THE REESTABLISHMENT OF *BAKERANTHA*, AND A NEW GENUS IN HECHTIOIDEAE (BROMELIACEAE) IN MEGAMEXICO, *MESOAMERANTHA*

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Abstract. The most recent phylogenetic analyses using molecular and morphological data of Hechtioideae revealed the presence of three well-supported, morphologically distinct clades related to each other as follows: (*Hechtia tillandsioides* complex [*Hechtia guatemalensis* complex (*Hechtia s.s.*)]). (1) *H. tillandsioides* complex is recognized here at the generic level (under the reestablished name *Bakerantha*), characterized by its grass-like leaves, which are almost entire or minutely dentate, central inflorescences with pedicellate flowers, and papyraceous, pendent fruits; this clade includes four species confined to the Veracruzan, Sierra Madre Oriental, Balsas Basin, and Transmexican Volcanic Belt biotic provinces. (2) The *H. guatemalensis* complex, here proposed as the new genus *Mesoamerantha*, is characterized by the presence of central inflorescences and flowers with ¾ superior ovaries and is confined to the Pacific Lowlands, Veracruzan, Mosquito, and Chiapas Highlands provinces (in Belize, Guatemala, Honduras, El Salvador, and Nicaragua). The remaining sampled taxa are grouped into a clade (3) that consists of three well-supported lineages: the *Hechtia glomerata* complex distributed in the drainage of the Gulf of Mexico; a clade conformed by two species (*H. deceptrix* and *H. epigyna*) from the Sierra Madre Oriental that share an inferior ovary, and a poorly resolved internal clade (Core *Hechtia*) with the remaining species containing several well-supported, geographically restricted clades.

Resumen. El análisis filogenético más reciente utilizando datos moleculares y morfológicos en Hechtioideae, reveló la presencia de tres clados bien soportados, relacionados de la siguiente manera: (*Hechtia tillandsioides* complex [*Hechtia guatemalensis* complex (*Hechtia* s.s.)]). (1) Complejo *H. tillandsioides,* reconocido aquí a nivel genérico (con el nombre de *Bakerantha*); caracterizado por inflorescencias centrales, hojas parecidas a gramíneas, casi enteras o diminutamente dentadas, con flores pediceladas, frutos papiráceos y colgantes, que incluye cuatro especies confinadas a las provincias bióticas de Veracruz, Sierra Madre Oriental, Depresión del Rio Balsas, y Eje Volcánico Transmexicano. (2) El segundo clado incluye especies del complejo *H. guatemalensis*, aquí propuesto como el nuevo género *Mesoamerantha*, caracterizado por la presencia de inflorescencias centrales, flores con ovarios ¾ superiores, con sus especies confinados a las provincias biogeográficas Tierras Bajas del Pacífico, Veracruzana, Mosquito, y Tierras Altas de Chiapas (en Belice, Guatemala, Honduras, El Salvador, y Nicaragua). (3) El resto de las especies se agrupan en un clado el cual consiste de tres linajes bien apoyados: complejo *Hechtia glomerata* distribuido en la vertiente del Golfo de México; (4) un clado conformado por dos especies (*H. deceptrix* y *H. epigyna*) de la Sierra Madre Oriental que comparten ovario ínfero; y un clado no resuelto con el resto de las especies de *Hechtia* (Grupo nuclear) con algunos clados bien apoyados y geográficamente restringidos.

Keywords: Dioecy, endemism, *Hechtia*, Megamexico

Hechtioideae (Bromeliaceae), as proposed by Givnish et al. (2007), included a single genus, *Hechtia* Klotzsch, characterized by dioecy, capsular fruits, winged or almost naked seeds, spiny foliar margins, and the lack of stellate sclerenchyma. Ramírez-Morillo et al. (2018) included as additional characters the terrestrial or lithophytic habit, often growing over limestone, gypsum, or volcanic rocks, as well as fragrant flowers (with the exception of at least *H. rosea* E. Morren ex Baker, *H. iltisii* Burt-Utley & Utley, and *H. meziana* L.B. Sm.). Furthermore, pistillate flowers show a sessile stigma and staminodia, whereas staminate flowers bear stamens as well as pistillodes. An exception is *H. gayorum* Lenz, from Baja California Sur in Mexico, which is a polygamomonoecious species (pistillate, staminate, and hermaphrodite flowers on the same individual; Lenz, 1995). Hechtioideae is confined to a region called Megamexico III (sensu Rzedowski, 1991), a region that extends from the Chihuahuan and Sonoran deserts to northern Nicaragua, although most of the species (94%) are restricted to Mexico proper, reaching its highest richness in the biogeographic

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provinces of Sierra Madre del Sur, Veracruz, Chiapas Highlands, Pacific Lowlands, Balsas Basin, Transmexican Volcanic Belt, and Mexican Plateau (circumscribed as in Morrone, 2014).

The most recent phylogenetic analysis of the Hechtioideae (Ramírez-Morillo et al., 2018), which included 82.6% of the known taxa, was based on plastid (ycf1, the rpl32-trnL intergenic spacer) and nuclear (PRK) DNA regions, as well as morphological characters. Using parsimony and Bayesian inference (Fig. 1), this analysis supported the monophyly of Hechtioideae, as well as the identification of three well-supported internal clades, the first two being (1) the *Hechtia tillandsioides* complex, as the sister group to the rest of Hechtioideae and proposed here at the generic level (with the reestablished name *Bakerantha* L.B. Sm.) and (2) the *H. guatemalensis* complex, here proposed as the new genus *Mesoamerantha*. The remaining sampled taxa are grouped into a clade that consists of three well-supported lineages: (3) the *Hechtia glomerata* complex, distributed in the drainage of the Gulf of Mexico, (4) a clade of two species (*H. deceptrix* I. Ramírez & C.T. Hornung and *H. epigyna* Harms) that share an inferior ovary and are distributed north of the Isthmus of Tehuantepec in the Sierra Madre Oriental, and (5) a poorly resolved internal clade (*Hechtia* s.s.) with the remaining species containing several well supported, geographically restricted clades.

The *Hechtia tillandsioides* complex currently comprises four species—*H. caerulea* (Matuda) L.B. Sm., *H. lundelliorum* L.B. Sm., *H. purpusii* Brandegee, and *H. tillandsioides* (André) L.B. Smith—and is characterized by acaulescent to caulescent rosettes, these round and flat when young, with strict sympodial growth, with or without a well-defined, prostrate to suberect stem (*H. caerulea* and *H. purpusii*); older plants growing on cliffs feature long, narrow, pendent leaves rendering the plants a grass-like aspect when seen from afar (somewhat suggesting species of the genus *Pitcairnia* L'Hér). The leaves are succulent, channeled above, usually very narrow, long, and pending, with minutely serrate margins or even entire in some portions; adaxially, the leaves are green, glaucous, and shiny, whereas abaxially they are always white-lepidote; the apex acute, sometimes dry, often coiled. The flowers show conspicuously thin pedicels, as long as or half the length of the ovaries; the petals are spreading, coiled/reflexed, exposing the entire ovary (or pistillode), and stamens (or staminodes). The thin-textured petals vary in color from white (as in *H. purpusii* and *H. lundelliorum*) to pink (*H. tillandsioides*), or lilac to caerulescent (as in *H. caerulea*); the fruits are capsules, erect when immature, then the pedicel bends down and the fruit becomes pendulous upon maturity with carpels turning papyraceous and releasing minute seeds, 3–3.5 mm long and 0.56–0.67 mm wide, with two apical wings. Most species from this clade grow on rocky volcanic soils. They occur in low caducifolious forests at several elevations, in some places always on steep, often continuously seeping, wet walls (as *H. lundelliorum*). Members of this clade are distributed in the Transmexican Volcanic Belt, Sierra Madre Oriental, and Veracruzan provinces, always on the Mexican Gulf slope (Pech-Cárdenas, 2015; Romero-Soler, 2017). The monophyly of this clade is also well supported by molecular features, along with a fairly circumscribed biogeographical distribution. Because of its distinctness and ease of diagnosis, here we propose its recognition at the generic level in

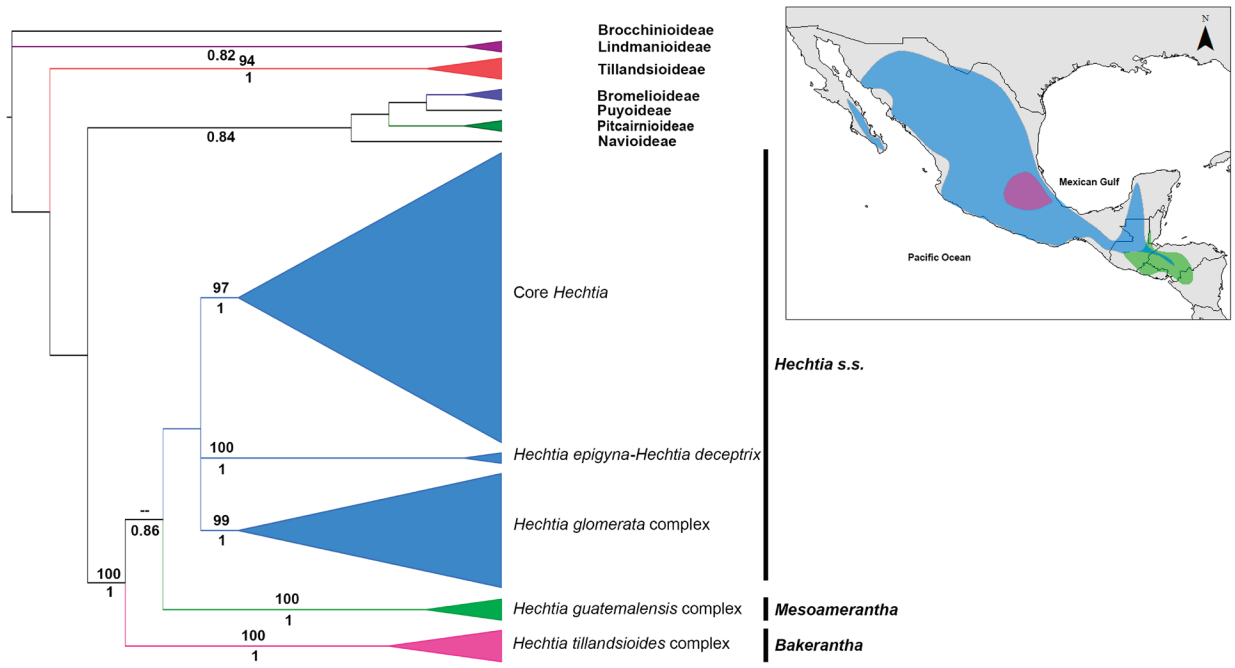

FIGURE 1. Consensus tree of 50% of the majority of the analysis of Bayesian Inference integrating total evidence from molecular characters (*matK-trnK*, *rpl32-trnL* + indels, fragments 4 and 6 of the gene *ycf1* and the nuclear region PRK) and morphological features. The values above the branches indicate the bootstrap support; the values under the branches indicate the posterior probabilities. Upper right: a map depicting the geographical distribution of the three genera in Hechtioideae (colors according to those in the cladogram).

Hechtioideae, reestablishing the name *Bakerantha* proposed by L. B. Smith (1934).

The second clade, the *Hechtia guatemalensis* complex, consists of three species distributed in the southern portion of Megamexico III. Its distribution spans the Veracruzan, Mosquito, Pacific Lowlands, and Chiapas Highlands provinces (in Belize, Guatemala, Honduras, El Salvador, and Nicaragua). They occur in caducifolious forests as well as pine-oak forests, as terrestrials or lithophytes. This species aggregation is characterized by rosettes with strict sympodial growth, serrate leaves, very short spines, which are non-uncinated but hard and rigid and homogenous in size and shape along the margin, otherwise, when long, they are soft and flexible; upon exposure to the sun, the foliar blades develop red pigments. Foliar surfaces are lustrous adaxially, white-lepidote abaxially. The flowers have green or red sepals, the corolla is spreading and the petals form a basal semi-cup; the star-like flowers have white petals and a ¾ inferior ovary; some species (*H. guatemalensis* Mez) have pendulous mature fruits. The inflorescences develop quickly but flowers open successively a few at a time, thus making the blooming period last for almost a month, more than any other species group in the subfamily, where the inflorescences usually bloom for just a week or so, also developing quickly but the flowers opening several at a time in quick succession. This clade is diagnosed by the following combination of characters: central inflorescences, flowers with ovary ¾ inferior, white (sometimes apically reddish) petals, and a distribution restricted to Central America, spanning the southern section of Megamexico III, from Belize through the dry areas south of the Motagua River close to the Guatemalan-Honduras border, then extending to northern Nicaragua, north of the lakes. This complex includes the following species: *H. malvernii* Gilmartin, *H. dichroantha* Donn. Sm., and *H. guatemalensis*. Because of its morphological distinctness and geographical circumscription, here we propose the new genus *Mesoamerantha* for this clade.

Taxonomy

All phylogenetically informative evidence available to us (morphology and both plastid and nuclear DNA) strongly supports the *Hechtia tillandsioides* complex and the *H. guatemalensis* complex as nested within Hechtioideae but distinct and readily diagnosable. Nuclear evidence, when analyzed on its own, supports the hypothesis that these two clades are sister to each other, forming a highly supported clade, sister to the rest of Hechtioideae (henceforth *Hechtia* s.s.) (Ramírez-Morillo et al., 2018). However, when considering solely cpDNA evidence, the *H. guatemalensis* complex is sister group of a clade formed by *H. tillandsioides* complex and *Hechtia* s.s.

We propose that the morphological and ecological diversity of Hechtioideae is better accounted for by treating the subfamily as composed by three strongly supported, easily diagnosed genera. Simultaneously, the conservation of species of Hechtioideae is most easily managed if their taxonomy reflects, nomenclaturally, their diversity. This is particularly relevant as the species of *Mesoamerantha* occur in four different countries (Belize [Holst et al., 2017], Nicaragua, El Salvador, Honduras, and Guatemala), affording these countries a better grasp of the conservation needs for these taxa.

Here we include the required new nomenclature for the newly described (*Mesoamerantha*) and the reestablished (*Bakerantha*), as well as the pertinent synonymy.

Members of Hechtioideae are often difficult to identify without well-preserved, fairly complete, informative herbarium material. Identifications are also more reliable when rosette features are available, especially showing where inflorescences are borne; the morphology of both staminate and pistillate flowers, as well as that of fruits, is usually important for species-level determination. In many cases, accurate determination to species is extremely difficult without geographical information and field data, particularly with less than perfect material. The following artificial key was explicitly devised to help identify the three genera of Hechtioideae. It is important to understand that most of these clades are internally variable, and variation patterns often partially overlap: the key below is therefore polythetic and thus several characters often have to be evaluated simultaneously to arrive at a positive identification.

Key to Major Clades of Hechtioideae

1a. Inflorescences lateral, originating from the lower internodes of a pseudomonopodial rosette 2

1b. Inflorescences terminal either on a fully grown rosette or from a rosette in development, which may or may not halt its growth after flowering, often both types present simultaneously . . . . . 3 (*Hechtia, pro parte*)

2a. Peduncle, rachis, bracts, and sepals with dense lanuginose pubescence; ovary superior . . . . . *Hechtia* (*H. glomerata* complex)

2b. Peduncle, rachis, bracts, and sepals glabrous or subglabrous; ovary ½ inferior . . . . . *H. epigyna–H. deceptrix* Clade

3a. Rosettes round and flat to funnel-shaped; leaves spreading to erect, never pendent; foliar margins armed with pungent, usually uncinate spines; flowers sessile or pedicellate, pedicel rarely thin (<1 mm diam.), usually thick (>2 mm diam.), corolla rotate or tubular, petals patent; ovary superior or rarely half-inferior . . . . . Core *Hechtia* (Fig. 2)

3b. Rosettes round and flat when young, usually becoming grass-like upon maturing, with leaves spreading to pendent, never erect; foliar margins armed but spines not pungent, or minutely serrate; inflorescences centrally borne on a fully grown rosette; flowers sessile to pedicellate, corolla with petals spreading, coiled/reflexed; ovary superior or ¾ inferior 4

4a. Flowers long-pedicellate, pedicel thin, with white, lilac, or pink petals, green or lilac sepals, ovary superior; fruits pendulous when mature, septicidal, carpels papyraceous, sepals and petals persistent on the fruit; seeds with white wings when dry; species native from the Veracruzan, Transmexican Volcanic Belt, Balsas Basin, and Sierra Madre Oriental provinces, endemic to Mexico . . . . . *Bakerantha* (Fig. 3)

4b. Flowers sessile, with white petals, or white with red apical portions, green or red sepals, ovary ¾ inferior; fruits erect or sometimes pendulous when mature, loculicidal, carpels rigid; seed with brown wings when dry; species native from the Chiapas Highlands, Pacific Lowlands, Mosquito, and Veracruzan biogeographical provinces, in Belize, Guatemala, Honduras, El Salvador, and Nicaragua . . . . . *Mesoamerantha* (Fig. 4)

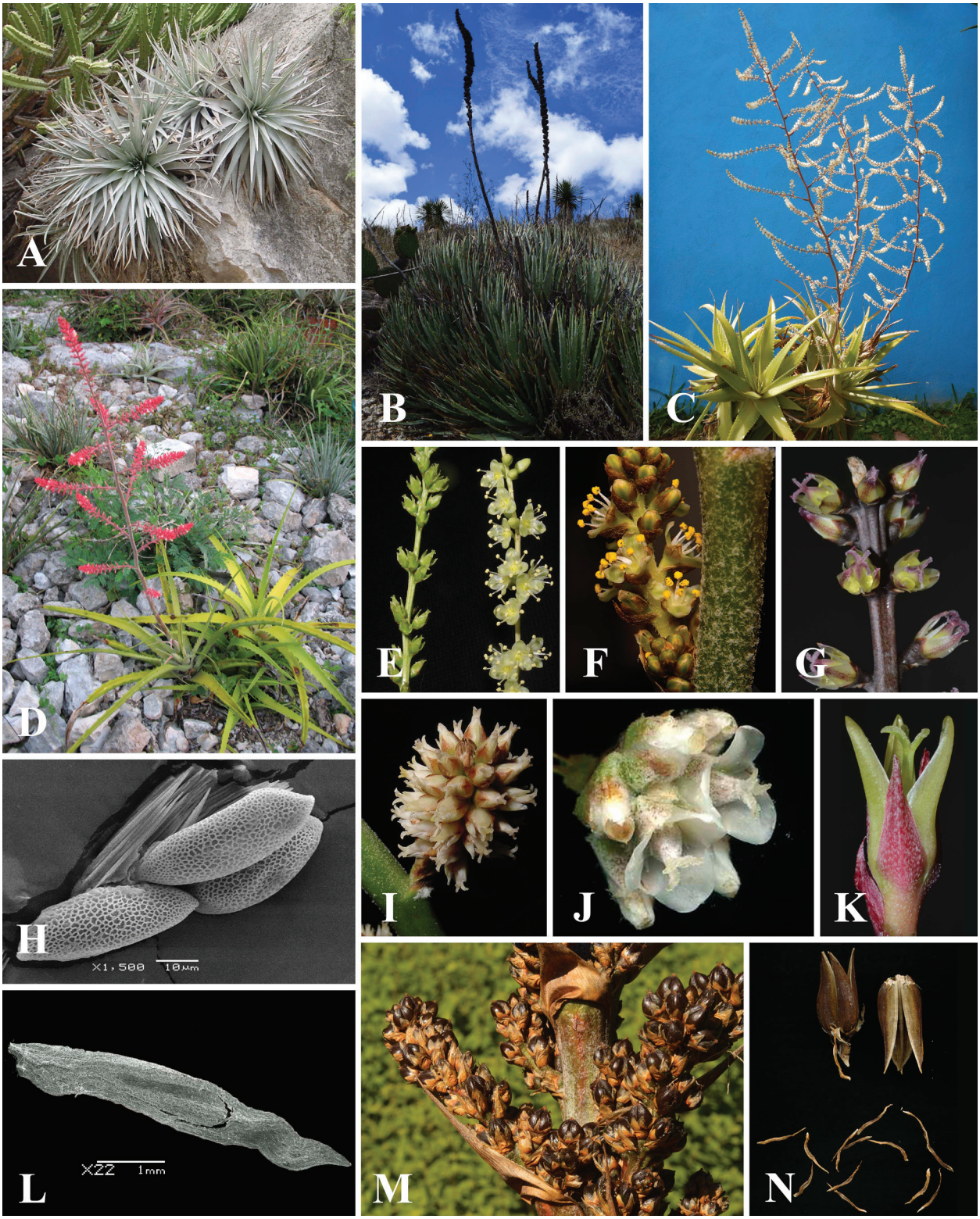

FIGURE 2. Some features of *Hechtia* s.s. **A**, *Hechtia zamudioi* Espejo, López-Ferr. & I. Ramírez showing its litophytic habit; **B**, *H. perotensis* I. Ramírez & Martinez-Correa in habitat; **C**, staminate plant of *H. fosteriana* L.B. Sm. under cultivation; **D**, *H. meziana* L.B. Sm. in bloom under cultivation; **E**, flowers of *H. aquamarina* I. Ramírez & C.F. Jiménez: pistillate (left) and staminate (right); **F**, staminate flowers of *H. confusa*; **G**, pistillate flowers of *H. huamelulaensis* I. Ramírez & Carnevali; **H**, pollen grain and raphides on *H. argentea* K. Koch; **I**, pistillate flowers of *H. nuusaviorum* Espejo & López-Ferr.; **J**, pistillate flowers of *H. glomerata* Zucc.; **K**, pistillate flower of *Hechtia iltisii* Burt-Utley & Utley; **L**, seed of *Hechtia stenopetala* Klotzsch; **M**, capsules of *Hechtia bracteata* Mez; **N**, open capsules and seeds of *Hechtia rosea* E. Morren ex Baker. Photograph and image credits: (A, C, D, E, I, J, K, M, N) I. Ramírez-Morillo, (B) C. Ramírez-Díaz, (F) G. Carnevali, (G) G. Romero-González, (H) E. Herrera and L. Can, (L) E. Gorocica and L. Can.

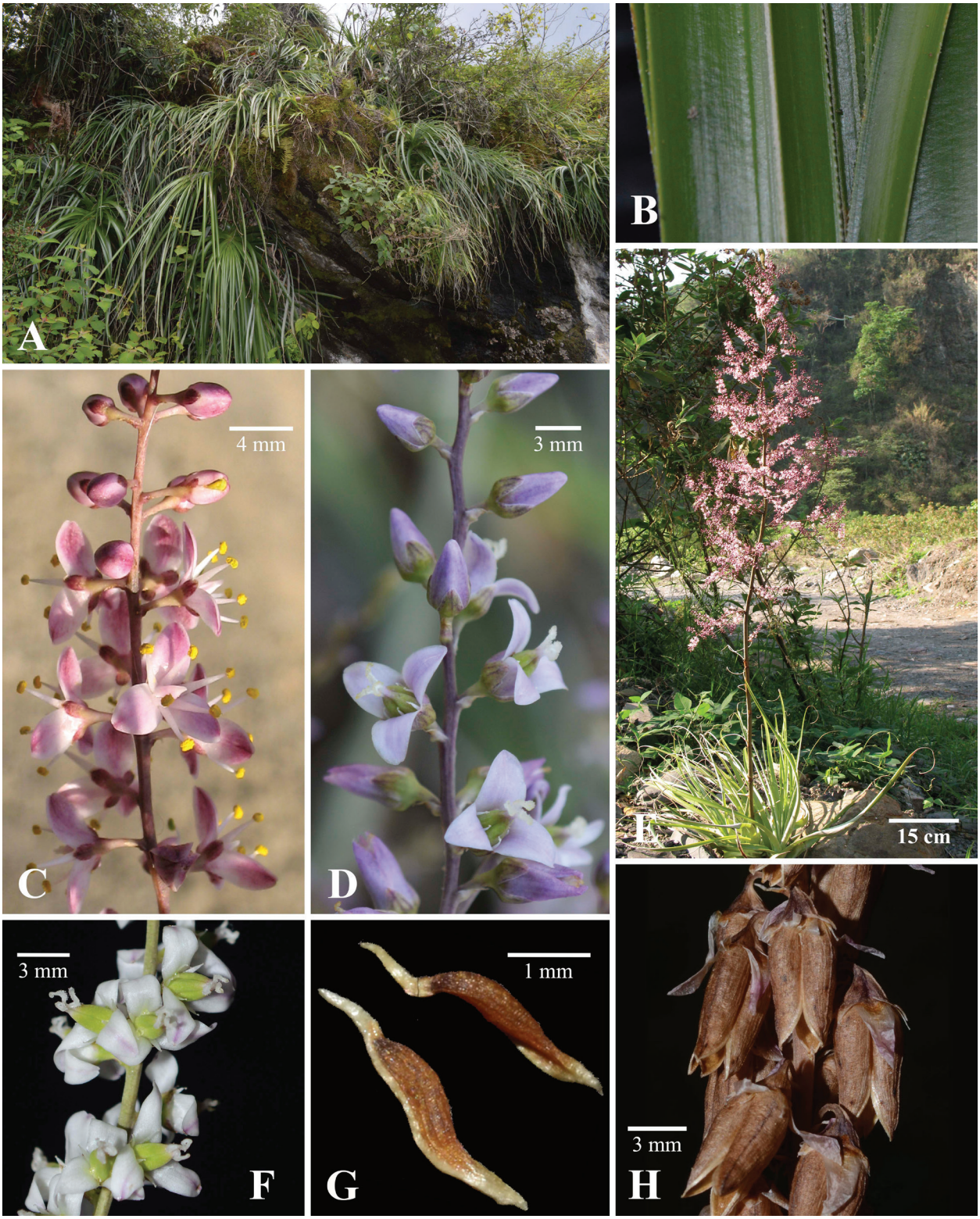

FIGURE 3. Main morphological features of the genus *Bakerantha* L.B. Sm. **A–B**, **F**. *Bakerantha lundelliorum* (L.B. Sm.) I. Ramírez & K. Romero. **A**, habit, note long and pending leaves; **B**, leaves with minute, sparsely distributed teeth on margins; **F**, pistillate flowers with white petals, note white staminodes around the ovary. **C**, **E**. *Bakerantha tillandsioides* (André) L. B. Sm. **C**, staminate flowers in anthesis; **E**, staminate plant in bloom. **D**, **G–H**. *Bakerantha caerulea* (Matuda) I. Ramírez & K. Romero. **D**, pistillate flowers; **G**, seeds; **H**, pendulous, dry fruits with persistent petals and sepals. Photograph credits: (A, B, D, F) K. Romero-Soler, (C, E) I. Ramírez-Morillo, (G, H) G. Salazar.

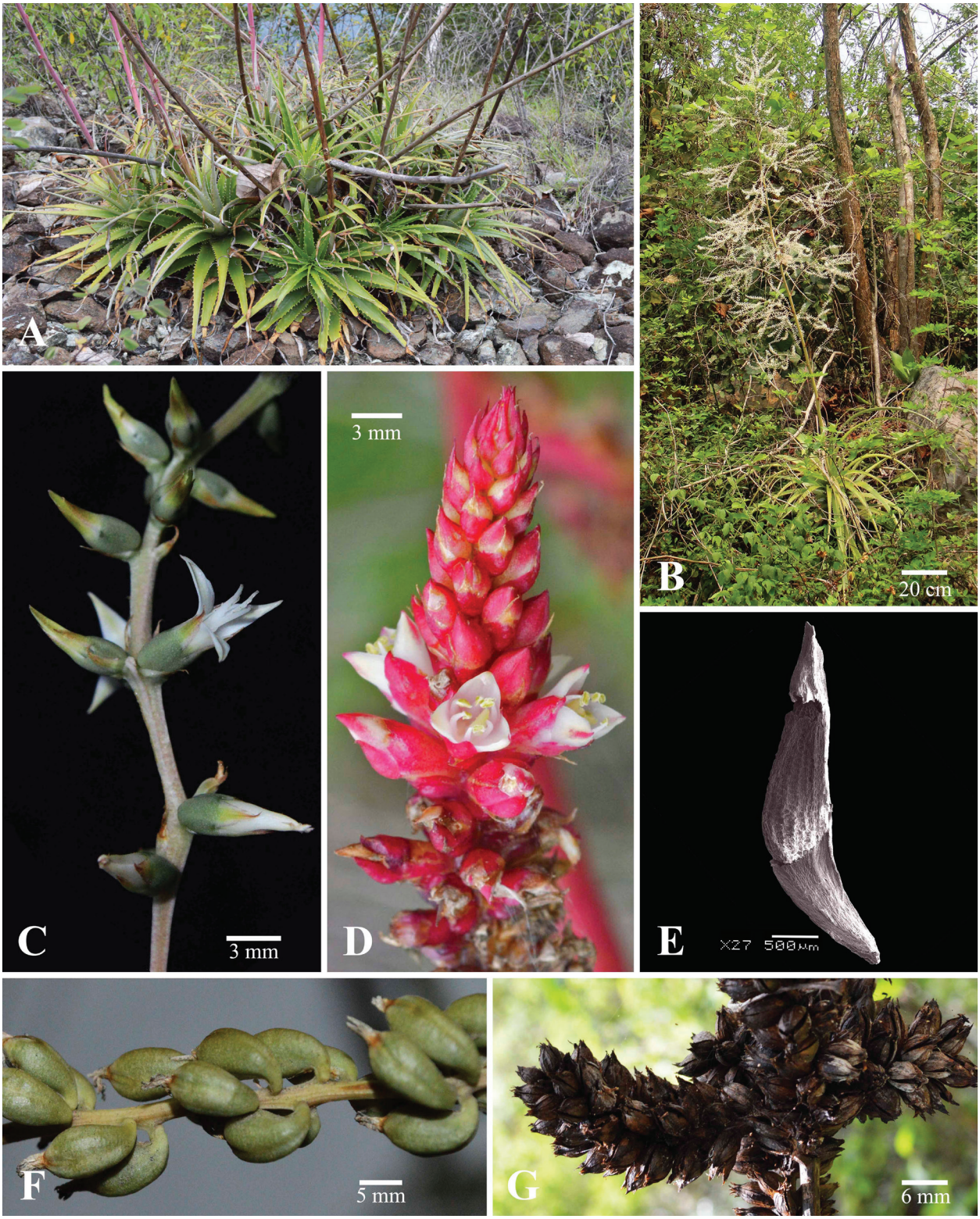

FIGURE 4. Main morphological features of the genus *Mesoamerantha* I. Ramírez & K. Romero, *gen. nov.* **A**, **D**, **G**. *Mesoamerantha dichroantha* (Donn. Sm.) I. Ramírez & K. Romero. **A**, habitat; **D**, staminate flowers **G**, fruits. **B**, **C**, **F**. *Mesoamerantha guatemalensis* (Mez) I. Ramírez & K. Romero. **B**, male plant in bloom; **C**, pistillate flowers; **F**, fruits. **E**. *Mesoamerantha malvernii* (Gilmartin) I. Ramírez & K. Romero. **E**, seeds. (A, C, D, F, G) K. Romero-Soler (B) I. Ramírez-Morillo, (E) E. Gorica and L. Can.

Bakerantha L.B. Sm., Contr. Gray. Herb. 104: 72 (1934).
Type species: *Bakerantha tillandsioides* (André) L.B. Sm.
Synonym: *Niveophyllum* Matuda, Cactáceas y Suculentas Mexicanas 10: 3–5, f. 2–4 (1965).
Type species: *Niveophyllum caeruleum* Matuda

Plants terrestrial or lithophytic herbs, acaulescent to caulescent, medium to large sized, forming rosettes but some becoming grass-like when adults. *Leaves* many per rosette; *foliar sheaths* square, ovate to transversely oblong, glabrous or white-lepidote abaxially; *foliar blades* narrowly triangular to linear-triangular, sometimes apically dry and curly, frequently pendulous, margins entire or minutely dentate, glabrous adaxially or scarcely lepidote, white and densely lepidote abaxially. *Inflorescences* central, paniculate, staminate (1)–3 divided, pistillate 1–3 divided, erect to pendulous, longer than leaves; scape and main axis glabrous; *flowers* polystichous, divaricate to diffuse, pedicellate, pedicels filiform; *sepals* petaloid, free; *petals* free, white, pink, cerulean, or lilac, membranaceous, multinerved, spreading, coiled/reflexed, exposing the entire ovary (or pistillode), and stamens (or staminodes) at anthesis; *staminodes* laminate; *ovary* superior, conical; *stamens* erect, filaments laminate; *anther* oblong, dorsifixed; *pistillode* conical, conspicuous; *stigma* sessile, lobes long and conspicuous; *fruits* dry capsules, septicidal, when immature erect, becoming pendulous when mature and seeds are free, carpels papyraceous, sepals and petals persistent on the fruit; *seeds* small and thin, fusiform, 3–3.5 mm long, 0.56–0.67 mm wide, bicaudate.

Distribution: Veracruzan, Transmexican Volcanic Belt, Balsas Basin, and Sierra Madre Oriental biogeographical provinces (sensu Morrone, 2014, and references therein) in Mexico (States of Hidalgo, Guerrero, México, Morelos, Puebla, Querétaro, San Luis Potosí, and Veracruz).

Nomenclatural history: in 1889, the French botanist Édouard François André, honoring the bromeliologist John G. Baker, proposed the genus *Bakeria* and described the first species referable to this genus (*B. tillandsioides*). André was apparently unaware that the generic name he coined was pre-occupied twice, once for a taxon in the Araliaceae (*Bakeria* Seemann, 1864), then again in the Rosaceae, when Michel Gandoger (1876) raised his own *Rosa* sect. *Bakeria* to the generic level. The great doyen of bromeliology, Lyman B. Smith, then proposed in 1934 the genus *Bakerantha* to accommodate *Bakeria tillandsioides* André (=*Bakerantha tillandsioides* (André) L.B. Smith). Later on, Smith (1951) placed *Bakerantha* in the synonymy of *Hechtia*. In 1965, a second species of this affinity was described as *Niveophyllum caeruleum* by Eizi Matuda, who referred his new taxon to Liliaceae. Smith realized this taxon was related to *H. tillandsioides* and transferred it to *Hechtia* in 1972 as *H. caerulea*. In the meantime, M. B. Foster had described *H. integerrima* in 1968, and Smith, realizing it was conspecific with Matuda's taxon, also placed it the synonymy of *H. caerulea* (Smith, 1972); Espejo et al. (2010) eventually referred the latter to the synonymy of *H. tillandsioides*. An analysis of the complex of taxa related to *H. tillandsioides* (Romero-Soler, 2017) required four species to account for the variability in geography and morphological space of the group. This analysis also strongly supported the notion that *H. tillandsioides* was more closely related to *H. lundelliorum* than to *H. caerulea*.

Bakerantha caerulea (Matuda) I. Ramírez & K. Romero, *comb. nov.*
Basionym: *Niveophyllum caeruleum* Matuda, Cactáceas y Suculentas Mexicanas 10: 3–5, f. 2–4 (1965).
TYPE: MEXICO. Mexico State: ravine, Santo Tomás de los Plátanos, S of Valle de Bravo, 1200 m, 15 March 1960, *E. Matuda 37440* ♀/♂ (Holotype: MEXU-273770, MEXU-273771).
Homotypic synonym: *Hechtia caerulea* (Matuda) L.B. Sm., Phytologia 24: 446, t. 5, f. 5 (1972).

Distribution: this species is known from a few localities in the Mexican states of Guerrero, Mexico, and Morelos, where it appears to be endemic. Localities are within the biogeographical region of the Balsas Basin, very close to the limits of the Transmexican Volcanic Belt. It grows on igneous rocks at elevations of 1100–1800 m in tropical dry forests. Espejo et al. (2010) proposed *Hechtia caerulea* as a synonym of *H. tillandsioides*, but our results (Ramírez-Morillo et al., 2018), based on cladistic analyses of DNA sequences (plastid and nuclear regions) and morphology and including all taxa in the complex, support the hypothesis that these entities are two different species.

Bakerantha lundelliorum (L.B. Sm.) I. Ramírez & K. Romero, *comb. nov.*
Basionym: *Hechtia lundelliorum* L.B. Sm., North American Flora 19: 97–98 (1938).
TYPE: MEXICO. San Luis Potosí, Tamazunchale, July 1937, C. *Lundell & A. Lundell 7265* ♀ (Holotype: MICH; Isotype: GH).
Heterotypic synonym: *Hechtia integerrima* M.B. Foster, Bromeliad Society Bulletin 18: 4, f. (1968). Type: Mexico: no exact locality, no date, *M. B. Foster 3072* ♀ (Holotype: US).

Distribution: populations of this species have been reported from the Mexican states of Hidalgo, Querétaro, and San Luis Potosí (where the type specimen comes from) or more properly from the Veracruzan and Sierra Madre Oriental biogeographical provinces, at elevations of 200–1250 m. There, mature rosettes grow on steep, continuously seeping rocky slopes, forming colonies of many individuals with pendent leaves, inflorescences, and infructescences.

Bakerantha purpusii (Brandegee) I. Ramírez & K. Romero, *comb. nov.*
Basionym: *Hechtia purpusii* Brandegee, University of California Publications in Botany 7: 325 (1920).
TYPE: MEXICO. Veracruz, Barranca de Tenampa, May 1919, C. A. *Purpus 8420* ♀ (Holotype: GH; Isotypes: NY, UC, US).
Heterotypic synonym: *Hechtia lindmanioides* L.B. Sm., Contributions from the Gray Herbarium of Harvard University 117: 14–15, t. 1, f. 24–26 (1937). TYPE:

MEXICO. Veracruz, stony slopes, Barranca de Consoquitla near El Fortin, *F. M. Liebmann 7951* ♀ (Holotype: F [photograph, GH]; Isotype: C, photograph available at JStor).

Distribution: this species is endemic to the Mexican state of Veracruz, where it is found in low caducifolious forests, on vertical walls of canyons in the Sierra Madre Oriental and Veracruzan biogeographical provinces, at 300–600 m of elevation.

Bakerantha tillandsioides (André) L. B. Sm., Contributions from the Gray Herbarium of Harvard University 104: 72 (1934). TYPE: [BRASIL] most likely MEXICO. Without precise locality, *ex Hort*. [Monsieur] A. de la Devansaye *sub E. André s.n*. (Holotype: K [K000307707]). Fig. 5–6.

Basionym: *Bakeria tillandsioides* André, Revue Horticole 61: 84, pl. (1889), *nom. illeg*. [Art. 52.1].

Homotypic synonym: *Hechtia tillandsioides* (André) L. B. Sm., Contributions from the United States National Herbarium 29(10): 431 (1951).

Distribution: populations of this species are known from the Sierra Madre Oriental biogeographical region, close to the limits of the Veracruzan Province, in the Mexican states of Hidalgo, Puebla, and Querétaro, at 750–850 m, on steep vertical walls along rivers in tropical dry forests.

Additional specimens examined: without country of origin, most likely MEXICO: K00030778 (Fig. 5); MEXICO. Puebla: Mun. Pahuatlán, El Río, a 3 Km al N de Pahuatlán, carr. a San Pablito, 20°18'N, 98°13'W [20°17'29.6"N, 98°08'49.1"W], 850 m, 04 Mayo 1989, *P. Tenorio 15730*♂ (MEXU); 20°17'33.5"N, 98°08'50"W, 767 m, 26 Abril 2007, *I. Ramírez, J.L. Tapia Muñoz y F. Chi May 1475a*♀, *1475*♂ (CICY); *I. Ramírez & G. Carnevali 1851*♂ (CICY).

Several features of this entity are relevant and are here discussed in detail as follows.

The first is the gender of the flowers in the holotype: in the protologue of the species, the androecium was described as "Étamines égalant les pétales, insérées suivant une ligne simple et régulière; anthères ovales, dorsifixies, versatiles" and the gynoecium as "*Ovaire semi-infère, dressé, trigone e triloculaire; ovules nombreux, superposés; style et stigmates très-courts, non tordus*." In order to determine whether the flowers were hermaphroditic or unisexual, the first author studied the holotype at K (K000307707; see Fig. 6) and concluded that the ovary did not have ovules. It is probable, but unlikely, that the supposedly hermaphroditic flower André examined (1889) had "ovules" in early stages of development; nonetheless, our examination of the ovary (pistillode) did not reveal ovules at all, and we conclude that the flowers are unisexual, staminate in this case, and support the transfer by Smith (1951) from *Bakerantha* to the dioecious genus *Hechtia*.

Another element we need to clarify is the place of origin of this species. When Édouard André (1889) described *Bakeria tillandsioides*, he was unsure as to the country of origin ("Brésil?"). Later, Mez (1896: 344) indicates at the very end of the description of *Bakeria* "(=*Bakeria*)… '*Patria dubia, verisimiliter Columbia*.'" Later on, Smith (1951) mentioned that stating "Colombia" as the place of origin "was another of those confusions so frequent in the description of novelties from horticultural material," concluding that the species was a native of Mexico. We have collected staminate plants in bloom in Puebla (Pahuatlán) and studied herbarium material from Querétaro (Moctezuma and Estórax rivers) that perfectly match the illustration, and we conclude that both populations represent the concept in the protologue of *Bakeria tillandsioides*, especially the illustration (Fig. 7), as well as the holotype, including drawings included thereon. Relevant herbarium material from Mexico here assigned to this species is cited above.

Mesoamerantha I. Ramírez & K. Romero, *gen. nov.*

Type species: *Hechtia guatemalensis* Mez

A genus of Hechtioideae closely related to *Hechtia* but diagnosable by means of the following character combination: central inflorescence, sessile flowers with a ¾ inferior ovary, and white, rarely apically red petals. It is also restricted to the extreme south of Megamexico.

Etymology and distribution: *Mesoamerantha* alludes to the fact that this new genus is restricted to the Mesoamerica region, particularly to Nicaragua, El Salvador, Honduras, Guatemala, and Belize, in pine-forest or low caducifolious forests.

Three species are recognized in this genus and are distributed in the biogeographical provinces of Chiapas Highlands, Pacific Lowlands, Mosquito, and Veracruzan (sensu Morrone, 2014).

Mesoamerantha guatemalensis (Mez) I. Ramírez & K. Romero, *comb. nov.*

Basionym: *Hechtia guatemalensis* Mez, Repertorium Specierum Novarum Regni Vegetabilis 3: 14. 1906.

TYPE: GUATEMALA. Guatemala: San Bernardo between Trapiche Grande and Las Canoras, April 1905, *H. F. Pittier 137*♂ (Holotype; US; Isotypes: B, GH).

Mesoamerantha guatemalensis is known from Belize to northern Nicaragua, commonly growing over rocky soils and road cuts. It usually forms dense colonies in open areas of tropical dry forests and xerophytic scrub. The populations of the species are distributed along the Chiapas Highlands, Pacific Lowlands, Mosquito, and Veracruzan biogeographical provinces (sensu Morrone, 2014), at elevations of 100–1600 m.

Mesoamerantha dichroantha (Donn. Sm.) I. Ramírez & K. Romero, *comb. nov.*

Basionym: *Hechtia dichroantha* Donn. Sm., Botanical Gazette 42(4): 299–300. 1906. TYPE: GUATEMALA. Baja Verapaz: slopes above Río Quililiha near Santa Rosa, May 1905, *O. F. Cook s.n.* ♂ (Holotype: US; Isotype: GH, US).

Mesoamerantha dichroantha is endemic in Guatemala, where it grows on rocky soils and cliffs, forming dense colonies in an area of pine-oak forests at 500–1600 m. Populations of *M. dichroantha* are apparently restricted to the central zone of the Chiapas Highlands biogeographical province (sensu Morrone, 2014).

FIGURE 5. Holotype of *Bakerantha tillandsioides* André. ex Hort. [Monsieur] A. de la Devansaye sub *E. André s.n.* (K000307707). Courtesy of Herbarium K. © by the Board of Trustees of the Royal Botanic Gardens, Kew. http://specimens.kew.org/herbarium/K000307707.

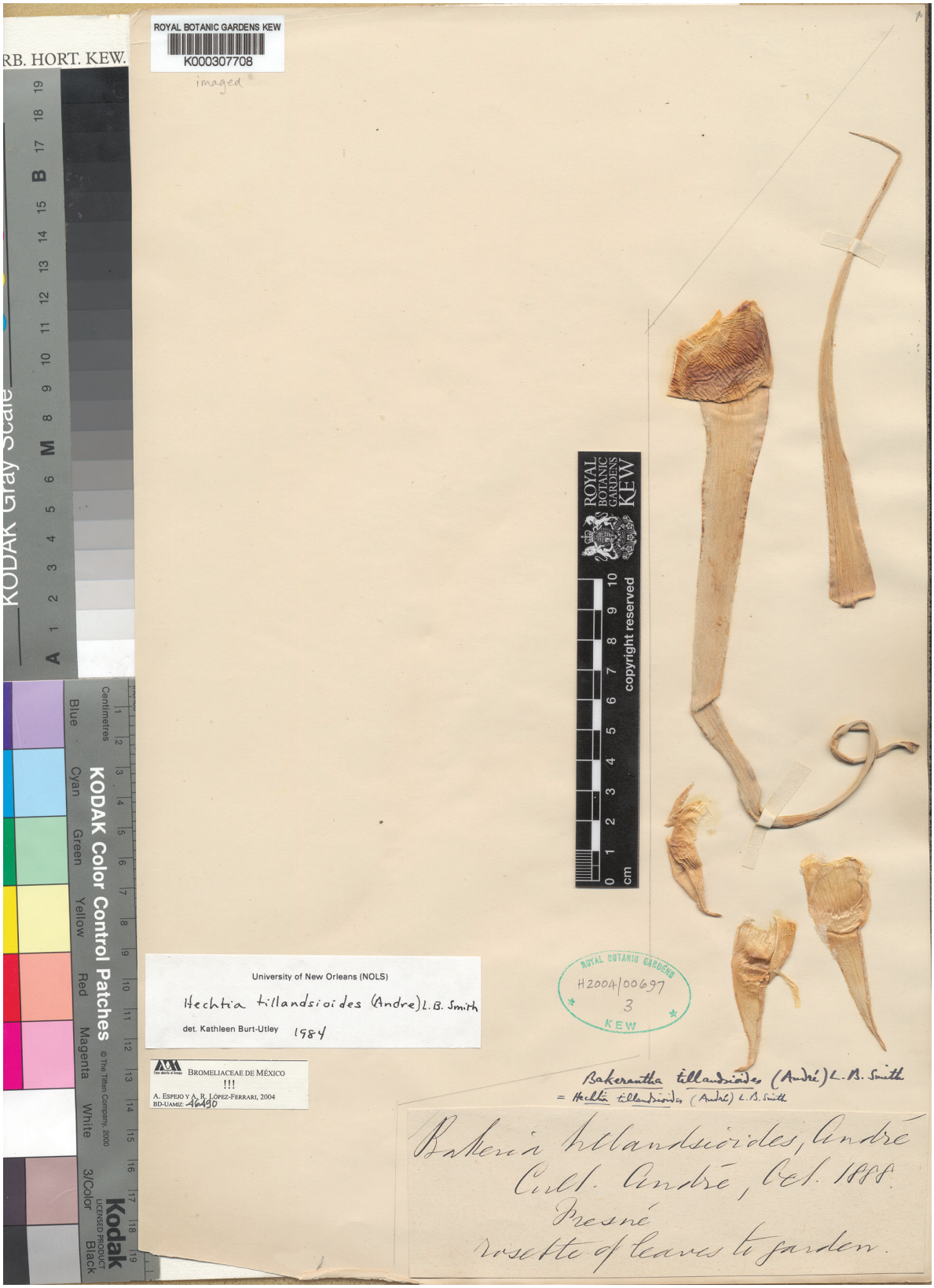

FIGURE 6. An additional specimen (K00030778) specifies "*Cult. André... 1888*," indicating that the plant was probably taken from a cultivated plant by André, which discards it as holotype. Courtesy of Herbarium K. © by the Board of Trustees of the Royal Botanic Gardens, Kew. http://specimens.kew.org/herbarium/K000307708.

FIGURE 7. *Bakerantha tillansioides* (André) L. B. Smith (sub *Bakeria*). Illustration in André (1889). Courtesy of the Botany Libraries, Harvard University Herbaria.

Mesoamerantha malvernii (Gilmartin) I. Ramírez & K. Romero, *comb. nov.*

Basionym: *Hechtia malvernii* Gilmartin, Ceiba 11(2): 9, f. 4. 1965.

TYPE: HONDURAS. El Paraiso: bank road cut near small ravine, km. 75 Tegucigalpa-Danli, 700 m, July 1964, *A. J. Gilmartin 966* ♀ (Holotype: US; Isotypes: EAP, US).

Mesoamerantha malvernii is endemic to Honduras where it inhabits pine-oak forests, more rarely tropical deciduous forests, in the eastern portion of the country, and in the southern portion of the Chiapas Highlands biogeographical province at 600–1800 m elevation.

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