



Three new species and growth patterns in *Hechtia* (Bromeliaceae: Hechtioideae)

IVÓN RAMÍREZ MORILLO^{1,3}, CARLOS F. JIMÉNEZ¹, GERMÁN CARNEVALI FERNÁNDEZ-CONCHA¹ & JUAN P. PINZÓN²

¹Centro de Investigación Científica de Yucatán, A. C., Unidad de Recursos Naturales-Herbario CICY, Calle 43 # 130. Colonia Chuburná de Hidalgo, Mérida, Yucatán 97200, México.

²Universidad Autónoma de Yucatán, Campus de Ciencias Biológicas y Agropecuarias, Departamento de Botánica, Carretera Mérida-Xmatkuil, Km. 15.5 Apdo. Postal: 4-116 Itzimná, Mérida, Yucatán 97100, México.

³E.-mail ramirez@cicy.mx (Author for correspondence)

Abstract

Three new species of *Hechtia* from the Mexican State of Oaxaca are herein proposed as new: *Hechtia flexilifolia*, *H. huamelulaensis*, and *H. nivea*, from the physiogeographical provinces of Mixteca Alta, Costas del Sur, and Sierras Centrales de Oaxaca respectively. All three species are described and illustrated. Iconography provided features plants in habitat and under cultivation. An assessment of their conservation status *sensu* IUCN criteria is presented as well. We also discuss and illustrate the three growth patterns identified at this time in the genus.

Keywords: Diversity, endemism, growth patterns, IUCN, Oaxaca, physiogeographical regions

Introduction

Oaxaca ranks third in vascular plant diversity among Mexican states only after Chiapas and Guerrero, with 251 families, comprising 1,824 genera and 8,431 species (García-Mendoza 2004). Among them, angiosperms are the most numerous with 7,752 species, whereas Bromeliaceae is the seventh most diverse family of monocots. However, Oaxaca houses the largest diversity of bromeliads of the country, the latest report accounting for 172 species in 15 genera (Espejo *et al.* 2007a), a figure that represents ca. 50% of all Bromeliaceae reported for Mexico (Espejo *et al.* 2004) and new species are continuously being added.

The genus *Hechtia* Klotzsch (1835: 401) is one of the most interesting members of the Mexican Bromeliaceae. Our latest estimate of the number of species is of 65 (Ramírez & Jiménez 2012), but this figure is becoming rapidly outdated by the discovery of new species every year. Mexico harbors the largest number of species of this genus with ca. 94% of them being endemic to the country, whereas the genus as a whole is restricted to Megamexico III. Espejo *et al.* (2004) reported 14 species of *Hechtia* for Oaxaca, but this number went up to 20 just in three years (Espejo *et al.* 2007a) and five more have been described since then [*H. colossa* Martínez-Correa *et al.* (2010: 746), *H. complanata* Burt-Utley (2012: 6), *H. ixtlanensis* Burt-Utley (2012: 1), *H. isthmusiana* Burt-Utley (2012: 10), and *H. oaxacana* Burt-Utley *et al.* (2011: 7)], and with the three newly species described here, the total number adds up to 28, becoming the leading state in *Hechtia* species richness; furthermore, most of the Oaxacan *Hechtia* species are restricted to the state. In Oaxaca only the genus *Tillandsia* Linnaeus (1753: 286) surpasses *Hechtia* as the most species-rich bromeliad genus with ca. 101 species (Espejo *et al.* 2007a). At present, *Hechtia* includes ca. 70 accepted species out of 89 published binomials. We still have a long way to go in order to reliably document bromeliad diversity in Mexico, until more regions are explored, particularly xerophytic shrublands or open rocky outcrops in remote and inaccessible places.

Givnish *et al.* (2007) proposed a new subfamily, Hechtioideae, with *Hechtia* as its sole member based on molecular evidence. Plants of *Hechtia* are terrestrial or more commonly lithophytic, on volcanic, karstic, or gypsophilous rocks; rosettes are cespitose or rarely caulescent, ranging in size from rather small [ca. 30 cm or smaller in diameter, i.e. *H. edulis* I. Ramírez *et al.* (2011: 363)] to fairly large dimensions [ca. 2 m diameter, i.e. *H. myriantha* Mez (1901: 6)], with succulent leaves, these strongly armed or rarely with serrulate margins. *Hechtia* species occupy mainly xerophytic shrublands, caducifolious tropical forests, and less commonly, *Quercus* Linnaeus (1753: 994) forests (*sensu* Rzedowski 1978). As most bromeliads, many species of *Hechtia* have central inflorescences, but ca. 20% of them have lateral

inflorescences [the *H. glomerata* Zuccarini (1840: 240) complex *sensu* Jiménez (2011)], a character shared with a few other species in the family but part of a unique combination of characters within the family along with unisexual flowers (*vs.* mainly bisexual), dioecious members (*vs.* usually hermaphroditic), and sessile stigma (*vs.* on top of a distinct style).

Materials and methods

Herbarium specimens were prepared from plants cultivated in Yucatan, Mexico, but previously collected sterile or only partially fertile (e.g. fruits) in Oaxaca from 2000 to 2013. Cultivating plants not only allowed obtaining fertile structures (flowers and fruits) but also observing changes under various regimes of water and nutrient availability (e.g., for several years watering was withheld during all of the dry season, whereas during other years plants were regularly watered the year around). Morphological variation of rosette features at the population level was previously evaluated in the field and later also in cultivation, where we usually observed greater size (rosette and inflorescence) development under optimal growth conditions, which not always led to flowering. The complete material (vegetative and floral) of the three species was cross examined to verify their status as new species against all species recorded from Oaxaca and neighboring states, carefully studying the information of the protologues, including type material (whenever available) or high resolution images of types and plants in the field. Each description includes characters observed in live material as well as dry material. For each new species, we included an assessment of conservation based on IUCN criteria (2010).

Growth patterns

Bromeliaceae is a clade composed mainly by taxa with monocarpic rosettes with central (terminal) inflorescence. As mentioned before, some members of *Hechtia* present lateral inflorescences and thus, polycarpic rosettes, a character shared by a few members in the subfamily Bromelioideae [*Disteganthus* Lemaire (1847: t. 227)] and *Greigia* Regel (1865: 137)] and a few species in subfamily Tillandsioideae (*Tillandsia* spp.) (Smith & Till, 1998). Yet, other species feature seemingly lateral inflorescences, and often described as so, which are here interpreted as terminal, see discussion below.

We have identified three different architectural patterns in *Hechtia* (Fig. 1 A–D). They are related to growth schemes of individual rosettes, and the position of the inflorescence relative to the degree of development of the new rosettes. Ongoing phylogenetic analyses should provide insight and testable hypothesis to understand these three different patterns and their evolution.

In a first architectural pattern (Fig. 1A, B), hereafter referred to as the “strict sympodium pattern” (SSP), the apical meristem of a fully grown rosette produces an inflorescence; after fruiting the rosette dies, producing one or more offsets in a basal position, resulting in cespitose plants, usually forming colonies [e.g. *H. purpusii* Brandege (1920: 325) and *H. podantha* Mez (1896: 549)]. This SSP is assumed to derive from a strongly dominant apical meristem that inhibits any other growth of the plant but that is strongly predetermined to make an early transformation into a floral meristem, at which point ceases its dominance, allowing basal vegetative meristems to activate. This pattern is the one commonly found in the rest of the family and is thus assumed to be plesiomorphic whilst the following two types are presumably apomorphic. Our preliminary phylogenetic analyses, using several DNA regions, consistently identify taxa characterized by this pattern as basal in the genus.

In the second pattern (Fig. 1C), hereafter referred to as the “pseudomonopodial pattern” (PMP), the long-lived rosettes produce truly lateral (mostly basal) inflorescences. Here, the apical meristem is also strongly dominant but is simultaneously extremely long lived, apparently never making a transition into a floral meristem. Thus, the rosettes have indefinite vegetative growth, eventually becoming very large (often bearing more than a hundred leaves, e.g. *H. myriantha*). As growth continues and the rosette elongates, the distance between the apical meristem and the most basal ones increases, resulting in a gradual lowering of the dominance degree. Eventually, the lowermost meristems activate, resulting in either inflorescences or new rosettes. Additional rosettes are formed either by rhizomes as in *H. schottii* Baker ex Hemsley (1884: 318), or by stolons (as in *H. glomerata*), or rarely by cespitose growths as is the case in *H. lepidophylla* I. Ramírez (2008: 65)]. Taxa featuring PMP are restricted to the Gulf of Mexico drainages and have been identified by our preliminary phylogenetic analyses as a well-supported clade.

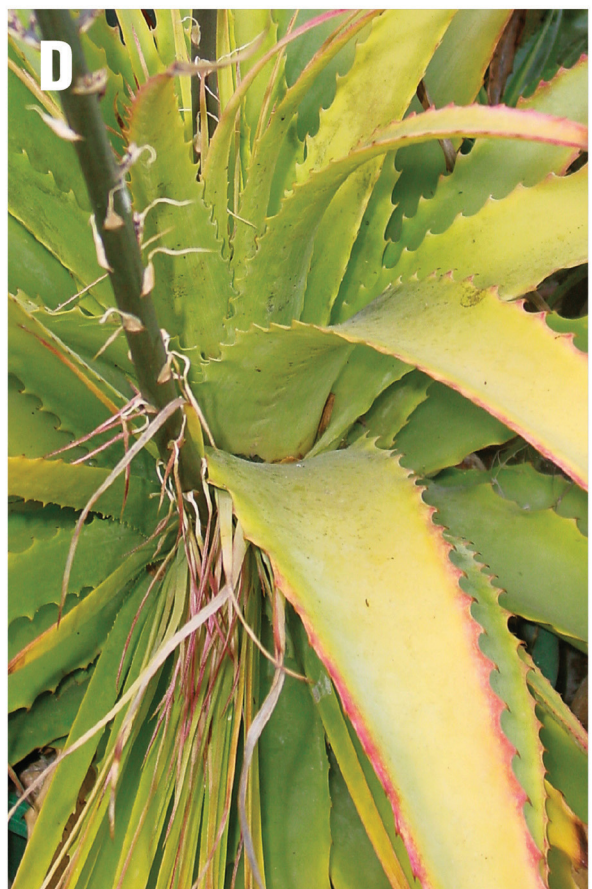


FIGURE 1. Growth patterns in *Hechtia*: A–B. Pattern SPP (strict sympodium pattern), A. *H. podantha*; B. *H. guatemalensis*. C. Pattern PMP (pseudomonopodial pattern), *H. schottii*. D. Pattern SPFP (sympodial with precocious-flowering pattern), *H. huamelulaensis*. (Photographs by Ivón Ramirez).

In the third and final pattern (Fig. 1D) hereafter called the “sympodial with precocious-flowering pattern” (SPFP), the inflorescence emerges from the center of a newly-forming shoot or rosette (thus precocious) that never fully develops. The older rosettes eventually stop growing, and may eventually flower [e.g. *H. rosea* E. Morren ex Baker (Baker 1889: 140)]. The SPFP is here hypothesized to be the result of a weakly dominant apical meristem that cannot prevent axillary meristems from developing into a flowering shoot (precocious flowering resembling lateral inflorescences). It is also predetermined to a temporarily relatively short growth. The SPFP results in relatively compact plants (small number of rosettes), which may or may not be cespitose and that produce both apparently “lateral” and terminal inflorescences. Axillary shoots, whether vegetative or precocious-flowering, may appear in basal or subapical positions, plants thus bearing a mixture of rosettes and inflorescences in several stages of development. Even if these inflorescences were interpreted as lateral, the SPFP remains distinctive because the combination of terminal and lateral inflorescences is unique. Nearly half of the known *Hechtia* species display the SPFP.

The description and characterization of these growth patterns in the genus *Hechtia* should allow us to better understand relationships within the genus and to standardize descriptions and comparisons through the usage of a common terminology based upon morphological and developmental homologies.

Taxonomy

Hechtia flexilifolia I. Ramírez & Carnevali, *spec. nov.* (Figs. 2, 3).

This new species is characterized by an unique combination of characters: leaves numerous, (20–)30–40 in number, proportionally long, narrow, flexible, margins densely spinose, abaxial epidermis glossy and wrinkled, shedding when dry, staminate inflorescence a 1–2 times divided panicle, with a long peduncle, branches at first secund, then horizontal, branches densely flowered, cylindrical, rachis green, sulcate, sterile bases of branches bracteate, petals white.

TYPE:—MEXICO. Oaxaca: Distrito de Tlaxiaco, Municipio Santiago Yosondúa, ca. 4 km después de Santiago de Yosondúa, rumbo a Yerba Santa, en las cascadas, riscos en bosque de pino-encino con algunos elementos mesófilos [ca. 4 km beyond Santiago de Yosondúa, toward Yerba Santa, by the waterfalls, cliffs with pine-oak forest with some mesophyll elements], 16° 50' 43" N, 97° 34' 52" W, 1990 m elevation, 1 July 2013, Ramírez & Carnevali 1868 ♂ (holotype CICY (x7)!; isotypes MEXU!, OAX!, SEL!, US!).

Plants lithophytic, forming a hemispherical rosette, 20–25 cm long, 50–55 cm in diameter. *Leaves* (20–)30–40 in number, erect, becoming slightly reflexed, flexible; *sheaths* broadly oblong, 3–4 x 5.5–6.5 cm, glabrous, drying white-yellowish at the base, dark brown, densely white lepidote and dentate close to the blade; blades sublinear triangular, acute, pungent, 12–60(–100) cm long, 1.5–2.5(–3) cm wide at the base, apical half reflexed, succulent, flexible, U-shaped in cross section, dark green, densely white lepidote abaxially, adaxially corrugated, covered by a thin, white layer (probably the cuticle) that peels off easily, especially when dry, margins spinose, white-yellowish; *spines* antrorse, ca. 2 mm long decreasing to ca. 1 mm long at the apex, 1–1.5 cm apart. *Inflorescence* central, emerging from the center of a newly-forming rosette (type SPFP), erect.

Staminate inflorescence one to twice-branched panicle, ellipsoid, erect or arcuate (only seen in cultivation), sometimes a few primary branches produce a secondary short branch at their base, 2.10–2.70 m long; peduncle terete, 92–97 cm long, 0.8–1.2 cm in diameter, green, longer than the leaves, internodes (2.3–)3.7–4.7 cm long; *peduncle bracts* narrowly triangular, long acuminate, (1.8–) 2.7–19.2 cm long, 1.8–2.4 cm wide at the base, entire to finely serrate, sheaths and blades well differentiated, the basal ones recurved, those at the base with the blades ca. 4 times longer than their sheaths, the apical ones erect, with blades and sheaths the same length; *main axis* 1.2–1.8 m long, 0.5–0.9 cm in diameter, green, 2–3 times longer than the leaves and ca. 2 times longer than the peduncle, internodes 1.3–3 cm long; *primary bracts* broadly triangular, acuminate, 0.5–1.8 x 0.3–1.6 cm, thin and brittle, yellowish to light brown, glabrescent, strongly nerved, clasping the peduncle of the branch but shorter than it, peduncle bracteate; *branches* (52–)77–81 in number, forming a 45° angle with the main axis then arching and subspreading to pendulous, 4.7–28 cm long, each with 31–250 flowers, apices of the branches (at least in cultivation) do not develop and remain light brown, with abortive floral buds; *rachis* 1–3 mm in diameter, flattened at the base, strongly sulcate, sterile bases of branches bracteate, light green in the first order branches (1–)2–3.5 cm long, in the second order branches (0.9–)1.5 cm long; *floral bracts* lanceolate, acute, 2.2–4.3 x 1–2 mm, erose to strongly erose, hyaline, yellowish, glabrous, 3–5 nerved, verrucose close to the central nerve. *Flowers* pedicellate, verticillate, 4–5.7 mm long; pedicels obconical, 1–1.4 mm long, green; *se-*

pals free, ovate, acute, 2–2.4 x 1.2–1.6 mm, entire, light brown, glabrous, 1–3-nerved; *petals* free, elliptic to broadly elliptic, acute to rounded, 2.4–3.5 x 1.4–2.3 mm, entire, white, glabrous, 5-nerved, arranged so as to seemingly form a three-pointed star in anthesis; *stamens* 1.7–3.1 mm long, 3 opposed to the sepals, three to the petals; *filaments* narrowly triangular, flat in cross section, 1.5–2.7 x 0.4 mm, white; *anthers* elliptic, 1–1.4 x 0.3–0.5 mm, dorsifixed; *pistillode* conical, ca. 0.3 mm long, sometimes inconspicuous, stigmatic blades inconspicuous.

Pistillate inflorescence (known and described based on photographs in habitat and on a dry infructescence, an once-branched panicle, cylindrical, erect, 1.4–1.5 m long; *peduncle* terete, 50–60 cm long, 0.8–1.2 cm in diameter, internodes 1.9–4.1 cm long; *peduncle bracts* similar with those of the staminate inflorescence; *main axis* 50–60 cm long, ca. 0.4 cm in diameter, internodes 0.5–2 cm long; *primary bracts* broadly triangular, acuminate, 1.1–1.2 x 0.6–0.7 cm, thin and brittle, margins entire and undulate, drying pale brown, glabrous, multinerved, enclosing the sterile bases of branches, shorter than or equaling the peduncle of the branch; *branches* (11–)14–18 in number, 0.5–1 cm long stipitate, spreading to ascending, 4–10.5 cm long, 45–120 flowered; *rachis* 2–2.5 mm in diameter, flattened at the base of the branches, slightly sulcate, drying dark brown; *floral bracts* ovate, acute, 2–3 x 1.5–2 mm, hyaline, yellowish, glabrous, 1-nerved. *Flowers* known and described based on the remaining structures on the fruit, subsessile, verticillate, densely grouped; *pedicel* obconical, 1–2 mm long, 0.5–1 mm in diameter, drying dark brown; *sepals* free, ovate, acute, 1.5–2.2 x 1.3–1.6 mm, entire, light brown, glabrous, 1-nerved; *petals* triangular, acute, 2.5–2.8 x 1–1.3 mm, entire, color unknown, 3-nerved; *staminodes* narrowly triangular, 1–1.4 x 0.3–0.5 mm; *ovary* unknown. *Fruits* narrowly ovoid, 5–6 mm long, 2 mm in diameter, dark brown with black spots, glabrous; sepals, petals, staminodes, and stigmatic lobes remaining on the capsule upon maturity; *seeds* 1–2 in number per locule, fusiform, 3.7–4.9 mm long, 0.6–1 mm in diameter, apical wing 0.6–1 mm long, basal wing 1–1.2 mm long.

Distribution and habitat:—*Hechtia flexilifolia* is known from a restricted geographical area near the village of Yosondúa, where it grows in close sympatry with *H. nuusaviorum* Espejo & López-Ferr. in Espejo *et al.* (2007b: 98). There it grows as a lithophyte on steep or vertical rock walls, at an elevation of ca. 1970 m, surrounded by humid forest. Most collections have been made from around the Yosondúa waterfalls, a well-known touristic site.

Etymology:—The specific epithet refers to the flexible foliar blades, an unique feature in the genus in Oaxaca since the rest of the species have succulent, rigid, inflexible leaves.

Additional specimens examined (paratypes):—MEXICO. Oaxaca: Distrito de Tlaxiaco, Municipio Santiago Yosondúa, de la desviación a Yerba Santa hacia la desviación a El Vergel, 16° 50' 43" N, 97° 34' 52" W, 1992 m elevation, 11 Noviembre 2005, *Carnevali et al.* 7136 fruits (CICY (x2)!); ca. 4 km después de Santiago de Yosondúa, rumbo a Yerba Santa, en las cascadas, riscos en bosque de pino-encino con algunos elementos mesófilos [ca. 4 km beyond Santiago de Yosondúa, toward Yerba Santa, by the waterfalls, cliffs with pine-oak forest with some mesophyll elements], 16° 50' 43" N, 97° 34' 52" W, 1990 m elevation, 24 Julio 2009, *Ramírez & Carnevali* 1745 ♂ (CICY!, ENCB!).

Discussion:—The species has been collected in the Mixteca Alta region near the limits with the Cordillera Costera Sur phytogeographical province (Cervantes-Zamora *et al.* 1990, Fig. 3), in the western area of the Mexican State of Oaxaca. It grows sympatrically with *Hechtia nuusaviorum*, a species well characterized by its glomerule-like pistillate inflorescence branches, and wider, more succulent foliar blades. In the field both species are readily recognized by leaf width and texture. *Hechtia flexilifolia* has narrower foliar blades that are white lepidote abaxially whereas the adaxial surface looks wrinkled. When the leaf blades dry, a thin layer from the adaxial epidermis peels off, apparently the cuticle because we did not observe foliar trichomes on the adaxial surface. This species is well characterized by its densely flowered spikes of both staminate and pistillate flowers. Plants were collected in fruit and cultivated but only staminate plants bloomed in 2009 and again in 2013. However, no pistillate plants produced inflorescences during eight years of cultivation. A recent trip to the type locality (2012) revealed small rosettes not ready to bloom and no recent evidence of previous flowering. However, vegetative features and staminate flower characteristics are sufficient to propose this species as new. A population of *Hechtia* occurring along the Oaxaca-Puerto Escondido road (*Ramírez & Carnevali* 1881, CICY, separated by ca. 90 km SE in straight line) strongly resembles *H. flexilifolia* in rosette features and the staminate inflorescence, but in this population some branches produced two small additional spikes at the base. Besides this, everything else is exactly the same. The problem of assuming this as the same species is that in some groups of *Hechtia* male flowers and inflorescences are extremely similar whereas pistillate inflorescences are strikingly different. As we are not sure if this is the case, we will await further evidence before we refer this population to any *Hechtia* species.

IUCN Conservation assessment:—Vulnerable (VU). *Hechtia flexilifolia* meets criteria D2 of the IUCN (2010). The species is known from an area of less than 2 km² within which it occurs only at a handful of small sites. Albeit local populations of the species can be rich in individuals and are often inaccessible, they are widely dispersed and isolated on the slopes and cliffs of the mountainous landscape.

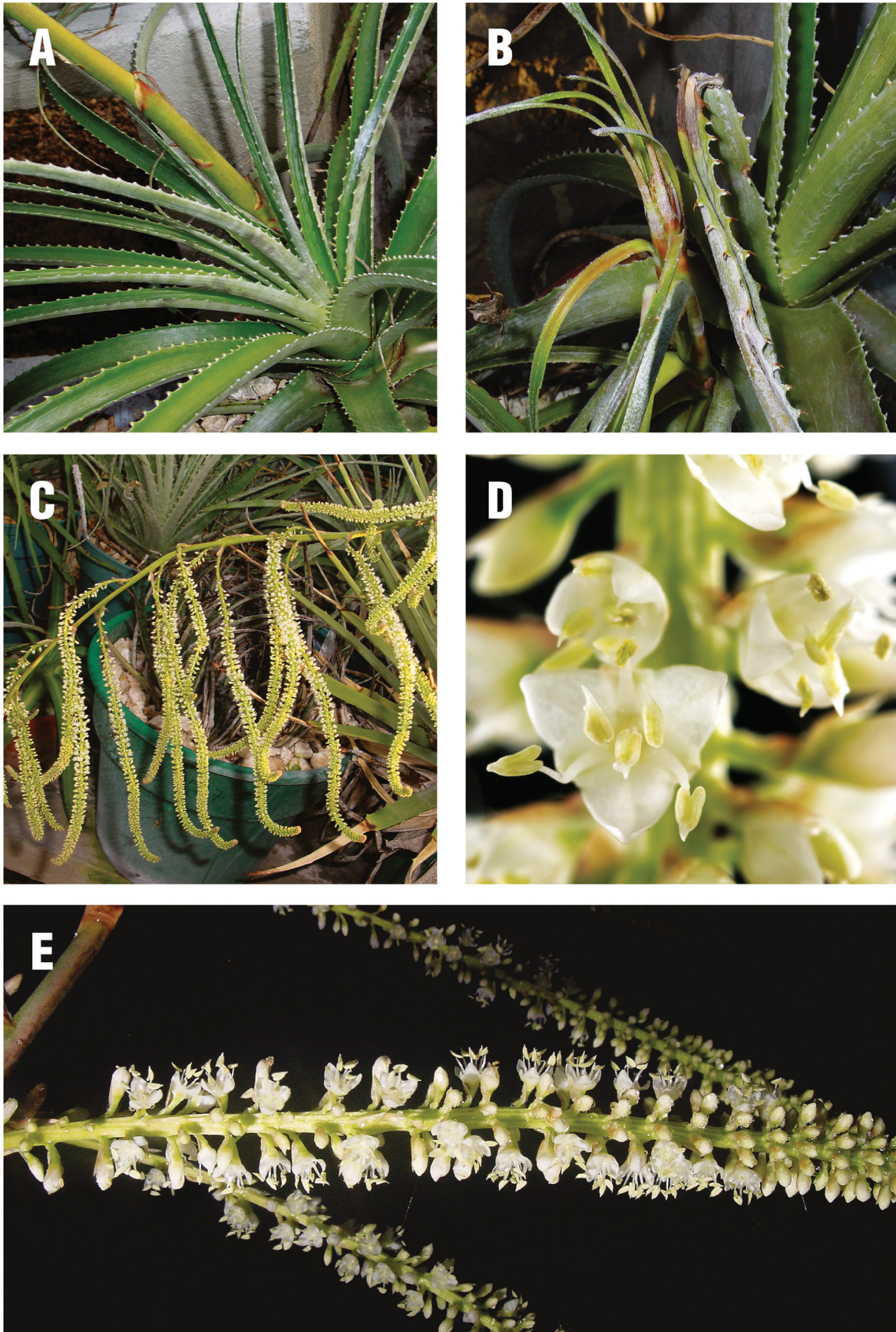


FIGURE 2. *Hechtia flexilifolia*. Staminate plant. A. Part of rosette and peduncle. B. Inflorescence originates in a young rosette (pattern SPFP). C. Branches of the inflorescences are initially pendulous. D. Flowers at anthesis. E. Branches. (Photographs by Ivón Ramírez)

Hechtia huamelulaensis I. Ramírez & Carnevali, *spec. nov.* (Figs. 3, 4, Table 1).

A species similar to *Hechtia glauca* but leaves dull matte green (*vs.* glaucous), the leaf margins not undulate (*vs.* undulate throughout), without tufts of hairs in axils of spines (*vs.* with tuft of hairs in axils of spines); peduncle of the pistillate inflorescence 20–23 cm long (*vs.* 40–75.5 cm long); staminate sepals 2.5–3.4 mm long (*vs.* 1.6–2.2 mm long), pistillate floral bracts longer (2.4–4.7 mm *vs.* 1–2.3 mm long); fruits ellipsoid, not pendulous, 9–12.3 x 4.5–5.7 mm (*vs.* ovoid, pendulous, (8)9–12 x 3.5–5 mm).

TYPE:—MEXICO. Oaxaca: Municipio San Pedro Huamelula, desvío de la Carretera Federal 200 a San Pedro Huamelula, ca. 1 km, desde la carretera Salina Cruz a Pochutla, [deviation from federal road 200 to San Pedro Huamelula, ca. 1 km, from the road from Salina Cruz to Pochutla], 15° 59' 44" N, 95° 39' 57" W, 62 m elevation, originally collected in March 2011, blooming under cultivation, 2 Marzo 2013, *Ramírez & Carnevali 1675c* ♀ (holotype, CICY (x2)!).

Plants lithophytic, rosettes globular, 50–60 cm in diameter, 25–30 cm tall. *Leaves* 30–40 in number, reflexed; *sheaths* transversely oblong, 7–8 x 10–12 cm, entire, yellowish green, glabrous, with flat or undulate margins only at base; *blades* narrowly triangular, long acuminate, 30–35 x 6–8 cm, recurved, succulent, broadly and shallowly channeled in cross section, dull mat green, occasionally the apical portion reddish, glabrous and opaque adaxially, white lepidote abaxially, margins straight, sometimes basally undulate, armed, red; spines antrorse, 3–5 mm long, 1–1.5 cm apart, red. *Inflorescence* central, emerging from lateral young rosettes (type SPFP), erect.

Staminate inflorescence (only known from dry specimens and pictures in habitat) an once-branched panicle, pyramidal, erect, 60–80 cm long; *peduncle* terete, ca. 20 cm long, 0.5–0.8 cm in diameter at the base, as long as the height of the rosette or shorter, internodes 1–1.5 cm long; *peduncle bracts* with broadly triangular sheaths, appressed to the peduncle, 2–3 x 4–7 mm, margins thin, narrowing abruptly into the blade; the blade narrowly triangular, long acuminate, 2–10 x 0.5–0.7 cm, entire to finely serrate, light brown, sparsely white-lepidote at the apex, multinerved; *main axis* 40–50 cm long, 0.5–0.6 cm in diameter at the base, upward to ca. 2 mm in diameter, dark olive green, internodes 1.5–3 cm long; *primary bracts* triangular, acuminate, 0.7–2 x 0.3–0.8 cm, margins entire and very thin, light brown, glabrous, multinerved, shorter than the branches; *branches* 47–53 in number, forming an angle of 90° or nearly so with the main axis, 2.5–13.2 cm long, with (8–)11–38 flowers, the distal flowers often not developing, color unknown; *rachis* ca. 1 mm in diameter, flattened at its base, then sulcate, drying light brown, glabrous, sterile basal portion 0.3–0.8 cm long, naked; *floral bracts* broadly ovate, acuminate, 2.3–2.6 x 2 mm, margins erose, minutely serrate at the apex, shorter than the sepals, glabrous, 5-nerved. *Flowers* (unknown at anthesis *in vivo*) shortly pedicellate, erect; *pedicels* obconic, ca. 1 mm long, ca. 0.5 mm in diameter, glabrous; *sepals* ovate to triangular-ovate, acute, 2.5–3.4 mm x 1.3–2 mm, erose, glabrous, 7-nerved, shorter than the petals; *petals* elliptic, rounded, 4.5–6.1 x 2.5–2.8 cm, entire, 7–9 nerved; *filaments* narrowly triangular, 4–4.7 x 0.7–1 mm; anthers oblong, 1.6–1.9 mm long; *pistillode* ovoid, reduced, 1–1.3 x 1.2–1.4 mm, stigmatic lobes 0.2–0.4 mm long.

Pistillate inflorescence (known from live material) a once-branched panicle, pyramidal, erect, rigid, 92–112(–121) cm long; *peduncle* terete, 20–23 cm long, 1.1–1.3 cm in diameter at the base, as long as the height of the rosette or slightly longer, internodes 1–1.5 cm long, olive green to purple; *peduncle bracts* with broadly triangular sheaths, these appressed to the peduncle, 3–5 x 5–9 mm, serrulate, narrowing abruptly into the spreading blades; the blade narrowly triangular, long acuminate, 2.2–12 x 0.7–1 cm, entire, light brown with some pinkish hue, base and apex reddish, sparsely white lepidote mainly at the apical abaxial surface, multinerved; *main axis* 70–98 cm long, 0.7–1.1 cm in diameter at the base, upward to ca. 2 mm in diameter, internodes 1–1.5 cm long; *primary bracts* triangular, acuminate, 0.7–2.8 x 0.3–0.7 cm, margins entire and very thin, light brown, glabrous, multinerved, much shorter than the branches except the lower ones equaling the shorter branches; *branches* 46–94 in number, forming an angle of ca. 90° or nearly so with the main axis, 1.5–13 cm long, with 4–40 flowers, the apex bearing abortive flowers; *rachis* 0.3–1(–3) cm long, ca. 0.2 cm in diameter, naked, dorsiventrally flattened at the base, then sulcate, dark purple, without sterile portion at its base; *floral bracts* variable in shape and size, oblong to triangular, acuminate, 2.4–4.7 x 1.5–2.8 mm, erose, with some scattered tiny spines at the apex, scarious, basally green, apically brown, glabrous, 8–9 nerved, as long as or longer than the pedicel. *Flowers* pedicellate, erect; *pedicel* terete, 1.5–3 mm long, ca. 1 mm in diameter, glabrous; *sepals* variable in size, deltoid, acute, 1.3–2.6 x 2–2.5 mm, entire to erose, purple, glabrous, 5–7-nerved, appressed to the petals; *petals* ovate, acute, 4–5.2 x 2–2.7 mm, ca. 7-nerved, arranged so as to form a star-like corolla, white, basally green, with a red longitudinal stripe, often with the red color spreading over the whole surface; *staminodes* narrowly triangular, 2.7–3.3 x 0.5–0.8 mm, sometimes apically capitate; *ovary* oblongoid to ovoid, 3.2–3.5 mm long, 1.8–2.3 mm in diameter, light green, apex purple, stigmatic lobes recurved, 1–1.2 mm long, light purple. *Fruits* narrowly ellipsoid, 9–12.3 mm long, 4.5–5.7 mm in diameter, glabrous, pendulous; *pedicel* stout, ca. 2 mm long, 1 mm

in diameter, the sepals, petals, and staminodes persistent; *seeds* fusiform, (4–)6.3–8.4 mm long, (0.5–)0.7–1.1 mm in diameter, apical wing 0.4–0.6 mm long, basal wing (2–)3–3.9 mm long.

Distribution:—*Hechtia huamelulaensis* occurs in the southeastern area of the State of Oaxaca (Fig. 3), on the Pacific slopes of the Tehuantepec Isthmus, an area belonging to the Costas del Sur Physiogeographical Province (Cervantes-Zamora *et al.*, 1990). So far it is only known from the vicinity of the village of San Pedro Huamelula in the municipality of the same name. The area where this species has been found coincides with a relatively small patch of hot arid climate (type BSo(h')w), which is embedded within a more extensive region of tropical subhumid climate (García 1998). At this single locality, *H. huamelulaensis* grows in xerophytic vegetation at an elevation of ca. 60 m and is associated with such other plants as *Agave ghiesbreghtii* Lemaire ex Jacobi (1864:545), *Plumeria rubra* Linnaeus (1753: 209), *Opuntia decumbens* Salm-Reifferscheid-Dyck (1834: 361), and a laxly-flowered form of *Hechtia rosea*.

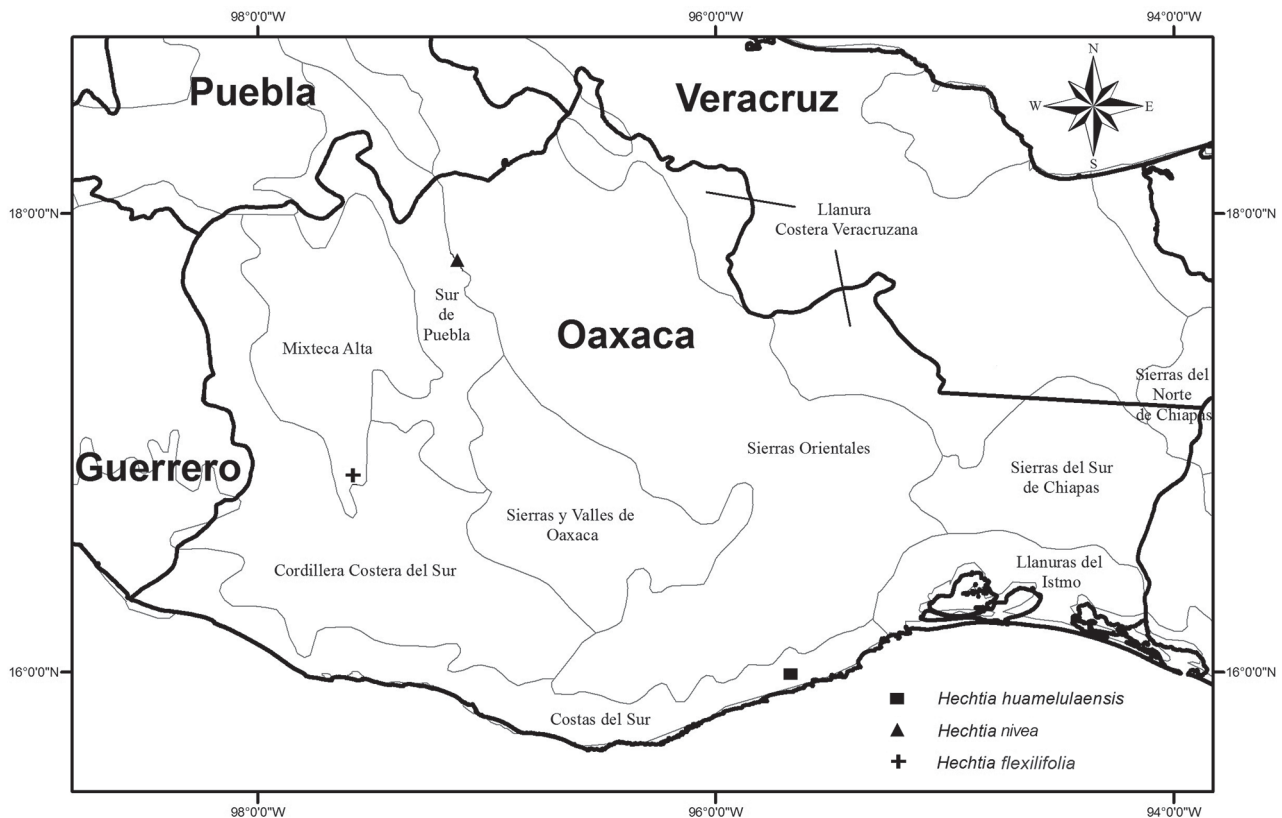


FIGURE 3. Geographical distribution of the three new species: *Hechtia flexilifolia*, *H. huamelulaensis*, and *H. nivea*.

Etymology:—The epithet refers to the locality where the new species was collected, San Pedro Huamelula in Oaxaca, Mexico.

Additional specimen examined (paratypes):—MEXICO. Oaxaca: Municipio San Pedro Huamelula, desvío de la carretera federal 200 a San Pedro Huamelula, ca. 1 km, desde la carretera de Salina Cruz a Pochutla, 15° 59' 44" N, 95° 39' 57" W, 62 m elevation, 25 March 2011, Ramírez & Carnevali 1675a ♂ (CICY!), 1675b fruits (CICY!, MEXU!, OAX!, US!), same locality, flowering on cultivation, 01 March 2013, Ramírez & Carnevali 1882 ♀ (MEXU!, US!).

Discussion:—*Hechtia huamelulaensis* is characterized by the following combination of characters: rosettes with broad, succulent leaves, these dull mat green, often reddish at apex and margins, and white lepidote abaxially; the inflorescences are central but emerging from a young, newly formed lateral shoot (type SPFP); the main axis of the pistillate inflorescences as well as the sepals are dark purple, the pistillate flowers have white petals, sometimes with a purple longitudinal mid line abaxially, and pink stigma lobes.

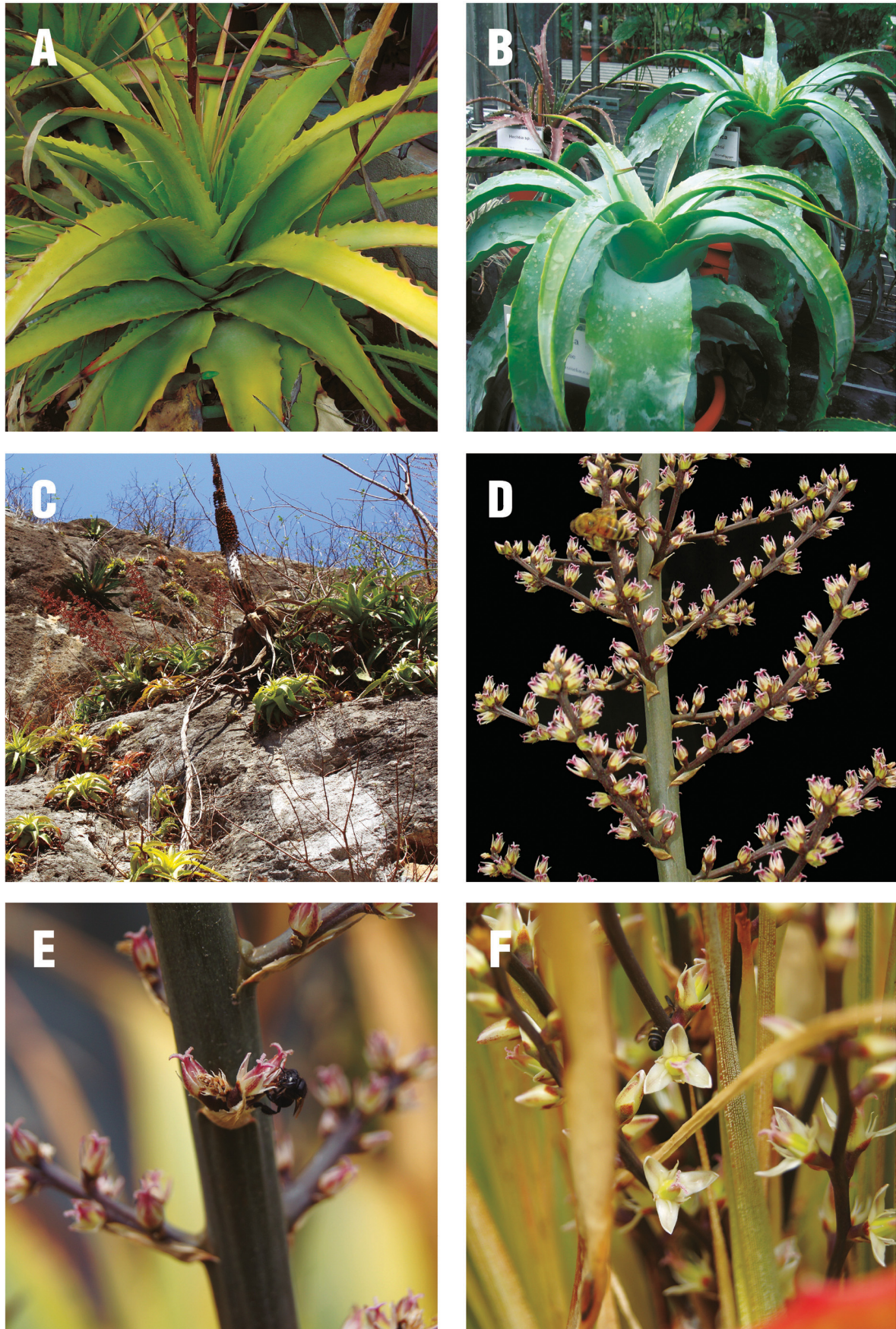


FIGURE 4. *Hechtia huamelulaensis* (A, C–F). A. Rosette (plant in cultivation). C. Plants in habitat, note the brown, erect infructescence. D. Pistillate inflorescence. E. Details of pistillate flowers, note the purple color on the floral parts. F. Different morph of pistillate flowers, patent and lighter petals. B. *Hechtia glauca*, its rosette resembles that of *H. huamelulaensis* (Photographs: A, B, D. Ivón Ramírez; C. Juan Pinzón, E–F. Débora Carnevali).

Actually, there are some other populations of *Hechtia* in the same phytogeographical region of the Tehuantepec Isthmus where *H. huamelulaensis* grows that share the same rosette architecture with some variations on leaf number, width and length, cross section and color, but with different floral and fruit features that allow differentiating them from the new species. These are referable to species such as *H. fosteriana* L. B. Sm. (1961:8) and *H. rubicunda* Espejo & López-Ferr. in López-Ferrari & Espejo (2014:154), and perhaps others yet to be formally recognized. Because the taxonomy of this group of taxa is unresolved at this time and no closest relative to our new species is obvious, we have chosen to compare our new species against an unrelated taxon that is, however, vegetatively similar. Thus, we contrast the new species with *H. glauca* Burt-Utley & Utley (1993: 220) (Table 1), native of the Mexican state of Michoacán, which is similar in rosette features.

TABLE 1. Comparison of the new species *Hechtia huamelulaensis* and *H. glauca*.

Characters	<i>H. huamelulaensis</i>	<i>H. glauca</i>
Foliar margins	straight, sometimes basally undulate	undulate throughout
Foliar blade spines	without tuft of hairs in axils of spines	with tuft of hairs in axils of spines
Peduncle (♀ inflorescence)	20–23 cm long	40–75.5 cm long
Staminate sepals	2.5–3.4 × 1.3–2 mm	1.6–2.2 × 1.5–2.3 mm
Staminate petals	4.5–6.1 × 2.5–2.8 mm	4.5–5 × 1.8–2.2 mm
Pistillate floral bracts	2.4–4.7 × 1.5–2.8 mm	1–2.3 × 1–1.3 mm
Pistillate petals	4–5.2 × 2–2.7 mm	3.5–5 × 1.3–2.1 mm
Fruits	ellipsoid, not pendulous, 9–12.3 × 4.5–5.7 mm	ovoid, pendulous, (8)9–12 × 3.5–5 mm
Locality and elevation	Oaxaca, ca. 60 m elevation	Michoacán, 270–300 m elevation

Hechtia huamelulaensis differs from *H. glauca* by its dull matte green leaves (*vs.* glaucous), blades with flat or undulate margins only at base (*vs.* undulate throughout), leaf surfaces densely lepidote abaxially, without tufts of hairs in axils of spines (*vs.* glabrous with tuft of hairs in axils on spines), peduncle of the pistillate inflorescence 20–23 cm long (*vs.* 40–75.5 cm long), staminate sepals 2.5–3.4 mm long (*vs.* 1.6–2.2 mm long), pistillate floral bracts longer (2.4–4.7 mm *vs.* 1–2.3 mm long); fruits ellipsoid, not pendulous, 9–12.3 × 4.5–5.7 mm (*vs.* ovoid, pendulous, (8)9–12 × 3.5–5 mm).

IUCN Conservation assessment: Vulnerable (VU). *Hechtia huamelulaensis* meets criteria D2 of the IUCN (2010). The species is known from an area of less than 2 km² within which it occurs only at a handful of small sites. Albeit local populations of the species can be rich in individuals and are often inaccessible, they are widely scattered and isolated on the slopes and tops of small rocky hills.

Hechtia nivea I. Ramírez & C. F. Jiménez, *spec. nov.* (Figs. 3, 5, Table 2).

This new species is similar to *Hechtia nuusaviorum* in its inflorescence architecture and condensed, conical or cylindrical branches in both sexes; however the new species differ in that foliar blades are 21–39 × 1.3–2.9 cm (*vs.* 30–75 × 1.5–4.5 cm), densely white lepidote on both surfaces (*vs.* glabrous above and white lepidote abaxially); staminate inflorescences are denser, featuring ca. 12 branches in a rachis of 20 cm length (*vs.* 5 branches in the same length), branches 1.2–3 × 1–1.4 cm (*vs.* 4 cm long × 2.5 wide), primary bracts much longer than or equaling the branch length (*vs.* always shorter than the branches); pistillate inflorescences are denser with ca. 16 branches in 20 cm length (*vs.* ca. 5), primary bracts vary from shorter to longer than the branches (*vs.* always shorter), branches are cylindrical, and up to 2.4 cm long (*vs.* 3 cm long and spheroid), floral bracts are equaling the flower, petals green, ovary reddish, and stigma white (*vs.* floral bracts shorter than the petals, petals white, ovary and stigma white in *H. nuusaviorum*).

TYPE:—MEXICO. Oaxaca: Municipio San Juan Bautista Cuicatlán, 4.10 km al S de San Pedro Nodón, camino de terracería hacia San Miguel Huautla, matorral crasicaule [unpaved road to San Miguel Huautla, shrubland with succulent elements], 17°46'32.2"N, 97°07'58.3"W, 1740 m elevation, 21 Marzo 2013, Ramírez, Jiménez & Flores 1826b ♀ (holotype CICY!; isotype MEXU!).

Plants terrestrial or lithophytic, cespitose, when blooming 1–1.20 m tall, heliophilous. *Rosettes* 35–45 cm in diameter, 25–30 cm long, new rosettes originating from the base of the older ones. *Leaves* 60–70 per rosette, straight and ascending; *sheaths* oblong, 2.5–3 × (2.6–)3.7–4.8 cm, basally entire, finely dentate toward the apex, white-yellowish adaxially and brownish abaxially when dry, sometimes with a darker brown distal area, glabrous on both surfaces; *blades* narrowly triangular, acuminate, pungent, 21–39 cm long, 1.3–2.9 cm wide at the base, 0.5–1.1 cm wide in the mid area, erect (central ones) to slightly recurved (outer ones), succulent, slightly concave, green, glabrous to sparsely

white lepidote adaxially, white lepidote abaxially, margins spinose; *spines* usually retrorse, uncinata, 4–7 mm long, (0.8–)1.6–4.4(–5.1) cm apart, laxly arranged toward the apex, reddish. *Inflorescence* central (type SSP), one branched panicle in both sexes, erect.

Staminate inflorescence cylindrical, erect, 120–135 cm long; *peduncle* terete, 60–67 cm long, 0.9–1 cm in diameter at the base, ca. 3 times longer than the rosette, brown, glabrous, internodes 1.2–3.2 cm long; *peduncle bracts* with broadly triangular sheaths, the blades appressed to the peduncle, abruptly long (basal bracts) to shortly (upper ones) acuminate, 4–11 x 0.8–1 cm, entire, margins thin, brownish, glabrous, strongly nerved, the basal ones longer than internodes, the upper ones equaling the internodes; *main axis* 70–74 cm long, 0.4–0.5 cm in diameter, cylindrical, sulcate when dry, light brown, glabrous, internodes 1–1.5 cm long; *primary bracts* narrowly triangular, acuminate, 1.3–3.5 x 0.4–1(–1.3) cm, wider than the peduncle bracts and enclosing the base of the branches, entire, brownish, glabrous, strongly nerved, equaling or longer than the branches; *branches* 70–72 in number, ascendent or appressed, 1.2–3 cm long, 1–1.4 cm in diameter, sessile, with 30–70 flowers, densely arranged along the main axis, longer than the internodes, green; *rachis* hardly visible, cylindrical, green, smooth; *floral bracts* elliptic to broadly elliptic, 6.3–8 x 3.7–5.5 mm, concave, acute, strongly erose, light brown, longer than the sepals and petals, glabrous, 5–9 nerved. *Flowers* subsessile, erect, 5.5–6.7 mm long, 2.4–3.2 mm in diameter; *pedicels* terete, 1–2 mm long, 1–1.5 mm in diameter, glabrous; *sepals* usually 3, sometimes 4, oblong, 3.5–4 x 2.2–3 mm, concave, acute, stramineous, erose, glabrous, 5–7(–8) nerved; *petals* elliptic, 4–4.4 x 2.2–2.5 mm, rounded, cucullate, entire, white, glabrous, 7–9-nerved; *stamens* erect, adnate to the petals and to the pistillode base, barely protruding at anthesis; *filaments* narrowly triangular, 4–4.6 x 0.5–0.7 mm, white; *anthers* ovoid, 1.7–2.2 mm long, 0.7–1 mm in diameter, green; *pistillode* conical, 0.8–1 mm long, 1 mm in diameter, white, stigmatic lobes usually absent, when present ca. 0.2 mm long.

Pistillate inflorescence cylindrical, ca. 160 cm long, erect; *peduncle* cylindrical, 91–99 cm long, 0.8–0.9 cm in diameter at the base, much longer than the leaves, glaucous, green; *peduncle bracts* broadly triangular, abruptly long (basal ones) to shortly (upper ones) acuminate, appressed to the peduncle, 2.5–9.2 x 0.8–0.9 cm, entire, brownish, glabrous, strongly nerved, margins thin, the basal ones longer than the internodes, the upper ones equaling the internodes, internodes 1.2–3.2 cm long; *main axis* ca. 69 cm long, 0.4–0.5 cm in diameter at the base, cylindrical, sometimes flexuous, green, glabrous, internodes 1–3 cm long; *primary bracts* triangular, acuminate, 0.8–2.5 x 0.5–1 cm, light brown, glabrous, entire, strongly nerved, subequaling or shorter than the branches; *branches* ca. 44 in number, ascending or erect, 0.8–2.4 cm long, 0.7–1 cm in diameter, sessile, with 25–50 flowers, densely arranged; *rachis* not visible; *floral bracts* triangular ovate, 5.2–6.8 x 3.2–4 mm, concave, acute, strongly erose, brown, glabrous, ca. 7-nerved, longer than the sepals and petals. *Flowers* sessile, appressed to the rachis, (4.4–)5.8–6.3 mm long, (2.4–)3–3.3 mm in diameter; *sepals* deltoid, 3–3.4 x 2.6–3(–3.7) mm, acute, entire at the base, apically erose, brown, glabrous, ca. 5-nerved; *petals* triangular to triangular-ovate, 3–4.3 x 2–2.8 mm, acute, entire, green, glabrous, ca. 7-nerved; *staminodes* narrowly triangular, 1.1–2.4 mm long, 0.4–0.8 mm wide at the base, without vestigial anthers; *filaments* adnate to the bases of the petals and the ovary, green; stigmatic lobes short, slightly recurved, ca. 1.2 mm long, white; *ovary* superior, oblongoid, 2.5–3 mm long, 1.4–2 mm in diameter, green, placentation central. *Fruits* ellipsoid to broadly ellipsoid, sometimes asymmetrical, 6.3–8.9 mm long, 4–5.8 mm in diameter, brown; sepals, petals, staminodes and stigmatic lobes remaining in fruit; *seeds* variable in shape, generally ovate, rarely oblong, 3.4–4 x 1.3–2 mm, brown, with 2 wings, apical wing 0.3–0.5 mm long, basal wing 0.8–1.2 mm long.

Distribution and habitat:—*Hechtia nivea* is known from a restricted geographical area in the vicinity of the village of San Pedro Nodón. It grows as a lithophyte on vertical walls where rosettes resemble silver stars from afar. It also grows at the foothills in a general area of low caducifolious forest along with species of *Agave* Linnaeus (1753: 323) (Agavaceae), *Brahea* Martius (1838: 243) (Arecaceae), *Cnidioscolus* Pohl (1827: 56) (Euphorbiaceae) and *Bursera* Jacquin ex Linnaeus (1762: 471) (Burseraceae), at elevations of about 1700 m. *Hechtia nivea* was collected in bloom during April 2013 and several plants of it are currently under cultivation.

Etymology:—The specific epithet refers to the white indumentum of the leaves lending the plant a snowy aspect.

Additional specimens examined (paratypes):—MEXICO. Oaxaca: Municipio San Juan Bautista Cuicatlán, 4.10 km al S de San Pedro Nodón, camino de terracería hacia San Miguel Huautla, matorral crasicaule, 17° 46' 32.2" N, 97° 07' 58.3" W, 1740 m elevation, 21 March 2013, Ramírez, Jiménez & Flores 1826a ♂ (CICY!, MEXU!), 1826c fruits (CICY!, MEXU!, OAX!).

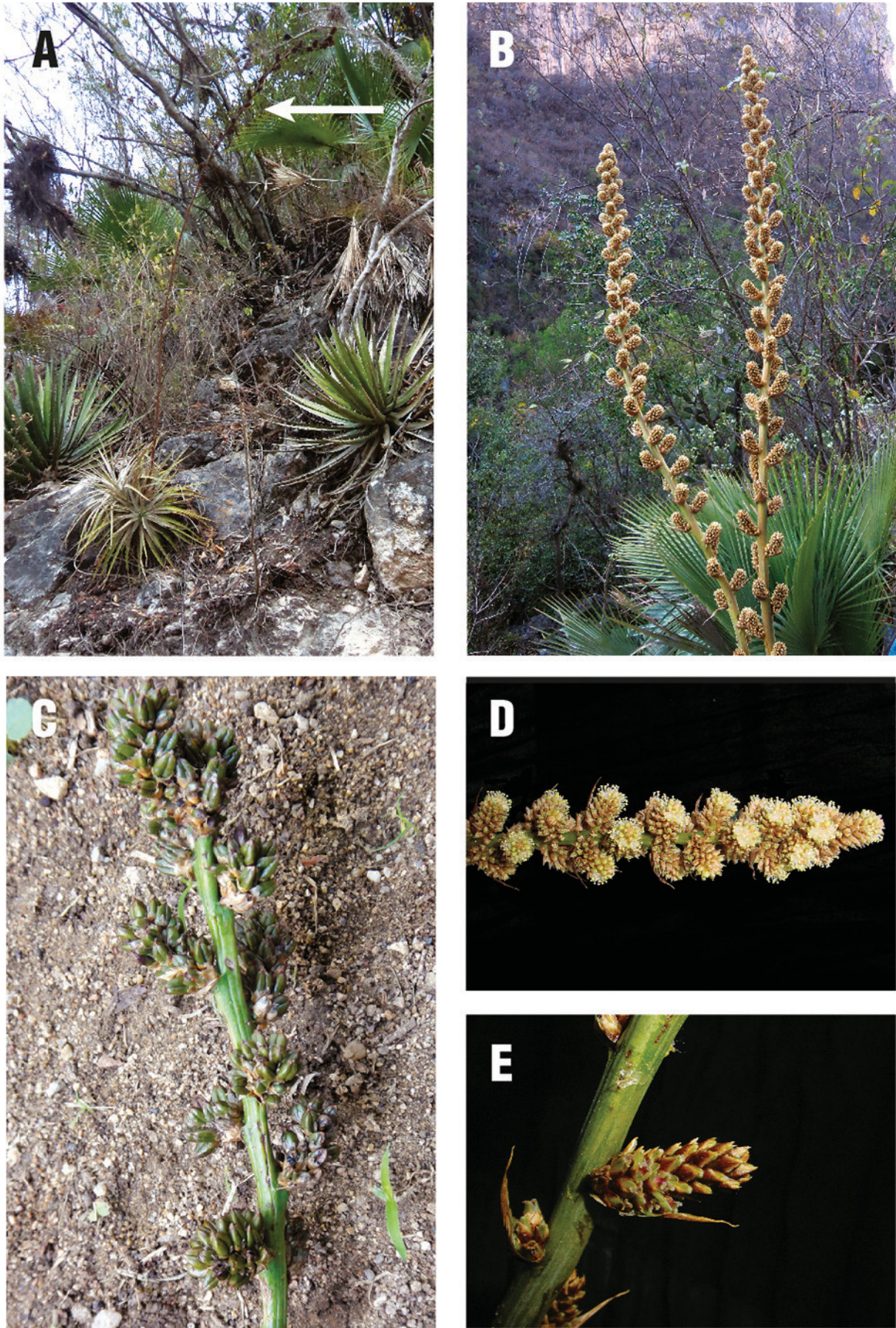


FIGURE 5. *Hechtia nivea*. A. Plant with infructescence in habitat (indicated by an arrow) B. Staminate inflorescences at anthesis. C. Young infructescens. D. Staminate branches with flowers at anthesis. E. Pistillate branches with flowers at anthesis (Photographs A, B, D & E. Ivón Ramírez; C. Prisciliano Flores).

TABLE 2. Main differences between *Hechtia nuusaviorum* and *H. nivea*

Feature	<i>H. nuusaviorum</i>	<i>H. nivea</i>
Rosette features	rosettes ellipsoid, wider than high, with leaves horizontally extended with apices deflexed	rosettes higher than wide, with leaves straight and ascending
Foliar blade color	green, may develop red color	green, not developing red color
Foliar sheaths	3–8.5 cm long	2.5–3 cm long
Floral bracts (♂ flower)	5–6 mm long, as long as the petals	6.3–8 mm long, longer than the petals
Petals (♂ flowers)	6–6.3 mm long, ovate to broadly elliptic	4–4.4 mm long, elliptic
Anthers	ca. 1.4 mm long	1.7–2.2 mm long
Floral bracts (♀ flower)	triangular-ovate to triangular, 4–7 mm long, equaling the petals	triangular-ovate, 5.2–6.8 mm long, longer than the petals
Sepals (♀ flower)	4.2–6 mm long	3.5–4 mm long
Ovary	ovoid, 4.7–5(7.7) mm long	oblongoid, 2.5–3 mm long
Staminodes	ca. 3.8 mm long	1.1–2.4 mm long
Fruits	ovoid	ellipsoid to broadly ellipsoid
Seeds	5.2–7.2 mm long	3.4–4 mm long

Discussion:—The species was collected in the Sierras Centrales de Oaxaca physiogeographical province (Fig. 3) and it can be recognized by the following combination of characters: rosettes are medium-sized with dense white lepidote leaves, branches of both sexes are reduced and short clavicate, pistillate flowers with green petals, the staminate ones with white petals. *Hechtia nivea* is compared with *H. nuusaviorum* (Table 2), a morphologically similar species and also native from northwestern Oaxaca. Main differences include the smaller branches of *H. nivea* that are more densely packed on the rachis and the much narrower leaves with white lepidote indumentum above as opposed to the broad leaves of *H. nuusaviorum* which are glabrous above.

IUCN Conservation assessment:—Vulnerable (VU). *Hechtia nivea* meets criteria D2 of the IUCN (2001). The species is known from an area of less than 2 km² within which it occurs only at a handful of small sites. Albeit local populations of the species can be rich in individuals and are often inaccessible, they are widely scattered and isolated on the slopes and tops of small hills where they are susceptible to fires and other anthropogenic disturbances.

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