition to the central ring of vascular bundles, the pith is vascularized with medullary bundles and the cortex vascularized with cortical bundles (Mauseth et al. 1998; Fig. 8). Medullary and cortical bundles are unique to all of subfamily Cactoideae except for the basal lineage *Blossfeldia* Werderm. (Mauseth 2006a).

Harrisia produces a hard, fibrous, lignified wood (Mauseth & Plemons-Rodriguez 1998; Mauseth et al. 1998) in the inner cortex (Schwager et al. 2013) that is longitudinally interwoven (e.g. *Franck 2370*, *2896*, *2897*, *2898*, *2899*). The wood fibers are septate (Metcalfe & Chalk 1950; Mauseth et al. 1998) and libriform (Gibson 1973; Mauseth et al. 1998). Wide-band tracheids have been observed in seedlings (Mauseth 2004) but are absent in adults (Arruda et al. 2004; Mauseth 2004). Relatively long vessel elements of the xylem have been observed (Gibson 1973) with irregularly divided, multiperforate plates (Metcalfe and Chalk 1950). The wood of *H. divaricata* has been characterized as a monomorphic fibrous wood (Stevenson & Mauseth 2004). At the stem base, plants are woodiest and produce bark from the epidermis (Mauseth et al. 1998). Heartwood is not produced and cactus wood does not undergo apoptosis (Mauseth 2006b), unlike the xylem of many other woody plants. Branch-stem junctions are often constricted in subfamily Cactoideae to increase stability (Schwager et al. 2013).

It is also a stem shoot that produces the outer tissue of the pericarpel and hypanthium (flower tube) and encases the flower within. Thus, the scales of the pericarpel and hypanthium can be considered leaves that subtend an areole (Mauseth 2016).

Roots. The base of the stem grades into one to several taproots from which arise several branches to form a fibrous root system. A ±parenchymatous monomorphic to dimorphic wood has been observed in the roots of *Harrisia divaricata* (Stevenson & Mauseth 2004).

Stem areoles. The areoles of the stem are tomentose with pellucid, septate, uniseriate trichomes (Fig. 9) and contain a cluster of spines. Long, scaly trichomes may sometimes appear on stem areoles of young long-shoots (Fig. 10). The spine clusters and trichomes arise near the adaxial base of a greatly reduced leaf. The tiny, inconspicuous leaf can be seen at the abaxial base of an areole of new stem growth near the shoot apical meristem (Britton & Rose 1920; Mauseth 2007). New growth, such as spines, trichomes, or long-shoots, may continually appear from the adaxial portion of the areoles over the life of the stem. Thus, older spines and trichomes are at the base of the areoles and newer ones near the top. Long-shoots that arise from areoles may become new stems or flowers (Fig. 11). Trichomes of the stem are usually white but newly emergent trichomes can be reddish or brownish.

Spines. The spines may be modified leaves of the axillary bud (Mauseth 2006b). Mature spines are generally gray, smooth (longitudinally striate under magnification), round to somewhat flattened basally, and dilated at the base. Newly-emergent spines are more brightly colored, varying from white to yellow-green to red, with darker or blackish tips. Young spines may become straw-colored, yellowish, or blackish before turning gray. Spine clusters at each areole consist of spines of varying lengths. Longer and thicker spines are usually produced later and the older spines at the base of the areole are often thinner and shorter. The longest and thickest spines are usually found at the base of the plant.

Flowers. The flowers are long-shoots, essentially a stem containing a flower within (e.g. *Calymmanthium substerile*). As on the stem, the flowers consist of tubercles each with an areole containing a leaf as a scale. In addition to uniseriate trichomes, the areoles of the flower usually contain semi-deciduous longer, scaly trichomes (Figs. 5, 7), which are rarely present on stems (Fig. 10). The scaly trichomes may sometimes grade into spine-like forms, especially near the base of the flower. Both types of trichomes are usually white on the flower but are sometimes reddish (e.g. *Harrisia regelii*). Areoles of the pericarpel and lower hypanthium may resemble stem areoles (having spines but no scaly trichomes) on some species of sect. *Eriocereus* (e.g. *H. martinii* and *H. tortuosa*).

The pericarpel is the tissue surrounding the ovary which matures into a fruiting structure and has areoles with scales (Figs. 12–13). The term hypanthium is here used to refer to the flower tube which contains visible areoles above the pericarpel and below the sepals (Figs. 12–13). Subtending the hairy areoles of the pericarpel and hypanthium are scales which are smallest on the pericarpel and gradually increase in size along the hypanthium, eventually grading into the larger sepals (Fig. 12). The scales and sepals are both succulent. The mid-hypanthium scales exhibit significant differences among species, and here were measured at the middle third of the hypanthium (well below the sepals and well above the pericarpel), from the tip to the base where the trichomes arise. The sepals are here defined as the non-white blades occurring after the hypanthium but may intergrade with the hypanthium scales and whitish petals. The petals are white, sometimes pinkish, very thin, and membranaceous.

Flower buds (Fig. 11) are produced on the stem areoles of the distal portions of the stem. The buds first appear as scaly protrusions which then slowly engorge to become acutely globose with densely imbricate scales. The buds then elongate, forming an incipient pericarpel and hypanthium. At maturity, the pericarpel is globose and narrows into a slender hypanthium which leads to an expanding tight cluster of 20–30 sepals and petals. The petals are only initially visible the night of anthesis. The sepals reflex backwards and the petals expand outwards (Fig. 12).

The stigma is at the center of the flower, exserted beyond the anthers in mature flowers (Figs. 12–14). The arrangement of the stamens is bilaterally symmetrical with a dense array of stamens in the lower portion of the flower (the abaxial stamen cluster and lower rim stamens) and few in the upper portion (the upper rim stamens). The rim stamens are adnate to the tip of the hypanthium and held in a ring around the inner circumference of the flower. The stamens that comprise the abaxial stamen cluster (Fig. 14) arise from the middle region of the hypanthium (Figs. 13–14) and the filaments are not sheathed together (cf. *Trichocereus*-type, Schick 2011). The filaments of both stamen types may curve upwards distally. At the basal portion of the hypanthium is the beige-colored nectar chamber (Fig. 13).

Pollen. The pollen is tricolpate (to hexacolpate?), ~50–70 μm in diameter (Kurtz 1963; Leuenberger 1976) with numerous spinulae (Figs. 15–17) (Leuenberger 1976).

Chromosomes. The karyotype of *Harrisia portoricensis* from Guayanilla, Puerto Rico has been recorded as diploid, $2n = 22$ (Spencer 1955). The base haploid number of Cactaceae is 11 with polyploidy being frequent (Ross 1981). Deviations from multiples of 11 chromosomes are extremely rare in Cactaceae (Ross 1981).

Fruits. The pericarpel matures into a yellow, orange, or red fruit containing a sweet, edible, white pulp and hundreds to thousands of tiny seeds (Rojas-Sandoval & Meléndez-Ackerman 2009c; McFadyen 2012; Fig. 18). The tubercles of the fruit are often well-defined by the sulci, especially when immature (Fig. 7). A withered flower often persists on the immature fruit (Fig. 7). The withered flower, scales, and trichomes are usually deciduous on the ripened fruit. The fruit scales are retained in *Harrisia bonplandii* and *H. jusbertii*. In sect. *Harrisia* the fruits are indehiscent, whereas in the other species the fruit splits open along lateral or apical tears, exposing the mesh of pulp and seeds (Fig. 6).

Seeds. The testa cells of the seedcoat are black, sometimes becoming reddish around the hilum-micropylar region (HMR) (Fig. 4). The testa cells are hollow and at junctures on the seed coat form pits (Gibson & Nobel 1986; Barthlott & Hunt 2000; Doweld 2001). The surface of the cells are vermiculate with striate cell junctures (Gibson & Nobel 1986; Barthlott & Hunt 2000; Doweld 2001). The top of the seed (opposite the HMR) has a curved crest of a few rows of testa cells noticeably larger (to 0.4 mm long; Fig. 4) than the rest of the seed coat (Zuccarini 1838; Barthlott & Voit 1979; Bregman 1988; Barthlott & Hunt 2000; Doweld 2001). The HMR is cavernous (Fig. 4), surrounded by the seed coat except at the bottom (Bregman 1988; Barthlott & Hunt 2000; Doweld 2001), and contains a medial sclerified band (Barthlott & Hunt 2000). The interior of the seed is composed of the embryo and endosperm (Bregman 1988). Perisperm is not evident (Bregman 1988). Each seed generally weighs ~1.5–2.0 mg (Serrano & Guzmán 1994; Alzugaray et al. 2007) and most appear to float in fresh water (pers. obs.).

Seedlings. Seedlings have a green, succulent hypocotyl to 1 cm tall, above which are two cotyledons (Zuccarini 1838; Buxbaum 1950). The cotyledons are deltoid or sometimes cleft (Ganong 1898; pers. obs.) and indistinct from the hypocotyl (Zuccarini 1838; Buxbaum 1950). The apical meristem of the epicotyl soon produces areolate tubercles (Zuccarini 1838). Ribs of seedlings are often fewer and spines more setaceous than in mature individuals. The epicotyl of *Harrisia bonplandii* reportedly first develops four ribs, then increases to eight, and finally reduces to 4–5 ribs (Ganong 1898).

ECOLOGY

Distribution and habitat. The genus ranges from the eastern Andes of Bolivia to the Gran Chaco region of south-central Argentina to the caatinga of northeast Brazil to western Puerto Rico to the Swan Islands of Honduras and up to northeast peninsular Florida (Figs. 1–3). A few species have also been naturalized in Australia (McFadyen 1986), South Africa (Henderson 2007; Shisani 2013), and Hawaii (Lorence et al. 1995). The genus is found in seasonally dry forest or shrubland. Where the species of *Harrisia* occur, the rainy season in South America is roughly Oct–Mar, and May–Oct in the West Indies and Florida. Annual precipitation is generally around 500–1200 mm. At its northern range in Florida and its southwestern range in Argentina and Bolivia, occasional freezing temperatures are experienced. Light frosts (1–2 per year) experienced by species in cultivation in Lake Sarasota, Florida, seemed well-tolerated and not detrimental. The highest elevation is experienced by *H. tetracantha* at ca. 2600 m (*Cárdenas 5021*), while some populations in the Caribbean region are near sea level and only a few meters inland from the high tide line (e.g. *H. fragrans*, *Franck 473*, *1236*).

Phenology. From the initial appearance of the flower buds, several weeks pass until anthesis occurs. Flower bud production and efflorescence seem to be dependent on temperature and rainfall. Flower bud formation in *Harrisia portoricensis* was strongly correlated with monthly mean temperature and monthly minimum temperature while efflorescence was strongly correlated with rainfall (Rojas-Sandoval & Meléndez-Ackerman 2011a). Efflorescence of *H. fragrans* was observed to have two peaks, in May and October (Rae 1995) coinciding with the beginning and end of the rainy season. Plants of *H. fragrans* in the shade rarely flowered but invested more energy in stem growth (Rae 1995), perhaps to gain access to sunnier locations. Efflorescence seems to peak after heavy rain in *H. adscendens* (Lima 2007) and in *H. tetracantha* (M. Mendoza & M. Nee, pers. comm.).

Pollination. The flowers are nocturnal and open only once, opening after sunset and remaining open until near sunrise. Kaiser and Tollsten (1995) characterized *Harrisia adscendens* as moth-pollinated due to its nocturnal anthesis and distinctly pleasant odors. Scogin (1985) identified

H. pomanensis as having a hawkmoth-pollinated syndrome as its nectar is low in energy. The flowers of *Harrisia* may also be chiropteriphilous due to the presence of clustered stamens and hexose sugars, characters amenable to pollination by the New World glossophagine bats (Fleming et al. 2009). Pollen from *Harrisia* has been reported in the stomach contents of two species of bats in Cuba (Silva Taboada 1979). Several different insects have been observed visiting flowers, including hawkmoths (Sphingidae) (*H. portoricensis*, Rojas-Sandoval & Meléndez-Ackerman 2011a), sap-feeding beetles (Nitidulidae) (*H. fragrans*, Dobson 1972; pers. obs.), long-horned beetles (Cerambycidae) (*H. fragrans*, Hutchinson & Pazara 2004), scarab beetles (Scarabaeidae) (*H. pomanensis*, *Nee 51239*), and stingless bees (Meliponidae) (*H. pomanensis*, Allier et al. 2010). Flowers appear to be self-compatible (Rojas-Sandoval & Meléndez-Ackerman 2009c; pers. obs.) and self-pollination may be assisted by the wind (Rojas-Sandoval & Meléndez-Ackerman 2011b; Rojas-Sandoval 2012).

Fruit set and consumption. Fruits take several weeks to mature, up to ~60 days after efflorescence (Rojas-Sandoval & Meléndez-Ackerman 2009c; pers. obs.) and to another ~30 days to dehisce and split open in South American species (pers. obs.). Splitting may depend on precipitation. Mature fruits can remain on the plant for months (Rae 1995; pers. obs.).

The internal pulp of the fruits of *Harrisia* is sweet, fleshy, and likely palatable to a variety of animals such as humans (pers. obs.; Fig. 18), birds (Rae 1995; Rojas-Sandoval & Meléndez-Ackerman 2009a), mice (Rojas-Sandoval & Meléndez-Ackerman 2009a), lizards (Rojas-Sandoval & Meléndez-Ackerman 2009a), crab-eating foxes (Bianchi 2009; Bianchi et al. 2013), brown-nosed coatis (Bianchi 2009; Bianchi et al. 2013), crabs (Areces-Mallea 2003), goats (Meléndez-Ackerman et al. 2008), and social wasps (Santos et al. 2007). The fruits are thought to be an important part of the diet of brown-nosed coatis in the wet season (Bianchi et al. 2013). The fruit rind is usually not consumed as it is essentially stem tissue. Seed dispersal of *Harrisia* has likely been assisted by birds (ornithochorous) and/or bats (chiropterochorous) as many populations are limited to isolated islands (i.e., West Indies). Species of the bat subtribe Stenodermatina (Chiroptera) are frugivores with distributions in South America, Central America, and the Caribbean (Dávalos 2007) and may potentially consume *Harrisia* fruits. Seed dispersal by water may also be possible (Bregman 1988).

Germination and growth. Seeds of *Harrisia* do not appear to experience much dormancy (~8 weeks, Rojas-Sandoval & Meléndez-Ackerman 2009c), as they sometimes germinate in the fruit (vivipary), e.g. in *H. eriophora* (Barrios et al. 2012), *H. fragrans* (Fig. 19), and *H. martinii* (Cota-Sánchez 2004). Vivipary may depend on the hydration of the plants (R. Kiesling, pers. comm.). Gibberellic acid and scarification by sulfuric acid have been used to increase germination (Dehgan & Pérez 2005) as well as soaking the seeds in water (L. Boehner, pers. comm. 2011). Seeds of *H. martinii* experienced maximum germination three days after sowing washed seeds (Alzugaray et al. 2007). Seeds of *H. fragrans* are viable for at least one year (pers. obs.) to 19 months (Bradley & Hines 2007). Seeds from cross-pollinated flowers were larger and germinated better than those from self-pollination in *H. portoricensis* (Rojas-Sandoval & Meléndez-Ackerman 2009c). Seeds germinate by a fissure between the HMR and upper seed coat like an operculum (Bregman & Bouman 1983). Possible functions of the cavernous HMR might be to assist in uptake and retention of water for germination or conversely to maintain an air pocket (for floating or oxygen requirements?), but neither has been studied. It could be speculated that the function of the large hollow apical testa cells is to assist in floating (R. Kiesling, pers. comm.).

Mycorrhizal arbuscles and vesicles were reported to be absent from the roots of *Harrisia fragrans* (Fisher & Jayachandran 2005), which is possibly common among cacti (Muller et al. 1994; Bashan et al. 2000). Seedlings of many cactus species benefit from nurse plants (Godínez-Álvarez et al. 2003) and nurse plant association has been implicated in species of series *Harrisia* (Rae 1995; Rojas-Sandoval & Meléndez-Ackerman 2009b; Moore 2011), with most seedlings of *H. fragrans* appearing in shade (Bradley & Hines 2007). Invasive plants have been correlated with negatively affecting the demography of *H. portoricensis* (Rojas-Sandoval 2007; Guerrero et al. 2011; Rojas-Sandoval & Meléndez-Ackerman 2012).

Vegetative reproduction is frequent when stems break and detach from the parent plant. The stems can proceed to produce roots along tissue nearest to the ground and produce a new plant. The ribs of the stem may contract during water stress. The stems (and likely the stem tissue of the flowers) function as the photosynthetic region of the plant, utilizing crassulacean acid metabolism or CAM photosynthesis, as documented in all cacti so far (Nobel 2002; Hernández-González & Villarreal 2007), with possible exceptions in *Leuenbergeria* and *Pereskia* (Rayder & Ting 1981; Edwards et al. 2005).

Herbivory. Various insects predate on the stems such as armored scale insects (Diaspididae) (Claps & de Haro 2001; pers. obs.), weevils (O'Brien 1976; McFadyen 1979a), long-horned beetles (McFadyen & Fidalgo 1976), moth larvae (McFadyen 1980), cochineal insects (Claps de Haro 2001), midges (McFadyen 2012), fly larvae (McFadyen 2012), mealybugs (McFadyen 1979b; Claps de Haro 2001), and possibly some cockroaches (*Eurycotis floridana* Walker). The mealybug *Hypogeococcus* (see Aguirre et al. 2016) has been successfully used to control invasive species of sect. *Eriocereus* in Australia (McFadyen 1986) and South Africa (Klein 1999), especially *H. martinii*. The invasive *Cactoblastis cactorum* Berg avoids *Harrisia* (Tate et al. 2009). Myxomycetes have been observed on decaying *Harrisia* (Eliasson 2004). Moth larvae (Pyralidae) consume developing fruits (McFadyen 2012; Fig. 19). One of the principal dry season foods of the Chacoan peccary may be the stems of *Harrisia* (Mayer & Brandt 1982). Exotic rhesus macaques have been observed feeding on stems of *H. portoricensis* (Brecken 2000). Introduced iguanas are reported to eat the flowers of *H. aboriginum* (Bradley et al. 2004) and gopher tortoises have been reported eating stem bases of *H. aboriginum* (Woodmansee et al. 2007). Introduced feral hogs were responsible for the death of at least one plant of *H. fragrans* (Bradley & Hines 2007).

ETHNOBOTANY

The internal flesh of the fruits of *Harrisia* are edible and used locally by humans (Fawcett & Rendle 1926; Morton 1962; Barton et al. 1990; Schmeda-Hirschmann 1994; Andrade 2002; Arenas and Scarpa 2007; Fig. 18), although they should be avoided if already visited by other animals because of the possibility of disease transmission (Martínez 2010). The flowers of *H. bonplandii* are sometimes boiled by the Ayoreo of Paraguay (*Schmeda 1185* & *1489*, Schmeda-Hirschmann 1994) and the Chorote of Argentina (*Scarpa 562*, Arenas and Scarpa 2007). The boiled or roasted roots of sect. *Eriocereus* are sometimes eaten (Scarpa & Arenas 2002). Decoctions of the roots of *H. adscendens* are used medicinally (Andrade et al. 2006; Agra et al. 2007; Rocha & Agra 2011). *Harrisia pomanensis* has been used for forage (Palacio et al. 2011). Use of the flowers and stems of *Harrisia* in homeopathy has been reported (Waizel-Bucay 2009). The dried woody stem of *H. gracilis* was said to be used as a torch, which baited fish for harpooning when held out from the canoe (Edwards & Lindley 1818; Fawcett & Rendle 1926). Descourtilz (1821: 281–284) described its use as a torch and the cautious use of the juice of the stem of *H. divaricata* in vinegar or castor oil topically as a depilatory and against toothache, warts, and ringworm fungi. Slats for mango crates were said to be sometimes made from *H. divaricata* (Curtis 1947).

CHEMISTRY

The *n*-alkane content of the cuticular wax was relatively high in *Harrisia tetracantha*, composed of a fairly even distribution of C_{18}–C_{34} and C_{36} *n*-alkanes (Maffei et al. 1997). The *n*-alkane content of *H. martinii* has been reported as dominant in C_{37} with significant fractions of C_{33}, C_{35}, and C_{39} (Herbin & Robins 1968). Presumably, the wax is biosynthesized from fatty acids and is partly responsible for the low epidermal absorbance of water (Barthlott & Capesius 1974). Alkaloids have been reported from species of *Harrisia* in Cuba (Martínez 1995), possibly similar to the phenylpropanoid alkaloids tyramine and hordenine which are common in the related genus *Echinopsis* s. lat. as well as other species of subfamily Cactoideae (Agurell 1969; Agurell et al. 1971). The toxicity of *Harrisia* was rated as relatively low (Levin & York 1978). The sap of *H. gracilis* is very dilute, in accord with other succulents (Harris & Lawrence 1917).

Monoterpenes (geraniol, geranial, and neral) and a phenylpropanoid (methyl benzoate) have been identified from the flowers of *Harrisia adscendens* (Kaiser & Tollsten 1995). Scogin (1985) found the flowers of *H. pomanensis* to have hexose as the dominant nectar sugar.

Betacyanin pigments (tetrahydropyridine-dihydroindole glycosides) have been characterized in the fruit of *Harrisia bonplandii*, with the total betacyanin content being 41% phyllocactin, 23% betanin, 18% isobetanin, and 18% isophyllocactin (Piattelli & Imperato 1969, as *H. guelichii*). Seeds of *H. pomanensis* are composed of ~11% protein, ~8% water ~2% ash, and a relatively low oil content (~15%) (Serrano & Guzmán 1994). The majority of the oil is 18:2 (62%) with significant amounts of 18:1 (21%) and 16:0 (13%) (Serrano & Guzmán 1994). The highest mineral content was, in descending order, potassium, magnesium, calcium, and sodium (Serrano & Guzmán 1994). Polyacrylamide gel electrophoresis of seed protein patterns of *H. pomanensis* have been compared to other cacti (Carreras et al. 1997). Caffeine has been reported in the seeds of *H. adscendens* (Friese 1935; see also Christenhusz 2008), though this is considered doubtful until corroborated.

PHYLOGENY

The monophyly of *Harrisia* and its infrageneric classifications are supported by molecular phylogenies and morphology (Schlumpberger & Renner 2012; Franck et al. 2013a). The generic relationships of *Harrisia* within subtribe Trichocereinae show a sister-group relationship with *Leucostele* Backeb. based solely on plastid data (Schlumpberger & Renner 2012; Franck et al. 2013a), while data from nuclear loci do not yet corroborate this relationship (Franck et al. 2013a). Species within sect. *Eriocereus* are very closely related (Franck et al. 2013a) and the same is true for the species of sect. *Harrisia* (Franck et al. 2013a, 2013b). Interspecies relationships in these two sections are difficult to assess and probably represent recent radiations (Franck et al. 2013a).

The monotypic ser. *Earlei* is supported as basal in sect. *Harrisia* (Franck et al. 2013a, 2013b). Within ser. *Harrisia*, three main groups emerge from molecular analyses (Franck et al. 2013b). The "Cuba group" comprises all the Cuban species of ser. *Harrisia* (*H. eriophora*, *H. fernowii*, *H. taetra*). The "Florida group" consists of both Florida species (*H. aboriginum* and *H. fragrans*). The "SEGAB group" contains all non-Cuban and non-Florida species (*H. brookii*, *H. caymanensis*, *H. divaricata*, *H. gracilis*, *H. portoricensis*). The "SEGAB group" may also contain or be most related to *H. fernowii* from southeast Cuba (Franck et al. 2013b), having relatively small seeds and flowers that are predominantly greenish.. Morphology suggests the Florida group is most closely related to *H. eriophora* and *H. taetra* from west Cuba, which all share fairly large seeds and flowers with reddish coloration (Franck et al. 2013b).

CHARACTER EVOLUTION

The best-defined apomorphy for *Harrisia* is the cavernous hilum-micropylar region of the seed (Fig. 4). The scaly trichomes of the flower (Fig. 5) also appear apomorphic in *Harrisia*, though it is speculative without having adequate knowledge of flower trichomes in the rest of Trichocereinae (e.g., *Leucostele*). Characters of the Bolivian *H. tetracantha* such as its many-ribbed, thick, erect stems may be plesiomorphic as these stems are common in subtribe Trichocereinae. Slender stems, few ribs, and flexible stems may then be apomorphic or homoplasious, being quite rare in subtribe Trichocereinae. If *Harrisia* is sister to the arborescent *Leucostele*, as suggested by the plastid data

(Schlumpberger & Renner 2012; Franck et al. 2013a), then arborescence may be a plesiomorphic feature in *H. tetracantha*.

Reduction in rib number may have occurred twice, with sect. *Eriocereus* and ser. *Earlei*. Splitting or dehiscing fruits are likely plesiomorphic, as they are present in three sections of *Harrisia* and absent in sect. *Harrisia*. Stigma lobes are relatively long, plesiomorphic in three sections of *Harrisia*, and reduced in sect. *Harrisia*. Yellow fruits are apomorphic, rare in sect. *Adscendens* and common in sect. *Harrisia*. The reappearance of red fruits in two Florida species in ser. *Harrisia* is possibly a reversion to the ancestral red fruits or homoplasious. Seeds are relatively large in sect. *Adscendens*, ser. *Earlei*, the west Cuban species, and the Florida species. The smaller seeds in some species of ser. *Harrisia* appear to be derived. The flower scales in subg. *Eriocereus*, sect. *Adscendens*, and ser. *Earlei* are usually reddish and the green to yellow-green scales in some species of ser. *Harrisia* are probably derived. Except for *H. bonplandii*, *H. jusbertii* and perhaps *H. regelii*, all species have ribs distinctly separated by a line at the sulcus.

BIOGEOGRAPHY

Diversification. Because of the high diversity and endemism of Cactaceae in the central Andes, sympatric with *Harrisia tetracantha*, the genus is presumed to have originated in the central Andes (Wallace 1997; Franck et al. 2013a). Its dispersal into Brazil from the central Andes would then match the distribution patterns of many other cacti (Franck et al. 2013a). Its diversification in the Gran Chaco (sect. *Eriocereus*) and in the West Indies and Florida is presumed a recent event in the Pleistocene (Franck et al. 2013a). Sect. *Harrisia* is disjunct from the Brazilian sect. *Adscendentes*. The colonization of the West Indies probably occurred by dispersal from Brazil to west Cuba (Franck et al. 2013a).

Range. Most species of *Harrisia* are narrow endemics, except for sect. *Eriocereus* of the Gran Chaco and *H. adscendens*, which have larger ranges. Given the narrow range of many species, it is likely that the distribution of *Harrisia* has repeatedly expanded and shrunk in response to climatic alterations of arid habitat. The climate was cooler and more arid 0.7–1.2 Ma ago (Clark et al. 2006), near the estimated dispersal of *Harrisia* into the Gran Chaco and West Indies (Franck et al. 2013a). Numerous cycles of increasing and decreasing aridity throughout the Pleistocene (Johnson 1982) are indicated by various regional studies from South America (van der Hammen 1974; Leyden 1985; Oliveira et al. 1999; Strecker et al. 2007; Werneck et al. 2011), nuclear Central America (Leyden 1984; Leyden et al. 1994), Jamaica (Street-Perrott et al. 1993), Haiti (Hodell et al. 1991), and Florida (Watts 1975; Grimm et al. 1993).

OFT-CONFUSED TAXA

Several genera of cacti are often misidentified as *Harrisia*. Besides seed and flower trichome morphology, the easiest characters to discern *Harrisia* are the presence of the abaxial stamen cluster, pilose areoles that are moderately densely arranged on the hypanthium and fruit, a tuberculate immature fruit, and the lack of aerial roots. Below is a list of commonly confused genera of cacti and examples of characters which differentiate them from *Harrisia*.

Acanthocereus (Engelm. ex A. Berger) Britton & Rose, stamens arranged radially symmetrical.
Cereus Mill., hypanthium areoles without conspicuous hairs, hypanthium and fruit with sparsely arranged areoles.
Hylocereus (A. Berger) Britton & Rose, stems with aerial roots.
Leptocereus (A. Berger) Britton & Rose, stamens arranged radially symmetrical
Monvillea Britton & Rose (=*Praecereus* Buxb.), hypanthium areoles without conspicuous hairs, hypanthium and fruit with sparsely arranged areoles.

Peniocereus (A. Berger) Britton & Rose, (=*Nyctocereus* (A. Berger) Britton & Rose), stamens arranged radially symmetrical.
Selenicereus (A. Berger) Britton & Rose, stems with aerial roots.
Stenocereus (A. Berger) Riccob., e.g. misidentified as *Harrisia* in Christenhusz (2008), stamens arranged radially symmetrical.

HERBARIUM SPECIMEN RECOMMENDATIONS

Well-made herbarium specimens greatly enhance the study of *Harrisia*, though spiny and bulky succulents like *Harrisia* are often neglected by herbarium personnel in the field. To make herbarium specimens of *Harrisia*, it is ideal to have mature flowers, fruits, a cutting of the apical stem, and whole areoles with spines from the base of the plant.

Healthy, vigorous shoots are often most diagnostic for exemplifying stem morphology. Length-wise sections of the stem help to retain their shape by decreasing rib contraction during pressed drying. A cross-section of the stem enables the easiest determination of rib number. Areoles from basal portions of the stems or trunk should be collected as they are diagnostic and often contain the longest and thickest spines. Stems, flowers, and fruits should be cut length-wise so that both sides can be viewed. The exterior of the stem, flower, and fruit is most informative for species identification. Some pollen can be packeted before mounting and the stigma can be protruded from the flower. The flower petals and pollen are extremely susceptible to insect damage, e.g. by book lice (*Liposcelis* Motschulsky) (Retief et al. 1995). To attempt to retain fruit dimensions and shape, seeds and pulp should be removed from a halved fruit. Color photographs can be included with the specimen, as they are informative of plant habit, shape, and color, all of which are easily lost from herbarium specimens.

TAXONOMY

Journal abbreviations follow Bridson et al. (2004), book abbreviations follow Stafleu et al. (1976–1988), author abbreviations follow Brummitt & Powell (1992), and herbarium acronyms follow Thiers (2016).

HARRISIA Britton, Bull. Torrey Bot. Club 35: 561. 1908. *Cereus* [unranked as “Gruppe”] *Eriophori* Vaupel in Engler, Nat. Pflanzenfam. ed. 2: 637–638. 1925 [fide Mottram 2014]. *Harrisiae* Buxb. [unranked as “linea”], Madroño 14: 182. 1958. **TYPE**: *Harrisia gracilis* (Mill.) Britton.

Columnar, succulent shrubs or trees. Bark smooth to slightly flaking. Stems green to glaucous-green, pendent, prostrate, decumbent, arching, reclining, clambering, ascending, or erect, occasionally falling over and rerooting, with 3–14 ribs; elongate, indeterminate, basally becoming woody. Stem sulci usually defined by a sinuous line, occasionally absent. Spines 3–20 on stem areoles, smooth, straw-colored to gray, microscopically striate longitudinally, subulate, round to somewhat flattened basally, to 8 cm long and 1.8 mm thick, fewest on distal areoles and becoming more numerous on basal areoles of stems. Young spines white to yellow to red to nearly black with darker tips. Stem areoles tomentose with short septate, uniseriate trichomes to 1.5 mm long. Tiny leaves evident on tips of vigorous shoot apical meristems, deltoid, 0.5–1.1 mm long. Flower buds globose, ovoid, or obovoid, usually hairy with scaly trichomes. Flowers lateral and distal on stems, 14–26 cm long and 8.5–16.5 cm wide, nocturnal, open only once. Pericarpel and hypanthium areoles villous to pilose with scaly trichomes, 2.5–12 mm long, sparse to copious, persistent to deciduous; trichomes sometimes grading into spines. Pericarpel green to purplish red, with deltoid to lanceolate scales, green to brown to red. Hypanthium green to brown to red, scales green to brown to red, rounded-truncate and somewhat erect basally, deltoid to lanceolate, acute to subulate at the tip. Sepals green to brownish to reddish, linear, acute. Petals white, rarely pinkish, ovate with slender limb, apiculate, margins roughened-entire to irregularly denticulate. Stamens adnate to inner hypanthium, filaments straight or often upcurved, arrangement bilaterally symmetrical, ca. 100 stamens concentrated in the lower region of the flower, ca. 50 sparsely arranged in upper ring. Filaments basally light green to white distally. Anthers beige. Pollen spherical, tricolpate (to hexacolpate?), covered with numerous spinulae, sulci very shallow. Pistil exserted beyond to sometimes level with the anthers, style light green to white, stigma 10–15 lobed, fimbriate. Fruits yellow to red, 3.5–8 x 3.5–8 cm, depressed globose to spherical to ellipsoidal, with hundreds to thousands of seeds, pulp white and sweet. Seeds black, oblong rectangular to squarish to clam-shaped, 1.3–2.4 x 1.8–3.35 mm (measured near the middle of their dimensions), hilum-micropylar region cavernous, apical margin testa cells enlarged.

Distribution. One species is restricted to the inter-Andean valleys of southeast Bolivia, five species occur in the Gran Chaco region of South America (Argentina, Bolivia, Brazil, Paraguay, and Uruguay), one species is found in the caatinga of northeast Brazil, and 11 species occur in the West Indies (Greater Antilles, Bahamas, southern coastal Florida) (Figs. 2–4); also naturalized in Australia, South Africa, and Hawaii; one species is known only from cultivation. 0–2600 m.

Etymology. For William Harris (1860–1920), of Scottish descent, resident botanist of Jamaica 1881–1920 (Johnson 1921).

Discussion. *Harrisia* is characterized by seeds with a cavernous hilum-micropylar region and enlarged apical testa cells (Fig. 4), scaly long trichomes (2.5–12 mm long) on the reproductive areoles (Fig. 5), large nocturnal flowers (14–26 cm long) with a cluster of stamens in the lower (abaxial) portion (Figs. 12–14), yellow to red fruits with hundreds of seeds and a sweet pulp (Fig. 18), and stems that do not put out adventitious roots (unless the stems are fragmenting and/or in contact with the ground). *Harrisia* is here divided into two subgenera, four sections, and two series. The main purpose in establishing these infrageneric taxa is to emphasize two speciose groups: the 6 shrubby to clambering species native to the Gran Chaco region (sect. *Eriocereus*) and the 10 shrubby species native to the West Indies (ser. *Harrisia*). In the original publication of *Harrisia* (Britton 1908), *H. gracilis* was explicitly cited as the type of the genus (Britton 1908: 563), contrary to the later typification cited by Mottram (2014).

Key to species of *Harrisia*

1. Seed length and width subequal, differing by < 0.5 mm, semi-lustrous (subg. *Eriocereus*).

  2. Trees, with a well-developed central trunk; stems mostly stiffly erect; ribs 7–9; fruits narrowly apically dehiscent (sect. *Roseocereus*); Bolivia .... **1. Harrisia tetracantha**
  2. Shrubs, trunk poorly developed or absent; stems erect, curvaceous, arching, scrambling, clambering, or prostrate; ribs 3–8; fruits widely & laterally dehiscent (sect. *Eriocereus*).

    3. All spines of mature stems short, to 5 mm long; known from cultivation only .... **3. Harrisia jusbertii**
    3. One to several spines of mature stems long, to 2–5 cm long.

      4. Most areoles with the radial spines appearing greatly reduced in length compared to the central spine(s), with the 1–4 central spines 1.5–2 times as long as most radials spines; ribs mostly 3–5, often strongly undulate with areoles on pronounced tubercles.

        5. Pericarpel and lower hypanthium areoles unlike stem areoles, with reddish scaly hairs and without spines; mid-hypanthium scales 7.9–11.5 mm long; fruit without spines (spines rare on flower or fruit); Argentina .... **6. Harrisia regelii**

5. Pericarpel and lower hypanthium areoles resembling stem areoles, often with spines, tufts of uniseriate trichomes, and without scaly hairs; scaly hairs white; mid-hypanthium scales 2.7–4.9 mm long; fruit usually with spines; Argentina, Paraguay .... **4. Harrisia martinii**

4. Most areoles with spines of relatively similar length, with the central spines less than 1.5–2 times as long as most radial spines; ribs 3–7, shallowly undulate with areoles on slightly pronounced tubercles.

6. Sulcus undefined, no line between ribs; ribs 3–5, often sharply angular; scales of mature fruit persistent and concolorous; Argentina, Bolivia, Brazil, Paraguay .... **2. Harrisia bonplandii**
6. Sulcus evident as line between ribs; ribs 4–8, often rounded; scales of mature fruit usually withering-deciduous and discolorous, occasionally persistent and red.

7. Ribs 4–6; pericarpel areoles without spines, unlike stem areoles; mid-hypanthium scales 13.6–18.3 mm long; fruit not spiny; Argentina, Bolivia, Paraguay .... **5. Harrisia pomanensis**
7. Ribs 6–8; pericarpel areoles resembling stem areoles, often with spines and tufts of uniseriate trichomes; mid-hypanthium scales 5.7–7.6 mm long; fruit often spiny; Argentina, Paraguay, Uruguay .... **7. Harrisia tortuosa**

1. Seeds oblong, > 0.5 mm longer than wide, lustrous (subg. *Harrisia*).

8. Stigma lobes 1.2–2 cm long; fruits dehiscent; stem glaucous-green to green (sect. *Adscendentes*); Brazil .... **8. Harrisia adscendens**
8. Stigma lobes 0.3–1.0 cm long; fruits indehiscent; stem green (sect. *Harrisia*).

9. Ribs 5–7; newly emergent spines bright red to dark red; decumbent, prostrate to pendent shrub (series *Earlei*); Cuba .... **9. Harrisia earlei**
9. Ribs 8–14; newly emergent spines white to yellow to brown, any reddish coloration faint; erect to reclining shrub (series *Harrisia*).

10. Spines similar on distal and basal areoles of stem (spines rarely longer and thicker on basal trunk areoles of *Harrisia gracilis*), spines of basal areoles not overlapping spines of adjacent areoles; longest spines < 3.5 cm long; fruit globose.

11. Pericarpel, hypanthium, and scales green to yellow-brown, without pink or red; mid-hypanthium scales 11.6–12.8 mm long; seeds 1.3–1.6 × 2.1–2.3 mm; Jamaica .... **17. Harrisia gracilis**
11. Pericarpel, hypanthium, and/or scales with pink or red; mid-hypanthium scales 4.5–10.3 mm long; seeds 1.7–2.0 × 2.7–3.0 mm.

12. Scales 7.0–10.3 mm long at mid-hypanthium; pericarpel and immature fruit purple to reddish green; mature fruit orange to red, rarely yellow; spines to 3.5 cm long; Florida .... **16. Harrisia fragrans**
12. Scales 4.5–8.0 mm long at mid-hypanthium; pericarpel and immature fruit green; mature fruit yellow (immature fruit sometimes orange); spines to 1.5 cm long; Florida .... **10. Harrisia aboriginum**

10. On basal areoles of stem, spines longer and thicker, usually spreading and ..overlapping spines of adjacent areoles; longest spines 3–12 cm long; fruit globose to ellipsoidal.

13. Longest spines (usually on basal areoles) 3–3.5 cm; mature fruit oblong, ellipsoidal; seeds 1.55–1.7 × 2.65–2.85 mm; Bahamas .... **11. Harrisia brookii**
13. Longest spines (usually on basal areoles) > 5 cm; mature fruit globose to ovate (rarely ellipsoidal); seeds 1.4–2.2 × 2.0–3.35 mm.

14. Most seeds 1.7–2.2 × 2.6–3.35 mm; sepals or upper scales purplish to reddish; mid-hypanthium scales 5.4–8.7 mm long.

15. Stem nearly inaccessible, spines densely crowded and overlapping;hypanthium and lower scales purplish to reddish; Cuba .... **19. Harrisia taetra**
15. Stem accessible, spines fairly sparse or moderately overlapping; hypanthium and lower scales green; Cuba .... **14. Harrisia eriophora**

14. Most seeds 1.4–1.7 × 2.0–2.8 mm; sepals and upper scales green to yellow-green to brown-green; mid-hypanthium scales 8.5–15.0 mm long.

16. Flowers to 15 cm long; mid-hypanthium scales 8.5–10.0 mm long; longest spines (usually on basal areoles) 0.7 mm thick; Cayman Islands, Swan Islands(?) .... **12. Harrisia caymanensis**
16. Flowers 16.5–21 cm long; mid-hypanthium scales 8.6–15.0 mm long; longest spines (usually on basal areoles) 1.0–1.2 mm thick.

17. Hypanthium scales ovate to ovate-lanceolate, faintly arched at base; immature fruit without well-defined sulci, moderately tuberculate; Cuba .... **15. Harrisia fernowii**
17. Hypanthium scales ovate-lanceolate, strongly arched at base; immature fruit strongly tuberculate with well-defined sulci.

18. Spines fairly sparse or moderately overlapping, stem accessible; mid-hypanthium scales 11–13.1 mm long; Hispaniola .... **13. Harrisia divaricata**
18. Spines densely crowded and overlapping, stem nearly inaccessible due to spines; mid-hypanthium scales 8.6–9.8 mm long; Hispaniola(?), Puerto Rico .... **18. Harrisia portoricensis**

I. HARRISIA subg. ERIOCEREUS (A. Berger) A.R. Franck, Syst. Bot. 38: 218. 2013. *Cereus* Mill. [unranked as "Reihe"] *Tortuosi* K. Schum., Gesamtbeschr. Kakt. 54, 135. 1899. *Cereus* Mill. subg. *Eriocereus* A. Berger, Rep. (Ann.) Missouri Bot. Gard. 16: 74. 1905. *Eriocereus* (A. Berger) Riccob., Boll. Reale Orto Bot. Palermo 8: 238. 1909. *Harrisia* Britton [unranked] *Eriocereus* (A. Berger) Britton & Rose. Cact. 2: 148. 1920. **TYPE**: *Harrisia tortuosa* (J. Forbes ex Otto & A. Dietr.) Britton & Rose.

Shrubs or large trees. Stems arching, reclining, clambering, ascending, or erect, 3–9 ribs. Spines to 4.6 cm long and 1.7 mm thick. Newly emergent spines yellow-green to red. Seed length and width subequal, 1.7–2.2 × 1.8–2.5 mm.

One species in the Eastern Cordillera of Bolivia and five species in the Gran Chaco region of southeast Bolivia, north Argentina, Paraguay, southwest Brazil, and west Uruguay (Fig. 1), and naturalized in Australia, South Africa, and Hawaii; scrub forest and scrubland; 50–2600 m.

This subgenus is defined by its seeds having a nearly equal length and width. Berger (1905) unambiguously designated the type of *Cereus* subg. *Eriocereus*, though Hunt et al. (2006) referred to Backeberg (1960) as typifying the name. Although Britton & Rose (1920) included a partitioned group *Eriocereus* under *Harrisia*, they did not clarify any rank (as they had done for infrageneric names of other genera like *Cereus* and *Opuntia*) and are not considered to have made the subgeneric combination for *H.* subg. *Eriocereus*.

Ia. HARRISIA sect. ROSEOCEREUS (Backeb.) A.R. Franck, Syst. Bot. 38: 218. 2013. *Roseocereus* Backeb., Blätt. Kakteenf. 1938–6. 1938. **TYPE**: *Harrisia tetracantha* (Labour.) D.R. Hunt.

1. Harrisia tetracantha (Labour.) D.R. Hunt, Bradleya 5: 92. 1987. *Cereus tetracanthus* Labour., Rev. Hort. (Paris) 4: 25. 1855. *Eriocereus tetracanthus* (Labour.) Riccob., Boll. Reale Orto Bot. Palermo 8: 244. 1909. *Trichocereus tetracanthus* (Labour.) Borg, Cacti: a gardener's handbook for their identification and cultivation 137. 1937. *Roseocereus tetracanthus* (Labour.) Backeb., Jahrbücher der Deutschen Kakteen-Gesellschaft, 30. 1942. *Echinopsis tetracanthus* (Labour.) Anceshi & Magli, cactusinhabitat 40. 2013. **NEOTYPE** (Franck 2012b): **Bolivia**. Santa Cruz Dept., [Manuel María] Caballero Prov., NE of Abra de Quiñe, shrubland, upper limit of arid woodlands, 31 Dec 1995, *Nee 46674* (NY; isoneotypes: LPB, MO, USZ).

Cereus tetracanthus var. *boliviana* F.A.C. Weber ex K. Schum., Gesamtbeschr. Kakt. 81. 1899. *Cereus bolivianus* (F. A. C. Weber ex K. Schum.) F. A. C. Weber ex K. Schum., Monatsschr. Kakteenk. 12: 21. 1902. *Eriocereus tetracanthus* (Labour.) Riccob. var. *bolivianus* (F. A. C. Weber ex K. Schum.) Backeb., Kaktus-ABC 179. 1936. *Trichocereus tetracanthus* (Lab.) Borg var. *boliviensis* (F. A. C. Weber ex K. Schum.) Borg, Cacti: a gardener's handbook for their identification and cultivation 137. 1937. **TYPE**: **Bolivia**. [Cochabamba Dept.], Cochabamba.

Tree to 6 m. Stems erect, ribs 7–9. Upper stems 3–5 cm wide, lower woody stems to 15 cm wide, basal trunk to 30 cm wide. Flowers 17–21 cm long. Pericarpel green. Hypanthium green. Mid-hypanthium scales 3.8–5.3 × 7.8–10.3 mm. Scales deltoid to deltoid-ovate, red to reddish green apically, green basally. Sepals brownish green. Fruit tearing apically. Figs. 4, 20–22.

Distribution. Eastern Cordillera of the Andes, Bolivia (Fig. 1); seasonally dry scrub forest of inter-Andean valleys; 1200–2600 m.

Specimens examined. **BOLIVIA**: COCHABAMBA DEPT.: San Pedro [Tarata?], *Cárdenas 5021* (US); Esteban Arce Prov., Tiataco, *Kamm s.n.* (USF). SANTA CRUZ DEPT.: Florida Prov.: Pampa Grande, *Nee & Vargas C. 44709* (MO, NY); Pampa Grande, *Rente 12* (ZSS). Manuel María Caballero Prov.: Comarapa, *Nee 46559* (MO, NY); Saipina, *Nee et al. 53697* (NY). Vallegrande Prov.: Torrecilla Río Mizque, *Betancur et al. 83* (MO). **CULTIVATED** (origin unknown): *Schumann 80* (NY); 27 Jun 1904, *Schumann s.n.* (NY); 30 Jul 1904, *Schumann s.n.* (NY); 17 Aug 1904, *Schumann s.n.* (NY); *Franck 2262, 2898* (USF).

Etymology. The protologue states that the areoles from the top to the bottom increase in the number of spines by four. The epithet has previously been suggested to mean spines in four series or that it is a misspelling of 'tephracanthus,' intended as ashy-spined (Hunt & Taylor 1987).

Discussion. *Harrisia tetracantha* is an arborescent species that consequently has the thickest trunk and constitutes the largest singular plants (with one root system) in *Harrisia*. In its native region, the most prolific flowering times seem to coincide with the peak of the wet season in December and January. The species may be well adapted to disturbance, apparently common in cleared forests with *Cleistocactus parviflorus* (K. Schum.) Gosselin (Barra Ricáldez 1998). The original material for the description in the protologue was said to be from Chuquisaca [Sucre], Bolivia from seeds supplied by Jacques Philippe Martin Cels, but no extant original material is known.

Ib. HARRISIA sect. ERIOCEREUS

Shrubs. Stems clambering, ascending, or erect, ribs 3–7. Flower buds white to reddish hairy. Pericarpel green. Hypanthium green to pinkish green. Scales deltoid to deltoid-subulate. Sepals brownish green. Fruits, tearing at sides to expose inner pulp and seed.

Five species in the Gran Chaco region (Fig. 1) and naturalized in Australia, South Africa, and Hawaii; chaco serrano, chaco arido, chaco semi-arido, chaco humedo, espinal, pantanal, pampeana; 50–1200 m; one species known only from cultivation.

This group of species is characterized by a clambering to shrubby habit with green stems, and few (3–8) ribs. In their native region, most flowering plants seem to occur during the wet season from Oct–Mar.

2. Harrisia bonplandii (Parm. ex Pfeiff.) Britton & Rose, Cact. 2: 157. 1920. *Cereus bonplandii* Parm. ex Pfeiff., Enum. Diagn. Cact. 108. 1837. *Eriocereus bonplandii* (Parm. ex Pfeiff.) Riccob., Boll. Reale Orto Bot. Palermo 8: 238. 1909. *Harrisia pomanensis* (F.A.C. Weber ex K. Schum.) Britton & Rose subsp. *bonplandii* (Parm. ex Pfeiff.) Braun & Esteves, Succulenta (Netherlands) 73: 131. 1995. **NEOTYPE** (Kiesling 1996): **Argentina**. Formosa Prov., Pilcomayo Dept., Parque Nacional Pilcomayo, 14 Dec 1988, *Guaglianone & Múlgura 2228* (SI; isoneotype: B).

Cereus acutangulus Pfeiff., Enum. diagn. Cact. 107. 1937. **NEOTYPE** (Leuenberger 2001): cult. hort. Berol., 9 Feb 1983, *Schwerdtfeger 15056* (neotype: B).

Cereus balansae K. Schum., Fl. bras. 4: 210. 1890. *Harrisia balansae* (K. Schum.) N. P. Taylor & Zappi, Cactaceae Consensus Init. 3: 7. 1997. **LECTOTYPE** (Kiesling 1996): **Paraguay**. Asunción, dans le forest, *Balansa 2504* (G; isolectotype: K, P). Holotype: B, destroyed]

Cereus guelichii Speg., Anales del Mus. Nac. Buenos Aires 11: 482. 1905. *Eriocereus guelichii* (Speg.) A. Berger, Kakteen 130. 1929. *Harrisia guelichii* (Speg.) Britton & Rose, Cact. 2: 158. 1920. **LECTOTYPE** (Kiesling 1996): Britton & Rose, Cact. 2: 158, Fig. 228. 1920. (isolectotype: NY, photo at NY is mounted along with 3 other photos presumably of same plant, “Chaco, Argentina, *Spegazzini*, Rec’d 1915”).

Cereus pomanensis F.A.C. Weber ex K. Schum. var. *grossei* Weing. ex A. Berger, Kakteen 128. 1929.

Stems green. Ribs not tuberculate, 3–5, indistinct with no demarcating line at sulcus. Spines of similar length. Pericarpel and lower hypanthium areoles not similar to stem areoles. Flowers 17–24 cm long. Pericarpel green. Hypanthium light green, scales lanceolate to subulate, red-brown to green basally, with reddish hairs. Mid-hypanthium scales 3.1–4.3 × 12.4–18.2 mm. Sepals brownish green to green. Fruits without spines, retaining scales. Figs. 23–25, 85.

Distribution. Southeast Bolivia, north Argentina, and Paraguay (Fig. 1), and naturalized in Hawaii and South Africa; chaco serrano, chaco árido, chaco semi-árido, chaco húmedo, espinal, pantanal; 80–900 m (*Nee 51221*).

Specimens examined. **ARGENTINA**. BUENOS AIRES PROV.: La Plata, *Rose & Russell 21095* (US) (probably from cultivation, R. Kiesling, pers. comm.). CORRIENTES PROV.: Estancia Santa Teresa, *Pedersen 3083* (A, S, US); Teniente Ochoa, *Schinini & Palacios 25594* (G). TUCUMÁN PROV.: Trancas Dept., Vipos, *Venturi 3555* (NY, US). Jujuy Prov.: Calilegua, *Shafer 70* (G, GH, MO, NY, US). Salta Prov.: Salta, *Shafer 39* (GH, MO, NY, US). **BOLIVIA**. SANTA CRUZ DEPT.: Boyuibe, *Cárdenas 5025* (US). Andres Ibáñez Prov.: Puerto Pailas, *Nee 44863* (MO, NY); Cotoca, *Nee 37764* (MO, NY); Río Grande Planta de Gas, *Nee et al. 44630* (MO, NY); Curuyuqui, *Gentry et al. 75172* (F). Cordillera Prov.: Comunidad Salinas, *Nee 51221* (MO, NY). **PARAGUAY**. Cordillera Central, *Hassler 6850* (G). ALTO PARAGUAY DEPT.: Cerro León, *Zardini & Rivas 58334* (MO). BOQUÉRON DEPT.: Campo Loro, *Schmeda 1185* (US). DISTRITO CAPITAL: Asunción, *Shafer 138* (NY, US). GUAIRÁ DEPT.: Olimpo, *Schmeda 1460* (US). ITAPÚA DEPT.: Trinidad, *Morong 268* (NY); Isla Alta, *Schmeda 1489* (US). PARAGUARÍ DEPT.: Paraguarí, *Shafer 150* (NY, US); Cerro León, *Spichiger et al. 362* (G); *Soria & Zardini 1897* (G); Cerro Mbatoví, *Zardini & Velásquez 10043* (ASU). PRESIDENTE HAYES DEPT.: *Bernardi 20121* (G); [Estancia] Santa Elisa, *Hassler 2743* (G). **USA**. HAWAII: Kauai, Poipu Distr.: Waihoai, *Dunn & Wood 288* (PTBG). Koloa Distr.: Poipu, *Lorence & Flynn 6279* (PTBG); Poipu, *Lorence 7698* (PTBG). **CULTIVATED** (origin unknown): *Franck 2642* (USF).

Etymology. Aimé Jacques Alexandre Bonpland (1773–1858), explorer and botanist.

Discussion. *Harrisia bonplandii* has a few-ribbed stem with an undefined sulcus, moderately long spines, and a fruit with persistent scales. Its stems are often erect, achiving a greater unsupported height than other species of *Harrisia* in the Gran Chaco region. This is the only species of *Harrisia* known to occurr in the Pantanal (Eggli 2002) where it is said to be a common occurrence (Junk et al. 2006). The picture of *Harrisia* depicted by Braun & Hofacker (2006: 294, top) from the Pantanal does not conform to the morphology of *H. bonplandii*. The nearly spineless and rounded stems seem to show a defined sulcus and the flower scales are rather short (Braun & Hofacker 2006: 294, top-left). This population is deserving of additional study to determine its identification.

The name *Harrisia bonplandii* is here retained, as its modern usage appears to be fairly consistent and widely adopted. Leuenberger (2001) exhaustively detailed the history of the name and elected to maintain use of the name *H. bonplandii*. In favor of the use of *H. balansae* and contrary to Art. 51 (McNeill et al. 2012), Hunt et al. (2006) stated that the name *H. bonplandii* is "to be rejected" although no formal proposal was put forth. The lectotype designated for *H. balansae* by Taylor and Zappi (1997) was superfluous following the typification by Kiesling (1996).

3. Harrisia jusbertii (Rebut) Frič, Möllers Deutsche Gärtner-Zeitung 36: 421. 1932. *Cereus jusbertii* Rebut, Catalogue des Cactées et Plantes Grasses Diverses de la Collection de P. Rebut a Chazay-D'Azergues (Rhône) 3. 1891(?). *Eriocereus jusbertii* (Rebut) Riccob., Boll. Reale Orto Bot. Palermo 8: 240. 1909. ×*Harrisnopsis jusbertii* (Rebut) P.V. Heath, Calyx 1: 111. 1992. ×*Eriocereopsis jusbertii* (Rebut) Doweld, Tsukkulenty 4: 34. 2001. **NEOTYPE** (Franck 2012b): accession no. 746, 18 Jul 1963, *Kimnach s.n.* (HNT [1739]). Figure 28.

Stems green. Ribs not tuberculate, 3–5, indistinct with no demarcating line at sulcus. Spines of similar length, and very short, to 5 mm long, very rarely longer. Pericarpel and lower hypanthium areoles not similar to stem areoles. Flowers 17–24 cm long. Pericarpel green. Hypanthium light green, scales lanceolate to subulate, red-brown to green basally. Mid-hypanthium scales 3.1–4.3 × 12.4–18.2 mm. Sepals brownish green to green. Fruits without spines, retaining scales. Figs. 26–28.

Distribution. Known only from cultivation.

Etymology. Presumably honoring someone by the name of "Jusbert" or "Joubert".

Discussion. For simplicity, *Harrisia jusbertii* is here recognized as a species, known only from cultivation and often used as a grafting stock. This taxon is often called a hybrid, but there is presently no corroborating evidence apart from the claims of others. The distinctively short, thick (~1–2 mm wide), conical blackish spines are diagnostic for *H. jusbertii*. It seems most related to *H. bonplandii* and perhaps is a cultivar or hybrid derived from it. Its characters are similar to *H. bonplandii*, such as the flowers, the dehiscent fruit with persistent scales (Haage 1963), the green stem often lacking a well-defined sulcus, the acicular juvenile spines, and often having 4–5 ribs. As short spines are also found on mature stems in *H. martinii* and *H. regelii,* perhaps these species are involved in its origin, but this is merely speculative.

Various other taxa have been hypothesized to be part of the genome of *Harrisia jusbertii*, but none are substantiated. The description from Schumann (1899: 137–138) gave origins of Argentina or Paraguay with material being in the collection of Hermann Gruson of Magdeburg, Germany. The species was alleged to originate from Abbé Beguin (of Brignoles, France), who claimed it to be a hybrid between unnamed taxa of an *Echinopsis* s. lat. and a *Harrisia* (Berger 1905), which would make ×*Harrisnopsis* the preferred generic name. This scenario seems highly unlikely as all the vegetative characters are quite consistent with known species of *Harrisia,* except that the spines never elongate. Young spines of *Harrisia* are often blackish at the base as in the spines of *H. jusbertii*. The flowers are very much like *Harrisia* and quite unlike *Echinopsis* s. lat. It has been postulated that it is a chimeric mutant of *H. bonplandii* (Rowley 1980), though the morphology is consistent on a plant. Additionally, the seeds are viable and retain the same phenotype (Haage 1963). Henke (1981) claimed to have produced this hybrid by crossing *Echinopsis eyriesii* Pfeiff. & Otto and *Echinocereus pentalophus* (DC.) Haage var. *procumbens* (Engelm.) P. Fourn., which seems extremely doubtful (Drawert 1983).

As far as is known, *Cereus jusbertii* was first published by Rebut (1891?; Fig. 27) in a catalogue, with a brief but sufficient description of short, black spines similar to "*Cereus palmeri*." Schumann (1899: 137–138) then provided a more detailed description and furnished an illustration. Frîc (1932) was apparently the first to make the combination *Harrisia jusbertii* with an indirect reference to the basionym *Cereus jusbertii*. Britton & Rose (1920: 158) made the suggestion that *C. jusbertii* belonged in *Harrisia* but never validated the actual combination.

4. Harrisia martinii (Labour.) Britton, Addisonia 2: 55. 1917. *Cereus martinii* Labour. Annales Soc. Hort. Haute-Garonne 1: 182. 1854. *Eriocereus martinii* (Labour.) Riccob., Boll. Reale Orto Bot. Palermo 8: 241. 1909. **NEOTYPE** (designated by Kiesling 1996): **Argentina**. Entre Ríos Prov., Colón Dept., Colón, 6 Feb 1985, *Kiesling 5069* (SI; isoneotype: CTES).

Cereus martinii Labour. var. *perviridis* Weing., Monatsschr. Kakteenk. 24: 72. 1914. *Harrisia perviridis* (Weing.) Borg, Cacti: a gardener's handbook for their identification and cultivation 145. 1937. **TYPE**: **Paraguay**. [Guairá Dept.], Estancia San Salvador, *Anisits 50*.

Stems green. Ribs tuberculate, 4–5, separated by a distinct line at sulcus. Central spines 1–4, 1.5–2 times as long as radial spines. Flowers 18–26 cm long. Pericarpel green, having areoles similar to stem areoles with spines and without scaly trichomes. Hypanthium green to reddish green, scales red-purple, deltoid, with white hairs, lower areoles often similar to stem areoles with spines and without scaly trichomes. Mid-hypanthium scales 1.3–3.8 × 2.7–4.9 mm. Sepals green to pinkish green. Fruits often spiny, scales deciduous. Figs. 17, 29–37.

Distribution. Southeast Paraguay and northeast Argentina (Fig. 1), and naturalized in Australia, South Africa, and Hawaii; chaco húmedo, espinal; 50–100 m.

Specimens examined. **ARGENTINA**. May 1904, *Weber s.n.* (P). CHACO PROV.: Colonia Benitez, *Krapovickas 15787* (P). CORRIENTES PROV.: Mburucyá Dept., *Pedersen 5871* (A, US); San Cosme, *Leuenberger & Arroyo 3969* (ZSS). FORMOSA PROV.: Patiño Dept., *Charpin & Eskuche 20342* (G). SANTA FE PROV.: San Cristóbal Dept., Ceres a Arrufó, *Kiesling 8365* (NY, P). **AUSTRALIA**. QUEENSLAND. Brisbane: Leichhardt, 7 Nov 2004, *Batianoff s.n.* (BRI). Darling Downs: Goondiwindi, *Telford 8875* (BRI). Moreton: Mt. Crosby Road, *Booth 5384* (BRI). **PARAGUAY**. CONCEPCIÓN DEPT.: Concepción, *Hassler 7388* (BM, G). ITAPÚA DEPT.: Trinidad, *Shafer 132* (NY, US). PRESIDENTE HAYES DEPT.: *Hahn 2152* (MO). **SOUTH AFRICA**. KWAZULU-NATAL PROV.: Ashburton, 18 Mar 1970, *Wells s.n.* (MO); Ashburton, May 1973, *Paterson s.n.* (PRE); near Pietermaritzburg, Jul 1975, *Pickworth s.n.* (PRE); Pietermaritzburg Distr., 13 Sep 1965, *Pickworth s.n.* (PRE); Ashburton area, Jul 1967, *Regional Officer s.n.* (PRE). WESTERN CAPE PROV.: Hout Bay, s.d., *Succulenta Nurseries s.n.* [cultivated?] (PRE). **USA.** HAWAII: Kauai: Koloa Distr.: Poipu, *Lorence 7697* (PTBG); Poi'pu Road, *Lorence 7987* (PTBG). Poipu Distr.: near Waiohai, *Dunn & Wood 303* (PTBG).

Etymology. Raymond Martin (?–?), cactus horticulturist.

Discussion. *Harrisia martinii* has a few-ribbed stem and short radial spines that are often present on the pericarpel, lower hypanthium, and fruit. The stems and fruit are often prominently tuberculate. It is the most successful species to naturalize outside of its native range, occurring in South Africa, Australia, and Hawaii. The authorship of *H. martinii* was confirmed by Leuenberger (2000a).

Based on Rec. 60C.2 in McNeill et al. (2012), "martini" as in "*Harrisia martini*" would be the preferred name over "*H. martinii.*" Since this is merely a recommendation and the spelling "*H. martinii*" is most common, I have retained the popular spelling.

5. Harrisia pomanensis (F.A.C. Weber ex K. Schum.) Britton & Rose, Cact. 2: 155. 1920. *Cereus pomanensis* F.A.C. Weber ex K. Schum., Gesamtbeschr. Kakt. 136. 1899. *Echinopsis pomanensis* (F.A.C. Weber ex K. Schum.) Anceschi & Magli, cactusinhabitat 39. 2013. **NEOTYPE** (designated by Kiesling 1996): **Argentina**. Santiago del Estero Prov., Ojo de Agua Dept., Quebrada de Pozo Grande, 18 Dec 1981, *Ulibarri 1366* (SI; isoneotype: SI).

Eriocereus polycanthus F. Ritter, Kakteen in Südamerika 2: 436. 1980. **TYPE**: **Argentina**. Catamarca, *F. Ritter 413* (holotype: U, not found).

Eriocereus tarijensis F. Ritter, Kakteen in Südamerika 2: 557. 1980. *Harrisia pomanensis* (F. A. C. Weber ex K. Schum.) Britton & Rose subsp. *tarijensis* Braun & Esteves, Succulenta (Netherlands) 73: 131.1995. **TYPE**: **Bolivia**. [Chuquisaca Dept.], Puente Azero, Grenze der Provinzen Azero und Tomina, *F. Ritter 619* (holotype: U, not found).

Stems glaucous green. Ribs not tuberculate, 4–6, separated by conspicuous line at sulcus. Spines of similar length. Pericarpel and lower hypanthium areoles not similar to stem areoles. Flowers 14–21 cm long. Pericarpel green. Hypanthium green, scales reddish green, lanceolate to subulate. Mid-hypanthium scales 4.0–5.0 × 13.6–18.3 mm. Sepals pale reddish green. Fruits without spines, scales usually withering-deciduous. Figs. 4, 38–42.

Distribution. Southeast Bolivia, west Paraguay, and northwest Argentina (Fig. 1) and naturalized in South Africa; chaco serrano, chaco árido, chaco semi-árido (Zak & Cabido 2002); 200–1200 m.

Specimens examined. **ARGENTINA**. CATAMARCA PROV.: *Leuenberger 4362* (USF). CÓRDOBA PROV.: Villa de Maria, *Leuenberger & Eggli 4639* (ZSS); Cruz del Eje, *Leuenberger & Eggli 4710* (ZSS); Cruz del Eje, *Leuenberger & Eggli 4485* (ZSS). TUCUMÁN PROV.: Trancas, 3 Dec

2003, *Leuenberger & Eggli 4901* (ZSS). **BOLIVIA**. SANTA CRUZ DEPT.: Caballero Prov.: Río Quiñal, *Saldias & Medellín 4409* (NY); Cordillera Prov.: Ipatí, *Nee 51239* (NY). TARIJA DEPT.: Yacuiba, *Pensiero & Marino 4475* (MO). **CULTIVATED** (origin unknown): *Franck 2640* (USF).

Etymology. Poman, pertaining to a place in Argentina, perhaps Pomancillo or Pomán.

Discussion. *Harrisia pomanensis* has a defined sulcus between the ribs, which can sometimes be difficult to see on specimens. It is also characterized by its spines normally being of a relatively similar length and having a spineless fruit with usually withering-deciduous scales.

6. Harrisia regelii (Weing.) Borg, Cacti: a gardener's handbook for their identification and cultivation 145. 1937. *Cereus regelii* Weing., Monatsschr. Kakteenk. 20: 33. 1910. *Eriocereus martinii* (Labour.) Riccob. var. *regelii* (Weing.) W.T. Marshall, Cactaceae, with illustrated keys of all tribes, sub-tribes and genera 98. 1941. *Eriocereus regelii* (Weing.) Backeb., Die Cactaceae 4: 2093. 1960. *Harrisia pomanensis* (F.A.C. Weber ex K. Schum.) Britton & Rose var. *regelii* R. Kiesling, Darwiniana 34: 395. **NEOTYPE** (designated by Leuenberger 1996): **Germany** [cultivated]. Berlin-Dahlem Botanical Garden, 10 Aug 1994, *Schwerdtfeger 12552a* (B; isoneotype: SI).

Stems green. Ribs tuberculate, 4–5, not separated by conspicuous line at sulcus. Central spines 1–4, 1.5–2 times as long as radial spines. Flower buds with reddish hairs. Flowers 19–22 cm long. Pericarpel and lower hypanthium areoles not similar to stem areoles. Pericarpel green. Hypanthium green, scales red to reddish green, deltoid-lanceolate. Mid-hypanthium scales 2.6–4.2 × 7.9–11.5 mm. Sepals pale reddish green. Fruits not spiny, scales deciduous or sometimes persistent. Figs. 5–6, 13, 43–45.

Distribution. Entre Ríos Province, Argentina (Fig. 1), reportedly naturalized in Queensland, Australia (Leuenberger 2000b; Paskins 2001); espinal; ~50 m.

Specimens examined. **CULTIVATED** (origin unknown): 19 Jun 2008 & 23 Sep 2008, *Franck s.n.* (USF); *Franck 2629*, *2662* (USF).

Etymology. Eduard August von Regel (1815–1892), botanist.

Discussion. *Harrisia regelii* has short radial spines like *H. martinii*, which it was noted as a possible variety of (Borg 1937; Hunt et al. 2006). Unlike *H. martinii*, areoles of the pericarpel and lower hypanthium of *H. regelii* typically have reddish scaly hairs and no spines. These two species are often confused and *H. regelii* appears to be common in cultivation. Kiesling (1996) regarded *H. regelii* as a variety of *H. pomanensis*, though Leuenberger (1995, 2000b) and Hunt et al. (2006) maintained it as a species. Both Kiesling (1996) and Leuenberger (2000b) identified specimens of this species from Entre Ríos Province, Argentina; previously this species had been known only from cultivation. *Harrisia regelii* is sympatric with *H. bonplandii* (Kiesling 1996; Leuenberger 2000b) while *H. pomanensis* is apparently widely disjunct (Fig. 1).

It seems possible that *Harrisia regelii* involves crosses between *H. bonplandii* and *H. martinii*. The angular ribs and occasional lack of a defined sulcus (Figs. 44–45) and fruit with persistent red scales (Fig. 43) are reminescent of *H. bonplandii* while the short radial spines (Figs. 43–45), occasionally defined sulcus (Fig. 43), tuberculate stems (Figs. 43–45), and tuberculate fruit (Fig. 45) seem similar to *H. martinii*. Its similarity to *H. pomanensis* (Fig. 43) cannot wholly be discounted, though this species is not known from the region (Fig. 1). It is not entirely clear that Figs. 43–45 are conspecific and ideally molecular data would be useful to clarify taxonomic relationships among these specimens and others in sect. *Eriocereus*.

7. Harrisia tortuosa (J. Forbes ex Otto & A. Dietr.) Britton & Rose, Cact. 2: 154. 1920. *Cereus tortuosus* J. Forbes ex Otto & A. Dietr., Allg. Gartenzeitung 6: 35. 1838. *Eriocereus tortuosus* (J. Forbes ex Otto & A. Dietr.) Riccob., Boll. Reale Orto Bot. Palermo 8: 245. 1909. NEOTYPE (Kiesling 1996): **Argentina**. Corrientes Prov., San L. del Palmar Dept., 18 km SE de San Luis del Palmar, 2 Nov 1979, *Schinini 19451* (CTES; isoneotype: SI).

Cereus arendtii Hildmann & Mathsson ex K. Schum., Monatsschr. Kakteenk. 4: 173. 1894. *Eriocereus arendtii* (Hildmann & Mathsson ex K. Schum.) F. Ritter, Kakteen in Südamerika 1: 242. 1979. NEOTYPE (designated here): **Argentina**. Corrientes Prov., San L. del Palmar Dept., 18 km SE de San Luis del Palmar, 2 Nov 1979, *Schinini 19451* (CTES; isoneotype: SI).

Cereus atropurpureus Hocay, Cacteencult 91. 1916.

Stems green. Ribs tuberculate, 6–8, separated by conspicuous line at sulcus. Spines of similar length. Flowers 19–22 cm long. Pericarpel brownish green, sometimes having areoles similar to stem areoles with spines and without scaly trichomes. Hypanthium pale pinkish green, scales red, ovate, with white hairs, sometimes the lower hypanthium areoles similar to stem areoles with spines and without scaly trichomes. Mid-hypanthium scales 2.2–3.4 × 5.7–7.6 mm. Sepals pale pinkish green-brown. Fruits with or without spines, scales deciduous. Figs. 46–49.

Distribution. Paraguay, northeast Argentina, and west Uruguay (Fig. 1) and naturalized in Australia; chaco húmedo, espinal; 80-300 m.

Specimens examined. **AUSTRALIA**. QUEENSLAND. Darling Downs: Boondandilla State Forest, *Forster 29482* (BRI). **ARGENTINA**. BUENOS AIRES: May 1904, *Weber s.n.* (P). **PARAGUAY**. CORDILLERA DEPT.: Río Piribebuy, *Zardini & Velazquez 19789* (MO). **URUGUAY**. MONTEVIDEO DEPT.: Montevideo, Apr 1836, *Gaudichaud s.n.* (P). RÍO NEGRO DEPT.: Estancia Nueva Mehlem, en limo pampeano, collected in 9 Apr 1922, *Schroeder s.n., Herb. Osten 16720* (MVM). **CULTIVATED** (origin unknown): *Franck 1281, 2628, 2897* (USF).

Etymology. Tortuous, twisting, winding.

Discussion. *Harrisia tortuosa* and *H. martinii* are the only taxa of *Harrisia* with stem-like areoles on the pericarpel, often being spiny. However, with its 6–8 ribs and longer radial spines, *H. tortuosa* is readily differentiated from *H. martinii.* Spination may be variable on the pericarpel, as a flower illustration (Fig. 49, Britton & Rose 1920) and a fruit specimen (Osten 1941) appear spineless.

Harrisia tortuosa is the only species in the genus known from Uruguay. The name *Harrisia tortuosa* var. *uruguayensis* was never given a Latin diagnosis and is illegitimate. The specimens ascribed to this name have 6–8 ribs, which agrees with its placement under *H. tortuosus*. The specimens at MVM also appear to have spiny pericarpels, but apparently the fruits may appear spineless (Osten 1941). Backeberg (1960) and Kiesling (1996) allied this specimen with *H. pomanensis*; however, the range of *H. tortuosa* var. *uruguayensis,* nom. illeg., is more agreeable with *H. tortuosa.*

Cereus arendtii is here regarded as a later synonym of *Harrisia tortuosa* as done by others (e.g. Schumann 1899; Britton & Rose 1920; Backeberg 1960; Aarsen 1983.), although the protologue of *C. arendtii* only mentioned a similarity to *H. tortuosa* and did not initially synonymize the two. The protologue of *C. arendtii* described a specimen having six ribs with shallow sulci, tuberculate areoles, and spines 2–3 cm long. This description is consistent with the morphology of *H. tortuosa* but does not distinguish it from many other species of cacti such as *H. pomanensis*. The provenance of *C. arendtii* was given as “Thale von Cordova in Uruguay” and only *H. tortuosa* is known from

Uruguay. I have been unable to confidently associate "Thale von Cordova" with any place in Uruguay (see Ritter 1979: 243). I have found only one reference to a place "Cordova" in Uruguay for the London & River Plate Bank (Homans 1874: 185). As Schumann (1899) recognized *H. pomanensis* and *H. tortuosa* as distinct and listed *C. arendtii* as a synonym of *H. tortuosa*, it is presumed this is consistent with the present treatment. It could be possible to interpret *C. arendtii* as actually from Córdoba, Argentina and more consistent with *H. pomanensis*. Therefore I proffer a neotype for *C. arendtii* to secure its application to *H. tortuosa*.

Ritter (1979: 242) chose to recognize *Eriocereus arendtii* and excluded *Cereus tortuosus* from *Eriocereus* (= *Harrisia*), suggesting it to more likely be a member of *Piptanthocereus* (A. Berger) Riccob. (= *Cereus* Mill. s. str.) and perhaps synonymous with *C. aethiops* Haw. *Harrisia tortuosa* has been neotypified (Kiesling 1996) and is in common usage for a cactus occurring in northeast Argentina, east Paraguay, and west Uruguay (Anderson 2001; Hunt et al. 2006; Franck 2012b). Reports of *H. tortuosa* in Bolivia are so far unverified by herbarium specimens (Kiesling et al. 2014).

II. HARRISIA subg. HARRISIA

Cereus Mill. [unranked] *Attenuati* Salm-Dyck, Cact. Hort. Dyck.: 27. 1842 [fide Mottram 2014].

Shrubs or small trees. Stems pendent, prostrate, arching, reclining, clambering, ascending, or erect, dark green to glaucous green, 5–14 ribs. Spines to 12 cm long, 1.5 mm thick. Newly emergent spines white to yellow to red with darker tips. Seeds oblong rectangular, 1.3–2.4 × 1.9–3.35 mm.

One species is found in the caatinga of northeast Brazil and 11 species occur in the West Indies (Greater Antilles, Bahamas, southern coastal Florida) (Figs. 2 and 3), naturalized in Hawaii; seasonally dry forest and scrubland; 0–600 m.

This subgenus contains species which have oblong seeds. Salm-Dyck (1850) may have recognized the similarity between the West Indian species and the Brazilian *Harrisia adscendens* if the name he used, *Cereus platygonus*, is the same plant as *H. adscendens*. These species were placed together in the unranked group *Attenuati* under the genus *Cereus* (Salm-Dyck 1850: 45; Labouret 1853: 335).

IIb. HARRISIA sect. ADSCENDENTES A.R. Franck, Syst. Bot. 38: 218. 2013. TYPE: *Harrisia adscendens* (Gürke) Britton & Rose.

This section is monotypic and might have been historically more widespread given the presence of other columnar cacti in northern South America (Franck et al. 2013a).

8. Harrisia adscendens (Gürke) Britton & Rose, Cact. 2: 155. 1920. *Cereus adscendens* Gürke, Monatsschr. Kakteenk.18: 66. 1908, nom. prop. cons. *Eriocereus adscendens* (Gürke) A. Berger, Kakteen 129. 1929. **LECTOTYPE** (Taylor & Zappi 2004): **Brazil**. Bahia, Tambury, den Niederungen der catinga, Oct 1906, *Ule 7072* (B; isolectotype: HBG, K [photo]).

Cereus platygonus Otto, Cacteae Horto Dyckensis Cultae, Anno 1849: 199. 1850, nom. prop. rej. *Eriocereus platygonus* (Otto) Riccob. 8: 242. 1909. *Harrisia platygona* (Otto) Britton & Rose, Cact. 2: 156. 1920. **NEOTYPE** (Franck 2015): "K. Sch. 99" (NY [02343599]).

Shrubs. Stems arching, reclining, clambering, ascending, or erect, glaucous green, 6–10 ribs. Spines to 3 cm long, spines of basal and distal areoles similar in size. Newly emergent spines red. Pericarpel and hypanthium green, scales lanceolate to subulate, green with reddish tips. Mid-hypanthium scales 1.5–3.2 × 3.3–8.2 mm. Sepals green to pale reddish green. Petals white. Fruits orange to red, rarely yellow-orange, tearing at sides to expose inner pulp and seed. Seeds 2–2.3 × 2.8–2.9 mm. Figs. 4, 9, 50–52.

Distribution. Northeastern Brazil (Fig. 2); caatinga; 100–600 m.

Specimens examined. **BRAZIL**. BAHIA: Juazeiro, *Rose & Russell 19730* (NY, US); Salgada, *Rose & Russell 19715* (NY, US); Barrinha, *Rose & Russell 19794* (NY); Joazeiro, *Zehntner 729* (US); Teofilandia, *Taylor et al. 1349* (ZSS); Uauá, *Taylor et al. 1362* (ZSS); Juazeiro, *Taylor et al. 1388* (ZSS); Iaçú, *Taylor et al. 1580* (ZSS); Ipirá, *Hofacker 403* (USF, ZSS). **CULTIVATED** (origin unknown): *Schumann 99* (NY); 1901, *Britton s.n.* (NY); *Franck 2641*, *2896* (USF).

Etymology. Climbing, ascendant.

Discussion. *Harrisia adscendens* is characterized by its oblong seeds, glaucous stem, dehiscent fruit, and long stigma lobes. This species has been treated in detail by Taylor & Zappi (2004). The unknown *Harrisia* reported from Unaí, Brazil (Junqueira et al. 2010) might be *H. adscendens*.

The name *Cereus platygonus* is here interpreted as conspecific with *Harrisia adscendens*. *Cereus platygonus* would have priority as an earlier published name, but it has been proposed and recommended for rejection (Franck 2015; Taxon 65: 1159. 2016.) since it was abandoned after being used by Riccobono (1909) and Britton & Rose (1920).

IIb. HARRISIA sect. HARRISIA

Shrubs or small trees. Stems pendent, prostrate, arching, reclining, clambering, ascending, or erect, dark to light green, 5–14 ribs. Spines to 12 cm long, spines of basal and distal areoles sometimes dissimilar in size. Newly emergent spines white to yellow to red. Pericarpel and hypanthium scales green to brownish to reddish, deltoid to lanceolate, sepals lanceolate. Petals white to pinkish. Fruits yellow to red, indehiscent. Seeds 1.25–2.0 × 2.0–3.35 mm.

Four species occur in Cuba, two in Florida, one (or two?) on Hispaniola, one in Puerto Rico, one in the Bahamas, one in Jamaica, and one in the Cayman Islands and the Swan Islands (Fig. 3), naturalized in Hawaii; scrubland and scrub forest; 0–400 mm.

IIb-1. HARRISIA ser. EARLEI A.R. Franck, Syst. Bot. 38: 218. 2013. TYPE: *Harrisia earlei* Britton & Rose.

It seems quite probable that this series was once more diverse or widespread historically, perhaps sympatric with other species of *Hylocereus* (A. Berger) Britton & Rose and *Strophocactus* Britton & Rose that occupy similar habitats, found prostrate on boulders in Central America and Mexico (Franck et al. 2013a).

9. Harrisia earlei Britton & Rose, Cact. 2: 154. 1920. **TYPE**: **Cuba**. Pinar del Río Prov., San Diego de los Baños, limestone rocks, 31 Aug–3 Sep 1910, *Britton et al. 6667* (holotype: NY).

Shrubs. Stems pendent, prostrate, clambering, only young stems ascending, or erect, 5–7 ribs. Young spines bright red with darker tips, becoming black to gray. Pericarpel green. Hypanthium light green, scales brownish, with reddish tips, deltoid to ovate. Mid-hypanthium scales 1.6–2.2 × 6.0–9.3 mm. Sepals pale yellow-greenish with brown-red tips. Immature fruit green. Fruits yellow. Seeds 1.65–1.8 x 2.55–2.95 mm. Fig. 53.

Distribution. Pinar del Rio Provínce, Cuba (Fig. 3); scrub forest over limestone boulders; 100–400 m.

Specimens examined. **CUBA**. PINAR DEL RÍO PROV.: Pan de Azucar, *Morton s.n.* (HNT, UC, US); Sumidero, *Shafer* [& *León*] *13397* (GH, HAC, NY, P, US); Sumidero, *Ekman 18222* (S); Río Guao, *Britton et al. 9653* (NY, US); Sierra Guayaba, *Shafer 13862* (NY, US); Sierra Guane, *Shafer 10524* (NY, US); Viñales, *Ardisson 99.15* (USF); San Diego de Los Baños, *Agathange 5045* (HAC, NY); San Diego de los Baños, *Earle s.n.* (NY); Guane, *Britton et al. 9747* (NY); San Diego de los Baños, *León 4231* (NY); 2 May 2006, *ZSS staff s.n.* (ZSS).

Etymology. Franklin S. Earle (1856–1929), mycologist.

Discussion. *Harrisia earlei* is the most distinctive species in the West Indies with its prostrate habit, 5–7 ribs, and reddish newly emergent spines. A description of the flowers was provided by Delanoy (2005) and a description of its habitat by Ardisson & Delanoy (2002).

IIb-2. HARRISIA ser. HARRISIA

Shrubs or small trees. Stems arching, reclining, clambering, ascending, or erect, 8–14 ribs. Spines to 8 cm long. Young spines white to straw-colored basally, becoming brown to red-black with a black tip, eventually becoming gray. Pericarpel green to red. Hypanthium yellow-green to green to red. Scales yellow-green to green to red. Sepals yellow-green to pale red. Fruits yellow to red. Seeds 1.25–2.0 × 2.0–3.35 mm.

Three species occur in Cuba, two in Florida, one (or two?) on Hispaniola, one in Puerto Rico, one in the Bahamas, one in Jamaica, and one in the Cayman Islands and the Swan Islands (Fig. 3), and an unknown species naturalized in Hawaii (*Dunn & Wood 298* (PTBG) and *Lorence 7623a* (PTBG)); scrubland and scrub forest; 0–400 m.

This study favors recognition of 10 species of series *Harrisia* in the West Indies. Four names that are sometimes recognized are here put into synonymy (*H. hurstii*, *H. nashii*, *H. simpsonii*, *H. taylorii*).

Most of the West Indian species are allopatric and morphologically uniform. Further morphological and molecular work in the West Indies would be ideal to verify taxonomic delimitation across multiple populations. The northwestern group of species (*Harrisia aboriginum* , *H. eriophora*, *H. fernowii*, *H. fragrans*, and *H. taetra*) all share relatively large seeds (1.7–2.2 × 2.6–3.35) and reddish coloration in the flowers. The other species of the West Indies (*H. brookii*, *H. caymanensis*, *H. divaricata*, *H. gracilis*, and *H. portoricensis*) are united by relatively small seeds (1.4–1.7 × 2.0–2.8 mm) and predominantly greenish flowers.

Characterization of the flower and overall spine morphology (especially at the base of plants in habitat) is critical for identification. Fresh, mature flowers of very few specimens have been studied and additional observations are desirable. Many morphological characters (flower bud shape, trichome color, petal margins, and stem thickness) which were claimed as diagnostic by others (e.g. Britton 1908; Britton & Rose 1920) are here abandoned because their utility is questionable or difficult to apply.

Flower buds of some species were distinguished as being depressed-truncate, subglobose, obovoid, or ovoid (Britton 1908; Britton & Rose 1920). The shape of the flower bud varies greatly as it ages and matures. This character is very difficult to assess or apply without having some indication of the age of the flower bud and measurements on its dimensions. Britton (1908) alleged pointed buds with curled hairs in some species, being obovoid in *Harrisia divaricata* (as *H. nashii*), ovoid in *H. brookii*, and subglobose in *H. fernowii* (as *H. taylorii*). Buds of *H. portoricensis* were stated to be rounded-truncate with curled hairs. Britton (1908) described pointed buds with straight hairs in *H. gracilis.*

Two species, *Harrisia aboriginum* and *H. fernowii*, were described as having tawny trichomes, probably an artifact of aging, as all observations of living material show white trichomes on the flowers (Hooten 1991; pers. obs.). Furthermore, all old herbarium specimens seem to have tawny trichomes. Additionally, the short, uniseriate trichomes of the stem areoles of many species can be tawny when first emerging (Fig. 95).

Flower petals margins have been described as denticulate or entire and used to characterize certain species (Britton 1908; Britton & Rose 1920). The margins of the flower petals of all species appear irregularly denticulate to varying degrees. None appear strictly entire and this character is very difficult to apply. The petals are delicate and thin, and as such, their margins are not well preserved on herbarium specimens. Multiple observations would be needed to verify if petal margins are consistently distinct between species. Entire petals were purported for *Harrisia brookii, H. divaricata* (as *H. nashii*), *H. eriophora, H. fragrans, H. portoricensis* and denticulate petals for *H. gracilis* and *H. fragrans* (as *H. simpsonii*) (Britton 1908; Britton & Rose 1920).

Stem thickness has also been used (Areces 1980) based upon the original descriptions (Britton 1908). This character widely varies with age, health, vigor, and the degree of hydration of the stem (Eggli & Giorgetta 2015) and it is difficult to conceive how this measurement could be standardized. Perhaps the distal mature stems of healthy, hydrated plants may be worthwhile to study.

10. Harrisia aboriginum Small ex Britton & Rose, Cact. 2: 154. 1920. *Cereus aboriginum* (Small ex Britton & Rose) Little, Amer. Midl. Naturalist 33: 495. 1945. *Cereus gracilis* Mill. var. *aboriginum* (Small ex Britton & Rose) L.D. Benson, Cact. Succ. J. (Los Angeles) 41: 126. 1969. *Harrisia gracilis* (Mill.) Britton var. *aboriginum* (Small ex Britton & Rose) D. B. Ward, Novon 14: 366. 2004. **LECTOTYPE** (Benson 1969): **USA**. Florida, [Manatee Co.], western shore Terra Ceia Island, hammock, 29 Apr 1919, *Small et al. s.n.* (NY; isolectotype: US).

Shrubs, trunk not evident or poorly developed. Spines not crowded, not overlapping spines of adjacent areoles, shorter than width of the stem, to 1.5 cm, 0.5 mm thick, spines of similar size on distal and basal areoles of stems. Flowers 18 cm long. Pericarpel green. Hypanthium pinkish brown, scales pinkish brown to red-brown, deltoid to deltoid-ovate. Mid-hypanthium scales 1.6–2.0 × 4.5–8.0 mm. Sepals pale pink. Immature fruit green and lightly tuberculate, turning orange and smooth near maturity. Mature fruit yellow, smooth. Seeds 1.7–2.0 × 2.7–3.0 mm. Figs. 54–58.

Distribution. Gulf coast, central peninsula of Florida, USA (Fig. 3); coastal strands and maritime hammock, on sandy or shell fragment soils; 0–5 m.

Specimens examined. **USA.** FLORIDA: Lee Co.: Buck Key, *Hooten s.n.* (US); Buck Key, 29 Oct 2007, *Franck s.n.* (USF); Buck Key, *Possley & Fellows 29* (FTG); Bokeelia Island, Jun 2007, *Franck s.n.* (USF); Buck Island, *Austin & Austin 6863* (FTG). Manatee Co.: Terra Ceia Island, 1917, *Swingle s.n.* (US); Terra Ceia, Jan 1920, *Robinson s.n.* (K). Sarasota Co.: Osprey, 1906, *Webb s.n.* (US); Osprey, 1911, *Webb s.n.* (NY); Longboat Key, *Lakela & Long 28145* (USF); Manasota Key, *Hansen & Richardson 6819* (USF); Longboat Key, *Lakela & Long 27609* (FLAS, USF); Little

Sarasota Key, *Coville 24* (US); Manasota Key, *Beckner 1715* (FLAS); Manasota Key, *Franck 1237* (USF); Longboat Key, Jun 2007, *Franck s.n.* (USF).

Etymology. For the "shell heaps formed by the aborigines" (Britton & Rose 1920).

Discussion. *Harrisia aboriginum* can be recognized by its consistently short spines, brownish hypanthium, green pericarpel, green immature fruit, and yellow mature fruit. The fruits often seem to change from green (immature) to orange (maturing) to yellow (fully mature). Vegetatively *H. aboriginum* is most like two other short-spined species, *H. gracilis* and *H. fragrans*, although longer spines are also observed in these two (< 3.5 cm).

Hooten (1991) used a strict interpretation of the protologue (i.e., tawny hairs) of *Harrisia aboriginum* to attempt to name a new species (*H. donae-antoinae*, nom. inval.) because of the white hairs observed in fresh material. All flower hairs seem to age to a tawny color on herbarium specimens, including the intended type specimen of *H. donae-antoinae*, nom. inval., making it agreeable with the sense of *H. aboriginum* in morphology and distribution. The name *H. donae-antoinae* is invalid as Hooten (1991) did not clearly designate a type specimen and then did not give a clear reference to the page number that gave the Latin diagnosis (Hooten 1992).

11. Harrisia brookii Britton, Bull.Torrey Bot. Club 35: 564. 1908. *Cereus brookii* (Britton) Vaupel, Monatsschr. Kakteenk. 23: 24. 1913. **TYPE**: **Bahamas**. Long Island, Clarence Town and vicinity, scrublands, 16–19 Mar 1907, *Britton & Millspaugh 6337* (holotype: NY; isotype: US). **EPITYPE** (Franck 2012b): **Bahamas**. Near Mortimers, dry open coppice on high rocky ridge, 24 Apr 1980, *Correll 51278* (FTG; isoepitype: NY).

Shrubs, trunk not evident or poorly developed. Spines of distal areoles sometimes overlapping spines of adjacent areoles, shorter than width of stem, to 1.5 cm long and 0.3 mm thick, spines of basal areoles somewhat crowded and overlapping, to 3 cm long and 0.6 mm thick. Flowers to 20 cm long. Pericarpel green. Hypanthium green to reddish, scales yellow-green to green distally, lanceolate to subulate. Mid-hypanthium scales 2.8–3.2 × 14.8–15.4 mm. Sepals pinkish brown-green. Immature fruit green, tuberculate. Mature fruit yellow, oblong, ellipsoid, lightly tuberculate. Seeds 1.55–1.7 × 2.65–2.85 mm. Figs. 59–62.

Distribution. Bahamas (Fig. 3); scrublands (Correll & Correll 1982) or coastal coppice (Correll 1979); 0–20 m.

Specimens examined. **BAHAMAS**. ELEUTHERA ISLAND: *Vincent 13393* (MU). LONG ISLAND: Clarence Town, *Britton & Millspaugh 6337* (NY,US); Mortimers, *Correll 44980* (FTG); Mortimers, *Franck 3033, 3116* (USF); Clarence Town, *Hill 2291* (FTG, NCU); Clarence Town, 11 May 1974, *O'Kelly s.n.* (A); Deadman's Cay, *Correll 45038* (FTG). NEW PROVIDENCE ISLAND: *Robinson 475* (K).

Etymology. Hon. Herbert A. Brook, Registrar of the Bahamas.

Discussion. *Harrisia brookii* can be recognized by its pinkish sepals, ellipsoid fruit (Vincent 2007), and spines that only become slightly longer and thicker on the lower stem. Only one flower has been observed for characterization of this species here. *Harrisia divaricata* is sometimes observed with ellipsoid fruits, but this species also seems to have strongly tuberculate immature fruits and longer, thicker spines on the lower stem compared to *H. brookii*. The scales of *H. brookii* are possibly consistently longer (14.8–15.4 mm long, again based on one flower) than those in *H. divaricata*. Although there is a specimen labeled year 1880 from New Providence Island (*Robinson 475*), recent observations have been made only from Eleuthera and Long Island. Correll & Correll

(1982) mentioned that the specimen *G.R. Proctor 8812* (IJ) from Grand Turk is possibly referable to this species, but the specimen was not located in a recent search at IJ. *Harrisia* should be searched for and characterized in the Turks and Caicos Islands.

12. Harrisia caymanensis A.R. Franck, Haseltonia 18: 98. 2012. **TYPE**: **Cayman Islands**. Cayman Brac, cutting grown in Florida, 10 June 2012, *A. R. Franck 3035* (holotype: USF; isotype: MO).

Shrubs, trunk not evident or poorly developed. Spines of distal areoles often overlapping those of adjacent areoles, often as long or longer than stem width, to 2.5 cm long and 0.5 mm thick, spines of basal areoles crowded and overlapping, to 6.5 cm long and 0.7 mm thick. Flowers to 15 cm long. Pericarpel green. Hypanthium light green, scales light green to green, ovate-lanceolate. Mid-hypanthium scales 2.1–2.7 × 8.5–10.0 mm. Sepals greenish brown. Immature fruit green, lightly tuberculate. Mature fruit yellow, smooth. Seeds 1.4–1.5 × 1.9–2.1 mm. Figs. 63–65.

Distribution. Cayman Islands, and Swan Islands, Honduras (?) (Fig. 3); coastal scrub and scrubby woodland on exposed limestone rock; 5–50 m.

Specimens examined. **CAYMAN ISLANDS**. CAYMAN BRAC: *Franck 2370*, *2371*, *2622*, *2630* (USF). **HONDURAS** (?). SWAN ISLANDS: Little Swan, 30 Jul 1974, *Clough s.n.* (IJ); Eastern Swan Island, 14 Nov 1973, *Moyne s.n.* (K).

Etymology. For the Cayman Islands.

Discussion. The shortest flowers in the genus occur in *Harrisia caymanensis*. This species is also characterized by long spines on the lower stem areoles and relatively small seeds. The flower color and shape of the hypanthium scales suggests an affinity with *H. fernowii*. The name *H. gracilis* had previously been misapplied to *H. caymanensis* (Adams 1972; Proctor 1984; Proctor 2012). The population of *Harrisia* on the Swan Islands, previously identified as *H. eriophora* (Sandoval et al. 2007), represents the most isolated occurrence of *Harrisia* and is here tentatively referred to *H. caymanensis* (Franck 2012b). The Swan Islands population needs additional study (i.e. the flower length, color of the flower parts, seed size, maximum spine width and length) to determine if it is conspecific with *H. caymanensis* or represents a differet taxon.

13. Harrisia divaricata (Lam.) Backeb., Die Cactaceae 4: 2101. 1960. *Cactus divaricatus* Lam., Encycl. 1: 540 1783. *Cereus divaricatus* (Lam.) DC., Prodr. 3: 466. 1828. *Pilocereus divaricatus* (Lam.) Lem., Rev. Hort. (Paris) 427. 1862. **LECTOTYPE** (Lourteig 1991): **Haiti**. Cul-de-sac, near Léogâne, Plumier illustration. Reproduced in Burman 1758, *Pl. Amer.* 8: tab. 193; in Hunt 1984, p. 57–58; and in Mottram 2002, p. 110–111.

Cereus divergens Pfeiff., Enum. diagn. Cact. 95. 1837. **TYPE**: Dominican Republic, Santo Domingo.

Harrisia nashii Britton, Bull.Torrey Bot. Club 35: 564. 1908. *Cereus nashii* (Britton) Vaupel, Monatsschr. Kakteenk. 23: 27. 1913. **TYPE**: **Haiti**. Between Gonaives and Plaisance, 1905, flowered [at] New York Botanical Garden 11 Jul 1907, *Nash & Taylor 1765* (holotype: NY).

Harrisia nashii Britton var. *straminea* W.T. Marshall, Cact. Succ. J. (Los Angeles) 15: 3. 1943. **TYPE**: **Dominican Republic**. Monte Cristi Prov., Hurst finca near Monte Christi, 25 Nov 1936, *Marshall s.n.* (holotype: GH).

Harrisia serruliflora (Haw.) Lourteig, Bradea 5: 408. 1991. *Cereus serruliflorus* Haw., Philos. Mag. Ann. Chem. 113. 1830. **LECTOTYPE** (Lourteig 1991): **Haiti**. Cul-de-sac, Plumier illustration. Reproduced in Burman 1758, *Pl. Amer.* 8: tab. 195, fig. 1; in Hunt 1984, p. 60; and in Mottram 2002, p. 113.

Shrubs or small trees, with well-developed erect trunk to 1 m. Spines of distal areoles not much overlapping those of adjacent areoles, shorter than stem width, to 2.0 cm long and 0.5 mm thick, spines of basal areoles crowded and overlapping, to 5.5 cm long and 1.0 mm thick. Flowers 17–23 cm long. Pericarpel green. Hypanthium green to brownish green distally, scales light green to green, ovate-lanceolate. Mid-hypanthium scales 2.2–3.3 × 11.0–13.1 mm. Sepals greenish brown. Immature fruit green and strongly tuberculate, becoming ellipsoid, yellow, and strongly tuberculate near maturity. Mature fruit yellow, smooth, globose. Seeds 1.4–1.65 × 2.05 –2.6 mm. Figs. 8, 15, 66–73.

Distribution. Lowlands and coastal areas of Hispaniola (Fig. 3); scrub forest and scrubland; 5–400 m.

Specimens examined. **DOMINICAN REPUBLIC**. AZUA PROV.: Azua, *Rose et al. 3831* (GH, NY, US); Azua, *Lavastre 2207* (NY); Puerto Tortuguero y Hatillo, *García et al. 137* (JBSD); Hatillo, *Zanoni 31122* (JBSD, USF); Palmar de Ocoa, *Clase & García 2859* (JBSD); Hatillo, *Veloz 1779* (JBSD); Hatillo, *Franck et al. 2305* (USF); Hatillo, *Franck et al. 2306* (USF); Azua, *Lavastre 1914* (NY). BARAHONA PROV.: Las Salinas, *Fuertes 974* (NY); Valley of Neiba, *Howard & Howard 8336* (GH, NY, US). INDEPENDENCIA PROV.: Municipio La Descubierta, Las Caritas, *Clase et al. 5637* (JBSD); Duverge, *Camejo & Feliz 60* (JBSD). MONTE CRISTI PROV.: Villa Elisa, *Franck et al. 2309* (USF); Monte Cristi, *Franck et al. 2307* (USF); Monte Cristi, *Franck et al. 2308* (USF); Villa Elisa, *Sauleda et al. 7546* (USF); Guayubín, *Abbott 1016* (US). PERAVIA PROV.: Punta Caballera, *Zanoni et al. 22005* (JBSD); Baní, *Zanoni et al. 14970* (JBSD). PERDENALES PROV.: Perdenales, *Liogier & Liogier 25260* (JBSD); Cabo Rojo, *Veloz et al. 942* (JBSD); Cabo Rojo, *Zanoni & Mejía 16753* (JBSD, NY); El Guano, *Zanoni & Pimentel 25903* (JBSD); Cabo Rojo, *Fisher-Meerow 793b* (FLAS). SAN JUAN PROV.: San Juan de la Maguana, *Liogier & Liogier 26641* (JBSD); Guanito, *Sauleda et al. 7579* (USF). SANTIAGO PROV.: Santiago to Jacagua, *Liogier 11041* (GH, NY, US); Navarrete, May 1985, *Kimnach s.n.* (HNT); Santiago de los Caballeros, *Read 1076* (FTG). VALVERDE PROV.: Mao, *Abbott 1043* (US). **HAITI**. ARTIBONITE DEPT.: Gonaïves, *Clover 19396* (US); Gonaïves, *Clover 11015* (US). NORD-OUEST DEPT.: Port de Paix, *Ekman 3994* (K, NY, S, US); Port de Paix, *Leonard & Leonard 15642* (GH, NY, US); Baie des Moustiques, *Leonard & Leonard 12003* (K, US); Île de la Tortue, *Ekman 4165* (S). OUEST DEPT.: Étang Saumâtre, *Leonard 3513* (NY, US); Étang Saumâtre, *Leonard 4249* (NY, US); Plaine du Cul de Sac, 1916, *Buch s.n.* (IJ, illustration); Anse-à-Galets, *Leonard 3256* (US). SUD DEPT.: Port-à-Piment, *Ekman 700* (S).

Etymology. Divaricate branching.

Discussion. *Harrisia divaricata* often forms a well-defined trunk with spreading branches in the sub-canopy and often has a strongly tuberculate immature yellowing fruit (Figs. 69–70). It also has relatively small seeds and long spines on the basal parts of the stem. It has been suggested that *H. divaricata* is the only species in the Dominican Republic (Corman 2005). Generally, geography has been relied upon for identification, in that all specimens on Hispaniola would seemingly be *H. divaricata*. The spines of *H. divaricata* are not as densely overlapping as those of *H. portoricensis* and the mid-hypanthium scales may be longer in *H. divaricata*. These species may be sympatric and interbreed, as several specimens from Hispaniola match the densely spinose morphology of *H. portoricensis*. Britton & Rose (1920) distinguished *H. divaricata* (as *H. nashii*) as having "flower-buds pointed" compared to "flower-buds depressed truncate" in *H. portoricensis*. Additional study among living specimens across multiple populations would, of course, be ideal to assess these and other characters. *Harrisia fernowii* seems to have scales that are more ovate on the flower than those in *H. divaricata*, but additional study is warranted to clarify their morphological similarties and differences.

The flower bud shapes might be relatable to the fruit shape, which led Marshall (1941, 1943) to distinguish *Harrisia hurstii* with obovate fruits from *H. nashii* var. *straminea* with ellipsoid fruits, both at the same locality on Hispaniola. Both names proposed by Marshall seem to fall within the range of variation exhibited by *H. divaricata* and *H. portoricensis* (and here *H. hurstii* is tentavely synonymized with *H. portoricensis*). Immature fruits are often ellipsoidal in *H. divaricata*, and usually globose when mature. The variety proposed by Marshall (1941, 1943) was said to differ by having areoles with 11 straw-colored spines compared to *H. nashii* (=*H. divaricata*) having 3–6 gray spines per areole. Young spines are typically yellowish in ser. *Harrisia* of the West Indies and become gray upon maturity, and thus this character is not diagnostic. The number of spines per areole is quite variable within one plant, with some areoles on the type of *H. nashii* var. *straminea* having only six spines. *Harrisia divaricata*, *H. hurstii*, and *H. nashii* have all been recognized as distinct entities (Moscoso 1941, 1943; García et al. 2007), but it is unclear how these taxa were distinguished.

Britton & Rose (1920) doubted that Plumier's plate, one of the earliest known illustrations of a species of *Harrisia* (Burman 1758), could be referred to any cactus species and as such introduced the name *H. nashii*. The plate is undoubtedly a *Harrisia* (Hunt 1984) and *H. nashii* appears entirely synonymous with *H. divaricata* with regard to provenance and morphology. Mottram (2002) chose to narrow the lectotype of *H. divaricata* down to one particular drawing, since the two plates could represent different specimens or gatherings. Nonetheless, I have chosen to follow Lourteig (1991) in recognizing them as a single specimen, with one drawing showing the habit and the other showing finer details. The combination of both drawings helps to fix the application of the name to *H. divaricata*, showing the long spines on the trunk and the non-overlapping shorter spines on the younger stems. Lourteig (1991) proposed the combination *H. divaricata*, apparently unaware that Backeberg (1960) had already made the same combination.

14. Harrisia eriophora (Pfeiff.) Britton, Bull. Torrey Bot. Club 35: 562. 1908. *Cereus eriophorus* Pfeiff., Enum. Diagn. Cact. 94. 1837, nom. cons. prop. **NEOTYPE** (Benson 1982): **Cuba**. Pfeiffer & Otto, Abbild. Beschr. Cact., Tab. 22. 1843, typ. cons. prop.

Shrubs or small trees, with well-developed erect trunk to 1 m. Spines of distal areoles not overlapping those of adjacent areoles, shorter than stem width, to 2.0 cm long and 0.5 mm thick, spines of basal areoles crowded and overlapping, to 6.5 cm long and 1.0 mm thick. Flowers 16–23 cm long. Pericarpel green. Hypanthium green, scales green to green with red tips, ovate. Mid-hypanthium scales 2.8–3.2 × 7.7–10 mm. Sepals greenish pink. Immature fruit green, tuberculate. Mature fruit yellow, smooth. Seeds 1.7–2.1 × 2.6–3.35 mm. Figs. 74–80.

Distribution. West-central and western Cuba (Fig. 3); scrub forest and scrubland; 5–50 m.

Specimens examined. **CUBA**. *Wright 2623* (BM, G, GH, K, NY, P, S). ARTEMISA PROV.: Mariel, *León 13415* (GH, HAC). CIENFUEGOS PROV.: Cienfuegos, *Jack 5406, 5527, & 5556* (GH); Paso Caballos, *Wood, Jr. & Atchison 7446* (A); Jagua, *Carabia 18058* (HAC). HAVANA PROV.: Cojimar, *León 7179* (GH, HAC, NY); Cojimar, *Baker 2828* (US). ISLA DE LA JUVENTUD PROV.: Sierra de los Caballos, *Britton & Wilson 15122* (NY, US); Isle of Pines, s.d., *Jennings s.n.* (US, acc. no. 3045199). MATANZAS PROV.: Espada, *León 16111* (HAC). MAYABEQUE PROV.: Cruz del Norte, *León & Daniel 7802* (HAC, NY); Jibacoa, *León 16833* (HAC). PINAR DEL RÍO PROV.: Sierra Mendoza, *Shafer 11135* (NY); Pan de Azúcar, *E. del Riseo et al. 27580* (HAC); Remates de Guane, *Roig 3938, 4604* (HAC). SANCTI SPÍRITUS PROV.: Las Villas, *Shafer 12091* (A); Sancti Spíritus, *León 4091 & 4093* (HAC, NY); Sancti Spíritus, *Shafer 12090* (NY, US). VILLA CLARA PROV.: Coralillo, *Bermúdez 14270* (HAC).

Etymology. Woolly, for the flower buds (e.g. Braun 1992).

Discussion. *Harrisia eriophora* has flowers with relatively short scales and reddish sepals, relatively large seeds, and long spines on the basal parts of the stem. The designated neotype (typ. cons. prop., Franck 2016) may be from the type specimen, although it is in not absolutely certain.

Areces (1980) explained that red-tipped scales are found in southern Havana Prov. (now Mayabeque Prov.) and that plants along the northern coast have green scales without red tips (Britton & Rose 1920, plate 28; Figs. 74 and 80). However, plate 28 (Fig. 80) shows that the upper scales and sepals are reddish.

I have here identified the specimens of Charles Wright based on the length of the mid-hypanthium scales, which for the most part seems straightforward. However, this does not readily distinguish *Harrisia eriophora* and *H. taetra*, and so I am only guessing these specimens are more likely to be *H. eriophora*, as it is more widespread. The Wright specimens typically do not contain any information about their location within Cuba and the numbers on the specimens only represent a taxon number, not a duplicate specimen (Underwood 1905; Howard 1988). Indeed, nearly all the “2623” specimens of Wright appear to be *H. eriophora* (Fig. 79), with short mid-hypanthium scales, except for “2623” at US which is clearly *H. fernowii*. The specimens of Wright are some of the earliest known herbarium specimens of *Harrisia*, aside from the *H. gracilis* specimen of Abbé Daenen at G. The name *C. pellucidus* Pfeiff. (with five ribs in its protologue) may have been misapplied to *H. eriophora* if the *Wright* “2623” specimen seen by Grisebach (1866: 116) was *H. eriophora*.

Pfeiffer (1837) cited two earlier names in syonymy, causing *Harrisia eriophora* to be an illegitimate name that ought to have adopted the type of *C. cubensis*. It is currently being proposed that *Cereus eriophorus* be conserved and made legitimate since the epithet has been widely used ever since its introduction in 1837 (Franck 2016). However, to avoid *H. eriophora* itself being treated as another illegitimate name citing the earlier *C. cubensis* and not based on the basionym *C. eriophorus* (e.g. *Harrisia eriophora* Britton, nom. illeg.), Proposal 235 (Wiersema et al. 2016) would need to be accepted to allow for a conserved basionym to retroactively be available for the combination *H. eriophora* (Pfeiff.) Britton, with *C. cubensis* necessitating rejection. The neotype of *C. eriophorus* (typ. cons. prop.) was previously designated by Benson (1982: 934) and was overlooked by Franck (2012b) who superfluously designated the same neotype. This type must be conserved to preserve the modern use of *H. eriophora*. Greuter & Rankin (2016) opted to use the name *H. cubensis* for this taxon, though the protologue of the basionym *C. cubensis* is incongruent as it describes thick stems similar to tree-like species of *Cereus*, which in *Harrisia* are only found in *H. tetracantha*.

15. Harrisia fernowii Britton, Bull.Torrey Bot. Club 35: 562. 1908. **LECTOTYPE** (Franck 2014): **Cuba**. Santiago de Cuba Prov., Río Grande to Río Ubero, 1906, *Taylor 254* (NY [flower buds only]).

Harrisia taylorii Britton, Bull.Torrey Bot. Club 35: 565. 1908. *Cereus taylorii* (Britton) Vaupel, Monatsschr. Kakteenk. 23: 37. 1913. **LECTOTYPE** (Franck 2012b): Britton & Rose, The Cactaceae 2: 153, Fig. 224. 1920. **EPITYPE** (Franck 2012b): **Cuba**. Guantánamo Prov., Novaliches, *Hioram 1806* (NY, isoepitype: HAC).

Cereus eriophorus var. *laetevirens* Salm-Dyck ex Pfeiff., Enum. Diagn. Cact. 94. 1837. **NEOTYPE** (designated here): **Cuba**. Santiago de Cuba Prov., Río Grande to Río Ubero, 1906, *Taylor 254* (NY [flower buds only]).

Shrubs or small trees with well-developed erect trunk to 1 m. Spines of distal areoles sometimes overlapping those of adjacent areoles, sometimes longer than stem width, to 3.0 cm long and 0.5 mm thick, spines of basal areoles crowded and overlapping, to 7.5 cm long and 1.2 mm thick.

Flower length 19–23.5 cm. Pericarpel green. Hypanthium olive green to slightly reddish distally, scales green, ovate to ovate-lanceolate. Mid-hypanthium scales 3.2–4.8 × 12.8–18.0 mm. Sepals yellow green. Immature fruit green, moderately tuberculate. Mature fruit yellow, smooth, globose. Seeds 1.4–1.65 × 2.05–2.6 mm. Figs. 16, 81–86.

Distribution. East Cuba (Fig. 3); scrub forest and scrubland; 0–50 m.

Specimens examined. **CUBA**. *Wright 2623* (US); *Wright 2624* (BM, GH, K, P). CAMAGÜEY PROV.: entre Nuevitas y Minas, *León & Dahlgren 23393* (HAC). GRANMA PROV.: Sierra Maestra, *Meszaros 6* (ZSS), Cabo Cruz, *León 16358* (HAC). GUANTÁNAMO PROV.: Novaliches, *Maxon 4517* (NY, S, US); Guantánamo, *León 3931* (HAC, NY); Novaliches, *Britton 2003* (NY, US); Guantánamo Bay, *Britton 1969* (NY, US); Imías, *León & Pérez 12557* (HAC, NY, US); Imías, *León & Pérez 12484* (HAC, NY); Imías, *León 16854* (HAC); Novaliches, *Ekman 2962* (G, K, S); Pueblo de Maisí, *León 18495* (HAC); Maisí, *León 20097* (HAC). HOLGUÍN PROV.: Holguín, Jan 1984, *Dice s.n.* (HNT). SANTIAGO DE CUBA PROV.: Reuter, *León 3744* (HAC, NY); Daiquirí, *Britton & Cowell 12656* (NY); Santiago de Cuba, *León 3745* (HAC, NY); Santiago de Cuba, *Ekman 7752* (S); Bacanao, *Rauh 70007* (ZSS); Renté, *Chrysogone 2620* (HAC); Cabañas Bay, *Britton & Cowell 12814* (NY). U.S. NAVAL STATION GUANTANAMO BAY: Cuzco Beach, *Areces-Mallea et al. 6619* (MAPR).

Etymology. Bernhard E. Fernow (1851–1923), forester.

Discussion. The hypanthium and ovate-lanceolate scales of *Harrisia fernowii* are yellow-green to green. Its spines are much longer on the lower areoles of the stem, and its seeds are smaller than other species of *Harrisia* in Cuba. Here it is only marginally separated from *H. divaricata* by the flower scales; additional study is needed to clarify if they are distinct. The smaller seeds, longer hypanthium scales, and predominantly greenish flowers seem to distinguish *H. fernowii* from the putatively allopatric *H. eriophora*.

The description of *Harrisia fernowii* is stated to be mainly from *Taylor 254* (Britton 1908), though only a fragment packet of flower buds is extant and available as the lectotype (Franck 2014). Britton (1908) also identified a collection by Charles Wright in the protologue, but did not indicate which specimen was seen. It would presumably be the one at NY ("2623"), but based on the short hypanthium scales, this specimen is more likely *H. eriophora*. The numbers on Wright specimens are merely taxon numbers; specimens with the same number could have been collected at different times and places (Mill & Stark Schilling 2010). Wright's specimens are also bereft of specific locations within Cuba, but some knowledge of his whereabouts are known (Underwood 1905; Howard 1988). All the "2624" specimens appear to be *H. fernowii*. The earlier lectotype selected for *H. fernowii* (Franck 2012b) appears to be inappropriate since the specimen selected by Franck (2012b) is not cited in the protologue (Franck 2014).

The seed depicted in Barthlott & Hunt (2000: *Rauh 70007*) would presumably be *Harrisia fernowii*, not *H. eriophora* as stated in the text. The name *Cereus pitajaya* (Jacq.) DC has been misapplied to *H. fernowii* (Grisebach 1866: 116).

Cereus eriophorus var. *laetevirens* was described to have a yellow-green stem, and is possibly a synonym of *Harrisia fernowii*, whose stem is often light green (Britton 1908). It could be applied to other West Indian species of *Harrisia*. Although an old name, since it was described at the varietal level, it has no priority at the species level and is unlikely to be disruptive to the nomenclature of *Harrisia*. A neotype is designated to secure its application to *H. fernowii*.

The name *Harrisia undata* (Pfeiff.) Britton is illegitimate as the basionym is a later homonym for *Cereus undatus* Haw. (=*Hylocereus undatus* (Haw.) Britton & Rose). It is here supposed that

Harrisia undata, nom. illeg., was intended to represent the species here known as *H. fernowii* (Fig. 86).

16. Harrisia fragrans Small ex Britton & Rose, Cact. 2: 149. 1920. *Cereus fragrans* (Small ex Britton & Rose) Little, American Midland Naturalist 33: 496. 1945. *Cereus eriophorus* Pfeiff. var. *fragrans* (Small ex Britton & Rose) L. D. Benson, Cact. Succ. J. (Los Angeles) 41: 126. 1969. *Harrisia eriophora* (Pfeiff.) Britton var. *fragrans* (Small ex Britton & Rose) D. B. Ward, Novon 14: 366. 2004. **LECTOTYPE** (Franck 2012b): **USA**. Florida, St. Lucie Co., 6 mi. S of Ft. Pierce, hammock on sand dune, 20 Dec 1917, *Small 8457* (NY [00385810], isolectotypes: FLAS, GH, NY [00385809], S, US).

Harrisia simpsonii Small ex Britton & Rose, Cact. 2: 152. 1920. *Cereus gracilis* Mill. var. *simpsonii* (Small ex Britton & Rose) L. D. Benson, Cact. Succ. J. (Los Angeles) 41: 126. 1969. *Harrisia gracilis* (Mill.) Britton var. *simpsonii* (Small ex Britton & Rose) D. B. Ward, Novon 14: 367. 2004. **LECTOTYPE** (designated here): **USA**. Florida, Monroe Co., Pumpkin Key, collected by Small in 1916, flowered 18 Jun 1917 [43933] (NY, isolectotype: US [00174217]).

Shrubs, trunk not evident or poorly developed. Spines of distal areoles sometimes overlapping those of adjacent areoles, sometimes as thick as stem width, to 3.5 cm long and 0.8 mm thick, spines of distal and basal areoles similar. Flowers 15–20 cm long. Pericarpel red-green. Scales of mid-hypanthium 1.5–2.0 mm wide. Hypanthium red basally to brownish yellow-green distally, scales brownish yellow-green with red tips, deltoid-subulate. Mid-hypanthium scales 1.4–2.3 × 7.0–10.3 mm. Sepals brownish yellow-green to pale pink-brown. Immature fruit reddish green to dark red-purple, tuberculate. Mature fruit red to pale red to yellow-orange, smooth to lightly tuberculate. Seeds 1.7–2.0 × 2.7–3.0 mm. Figs. 4, 11, 14, 19, 36, 87–91.

Distribution. Atlantic Coast of peninsula, lower Everglades and Keys, Florida, USA (Fig. 3); coastal berm, scrub, shell mound, rockland hammock, and maritime hammock; 0–10 m.

Specimens examined. **USA.** FLORIDA: Between Indian River and ocean, *Curtiss 963* (NY, US). Brevard Co.: Malabar, 30 Jul 1912, *Small s.n.* (NY); Malabar, *Rolfs 78* (NY); Melbourne Beach, 7 Jan 1983, *Hames s.n.* (FLAS). Indian River Co.: Vero Beach, *Popenoe 2411* (FTG). Miami-Dade Co.: Madeira Hammock, 10 May 1919, *Small et al. s.n.* (NY); Cuthbert Lake, Apr 1916, *collector not given* (NY); Biscayne Bay, *Franck 1236*, *1465*, *2845*, *2899* (USF). Monroe Co.: Pumpkin Key, 1919, *Small s.n.* (NY, US); Flamingo, May 1919, *Small s.n.* (NY); Key Largo, 22 May 1919, *Small & DeWinkeler s.n.* (NY); Key Largo, *Small 29964*. (NY); Cape Sable, *Moldenke 5861* (NY); Upper Matecumbe Key, *Moldenke 5832* (NY); Everglades National Park, *Hill 2948* (FTG, UNC); Key Largo, *Long et al. 1863* (USF); Key Largo, 23 Feb 1968, *Skinner & Weymouth s.n.* (FTG); Flamingo, 16 May 1965, *Craighead s.n.* (FTG); Everglades, 16 Apr 1965, *Craighead s.n.* (USF); Tavernier, *Franck 1278* (USF); Everglades National Park, *Franck 1277* (USF); Everglades National Park, *Benson 16578* (RSA); Plantation Key, *Franck 1279* (USF); Harry Harris Park, *Franck 2203*, *2722* (USF); Key Largo, *Franck 2204* (USF); Key Largo, *Austin et al. 6880* (FTG); Key Largo, *Austin & Austin 6868* (FTG); Turkey Gobbler Key, *Austin et al. 6896* (FTG); Big Pine Key: 8–9 May 1919, *Small et al. s.n.* (NY, US); *Miller, Jr. 1713* (US); *Killip 41330* (US); *Killip 32033* (FLAS, K, US); *Killip 44348* (US); *Benson et al. 16575* (RSA); *Austin et al. 6942* (FTG), 1986, *Tabb s.n.* (FTG); *Franck 2627* (USF). Palm Beach Co.: *Avery 1920* (FLAS), *Avery 1893* (FTG). St. Lucie Co.: Ft. Pierce, Aug 1916, *Vosburg s.n.* (US); Savannas Preserve State Park, *Franck 472* (USF); Ft. Pierce, *Benson & Benson 15375* (RSA); S of Ft. Pierce, May 1919, *Dahlgren s.n.* (F); Stuart, *McCart 11289* (FLAS), Savannas Preserve State Park, *Bradley et al. 2426* (FTG). Volusia Co.: Cape Canaveral National Seashore, *Franck 473* (FTG, USF); Turtle Mound, *Norman 101* (RSA).

Etymology. Fragrant, pertaining to the flower.

Discussion . *Harrisia fragrans* is the northernmost representative of the genus. It is the only West Indian species of *Harrisia* with red fruit (Small 1932). Observations of yellowish fruits appear to be incipient in maturation and later change to red or orangeish (Austin 1984). The lower hypanthium and pericarpel of the flowers are reddish and the spines are not noticeably longer on the basal parts of the plant. In one population, pinkish petals were observed (Fig. 81B), the only occurrence known so far in *Harrisia*.

The name *Harrisia simpsonii* is here treated as a synonym of *H. fragrans*. The DNA sequence data and morphology support synonymization of *H. simpsonii* with *H. fragrans* (Franck 2012b; Franck 2013; Franck et al. 2013b). Current known extant populations suggest a large disjunction between northern and southern populations along the east coast of Florida, however, this may have not been true historically (Franck 2012b). Vouchers are here cited from Volusia through to Monroe Cos., with the exception of Martin and Broward Cos. The St. Lucie Co. population of *H. fragrans* experienced an introgression of the plastid haplotype from *H. aboriginum* (Franck et al. 2013b). Of the two Florida species, *H. fragrans* has received the most study, mainly the upper-central peninsula populations which were treated as distinct from *H. simpsonii* (Rae 1995; Rae & Ebert 2002; Hutchinson & Pazara 2004; Bradley & Hines 2007).

The cited holotype of *Harrisia simpsonii* has never been located, however two others were cited in the protologue (Britton & Rose 1920), a photograph (Fig. 223) and Pumpkin Key specimens cultivated by the New York Botanical Garden and Charles Deering. Benson (1969) designated a lectotype congruent with the locality of the cited type. This specimen was not cited but was presumably available to Britton at NY as the label appears to bear his handwriting. In a strict interpretation of Art. 9.12 (McNeill et al. 2012), it would seem that a cited specimen must be chosen as lectotype over an uncited specimen, which is done here, however peevish it may be for a name whose application is fairly sound.

The name *Harrisia brookii* has been misapplied to this species (Small 1913a, 1913b). Backeberg (1977) listed *H. deeringii* as 2 m tall from Pumpkin Key, Florida but did not validly publish it. It presumably represents a population of *H. fragrans*.

17. Harrisia gracilis (Mill.) Britton, Bull. Torrey Bot. Club 35: 563. 1908. *Cereus gracilis* Mill., Gard. dict., ed. 8. 1768. *Cactus gracilis* (Mill.) Weston, Bot. univ. 1: 33. 1770. **LECTOTYPE** (Franck 2012b): Trew, Pl. Select., Tab. 14. 1751.

Shrubs, or small trees, with well developed trunk to 1m. Spines not overlapping those of adjacent areoles, shorter than stem width, to 2.5(–3.5) cm long and 0.5 mm thick, distal and basal spines similar. Flowers 21 cm long. Pericarpel green. Hypanthium greenish brown, scales yellow-green to green, subulate. Mid-hypanthium scales 2.5–3.3 × 11.6–12.8 mm. Sepals pale greenish brown. Immature fruit green, moderately tuberculate. Mature fruit yellow, smooth. Seeds 1.3–1.6 × 2.1–2.3 mm. Figs. 7, 12, 18, 37, 92–104.

Distribution. Coastal southern Jamaica (Fig. 3); scrubland forest; 5-100 m.

Specimens examined. **JAMAICA**. CLARENDON PAR.: Salt Island, *Britton 3070* (NY); Harris Savannah, Dec 1998, *Douglas s.n.* (UCWI); Harris Savannah, *Franck 2661* (USF). ST. ANDREW PAR.: Palisadoes, *Franck et al. 2265* (IJ, USF); Palisadoes, *Asprey et al. 2422* (UCWI); Palisadoes, *West & Arnold 468* (FLAS); Sandy Gully, *Robertson 2333* (UCWI); Hope, *Harris 6946* (UCWI); Kingston and Gregory Park, *Maxon & Killip 335* (F, GH, NY, US); Kingston, *Britton 413* (NY); Port Henderson, *Higgins s.n.* (photo, NY!). ST. CATHERINE PAR.: Hellshire Hills, *Scott 288* (UCWI); Hellshire Hills, *duQuesnay 453* (UCWI); Hellshire Hills, s.d., *Fleming s.n.* (ZSS, acc. no.

AX 12819); Spanish Town, *Proctor 36874* (FTG). ST. ELIZABETH PAR.: Great Pedro Bay, *Britton 1255* (NY).

Etymology. Gracile, slender stems.

Discussion. *Harrisia gracilis* is the only short-spined species outside of Florida. It differs from the Florida species by having a greenish brown hypanthium (Britton 1917a) and smaller seeds. The name *C. eriophorus* had been misapplied to this species (Grisebach 1860). Some of the earliest known descriptions of *Harrisia* are of *H. gracilis* from Jamaica (Sloane 1696; Trew 1751). The earliest known specimen of *Harrisia* is also likely of this species from the herbarium of Abbé Daenen (Fig. 101), who published on the medicinal applications of plants (Daenen 1852). It is unknown when the specimen was made as only the date of reception at G is noted.

The name *Cereus repandus* (L.) Mill. is modernly applied to a thick-stemmed, tree-like cactus of *Cereus* s. str. (Hunt et al. 2006), though *Cereus repandus* sensu Haworth (1812) cited the lectotype and basionym of *Harrisia gracilis*. Haworth (1812: 183) provided the exact same Latin diagnosis of *Cereus repandus* as Linnaeus did for *Cactus repandus* L., but Haworth cited other elements. It seems Haworth (1812: 183, 1819: 78) was proposing that *Cactus repandus* L. and *Cereus gracilis* Mill. were synonymous. However, Miller had already published the name *Cereus repandus*, thus making Haworth's sense of *C. repandus* misapplied or a later homonym. Furthermore, Miller's *Cereus repandus* cited the now lectotype of *Cactus lanuginosus* L. (lectotypified by Zappi 1994: 145) as well as repeating the nearly exact corresponding phrase from Linnaeus (1737: 182, no. 7) and Royen (1740: 279, no. 5) associated with *Cactus languinosus*, not citing the same elements in the Linnaean *Cactus repandus*. For *Cereus lanuginosus* Mill., Miller cited the page before the Hermann lectotype. The name *Cereus lanuginosus* Mill. has not been regarded as a new combination from the basionym *Cactus lanuginosus* L. and *Cereus lanuginosus* was not cited in synonymy for *Pilosocereus lanuginosus* (L.) Byles & G.D. Rowley (=*Cactus lanuginosus* L.) by Zappi (1994). Miller's *Cereus repandus* is not a clear new combination from the basionym *Cactus repandus* L., especially considering *Cereus lanuginosus* Mill. is not treated as such. The combination and application of *Cereus repandus* (L.) Mill. are not at all straightforward (see Kiesling 1982; Heath 1992; Hunt & Taylor 1992) and the name is in need of typification and clarification. Perhaps it should just be considered that Miller made valid combinations of all Linnaean epithets of *Cactus* that he cited in 1768 under *Cereus* but made errors in doing so.

18. Harrisia portoricensis Britton, Bull.Torrey Bot. Club 35: 563. 1908. *Cereus portoricensis* (Britton) Urb., Symb. antill. 4: 430. 1910. **NEOTYPE** (Franck 2012b): **Puerto Rico**. mainland, near Ponce, 1906, *Britton & Cowell 1324*, flowered 21 Aug 1912 (NY). **EPITYPE** (Franck 2012b): **Puerto Rico**. Mona Island, 6 Mar 1994, *Areces-Mallea s.n.* (2 sheets, NY).
Harrisia hurstii W.T. Marshall, Cactaceae, with illustrated keys of all tribes, sub-tribes and genera, 96. 1941. **TYPE**: **Dominican Republic**. Monte Cristi Prov., Hurst finca near Monte Cristi, 25 Nov 1936, *Marshall s.n.* (holotype: GH).

Shrubs, trunk not evident or poorly developed. S pines of distal areoles usually overlapping those of adjacent areoles, often as long or longer than stem width, to 3.0 cm long and 0.7 mm thick, spines of basal areoles to 7.5 cm long, 1.0 mm thick. Flowers 17–22 cm long. Pericarpel green. Hypanthium green to greenish brown, scales yellow green to green, ovate-lanceolate. Mid-hypanthium scales 2.8–3.4 × 8.6–9.8 mm. Sepals pale greenish brown. Immature fruit green. Mature fruit yellow, smooth. Seeds 1.4–1.7 × 2–3 mm. Figs. 105–107.

Distribution. Southwest mainland and western and southern islands of Puerto Rico, and maybe west Dominican Republic (?) (Fig. 3); scrubland on exposed limestone rock; 0-150 m.

Specimens examined. **DOMINICAN REPUBLIC**(?). INDEPENDENCIA PROV.: Isla Cabritos, *Mejía & Pimentel 17228* (JBSD). MONTE CRISTI PROV.: El Morro, *Judd et al. 3002* (FLAS, JBSD); Monte Cristi, 25 Nov 1936, *Marshall s.n.* (GH). SANTIAGO PROV.: Jaiqui Picado, *Liogier 11241* (GH, NY, US). **PUERTO RICO**. *Britton 1957* (BM). PONCE MUNICIP.: Ponce to Playa Las Cucharas, *Britton et al. 1959* (NY, US); Caja de Muertos Island, *Breckon & López 7095* (MAPR). DESECHEO ISLAND: *Britton et al. 1599* (NY, US); *Woodbury et al. D-152* (MO, NY); *Breckon & Carraro 4780* (MAPR). MONA ISLAND: *Britton et al. 1737* (NY, US); *Chardon & Otero 1001* (NY); *Little, Jr. & Kuns 16540* (NY, US); s.d., *Fumero-Cabán & Meléndez-Ackerman s.n.* (USF, acc. no. 252611); *Breckon & Kolterman 6747* (MAPR). MONITO ISLAND: *Breckon et al. 5185* (MAPR). **CULTIVATED** (origin unknown) (?): *Peláez 1474* (JBSD).

Etymology. Puerto Rico.

Discussion. *Harrisia portoricensis* is here recognized by its densely overlapping and numerous spines in combination with its green scales and hypanthium. It is apparently extirpated from mainland Puerto Rico (Liogier 1994; Medina & Cuevas 2009) where it was found near Ponce (Britton 1908) and Guayanilla (Spencer 1955). The ecology of *H. portoricensis* in Puerto Rico has been extensively studied (Rojas-Sandoval & Meléndez-Ackerman 2013).

It would be easy and intuitive to state that *Harrisia portoricensis* is endemic to Puerto Rico, and this may indeed be the case. However, this assertion seems to presently rely solely on geography instead of demonstrated morphological differences. Based on the biogeography, it seems clear that populations from Hispaniola dispersed to give rise to the populations in Puerto Rico (Franck et al. 2013b), the easternmost extent of *Harrisia* in the West Indies. Several specimens cited here from coastal and dry limestone areas in the Dominican Republic match the densely spinose morphology of *H. portoricensis*. The length of the flower scales of these specimens is not known, which may differ between *H. divaricata* and *H. portoricensis*. Presently it is unclear if there is a proven morphological character that could define populations in Puerto Rico as endemic or if *H. portoricensis* should be regarded as present in the Dominican Republic. Britton & Rose (1920) claimed that Puerto Rican populations were distinct because of their depressed-truncate flower buds. Additional study is needed to verify or refute the geographic distribution of *H. portoricensis*.

The description given for *Harrisia hurstii* does not warrant recognition apart from *H. divaricata* and *H. portoricensis* based on current evidence. The holotype of *H. hurstii* seems to resemble *H. portoricensis*, given its strongly overlapping spines on the relatively thick stem. Apical stems of *H. portoricensis* often seem to be relatively thick, compared to *H. divaricata*, although slender stems can be observed on *H. portoricensis*, too. *Harrisia nashii* var. *straminea* (=*H. divaricata*) is seemingly from the exact same type locality as *H. hurstii*. Given that the two names proposed by Marshall (1941, 1943) have their provenance in the Dominican Republic, they may both be synonyms of *H. divaricata*, if *H. portoricensis* is proven to be endemic to Puerto Rico. *Harrisia hurstii* was distinguished as having “strict branches” and obovate fruits compared to the “divergent branches” and ellipsoid fruits of other nearby specimens in Monte Cristi Province, Dominican Republic. Photos are shown (Marshall 1941) to exemplify these characters, though they seem to depict rooted cuttings and not mature plants in habitat. The plants in the photo of the proposed *H. hurstii* (Marshall 1941: Fig. 46) do not appear to be old or tall enough to show any branching patterns. Though *H. divaricata* sometimes has divergent branches, ascendent branches are also observed. The branching angles of *H. divaricata* and *H. portoricensis* do not appear to be reliable characters for identification.

19. Harrisia taetra Areces, Revista Jard. Bot. Nac. Univ. Habana 1: 17. 1980. **TYPE**: **Cuba**. Pinar del Río Province, Peninsula de Guanahacabibes, Terraza, costera la Iguana, en la carretera al cabo de San Antonio, 27 Mar 1973, *Areces 37991* (holotype: HAJB).

Shrubs, trunk not evident or poorly developed. Spines of distal areoles usually overlapping those of adjacent areoles, often as long or longer than stem width, to 10.3 cm long and 0.9 mm thick, spines of basal areoles to 12 cm long, 1.5 mm thick. Flowers 16.5–20 cm long. Pericarpel pale green. Hypanthium vinaceous to rose-purple to rose-pink, sometimes reddish green distally, scales pale purple to yellowish with red tips, deltoid-ovate. Mid-hypanthium scales 2.8–3.0 × 5.4–7.8 mm. Sepals purple, slightly pinkish. Immature fruit greenish red to dark red-purple, moderately tuberculate. Mature fruit yellow, smooth to lightly tuberculate. Seeds 1.8–2.0 × 2.9–3.2 mm. Figs. 108–110.

Distribution. Southwest Pinar del Río Prov., Cuba (Fig. 3); scrubland on exposed limestone rock; 5–20 m.

Specimens examined. **CUBA**. PINAR DEL RÍO PROV.: Guanahacabibes, 17 Sep 2008, *ZSS staff s.n.* (ZSS); Corrientes Bay, *Britton & Cowell 9880* (NY); Península Corrientes, *Alain 6917* (HAC); Las Martinas, *Shafer 11096* (A, NY); Bay of Mariel, *Britton & Gager 7600* (K, NY, US).

Etymology. From *taeter*, meaning horrid, repulsive, etc. referring to the thick, spiny stems.

Discussion. *Harrisia taetra* has densely overlapping spines and flowers with red-purplish scales and a red-purplish hypanthium. Though apparently not very closely related, this species has a similar vegetative morphology to *H. portoricensis*, also occurring on exposed limestone rock and having densely overlapping spines. The distinctiveness of *H. taetra* from *H. eriophora* would benefit from further examination, as *H. eriophora* is apparently found nearby in Pinar del Río Province and on Isla de la Juventud.

NOTHOTAXA

×Guillauminara P.V. Heath, Calyx 1: 111. 1992. = *Echinopsis* Zucc. × *Harrisia* × *Trichocereus* (A. Berger) Riccob.

This is a hybrid allegedly between *Harrisia jusbertii* and *Trichocereus lamprochlorus* (Lem.) Britton & Rose, but this has not been verified.

×Harricereus G.D. Rowley, Natl. Cact. Succ. J. 37: 76. 1982. = *Cereus* Mill. × *Harrisia*.

Cereus and *Harrisia*, though both in tribe Cereeae, are in different subtribes (sensu Nyffeler & Eggli 2010) and the reported hybrid seems dubious. Ritter (1980) reported a natural hybrid between *H. bonplandii* and *C. stenogonus* K. Schum. in Puerto Casado, Paraguay.

×Harrisnopsis G.D. Rowley, Natl. Cact. Succ. J. 37: 77. 1982. ×*Eriocereopsis* Doweld, Tsukkulenty 4: 34. 2001. = *Echinopsis* × *Harrisia*. **TYPE**: ×*Harrisnopsis jusbertii* (Rebut ex K. Schum.) P.V. Heath.

It is claimed that *Harrisia jusbertii* is a hybrid of *Echinopsis* and *Harrisia* (Berger 1905), and hence there exists the name *Harrisnopsis*. There is currently no evidence, however, that any hybrid between these two genera has ever been made.

×Selenirisia G. D. Rowley, Natl. Cact. Succ. J. 37: 79. 1982. = *Harrisia* × *Selenicereus* (A. Berger) Britton & Rose.

This hybrid is allegedly between *Harrisia bonplandii* and *S. pteranthus* (Link ex A. Dietr.) Britton & Rose but as these two genera are distantly related across divergent tribes, it is extremely dubious. Their morphological similarity is probably the cause of misidentification.

EXCLUDED NAMES

Cereus bonplandii Parm. ex Pfeiff. var. *brevispinus* Maass-Zehlendorf, Monatsschr. Kakteenk. 15: 119. 1905, nom. nud.

Cereus bonplandii Parm. ex Pfeiff. var. *pomanensis* F.A.C. Weber ex K. Schum. Gesamtbeschr. Kakt. 137. 1899, nom. nud.

Cereus repandus Haw., Syn. Pl. Succ. 183. 1812, nom. illeg. [McNeill et al. 2012: Art. 53.1].

Cereus undatus Pfeiff., Enum. Diagn. Cact. 94. 1837, nom. illeg. *Harrisia undata* (Pfeiff.) Britton, Bull.Torrey Bot. Club 35: 564. 1908, nom. illeg. [McNeill et al. 2012: Art. 53.1].

Eriocereus (A. Berger) Riccob. subg. *Pseudoharrisia* Backeb., Blätt. Kakteenf. 1934–3, 1936–6. 1934–1936, nom. inval. [McNeill et al. 2012: Arts. 22.2 & 39.1]. This taxon ought to have been *Eriocereus* subg. *Eriocereus* since it included *H. tortuosa*.

Eriocereus (A. Berger) Riccob. subg. *Roseocereus* Backeb., Blätt. Kakteenf., 1934–3. 1934, nom. nud.

Eriocereus (A. Berger) Riccob. subg. *Roseocereus* Backeb., Blätt. Kakteenf., 1936–6: 5–6. 1936, nom. inval. [McNeill et al. 2012: Art. 39.1].

Eriocereus (A. Berger) Riccob. series *Acanthocarpi* Backeb., Blätt. Kakteenf. 1938–6. 1938, nom. nud.

Eriocereus (A. Berger) Riccob. series *Eriocarpi* Backeb., Blätt. Kakteenf. 1938–6. 1938, nom. nud.

Eriocereus cavendishii (Monv.) Riccob., Boll. Reale Orto Bot. Palermo 239. 1909. = *Monvillea cavendishii* (Monv.) Britton & Rose, Cact. 2: 21. 1920.

Eriocereus crucicentrus Ritter ex Backeb., Das Kakteenlexicon. 1966, nom. nud.

Eriocereus martianus (Zucc.) Riccob., Boll. Reale Orto Bot. Palermo 240. 1909. = *Disocactus martianus* (Zucc.) Barthlott, Bradleya 9: 88. 1991.

Eriocereus spinosissimus Buining & Brederoo. = *Arthrocereus spinosissimus* (Buining & Brederoo) F. Ritter, Kakteen in Südamerika 1: 244.

Estevesia P.J. Braun. Probably synonymous with *Cereus* or *Monvillea*.

Estevesia alex-bragae P.J.Braun & Esteves. Probably a species of *Cereus* or *Monvillea*.

Harrisia Lundblad, K. Svenska Vetensk. Akad. Handl. 4: 71. 1950, nom. illeg. [McNeill et al. 2012: Art. 53.1].

Harrisia Robineau-Desvoidy, Mem. Pres. Div. Sav. Acad. R. Sci. Inst. Fr. - Paris 2: 323. 1830, [kingdom Animalia, order Diptera].

Harrisia Britton [unranked] *Euharrisia* Britton & Rose, Cact. 2:148, nom. inval. [McNeill et al. 2012: Arts. 21.3 & 22.2].

Harrisia brailovskyi Carvalho, Rev. Bras. Bio. 43: 148. 1983, [kingdom Animalia, order Diptera].

Harrisia brasiliensis Robineau-Desvoidy, Mem. Pres. Div. Sav. Acad. R. Sci. Inst. Fr. - Paris 2: 324. 1830, [kingdom Animalia, order Diptera].

Harrisia deeringii Backeb., Das Kakteenlexicon. 1966, nom. inval.

Harrisia donae-antoniae M.L. Hooten, Cact. Succ. J. (Los Angeles) 63: 65. 1991 and Cact. Succ. Succ. J. (Los Angeles) 64: 2. 1992., nom. inval. [McNeill et al. 2012: Arts. 38.13 & 40.1].

Harrisia fimbriata (Lam.) F.M. Knuth, Kaktus-ABC 309. 1936. = *Stenocereus fimbriatus* (Lam.) Lourteig, Bradea 5: 408. 1991.

Harrisia fimbriata (Lam.) F.M. Knuth var. *straminia* W.T. Marshall, Cactaceae, with illustrated keys of all tribes, sub-tribes and genera, 96. 1941, nom. illeg. [McNeill et al. 2012: Art. 39.1].

Harrisia floridana Vosburg, nom. nud. Name on Vosburg's specimen at US.

Harrisia floridana Rose ex J.G. Webb, nom. nud. Name on Webb's specimen at NY.

Harrisia hahniana (Backeb.) Kimnach & Hutchison ex Kimnach, Cact. Succ. J. (Los Angeles) 59: 59. = *Echinopsis hahniana* (Backeb.) R. S. Wallace, Cactaceae Consensus Init. 4: 12. 1997.

Harrisia marsilioides Lundblad, K. Svenska Vetensk. Akad. Handl. 4: 71. 1950. = *Harrisiothecium marsilioides* (Lundblad) Lundblad, Taxon 10: 23. 1961.

Harrisia rumpalensis Moravec [Trilobita, publication details unknown, cited in Mergl, M., & P. Budil. 2010. Exceptional preservation of trilobite exoskeletons in the Řevnice Quartzite (Libeň Formation, Ordovician) from Ejpovice in the Rokycany area. Paleontologie 2010: 109–112.].

Harrisia scutellaris Robineau-Desvoidy, Mem. Pres. Div. Sav. Acad. R. Sci. Inst. Fr. - Paris 2: 324. 1830, [kingdom Animalia, order Diptera].

Harrisia tortuosa var. *uruguayensis* Osten, Notas sobre Cactáceas 66. 1941, nom. inval. [McNeill et al. 2012: Art. 39.1]. *Eriocereus pomanensis* var. *uruguayensis* (Osten) Backeb., Die Cactaceae 4: 2095. 1960, nom. inval. TYPE: Uruguay, Río Negro, Estancia Nueva Mehlem, en limo pampeano, 9 Apr 1922, *Schroeder s.n., Herb. Osten 16720* (MVM).

INCERTAE SEDIS

Cereus cubensis Zucc., Allg. Gartenzeitung 2: 244. 1834, nom. rej. prop. **TYPE**: **Cuba** (cultivated at Munich Botanical Garden).

Pfeiffer (1837) listed *Cereus cubensis* as a synonym of *C. eriophorus*. The description of *C. cubensis* described flowers like *C. grandiflorus* L. (= *Selenicereus grandiflorus* (L.) Britton & Rose), nocturnal, and stems thick like *C. peruvianus* (L.) Mill. As *Harrisia* in Cuba tends to have slender stems that are not distinctly thicker than *S. grandiflorus*, *C. cubensis* may refer to *Dendrocereus* Britton & Rose which has nocturnal flowers and thick stems. It has been proposed to reject the name *Cereus cubensis* since its usage, if applied to other Cuban cacti having names with a long history of use, is nomenclaturally disruptive. The protologue of *C. cubensis* is not sufficient to clearly apply it to any one taxon of cacti in Cuba and no original material is known (Franck 2016).

Cereus subrepandus Haw., Suppl. Pl. Succ. 78. 1819. *Eriocereus subrepandus* (Haw.) Riccob., Boll. Reale Orto Bot. Palermo 8: 243. 1909, nom. rej. prop. **TYPE**: Vigebat in hort. Chels. ante A.D. 1817.

This was said to be similar to *Harrisia gracilis* (as *C. repandus* Haw.) except with longer spines, possibly representing a taxon from Cuba or Hispaniola or simply slight variation consistent with *H. gracilis*. Riccobono (1909) mentioned a yellow fruit that is completely red at maturity, suggesting it to be *H. fragrans*, the only Caribbean species with red fruits. However, it is unclear what material Riccobono was examining as only the original material would seem to be relevant. *Cereus subrepandus* has been proposed for rejection since its description is too vague to clarify its application (Franck 2016).

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