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A synopsis of the *Bromeliaceae* of Panama, including new records for the country

Abstract

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Based on extensive field and herbarium studies, twenty species of *Bromeliaceae* are newly reported for Panama: *Aechmea beeriana*, *A. penduliflora*, *A. pittieri*, *A. strobilacea*, *Bromelia hemispherica*, *Guzmania graminifolia*, *G. hollinensis*, *Pitcairnia halophila*, *P. wendlandii*, *Tillandsia dexteri*, *T. ionantha*, *T. longifolia*, *T. utriculata*, *Werauhia bracteosa*, *W. kathyae*, *W. macrantha*, *W. macrochlamys*, *W. notata*, *W. paniculata*, *W. viridis*. Former reports of six bromeliad species for Panama are revised as erroneous. The bromeliad flora of Panama now comprises 206 species. Endemism of the *Bromeliaceae* in Panama and Costa Rica is newly evaluated based on this revised inventory: 33 species are endemic to Panama, 32 to Costa Rica, 36 species to both countries. Only 3 of the 8 presently recognised subfamilies occur in Panama. The genus *Werauhia* has its centre of diversity in Panama (47 of 87 species) and Costa Rica. A distribution map is presented for the newly reported species.

Resumen

Basado en estudios extensivos de campo y de herbarios, veinte especies de Bromeliaceae son reportadas por primera vez para Panamá: *Aechmea beeriana*, *A. penduliflora*, *A. pittieri*, *A. strobilacea*, *Bromelia hemispherica*, *Guzmania graminifolia*, *G. hollinensis*, *Pitcairnia halophila*, *P. wendlandii*, *Tillandsia dexteri*, *T. ionantha*, *T. longifolia*, *T. utriculata*, *Werauhia bracteosa*, *W. kathyae*, *W. macrantha*, *W. macrochlamys*, *W. notata*, *W. paniculata*, *W. viridis*. Se informa la revisión de seis especies de bromelias de Panamá, erróneamente reportadas. La flora de bromelias de Panamá ahora comprende 206 especies. El alto endemismo de Bromeliaceae en Panamá y Costa Rica es revisado en este estudio: 33 especies son endémicas de Panamá, 32 de Costa Rica y 36 especies entre ambos países. Sólo 3 de las 8 subfamilias actualmente reconocidas, ocurren en Panamá. El género *Werauhia* tiene su centro de diversidad en Panamá (47 de 87 especies) y Costa Rica. Se presenta un mapa con la distribución de las nuevas especies reportadas.

Additional key words: bromeliads, endemism, life-form, taxonomy, systematic diversity, epiphytes

Introduction

Among the Central American countries, Panama (8560 species, Correa & al. 2004) and Costa Rica (8249 species, Hammel & al. 2004) are the countries with the highest diversity of flowering plants, which is well correlated with the overall biodiversity. The diversity of flowering plants

scientifically documented for Panama has increased considerably in the last decades: from 5314 species in the “Flora of Panama” founded by Woodson and completed between 1943 and 1987 (D’Arcy 1987), to 7345 species in the checklist by D’Arcy (1987) and 8560 species in the most recent checklist by Correa & al. (2004). Keeping the

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comparatively small surface area of 75 845 km² (IGNTG 2007) in mind, Panama is obviously one of the hotspots of plant diversity in the Neotropics.

The *Bromeliaceae* (bromeliads) of Panama, though clearly outnumbered by the orchids, are one of the major groups of epiphytes and contribute considerably to overall forest diversity. Because of their ecological versatility they have attracted special attention from botanists, ecologists and physiologists (e.g. Smith & Downs 1974, 1977, 1979, Croat 1978, Laube & Zotz 2006 and Zotz & Schultz 2008).

Within a few decades, our knowledge of the Panamanian bromeliad flora has increased considerably. Smith (1944) reported 87 species, D'Arcy (1987) 136, Utley (1994) 148 and Correa & al. (2004) 178 species. Further additions were recently published by Morales (2009) (*Werauhia brunei*, *W. camptoclada*) and Wester & al. (2011) (*Aechmea mariae-reginae*, *Tillandsia pruinosa*, *Werauhia singuliflora*).

Here we present updated and amended information on the diversity of *Bromeliaceae* in Panama, including patterns of endemism and systematic diversity. The results are based on detailed studies of the relevant herbarium collections and extensive fieldwork.

Material and methods

The herbarium collections of *Bromeliaceae* from 31 herbaria (B, BM, COL, CR, DS, DUKE, F, FR, GH, HEID, HUH, INB, K, LG, LI, MEXU, MICH, MO, NEU, NY, QCNE, PMA, SCZ, SEL, TEX, UC, UMO, US, USJ, W and WU; abbreviations following Thiers 2008+) were studied. Altogether 2968 herbarium specimens of *Bromeliaceae* from Panama and 4523 from Costa Rica were revised.

Field work in western Panama in 2004, 2008 and 2009 added 363 collections and 858 occurrence observations for *Bromeliaceae*. The specimens collected by Cáceres & al. are deposited in the herbaria of the Universidad de Panama, Panama City (PMA) and the Senckenberg Research Institute, Frankfurt/Main (Herbarium Senckenbergianum, FR).

These data provide the basis for a critical evaluation of the published records of *Bromeliaceae* in Panama and are also the basis of the quantitative, life form and endemism analysis of the *Bromeliaceae* presented.

Each entry in our list of bromeliad species of Panama is substantiated by the citation of representative specimens, which allow critical examination of the report.

Nomenclature and generic delimitation follow Luther (2008) and IPNI (2011).

Results

Bromeliaceae diversity in Panama

Twenty species are recorded here for Panama for the first time: *Aechmea beeriana*, *A. penduliflora*, *A. pittieri*, *A.*

strobilacea, *Bromelia hemispherica*, *Guzmania gramini-folia*, *G. hollinensis*, *Pitcairnia halophila*, *P. wendlandii*, *Tillandsia dexteri*, *T. ionantha*, *T. longifolia*, *T. utriculata*, *Werauhia bracteosa*, *W. kathyae*, *W. macrantha*, *W. macrochlamys*, *W. notata*, *W. paniculata* and *W. viridis*. Including these additions, the *Bromeliaceae* in Panama now comprise 206 species and account for 2.4 % of the total angiosperm flora of Panama. The whole family comprises 3172 species in 58 genera (Luther 2008), so 6.5 % of the species and 27.6 % of the generic diversity are represented in the country.

Only three of eight subfamilies of the *Bromeliaceae* are represented in Panama, with a strong predominance of the *Tillandsioideae* (7 genera/147 species; 71.4 % of all Panamanian bromeliad species), followed by the *Bromelioideae* (7/34; 16.5 %) and the *Pitcairnioideae* s.str. (2/25; 12.1 %) (Table 1).

At the generic level, *Werauhia* is the most diverse taxon in Panama with 47 species (22.8 % of the bromeliad flora), followed by *Guzmania* (45 species, 21.8 %), *Tillandsia* (34 species, 16.5 %), *Pitcairnia* (28 species, 11.2 %) and *Aechmea* (22 species, 10.7 %) (Table 1).

All species are listed below with information on their life form (Lf: E = epiphytic, T = terrestrial, S = saxicolous) and endemism (En: PA = endemic to Panama, CR = Costa Rica, CO = Colombia). Three revised herbarium collections are listed for each species, except in cases where the number of available collections was less than three. Type specimens are indicated (holo = holotype, iso = isotype, lecto = lectotype). Three species still have to be described and are cited here as "sp.". The new species records for Panama are marked in bold and treated in more detail with information also on the distribution range of the species and with citation of all herbarium collections known from Panama. Six species recorded as erroneous for Panama are given in a separate list at the end.

Aechmea allenii L. B. Sm. – Lf: E, T; En: PA; *McPherson* 8533 (MO), *Croat* 37486 (MO), *Dressler* 4603 (PMA).

Aechmea angustifolia Poepp. & Endl. – Lf: E; *Carrasquilla & Mendoza* 1228 (PMA), *Allen* 2378 (US, holo), *Cáceres & Pérez* 3973 (FR, PMA).

Aechmea beeriana L. B. Sm. & M. A. Spencer – Lf: E. Distribution: Panama (Fig. 1), Peru, Guianas, Brazil. Panama: Darien, Chepigana, 7.8.1986, *McDonagh & al.* 541 (MO).

Aechmea bracteata (Sw.) Griseb. – Lf: E; *von Wedel* 2922 (MO), *de Nevers & al.* 7686 (MO).

Aechmea dactylina Baker – Lf: E, T; *Fendler* 450 (MO, holo). *Dwyer & Gentry* 9508 (MO), *Cáceres & Fátima* 4027 (FR, PMA).

Aechmea germinyana (Carrière) Baker – Lf: E; En: PA & CO; *Williams* 960 (NY).

Aechmea haltonii H. Luther – Lf: E, S; En: PA; *Churchill & al.* 5988 (MO), *Halton* 85-1447 (SEL, holo), *Luther s.n.* (SEL).

- Aechmea jungurudoensis* H. Luther & K. F. Norton – Lf: E; En: PA; Kiehl s.n. (SEL, holo).
- Aechmea lingulata* (L.) Baker – Lf: E; Sytsma 1893 (MO), Davidse & Hamilton 23698 (MO), Cáceres & Fuentes 4023 (FR, PMA).
- Aechmea magdalenae* (André) André ex Baker – Lf: T; Folsom 2552 (MO), D'Arcy 9306 (MO), Cáceres 4185 (FR, PMA).
- Aechmea mariae-reginae* H. Wend. – Lf: E, S; Roubick & al. 1109 (PMA), Cáceres & Pérez 3883 (FR, PMA), Cáceres & Pérez 4129 (FR, PMA).
- Aechmea mexicana* Baker – Lf: E, T; Churchill & Rauh 4999 (MO), Antonio 3437 (MO), Cáceres 4049 (FR, PMA).
- Aechmea nudicaulis* (L.) Griseb. – Lf: E; Zizka Z50 (FR), Correa & Dressler 1034 (PMA), Cáceres & Pérez 3966 (FR, PMA).
- Aechmea penduliflora*** André – Lf: E.
Distribution: Nicaragua, Costa Rica, Panama (Fig. 1), Colombia, Venezuela, Ecuador, Peru, Bolivia.
Panama: Bocas del Toro, Changuinola Distr., community of Junquito, 11.7.2008, Cáceres & Pérez 3882 (FR, PMA), 3884 (FR, PMA); Chiriquí, Baru Distr., Puerto Armuelles (Chorogo), 22.6.2008, Cáceres & al. 3839 (FR, PMA).
- Aechmea pittieri*** Mez – Lf: E.
Distribution: Costa Rica, Panama (Fig. 1).
Panama: Chiriquí, Renacimiento Distr., 7.6.2009, Cáceres 4047 (FR, PMA).
- Aechmea pubescens* Baker – Lf: E, T; Hammel 4260 (MO), Hayes 538 (NY), Cáceres & Pérez 4136 (FR, PMA).
- Aechmea setigera* Mart. ex Schult. f. – Lf: E; Duke 10945 (MO), Correa & al. 4682 (PMA), Croat 8195 (SCZ).
- Aechmea strobilacea*** L. B. Sm. – Lf: E.
Distribution: Panama (Fig. 1), Ecuador, Peru.
Panama: Panama Distr., east slope of Cerro Jefe, 15.2.1982, Knapp 3563 (MO); Comarca Kuna Yala, Nargana, El Llano–Carti road, 16.1.1985, de Nevers 4583 (MO); Darien, Comarca Embera–Wounaan 1, 25.8.1974, Croat 27202 (MO).
- Aechmea strobilina* (Beurl.) L. B. Sm. & Read – Lf: E, T; En: PA; Antonio 1185 (MO), D'Arcy & Sytsma 14722 (MO), de Nevers & al. 4740 (MO).
- Aechmea tillandsioides* (Mart. ex Schult. f.) Baker – Lf: E; Hamilton & Davidse 2822 (PMA), Luther 1128 (SEL), Cáceres & Pérez 3861 (FR, PMA).
- Aechmea tonduzii* Mez & Pittier ex Mez – Lf: E, T; Hamilton & D'Arcy 668 (MO), Hammel & al. 16422 (MO), McPherson 12656 (MO).
- Aechmea veitchii* Baker – Lf: E, T; Monro & al. 5972 (PMA), Ibáñez & al. AI5834 (SCZ), Cáceres & Pérez 3930 (FR, PMA).
- Ananas ananassoides* (Baker) L. B. Sm. – Lf: T; Cáceres 4187 (FR, PMA).
- Ananas comosus* (L.) Merr. – Lf: T; Dwyer 1604 (MO), Müller-Schwarze 145 (PMA), Cáceres 4171 (FR, PMA).
- Araeococcus pectinatus* L. B. Sm. – Lf: E; Whitefoord & Eddy 176 (MO), Antonio & Hahn 4386 (PMA), McPherson & al. 15396 (PMA).
- Billbergia macrolepis* L. B. Sm. – Lf: E; Shattuck 373 (MO), Croat 11247 (MO), Cáceres & Pérez 3879 (FR, PMA).
- Bromelia hemispherica*** Lam. – Lf: T.
Distribution: Mexico, Nicaragua, Costa Rica, Panama (Fig. 1).
Panama: Cocle, Penonome Distr., 27 km north of Penonome on road to Coclesito, 20.2.1978, Hammel 1640 (MO).
- Bromelia karatas* L. – Lf: T; Saunders 525 (MO), Nee 7455 (MO, PMA), Cáceres & al. 4088 (FR, PMA).
- Bromelia pinguin* L. – Lf: T; Tyson 2737 (MO, SCZ), Croat 9746 (NY), Aizprúa & Alvarez B4357 (PMA).
- Catopsis berteroniana* (Schult. & Schult. f.) Mez – Lf: E; Seibert 646 (MO), Allen 738 (MO), Gentry & al. 3415 (MO).
- Catopsis juncifolia* Mez & Wercklé – Lf: E; Miller 1754-A (US, n.v.).
- Catopsis micrantha* L. B. Sm. – Lf: E; Tyson & al. 4423 (MO, PMA), Pierce 00-27 (SCZ), Cáceres 4101 (FR, PMA).
- Catopsis nitida* (Hook.) Griseb. – Lf: E, T, S; Davidson 863 (MO), Folsom & al. 5470 (PMA), Cáceres & Pérez 3853 (FR, PMA).
- Catopsis nutans* (Sw.) Griseb. – Lf: E; Dodge 16585 (MO), Croat 12310 (PMA), Cáceres & al. 4058 (FR, PMA).
- Catopsis pisiformis* Rauh – Lf: E; En: PA; Rauh 58635 (HEID, holo).
- Catopsis sessiliflora* (Ruiz & Pav.) Mez – Lf: E; Correa & Dressler 423 (PMA), Ibáñez & al. AI5717 (SCZ), Cáceres 4166 (FR, PMA).
- Catopsis wangerinii* Mez & Wercklé – Lf: E; Stern & al. 1117 (MO), Croat 26280 (MO), Cáceres & Pérez 3921 (FR, PMA).
- Greigia columbiana* L. B. Sm. – Lf: T; Davidse & al. 25247 (MO), Cáceres 4141 (FR, PMA).
- Greigia sylvicola* Standl. – Lf: T; En: CR, PA; Gómez & al. 22416 (MO, SEL), Aranda & al. 1481 (PMA), Cáceres & Pérez 3957 (FR, PMA).
- Guzmania angustifolia* (Baker) Wittm. – Lf: E; Croat 37106 (MO), Terry & Terry 1579 (MO), Cáceres 4116 (FR, PMA).
- Guzmania armeniaca* H. Luther – Lf: E; En: PA; Luther s.n. (SEL, holo).
- Guzmania attenuata* L. B. Sm. & Read – Lf: E; Gentry & al. 16866 (MO, holo).
- Guzmania berteroniana* (Schult. & Schult. f.) Mez – Lf: E; Allen 3957 (MO, n.v.).
- Guzmania butcheri* Rauh – Lf: E; En: CO, PA; Antonio 3747 (MO), Herrera 850 (MO).
- Guzmania calamifolia* André ex Mez – Lf: E, T; Antonio

- 1124 (MO, NY), *Nee 11221* (MO), *Luther & al. 1116* (PMA).
- Guzmania cerrohoyaensis* H. Luther – Lf: T; En: PA; *Skotak s.n.* (SEL, holo).
- Guzmania cinnabarina* H. Luther & K. F. Norton – Lf: E; En: PA; *Luther s.n.* (SEL, iso).
- Guzmania circinnata* Rauh – Lf: E, T; En: CR, PA; *Grant 97-2665* (MO, SEL), *Carrasquilla 3061* (PMA), *Cáceres 3998* (FR, PMA).
- Guzmania coriostachya* (Griseb.) Mez – Lf: E; *Bristan 491* (MO), *Pierce 00-26* (PMA), *Luther s.n.* (SEL).
- Guzmania darienensis* H. Luther – Lf: E; En: PA; *Herrera & al. 1006* (MO, holo), *Skotak s.n.* (SEL), *Anon. s.n.* (SEL).
- Guzmania desautelsii* Read & L. B. Sm. – Lf: E, S; *Sytsma & Stevens 2213* (MO), *de Nevers 4529* (PMA), *Cáceres & Pérez 3900* (FR, PMA).
- Guzmania dissitiflora* (André) L. B. Sm. – Lf: E; *Sytsma 2972* (MO), *McPherson 20766* (MO), *Carrasquilla 3060* (PMA).
- Guzmania donnellsmithii* Mez ex Donn. Sm. – Lf: E, T; *Sytsma & Antonio 2984* (MO), *D'Arcy 10342* (MO), *Cáceres & Pérez 3813* (FR, PMA).
- Guzmania elvallensis* H. Luther – Lf: E; En: PA; *Knapp 5320* (MO, holo), *Read 84* (SEL), *Berg P40* (SEL).
- Guzmania filiorum* L. B. Sm. – Lf: E; En: PA; *Antonio & al. 3405* (MO), *Mori & al. 3743* (MO), *Pierce 00-37* (PMA).
- Guzmania flagellata* S. Pierce & J. R. Grant – Lf: E, T; En: PA; *Duke 8022* (MO), *Tyson 3532* (SCZ), *Berg s.n.* (SEL).
- Guzmania glomerata* Mez & Wercklé – Lf: E, T; *Dwyer & Lallathin 8694* (NY), *Luther 1095* (SEL), *Cáceres & Pérez 3894* (FR, PMA).
- Guzmania graminifolia*** (André ex Baker) L. B. Sm. – Lf: E.
Distribution: Panama (Fig. 1), Colombia, Ecuador, Peru.
Panama: Darien, Chepigana, Darien National Park, Cerro Pirre, 7.2.1991, *Herrera & al. 880* (MO, PMA).
- Guzmania hollinensis*** H. Luther – Lf: T.
Distribution: Panama (Fig. 1), Colombia, Ecuador, Peru.
Panama: Chiriqui, Gualaca Distr., Fortuna Forest Reserve (Bijao, Chiriqui river-top), 20.6.2009, *Cáceres 4062* (FR, PMA).
- Guzmania kennedyae* L. B. Sm. & Read – Lf: E; En: CO, PA; *Churchill & al. 4931* (MO), *Croat 22674* (MO), *Hammel 2326* (MO).
- Guzmania lingulata* (L.) Mez – Lf: E, T; *Gentry 8776* (MO), *Hamilton & Davidse 2605* (PMA), *Cáceres & Fuentes 4012* (FR, PMA).
- Guzmania loraxiana* J. R. Grant – Lf: E; En: PA; *Grant & Rundell 97-2660* (US, holo, n.v.). *Cáceres & Pérez 3964* (FR, PMA).
- Guzmania macropoda* L. B. Sm. – Lf: E, T; En: PA; *Tyson & al. 4446* (MO, iso), *McPherson 12114* (MO), *Pierce 00-25* (PMA).
- Guzmania membranacea* L. B. Sm. & Steyerl. – Lf: T; *McPherson 10625* (MO), *Skotak s.n.* (SEL).
- Guzmania mitis* L. B. Sm. – Lf: E; *Sytsma & al. 2734* (MO).
- Guzmania monostachia* (L.) Rusby ex Mez – Lf: E; *Croat 22011* (MO), *Liesner 1089* (PMA), *Cáceres & Pérez 4134* (FR, PMA).
- Guzmania multiflora* (André) André ex Mez – Lf: E; *Churchill & Rauh 4997* (MO, n.v.).
- Guzmania musaica* (Linden & André) Mez – Lf: E, T; *Sytsma & D'Arcy 3573* (MO), *Folsom 3618* (PMA), *Cáceres & Pérez 3893* (FR, PMA).
- Guzmania nicaraguensis* Mez & C. F. Baker ex Mez – Lf: E, T; *Kirkbride & Duke 1290* (MO, NY), *Mori & Kallunki 5842* (PMA), *Cáceres & Pérez 3913* (FR, PMA).
- Guzmania obtusiloba* L. B. Sm. – Lf: E; *Knapp 5063* (MO), *Croat 69032* (MO), *Cáceres 4066* (FR, PMA).
- Guzmania patula* Mez & Wercklé – Lf: E; *Mori & Kallunki 2725* (MO), *Gentry 2133* (MO, SCZ), *Dressler 4121* (PMA).
- Guzmania plicatifolia* L. B. Sm. – Lf: E, T; En: CR, PA; *Knapp 1152* (MO, NY), *Foster 1902* (PMA), *Cáceres & Pérez 3906* (FR, PMA).
- Guzmania polycephala* Mez & Wercklé ex Mez – Lf: E, T; *Croat 15691* (MO), *Hammel 4731* (MO), *Luther s.n.* (SEL).
- Guzmania sanguinea* (André) André ex Mez – Lf: E; *Antonio 5126* (MO), *Cáceres 4100* (FR, PMA).
- Guzmania scandens* H. Luther & W. J. Kress – Lf: E, T; En: CR, PA; *Gentry & Clewell 7006* (MO), *Croat 68929* (MO), *Cáceres 4152* (FR, PMA).
- Guzmania scherzeriana* Mez – Lf: E; *de Nevers & al. 5264* (MO), *Hamilton & Davidse 2838* (PMA), *Cáceres & Pérez 3801* (FR, PMA).
- Guzmania* sp. – Lf: E; En: PA; *Luther 1093* (SEL).
- Guzmania speciosa* H. Luther – Lf: E; En: PA; *Luther s.n.* (SEL), *Skotak s.n.* (SEL).
- Guzmania sphaeroidea* (André) André ex Mez – Lf: E; *Stevens 18434* (MO), *de Nevers & al. 5574* (MO), *Carrasquilla 2099* (MO, PMA).
- Guzmania sprucei* (André) L. B. Sm. – Lf: E, T; *Liesner 698* (MO), *Peña & al. 441* (PMA), *Cáceres & Pérez 3815* (FR, PMA).
- Guzmania stenostachya* L. B. Sm. – Lf: E, T; En: CR, PA; *Kirkbride Jr. & Duke 929* (MO, NY), *Van der Werff & Van Hardeveld 6738* (PMA), *Cáceres & Pérez 3789* (FR, PMA).
- Guzmania subcorymbosa* L. B. Sm. – Lf: E; *Duke 14205* (MO), *Herrera & al. 1491* (MO), *Hamilton & D'Arcy 1394* (MO).
- Guzmania teucamae* H. Luther & K. F. Norton – Lf: E; En: PA; *Skotak s.n.* (SEL, iso).
- Guzmania zahonii* (Hooker f.) Mez – Lf: E; *Croat 37894* (MO), *D'Arcy & McPherson 16200* (MO), *Cáceres 4114* (FR, PMA).



Fig. 1. Distribution of bromeliad species newly recorded for the flora of Panama. – Details see text.

Table 1. *Bromeliaceae* of Panama: species richness and endemism.

Subfamily & genera	Number of species	% of bromeliad flora	Number of endemic species	% of endemic species
<i>Tillandsioideae</i>				
<i>Catopsis</i>	8	3.9	1	3
<i>Guzmania</i>	45	21.8	12	36.4
<i>Mezobromelia</i>	1	0.5	0	0
<i>Racinaea</i>	5	2.4	0	0
<i>Tillandsia</i>	34	16.5	0	0
<i>Vriesea</i>	7	3.4	3	9.1
<i>Werauhia</i>	47	22.8	6	18.2
Subtotal = 7	147	71.4	22	66.7
<i>Bromelioideae</i>				
<i>Aechmea</i>	21	10.2	4	12.1
<i>Ananas</i>	2	1	0	0
<i>Araeococcus</i>	1	0.5	0	0
<i>Billbergia</i>	1	0.5	0	0
<i>Bromelia</i>	3	1.5	0	0
<i>Greigia</i>	2	1	0	0
<i>Ronnbergia</i>	3	1.5	0	0
Subtotal = 7	34	16.5	4	12.1
<i>Pitcairnioideae</i>				
<i>Pepinia</i>	2	1	1	3
<i>Pitcairnia</i>	23	11.2	6	18.2
Subtotal = 2	25	12.2	7	21.2
Total = 16	206	100	33	100



Fig. 2. A: *Pitcairnia halophila*, Gulf of Chiriqui Marine National Park, Paridas Islands; B: *Tillandsia dexteri*, Remedios Distr.; C: *T. utriculata*, Changuinola Distr., after the community of El Silencio; D: *Werauhia paniculata*, Boquete Distr., El Pianista Trail to Culebra. – Photographs A, B, D by D. Cáceres; photograph C by L. Pérez.

Mezobromelia pleiosticha (Griseb.) Utley & H. Luther – Lf: E; Dwyer & Lallathin 8748 (MO, NY), Cáceres & Pérez 3850 (FR, PMA).

Pepinia aphelandriflora André – Lf: T, S; Aizprúa & Alvarez B4181 (F n.v., MO, PMA, SCZ), von Wedel 2282 (MO), McPherson 10706 (MO, PMA).

Pepinia hammelii (H. Luther) H. Luther – Lf: T, S; En: PA; Hammel 3182 (MO), Hammel & de Nevers 13599 (MO, iso; SEL, holo).

Pitcairnia arcuata (André) André – Lf: E, T; Folsom & Page 5945 (MO, NY), Churchill 3950 (SCZ), Cáceres & Pérez 3795 (FR, PMA).

Pitcairnia atrorubens (Beer) Baker – Lf: E, T, S; Gentry & al. 3483 (MO, NY), Kennedy 1533 (SCZ), Cáceres & Pérez 3793 (FR, PMA).

Pitcairnia brittoniana Mez – Lf: E; Gentry & Mori 14017

(MO), Cáceres & Pérez 3951 (FR, PMA).

Pitcairnia carnea Beer – Lf: T; En: PA; Manzanares 7433 (MO, QCNE), Warszewicz s.n. (MO photo; NY photo).

Pitcairnia chiriquensis L. B. Sm. – Lf: T, S; En: PA; Allen 5016 (MO, iso), Grant & Rundell 97-2826 (MO, NY, SEL), Cáceres & Pérez 3829 (FR, PMA).

Pitcairnia croatii H. Luther – Lf: T; En: PA; Croat 66448 (MO, holo).

Pitcairnia diffusa L. B. Sm. – Lf: E, T; Hammel 2405 (MO), Bruce & Hamilton 1106 (MO), de Nevers & al. 6734 (MO).

Pitcairnia geotropa J. R. Grant – Lf: T; En: PA; Grant & Rundell 97-2645 (SEL, iso), Grant 97-2816 (SEL).

Pitcairnia halophila L. B. Sm. – Lf: S, T.

Distribution: Costa Rica, Panama (Fig. 1, 2A).

- Panama: Chiriqui, San Lorenzo Distr., Horconcos (Hermosa Beach), 8.8.2008, *Cáceres & al.* 3939 (FR, PMA); *ibid.*, 16.5.2009, *Cáceres & al.* 3994 (FR, PMA); David Distr., Pedregal, Golfo de Chiriqui Marine National Park, Paridas Islands, 25.6.2009, *Cáceres & al.* 4093 (FR, PMA); Veraguas, Montijo Distr., Coiba Island, 27.8.1970, *Foster* 1639 (MO, PMA); Montijo Distr., Coiba Island, 1.12.1996, *Galdames & al.* 3566 (MO, NY, SCZ); Montijo Distr., Coiba National Park, 3.12.1996, *Galdames & al.* 3616 (SCZ); Las Palmas Distr., Coiba National Park (Uva Island), 3.6.2004, *Ibáñez s.n.* (SEL). Los Santos, Pedasi, Punta Mala, 14.4.1970, *Croat* 4216 (MO); Pedasi, Venado Beach, 30.10.1978, *Hammel* 5474 (MO, SCZ).
- Pitcairnia heterophylla* (Lindl.) Beer – Lf: E, T, S; *Dodge & Allen* 17467 (MO), *Croat* 13587 (SCZ), *Cáceres & Pérez* 3916 (FR, PMA).
- Pitcairnia imbricata* (Brongn.) Regel – Lf: T, S; *Schmalzel & al.* X38 (MO), *Hamilton & Krager* 3792 (MO), *Cáceres* 4048 (FR, PMA).
- Pitcairnia kalbreyeri* Baker – Lf: T; *Knapp & al.* 4232 (MO), *Davidson* 300 (MO), *Cáceres* 4081 (FR, PMA).
- Pitcairnia kressii* H. Luther – Lf: E, T; En: PA; *Croat* 66836 (MO), *Luther & al.* 1131 (SEL, holo), *Cáceres* 4000 (FR, PMA).
- Pitcairnia lymansmithiana* H. Luther – Lf: E, T; En: CR, PA; *McPherson* 12577 (MO), *Luther* 1099 (SEL, holo), *Cáceres & Pérez* 3891 (FR, PMA).
- Pitcairnia maidifolia* (C. Morren) Decne. – Lf: E, T, S; *D'Arcy* 9552 (MO), *Lewis & al.* 3156 (MO), *Croat* 12380 (MO).
- Pitcairnia megasepala* Baker – Lf: E, T; *Sytsma & D'Arcy* 3456 (MO), *Hernández & al.* FH1295 (SCZ), *Cáceres & Pérez* 3851 (FR, PMA).
- Pitcairnia multiflora* L. B. Sm. – Lf: E, T; En: PA & CO; *Hamilton & Davidse* 2681 (MO), *Ibáñez & al.* AI5841 (SCZ), *Cáceres* 4064 (FR, PMA).
- Pitcairnia nigra* (Carrière) André – Lf: E, T; *Zizka* Z40 (FR), *Luther* 1041 (SEL), *Cáceres & Pérez* 3947 (FR, PMA).
- Pitcairnia rundelliana* J. R. Grant – Lf: T; En: PA; *D'Arcy* 16279 (MO, PMA), *Grant* 97-2882 (SEL, iso), *Cáceres & Pérez* 3787 (FR, PMA).
- Pitcairnia saxicola* L. B. Sm. – Lf: S; *Warszewicz s.n.* (MO photo).
- Pitcairnia schultzei* Harms – Lf: T, S; *Luteyn & Foster* 1384 (MO), *Croat* 37040 (MO).
- Pitcairnia valerioi* Standl. – Lf: E, T; En: CR, PA; *Hamilton & Davidse* 2629 (MO), *Luther* 1078 (SEL), *Cáceres* 4155 (FR, PMA).
- Pitcairnia wendlandii*** Baker – Lf: T.
Distribution: Mexico, Belize, Guatemala, Costa Rica, Panama (Fig. 1).
Panama: Panama Distr., Cerro Azul, 8.1985, *Halton s.n.* (SEL).
- Racinaea adpressa* (André) J. R. Grant – Lf: E; *Zizka* Z35 (FR), *Gentry & al.* 28697 (MO), *Croat* 48626 (MO).
- Racinaea contorta* (Mez) M. A. Spencer & L. B. Sm. – Lf: E; *Antonio* 2820 (MO), *Dwyer & Gentry* 9386 (MO, NY, PMA), *Cáceres & Pérez* 3816 (FR, PMA).
- Racinaea crispa* (Baker) M. A. Spencer & L. B. Sm. – Lf: E; *Folsom* 4306 (MO), *Foster* 14131 (PMA), *Gentry & Mori* 13670 (SCZ).
- Racinaea schumanniana* (Wittm.) J. R. Grant – Lf: E; *Blum & Dwyer* 2662 (MO, SCZ), *Luther* 1090 (SEL), *Cáceres & al.* 3984 (FR, PMA).
- Racinaea spiculosa* (Griseb.) M. A. Spencer & L. B. Sm. – Lf: E; *McPherson* 10586 (MO), *Antonio* 5141 (MO, NY), *Cáceres & Pérez* 3892 (FR, PMA).
- Ronnbergia explodens* L. B. Sm. – Lf: E, T; *De Nevers & al.* 5380 (MO, PMA), *Correa & Dressler* 42 (PMA), *Ibáñez & al.* AI6108 (SCZ).
- Ronnbergia hathewayi* L. B. Sm. – Lf: E, T; *Zizka* Z48 (FR), *McPherson* 7340 (MO), *Cáceres* 4068 (FR, PMA).
- Ronnbergia maidifolia* Mez – Lf: T; En: PA & CO; *Allen* 4493 (MO, n.v.).
- Tillandsia anceps* Lodd. – Lf: E; *Davidse & Hamilton* 23618 (MO, PMA), *Liesner* 1097 (PMA), *Cáceres & Pérez* 3825 (FR, PMA).
- Tillandsia balbisiana* Schult. f. – Lf: E; *Croat* 12309 (MO, NY), *Nee* 10103 (MO, PMA), *Cáceres & Pérez* 4135 (FR, PMA).
- Tillandsia biflora* Ruiz & Pav. – Lf: E; *Stevens* 18164 (MO), *Gentry* 5981 (MO, PMA), *Cáceres* 4145 (FR, PMA).
- Tillandsia brachycaulos* Schldtl. – Lf: E; *Allen* 3478 (MO), *Cáceres & Pérez* 3836 (FR, PMA), *Cáceres & Pérez* 3944 (FR, PMA).
- Tillandsia bulbosa* Hook. – Lf: E; *Peterson & Annable* 6740 (MO, SEL), *Croat* 7048 (SCZ), *Cáceres & Pérez* 3826 (FR, PMA).
- Tillandsia butzii* Mez – Lf: E; *Allen* 1592 (MO), *Pittier* 3011 (NY), *Cáceres* 3997 (FR, PMA).
- Tillandsia caput-medusae* E. Morren – Lf: E; *Zizka* Z9 (FR), *Folsom* 3998 (MO), *Cáceres & al.* 4095 (FR, PMA).
- Tillandsia complanata* Benth. – Lf: E; *Woodson Jr. & Schery* 602 (MO), *Jerry* 1369 (SCZ), *Cáceres* 4142 (FR, PMA).
- Tillandsia compressa* Bert. ex Schult. f. – Lf: E; *Woodson Jr. & Schery* 823 (MO).
- Tillandsia dexteri*** H. Luther – Lf: E.
Distribution: Costa Rica, Panama (Fig. 1, 2B).
Panama: Chiriqui, Remedios Distr., 12.7.2008, *Cáceres & Pérez* 3888 (FR, PMA); *ibid.*, 21.4.2009, *Cáceres* 3971 (FR, PMA).
- Tillandsia elongata* Kunth – Lf: E; *Croat & Porter* 15449 (MO), *Allen* 4152 (SCZ), *Cáceres* 4005 (FR, PMA).
- Tillandsia excelsa* Griseb. – Lf: E; *Liesner* 936 (MO,

- PMA), *Grant 00-3714* (SEL), *Cáceres & Pérez 3945* (FR, PMA).
- Tillandsia fasciculata* Sw. – Lf: E; *Carrasquilla 2137* (MO, PMA), *Peterson & Annable 7082* (MO, SEL), *Cáceres & al. 4086* (FR, PMA).
- Tillandsia festucoides* Brongn. ex Mez – Lf: E; *Kirkbride & Bristan 1532* (MO, NY), *Whitefoord & Eddy 493* (PMA), *Cáceres & Pérez 4133* (FR, PMA).
- Tillandsia flexuosa* Sw. – Lf: E; *Woodson Jr. & al. 1488* (MO, NY), *Knapp 1926* (MO, PMA), *Cáceres & Pérez 3831* (FR, PMA).
- Tillandsia guatemalensis* L. B. Sm. – Lf: E; *Allen 4361* (MO, n.v.).
- Tillandsia ionantha*** Planch. – Lf: E.
Distribution: Mexico, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama (Fig. 1), Peru. Panama: Chiriquí, Boquete Distr., Alto Boquete, 24.1.1969, *Partch 69-107* (MO).
- Tillandsia juncea* Poir. – Lf: E; *Sytsma & D'Arcy 3455* (MO, NY), *Liesner 120* (MO, PMA), *Cáceres 4084* (FR, PMA).
- Tillandsia kegeliana* Mez – Lf: E; *Tyson & Smith 4158* (MO), *Hammel 7325* (MO), *Duke 14314* (MO, NY).
- Tillandsia leiboldiana* Schltdl. – Lf: E; *Stevens 18438* (MO), *Laube & al. SL133* (PMA, SCZ), *Cáceres 3993* (FR, PMA).
- Tillandsia longifolia*** Baker – Lf: E.
Distribution: Costa Rica, Panama (Fig. 1), Peru, Venezuela, Bolivia.
Panama: Chiriquí, Dolega Distr., El Burro, Potrerillos, 18.6.2009, *Cáceres & al. 4060* (FR, PMA); Boquete Distr., 16.7.2009, *Cáceres 4146* (FR, PMA).
- Tillandsia monadelpha* (E. Morren) Baker – Lf: E; *Gentry & al. 3453* (MO, NY, PMA), *Hamilton & Davidse 2657* (MO, PMA), *Cáceres & Pérez 3805* (FR, PMA).
- Tillandsia multicaulis* Steud. – Lf: E; *Croat 26966* (MO), *Dressler & Williams 4007* (PMA), *Cáceres & Pérez 3922* (FR, PMA).
- Tillandsia oerstediana* L. B. Sm. – Lf: E; En: CR, PA; *Carrasquilla 3054* (MO), *Cáceres 4004* (FR, PMA), *Cáceres 4149* (FR, PMA).
- Tillandsia pinnata* Mez & Sodiro – Lf: E; *Croat 60500* (MO), *Dressler 4592* (PMA), *Skotak s.n.* (SEL).
- Tillandsia pruinosa* Sw. – Lf: E; *Laube & al. SL460* (SCZ), *Luer 10597* (SEL).
- Tillandsia punctulata* Schltdl. & Cham. – Lf: E; *Hamilton & al. 1225* (MO), *Woodson Jr. & al. 991* (MO, NY), *Cáceres & Pérez 3846* (FR, PMA).
- Tillandsia singularis* Mez & Wercklé – Lf: E, T; *Croat 25888* (MO, PMA), *Blance 3001* (SEL), *Cáceres 4074* (FR, PMA).
- Tillandsia subulifera* Mez – Lf: E; *Cáceres & Pérez 3935* (FR, PMA).
- Tillandsia tricolor* Schltdl. & Cham. – Lf: E; *Antonio 5142* (MO), *Liesner 259* (MO, PMA), *Cáceres 3996* (FR, PMA).
- Tillandsia usneoides* (L.) L. – Lf: E; *Allen 3667* (MO, NY), *Dressler 4296* (MO, PMA), *Cáceres & Pérez 3887* (FR, PMA).
- Tillandsia utriculata*** L. – Lf: E.
Distribution: Mexico, Belize, Guatemala, Costa Rica, Honduras, Nicaragua, Panama (Fig. 1, 2C), Dominican Republic, Haiti, Jamaica, Puerto Rico, United States (Florida) and Virgin Islands, Trinidad and Tobago.
Panama: Bocas del Toro, Changuinola Distr., after the community of El Silencio, 2.8.2008, *Cáceres & Pérez 3933* (FR, PMA); Changuinola Distr., Las Tablas, near the river and community of Sibube, 14.7.2009, *Cáceres & Pérez 4128* (FR, PMA).
- Tillandsia variabilis* Schltdl. – Lf: E; *von Wedel 1395* (MO), *Dodge & Steyermark 17033* (MO), *Cáceres & al. 3976* (FR, PMA).
- Tillandsia venusta* Mez & Wercklé – Lf: E; *Mori & al. 4205* (MO, PMA), *Laube & al. SL274* (SCZ), *Luther s.n.* (SEL).
- Vriesea alta* E. Morren ex Baker – Lf: E; En: PA; *Morren s.n.* (K, n.v.).
- Vriesea chontalensis* (Baker) L. B. Sm. – Lf: E; *Croat 23073* (MO), *Liesner 260* (MO, PMA), *Cáceres 3988* (FR, PMA).
- Vriesea heliconioides* Lindl. – Lf: E; *Tyson & Dwyer 4470* (SCZ), *de Nevers 5960* (MO, PMA), *Cáceres & Pérez 3843* (FR, PMA).
- Vriesea incurva* (Griseb.) Read – Lf: E; *Folsom & Collins 1831* (MO), *Hammel & al. 6908* (MO), *Cáceres 4105* (FR, PMA).
- Vriesea monstrum* (Mez) L. B. Sm. – Lf: E, T; *Croat 27083* (MO, PMA), *Pierce 01-42* (SCZ), *Cáceres & Pérez 3817* (FR, PMA).
- Vriesea* sp. – Lf: E; En: PA; *Hammel & al. 16454* (MO), *Kirkbride & Duke 1376* (MO, NY, SEL), *Skotak s.n.* (SEL).
- Vriesea* sp. – Lf: E; En: PA; *Sytsma 3808* (MO), *McPherson 10742* (MO).
- Werauhia acuminata* (Mez & Wercklé) J. R. Grant – Lf: E, T; En: CR, PA; *Mori & Kallunki 3451* (MO), *Luther 1088* (SEL), *Cáceres 4080* (FR, PMA).
- Werauhia attenuata* (L. B. Sm. & Pittendr.) J. R. Grant – Lf: E; En: CR, PA; *Mori & Kallunki 4854* (MO), *Nee 9732* (MO), *Croat 67013* (MO).
- Werauhia bicolor* (L. B. Sm.) J. R. Grant – Lf: E; En: CR, PA; *Luther 1043* (SEL), *Luther 1091* (SEL), *Cáceres 4083* (FR, PMA).
- Werauhia bracteosa*** (Mez & Wercklé) J. R. Grant – Lf: E.
Distribution: Costa Rica, Panama (Fig. 1).
Panama: Chiriquí, Boquete Distr., Los Naranjos, El Pianista Trail to Culebra, 15.8.2008, *Cáceres & Pérez 3946* (FR, PMA); Cocle, Ola Distr., Nature Reserve El Cope (General de División Omar Torrijos Herrera National Park), 3.3.2004, *Zizka Z55* (FR).
- Werauhia brunei* (Mez & Wercklé) J. R. Grant – Lf:

- E; En: CR, PA; *Stevens 18426* (MO), *Croat 15787* (MO), *Croat 48630* (MO).
- Werauhia burgeri* (L. B. Sm.) J. R. Grant – Lf: E; En: CR, PA; *Hamilton & Stockwell 3531* (MO), *Cáceres & Pérez 3792* (FR, PMA), *Cáceres 4112* (FR, PMA).
- Werauhia camptoclada* (Mez & Wercklé) J. F. Morales – Lf: E; En: CR, PA; *Zizka Z29* (FR), *Schmalzel 1928* (MO).
- Werauhia capitata* (Mez & Wercklé) J. R. Grant – Lf: E; En: CR, PA; *Mori & Kallunki 3619* (MO), *Pierce 10* (PMA), *Pierce 2* (SEL).
- Werauhia comata* (Mez & Wercklé) J. R. Grant – Lf: E, T, S; En: CR, PA; *Liesner 924* (MO), *Foster 2072* (PMA), *Luther 1057* (SEL).
- Werauhia dressleri* (Rauh) J. R. Grant – Lf: T; En: PA; *Dressler s.n.* (HEID).
- Werauhia gladioliflora* (H. Wendl.) J. R. Grant – Lf: E, T; *Croat 22202* (MO), *Knapp & Chazdon 1406* (MO), *Cáceres 4051* (FR, PMA).
- Werauhia graminifolia* (Mez & Wercklé) J. R. Grant – Lf: E; *Hammel 2602* (MO), *Correa & al. 2324* (PMA), *Cáceres 4150* (FR, PMA).
- Werauhia greenbergii* (Utley) J. R. Grant – Lf: E, T, S; *Grant & Rundell 97-2814* (MO, SEL), *Luther 1120* (SEL), *Cáceres 4053* (FR, PMA).
- Werauhia hygrometrica* (André) J. R. Grant – Lf: E, T, S; *Liesner 888* (MO), *Grant 96-2411* (SEL), *Cáceres 4164* (FR, PMA).
- Werauhia insignis* (Mez) W. Till, Barfuss & M. R. Samuel – Lf: E, T, S; En: CR, PA; *Knapp & al. 2157* (MO, PMA), *Luther 1051* (SEL), *Cáceres & Pérez 3908* (FR, PMA).
- Werauhia jenii* S. Pierce – Lf: E; En: PA; *Pierce 15* (SEL, holo).
- Werauhia kathyae*** (Utley) J. R. Grant – Lf: E.
Distribution: Costa Rica, Panama (Fig. 1).
Panama: Chiriqui, Gualaca Distr., between Quebrada Higueron and Gutiérrez, Chiriquicito-Caldera Trail, 18.4. 1968, *Kirkbride & Duke 767* (MO, NY); Fortuna Dam area, Quebrada Bonito to N of reservoir, 30.7.1984, *Churchill 5760* (MO); Hornito, trail to Hornito River, Fortuna Forest Reserve, 16.7.2008, *Cáceres & Pérez 3897* (FR, PMA); Fortuna Forest Reserve, Quebrada Alemán, 7.7.2009, *Cáceres 4098* (FR, PMA).
- Werauhia kupperiana* (Suess.) J. R. Grant – Lf: E, T; *Churchill & al. 4171* (MO), *Luther 1134* (SEL), *Cáceres & Fuentes 4036* (FR, PMA).
- Werauhia latissima* (Mez & Wercklé) J. R. Grant – Lf: E, T; En: CR, PA; *Croat 14785* (MO), *Luther s.n.* (SEL), *Cáceres 4115* (FR, PMA).
- Werauhia laxa* (Mez & Wercklé) J. R. Grant – Lf: E, T, S; En: CR, PA; *McPherson 7830* (MO), *Luther 1118* (SEL), *Cáceres 4117* (FR, PMA).
- Werauhia leucophylla* (L. B. Sm.) J. R. Grant – Lf: E, T; En: CR, PA; *Dwyer & Hayden 7756* (MO), *Grant 00-3717* (SEL).
- Werauhia lutheri* S. Pierce & J. E. Aranda – Lf: E; En: PA; *Pierce 13* (SEL, holo), *Cáceres 4099* (FR, PMA), *Cáceres 4163* (FR, PMA).
- Werauhia macrantha*** (Mez & Wercklé) J. R. Grant – Lf: E.
Distribution: Costa Rica, Panama (Fig. 1).
Panama: Chiriqui, Las Nubes near Cerro Punta, 7.8.1974, *Croat 26445* (MO), *26446* (MO).
- Werauhia macrochlamys*** (Mez & Wercklé) J. F. Morales – Lf: E.
Distribution: Costa Rica, Panama (Fig. 1).
Panama: Chiriqui, Boquete Distr., ridgetop above Alto Boquete, 9.4.1979, *D'Arcy & al. 13126* (MO); Bugaba Distr., slopes of Las Cumbres near Cerro Punta, 20.2.1971, *Croat 13773* (MO); Bugaba Distr., 2.2 km SW of Cerro Punta, 7.8.1974, *Croat 26310* (MO).
- Werauhia marnier-lapostollei* (L. B. Sm.) J. R. Grant – Lf: E; En: CR, PA; *Croat 22204* (MO).
- Werauhia millennia* J. R. Grant – Lf: E, T; En: PA; *Hammel 2362* (MO), *Tyson & al. 4390* (SCZ), *Grant & Rundell 97-2697* (SEL, iso).
- Werauhia nephrolepis* (L. B. Sm. & Pittendr.) J. R. Grant – Lf: E, T; *D'Arcy & al. 12945* (MO), *Gentry 6007* (MO, SCZ), *Cáceres & Pérez 3928* (FR, PMA).
- Werauhia notata*** (L. B. Sm. & Pittendr.) J. R. Grant – Lf: E, T.
Distribution: Costa Rica, Panama (Fig. 1).
Panama: Bocas del Toro, Bosque Protector Palo Seco, Fortuna Forest Reserve (Cordillera Central), 16.7. 2008, *Cáceres & Pérez 3902* (FR, PMA).
- Werauhia ororiensis* (Mez) J. R. Grant – Lf: E, T; *Antonio 1587* (MO), *Hammel & al. 7140* (MO), *Cáceres 4139* (FR, PMA).
- Werauhia panamaensis* (E. Gross & Rauh) J. R. Grant – Lf: E, T; En: PA; *Pierce 99-10* (PMA), *Cáceres 4065 & 4160* (FR, PMA).
- Werauhia paniculata*** (Mez & Wercklé) J. R. Grant – Lf: E.
Distribution: Costa Rica, Panama (Fig. 1, 2D).
Panama: Chiriqui, Boquete Distr., corregimiento de Los Naranjos, El Pianista Trail to Culebra, 16.8.2008, *Cáceres & Pérez 3961* (FR, PMA); Gualaca Distr., Fortuna Dam region, along trail to Cerro Hornito (Pata de Macho), 17.1.1989, *McPherson 13562* (MO); Comarca Ngöbe Bugle, Nole Duima Distr., Cerro Colorado, along road between San Felix River and mining exploration camp, 7 mi W of Chami, 8.7.1988, *Croat 69176* (MO); Darien, Chepigana, Alto de Nique, southernmost peak of Pirre Massif, 19.4.1980, *Gentry & al. 28626* (MO).
- Werauhia pedicellata* (Mez & Wercklé) J. R. Grant – Lf: E, T; *Croat 48590* (MO), *McPherson 9390* (MO), *Cáceres & Pérez 3948* (FR, PMA).
- Werauhia picta* (Mez & Wercklé) J. R. Grant – Lf: E; En: CR, PA; *Hammel 7368* (MO), *Croat 37107* (MO), *Cáceres & Pérez 3952* (FR, PMA).
- Werauhia pittieri* (Mez) J. R. Grant – Lf: E; En: CR, PA;

Zizka Z36 (FR), *Hammel* 1420 (MO), *Luther* 1115 (SEL).

Werauhia ringens (Griseb.) J. R. Grant – Lf: E; *Kennedy* 2713 (MO), *Liesner* 1082 (MO, PMA), *Cáceres & Pérez* 3820 (FR, PMA).

Werauhia rubra (Mez & Wercklé) J. R. Grant – Lf: E, T; En: CR, PA; *Mori & Bolten* 7333 (MO), *Luther* 1089 (SEL), *Cáceres & Pérez* 3949 (FR, PMA).

Werauhia sanguinolenta (Linden ex Cogn. & Marchal) J. R. Grant – Lf: E, T, S; *Croat* 15883 (MO, NY), *Carrasquilla* 3067 (MO, PMA), *Cáceres & Pérez* 3885 (FR, PMA).

Werauhia singuliflora (Mez & Wercklé) J. R. Grant – Lf: E; En: CR, PA; *Berg s.n.* (SEL).

Werauhia stenophylla (Mez & Wercklé) J. R. Grant – Lf: E, T; En: CR, PA; *Churchill & al.* 4788 (MO), *Knapp & Sytsma* 2642 (MO), *Sullivan* 349 (MO).

Werauhia subsecunda (Wittm.) J. R. Grant – Lf: E; *Kirkbride & Duke* 1228 (MO).

Werauhia umbrosa (L. B. Sm.) J. R. Grant – Lf: E, T; *McPherson* 9940 (MO), *Croat* 33469 (MO), *Mori & Kallunki* 2344 (MO).

Werauhia viridiflora (Regel) J. R. Grant – Lf: E; *Dwyer & Gentry* 9470 (MO), *Luther* 1024 (SEL), *Cáceres & Pérez* 3896 (FR, PMA).

Werauhia viridis (Mez & Wercklé) J. R. Grant – Lf: E.

Distribution: Costa Rica, Panama (Fig. 1).

Panama: Chiriqui, Bugaba Distr., Las Nubes near Cerro Punta, 7.8.1974, *Croat* 26471 (MO).

Werauhia vittata (Mez & Wercklé) J. R. Grant – Lf: E; *Croat & Folsom* 33912 (MO), *Pierce* 6 (PMA, SEL), *Cáceres & Pérez* 3963 (FR, PMA).

Werauhia werckleana (Mez) J. R. Grant – Lf: E, T; *Liesner* 708 (MO, PMA), *Grant* 00-3672 (SEL), *Cáceres* 4106 (FR, PMA).

Werauhia williamsii (L. B. Sm.) J. R. Grant – Lf: E; *Knapp* 1632 (MO), *Sytsma* 1864 (MO), *Cáceres* 4085 (FR, PMA).

Werauhia woodsoniana (L. B. Sm.) J. R. Grant – Lf: E; En: PA; *Woodson Jr & al.* 1029 (MO, holo).

Species erroneously reported for Panama

Catopsis brevifolia Mez & Wercklé (= *Catopsis morreniana* Mez) – The species was reported for Panama



Fig. 3. Systematic diversity of bromeliad floras. – Pie charts show subfamily composition, size corresponds to total number of species per selected area or country, respectively, in Central and South America.

based on *H. von Wedel* 233 from Bocas del Toro (MO) by Utley (1994) and Correa & al. (2004). We revised the specimen as *Guzmania donnellsmithii* Mez ex Donn. Sm. Utley, and Correa probably referred to another specimen, *H. von Wedel* 2233 (MO), also from Bocas del Toro. That one, however, represents *Catopsis sessiliflora*.

Guzmania sibundoyorum L. B. Sm. – The report by D’Arcy (1987) and Correa & al. (2004) was based on *K. Utley* 5643 (DUKE) and *Folsom & Page* 5941 (MO). We revised these specimens as *Guzmania circinnata*.

Guzmania tarapotina Ule – Listed by D’Arcy (1987) and Correa & al. (2004) based on *Tyson, Dwyer & Blum* 3208 (MO, SCZ). This collection represents *Guzmania calamifolia*.

Pitcairnia attenuata L. B. Sm. – The records by D'Arcy (1987) and Correa & al. (2004) are based on the collection *Mass, Berg & Dressler 2780* (MO, PMA, SCZ). This collection belongs to *Pitcairnia multiflora*.
Tillandsia acostae Mez & Tonduz – The records by D'Arcy (1987) and Correa & al. (2004) are based on *Woodson Jr. & Schery 823* (MO) collected in 1940. The specimen belongs to *Tillandsia compressa*.
Tillandsia lampropoda L. B. Sm. – Listed by Correa & al. (2004) based on Utley (1994). The specimen cited, *Croat 26951* (MO) from 1974, actually represents *Tillandsia multicaulis*.

Discussion

Endemism — The comprehensive study of herbarium specimens from Panama and Costa Rica revealed not only additions to the bromeliad flora of Panama and some erroneous records but also provided some insight into the species endemism of bromeliads in Panama. Previously, 43 species were regarded to be endemic to Costa Rica (Morales 2003: 22.1 % of the total bromeliad flora) and 17 species to Panama (Correa & al. 2004: 9.6 % of bromeliad flora). Our results now give a different picture, with 33 species endemic to Panama, 32 species endemic to Costa Rica (own unpublished data) and 34 species occurring only in both countries. Seen in comparison to land surface area, the bromeliad endemism is considerably high in Panama. Western Panama with its higher geodiversity and altitudinal range of 0–3475 m displays higher endemism per area than eastern Panama.

In Panama, endemism in the family *Bromeliaceae* is distributed among the subfamilies as follows: the *Tillandsioideae* comprise most endemics (22 species (66.7 %), followed by *Pitcairnioideae* with 7 species (21.2 %) and *Bromelioideae* with 4 species (12.1 %) (Table 1).

Systematic diversity — The systematic diversity of the Panamanian bromeliad flora is confined to three subfamilies, with by far the highest diversity found in *Tillandsioideae* (147 species, *Bromelioideae*: 34 species, *Pitcairnioideae*: 25 species). The five other currently recognised bromeliad subfamilies (*Brocchinioideae*, *Lindmanioideae*, *Hechtioideae*, *Navioideae* and *Puyoideae*; Givnish & al. 2007, 2011) are not represented in the Panamanian flora. Table 2 gives a brief summary of the species diversity of subfamilies in selected areas respective countries. A strong dominance of *Tillandsioideae* can also be found in Costa Rica (Morales 2003), Mexico (Espejo-Serna & al. 2004), Colombia (Holst 1994), Ecuador (Holst 1994), Peru (Holst 1994) and Bolivia (Krömer & al. 1999). This can thus be regarded as characteristic for Central American bromeliad floras and those of South American countries comprising considerable parts of the Andes. The bromeliad flora of the Guianas (Gouda 1999) includes 6 subfamilies, *Bromelioideae* and *Tillandsioideae* comprising the greatest number of species with each being similarly diverse.

In the state of Minas Gerais, Brazil, the data present a different picture (Versieux & Wendt 2006). There the *Bromelioideae* are most diverse (120 species) followed by *Tillandsioideae* (82 species) and *Pitcairnioideae* (63 species) (Fig. 3, Table 2). There is a similar situation in

Table 2. *Bromeliaceae* diversity (subfamilies and total) in selected political units; BRC = *Brocchinioideae*, BRO = *Bromelioideae*, HEC = *Hechtioideae*, LIN = *Lindmanioideae*, NAV = *Navioideae*, PIT = *Pitcairnioideae* s.str., PUY = *Puyoideae*, TIL = *Tillandsioideae*. – Data: ¹ this publication; ² Utley & al. (2001); ³ Morales (2003); ⁴ Espejo-Serna & al. (2004); ⁵ Holst (1994); ⁶ Gouda (1999); ⁷ Krömer & al. (1999); ⁸ Versieux & Wendt (2006); ⁹ Fontoura & al. (1991); ¹⁰ Morrone & Zuloaga (1996); ¹¹ Zizka & al. (2009); ¹² Luther & Benzing (2009). Size of countries taken from Wikipedia (2011).

Country	BRC	BRO	HEC	LIN	NAV	PIT	PUY	TIL	Total	Size (km ²)
Panama ¹		34				25		147	206	75 517
Panama: W Panama ¹		23				22		121	167	28 789
Nicaragua ²		19	3			4		81	107	129 494
Costa Rica ³		28				19	2	147	105	50 660
Mexico ⁴		21	49			48		224	342	1 964 375
Colombia ⁵	4	70			10	82	29	196	391	1 141 748
Venezuela ⁵	17	56		38	84	41	8	120	364	916 445
Guianas ⁶	6	46		4	11	12		44	123	214 970
Ecuador ⁵		56				48	22	242	368	283 561
Peru ⁵		59				83	70	199	411	1 285 215
Bolivia ⁷		30				53	57	141	281	1 098 581
Brazil: Minas Gerais ⁸		120				63		82	265	588 528
Brazil: Rio de Janeiro ⁹		131				11		103	245	43 766
Argentina ¹⁰		14				26	14	56	110	2 766 400
Chile ¹¹		9				1	7	6	23	756 096
U.S.A.: Florida ¹²								16	16	170 305



Fig. 4. *Bromeliaceae* of Panama: life form spectrum. E: epiphytic, T: terrestrial, S: saxicolous.

the bromeliad flora of Río de Janeiro: *Bromelioideae* (131 species), *Tillandsioideae* (102 species) and *Pitcairnioideae* (11 species) (Fontoura & al. 1991) (Fig. 3, Table 2). This is in line with the reconstruction of the evolution of the *Bromelioideae*, which underwent recent and massive radiation in the coastal forests of Brazil (Schulte & al. 2005; Schulte & Zizka 2008).

The bromeliad flora of Chile is much poorer (23 species) with *Bromelioideae*, *Puyoideae* and *Tillandsioideae* being the most diverse subfamilies (Zizka & al. 2009) (Fig. 3, Table 2). The bromeliad flora of Venezuela, putative cradle of the family, is more diverse and varied with 7 subfamilies being represented, probably due to the variety of habitats, including the geologically ancient table mountains: *Tillandsioideae* (120 species), *Navioideae* (84), *Bromelioideae* (55), *Pitcairnioideae* (41), *Lindmanioideae* (38), *Brocchinioidae* (16) and *Puyoideae* (8) (Holst 1994) (Fig. 3, Table 2).

Life form — Fig. 4 sums up the life-forms of bromeliads in Panama. 120 species grow epiphytically and 18 as terrestrials. 48 species can be found both as epiphytic or terrestrials (e.g. *Pitcairnia heterophylla*, *P. valerioi*, *Werauhia rubra*), 11 additionally as saxicoles, 3 species were found growing both as epiphytes and saxicoles. Of the 206 reported species, 182 (88.4 %) are obligatory or facultative epiphytes. 83 species (40.3 %) are found exclusively or facultatively growing in soil or on rocks. The high proportion of epiphytes in the flora of Panama can be best explained by the natural vegetation of the country, which consisted of different types of tropical forest throughout the majority of its land area.

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References

- Correa A. M. D., Galdames C. & de Stapf M. S. 2004: Catálogo de plantas vasculares de Panamá. – Panama City: Smithsonian Tropical Research Institute.
- Croat, T. B. 1978: Flora of Barro Colorado Island. – Stanford: Stanford University.
- D'Arcy W. G. 1987: Flora of Panama. Checklist and Index. – Monogr. Syst. Bot. Missouri Bot. Gard. **17**(1): 1–325.
- Espejo-Serna A., López-Ferrari A. R., Ramírez-Morillo I., Holst B. K., Luther H. E. & Till W. 2004: Checklist of Mexican *Bromeliaceae* with notes on species distribution and levels of endemism. – *Selbyana* **25**(1): 33–86.
- Fontoura T., Costa A. & Wendt T. 1991: Preliminary checklist of the *Bromeliaceae* of Rio de Janeiro State, Brazil. – *Selbyana* **12**: 5–45.
- Givnish T. J., Milliam K. C., Berry P. E. & Sytsma K. J. 2007: Phylogeny, adaptive radiation, and historical biogeography of *Bromeliaceae* inferred from *ndhF* sequence data. – *Aliso* **23**: 3–26.
- Givnish T. J., Barfuss M. H. J., Van Ee B., Riina R., Schulte K., Horres R., Gonsiska P. A., Jabaily R. S., Crayn D. M., Smith J. A. C., Winter K., Brown G. K., Evans T. M., Holst B. K., Luther H., Till W., Zizka G., Berry P. E. & Sytsma K. J. 2011: Phylogeny, adaptive radiation, and historical biogeography in *Bromeliaceae*: Insights from an eight-locus plastid phylogeny. – *Amer. J. Bot.* **98**: 827–895.
- Gouda E. J. 1999: Studies on the flora of the Guianas no. 90: Checklist of *Bromeliaceae* of the Guianas with notes on critical species. – *Selbyana* **20**(1): 30–39.
- Hammel B. E., Grayum M. H., Herrera C. & Zamora N. (ed.) 2004: Manual de plantas de Costa Rica 1. Introducción. – Monogr. Syst. Bot. Missouri Bot. Gard. **97**: 1–299.

- Holst B. K. 1994: Checklist of Venezuelan *Bromeliaceae* with notes on species distribution by state and levels of endemism. – *Selbyana* **15(1)**: 132–149.
- IGNTG (Instituto Geográfico Nacional Tommy Guardia) 2007: Atlas nacional digital de la República de Panamá. – Panama City: Ministerio de Obras Públicas.
- IPNI 2011: International Plant Names Index. – Published at <http://www.ipni.org/index.html>.
- Krömer T., Kessler M., Holst B. K., Luther H. E., Gouda E., Ibsch P. L., Till W. & Vasquez R. 1999: Checklist of Bolivian *Bromeliaceae* with notes on species distribution and levels of endemism. – *Selbyana* **20(2)**: 201–223.
- Laube S. & Zotz G. 2006: Neither host-specific nor random: vascular epiphytes on three tree species in a Panamanian lowland forest. – *Ann. Bot. (Oxford)* **97**: 1103–1114.
- Luther H. E. 2008: An alphabetical list of bromeliad binomials. – Bromeliad Society International: published at <http://www.selby.org/research/papers/alpha-phabetical-list-bromeliad-binomials>.
- Luther H. E. & Benzing D. H. 2009: Native bromeliads of Florida. – Sarasota: Pinapple Press.
- Morales J. F. 2003: *Bromeliaceae*. – In: Hammel B. E., Grayum M. H., Herrera C. & Zamora N. (ed.), *Manual de plantas de Costa Rica 2*. – *Monogr. Syst. Bot. Missouri Bot. Gard.* **92**: 397–375.
- Morales J. F. 2009: Novedades y notas misceláneas en las *Bromeliaceae* de Mesoamérica. – *J. Bot. Res. Inst. Texas* **3**: 113–116.
- Morrone O. & Zuloaga F. O. 1996: *Bromeliaceae*. – In: Zuloaga F. O. & Morrone O. (ed.), *Catálogo de las plantas vasculares de la República Argentina*. – *Monogr. Syst. Bot. Missouri Bot. Gard.* **60**: 106–121.
- Schulte K., Horres R. & Zizka G. 2005: Molecular phylogeny of *Bromelioideae* and its implications on biogeography and the evolution of CAM in the family (*Poales*, *Bromeliaceae*). – *Senckenberg. Biol.* **85**: 113–125.
- Schulte K. & Zizka G. 2008: Multi locus plastid phylogeny of *Bromelioideae* (*Bromeliaceae*) and the taxonomic utility of petal appendages and pollen characters. – *Candollea* **63**: 209–225.
- Smith L. B. 1944: *Bromeliaceae*. – In: Woodson R. E. & Schery R. W. (ed.), *Flora of Panama*. – *Ann. Missouri Bot. Gard.* **31**: 477–541.
- Smith L. & Downs R. J. 1974: *Pitcairnioideae* (*Bromeliaceae*). – *Fl. Neotrop. Monogr.* **14(1)**: 1–662.
- Smith L. & Downs R. J. 1977: *Tillandsioideae* (*Bromeliaceae*). – *Fl. Neotrop. Monogr.* **14(2)**: 663–1492.
- Smith L. & Downs R. J. 1979: *Bromelioideae* (*Bromeliaceae*). – *Fl. Neotrop. Monogr.* **14(3)**: 1493–2142.
- Thiers B. 2008+ [continuously updated]: Index herbariorum: A global directory of public herbaria and associated staff. – New York Botanical Garden: published at <http://sweetgum.nybg.org/ih/>.
- Urtley J. F. 1994: *Bromeliaceae*. – Pp. 89–156 in: Davidse G., Sousa S. M. & Chater A. O. (ed.), *Flora Mesoamericana* **6**. – México D.F.: Universidad Nacional Autónoma de México, etc.
- Urtley J. F., Burt-Urtley K. & Huft M. J. 2001: *Bromeliaceae*. – In: Stevens W. D., Ulloa Ulloa C., Pool A. & Montiel O. M. (ed.), *Flora de Nicaragua 1*. – *Monogr. Syst. Bot. Missouri Bot. Gard.* **85(1)**: 460–495.
- Versieux L. M. & Wendt T. 2006: Checklist of *Bromeliaceae* of Minas Gerais, Brazil, with notes on taxonomy and endemism. – *Selbyana* **27**: 107–146.
- Wester S., Mendieta-Leiva G., Nauheimer L., Wanek W., Kreft H. & Zotz G. 2011: Physiological diversity and biogeography of vascular epiphytes at Río Changuinola, Panama. – *Flora* **206**: 66–79.
- Wikipedia 2011: Wikipedia, die freie Enzyklopädie. – Published at <http://de.wikipedia.org/>.
- Zizka G., Schmidt M., Schulte K., Novoa P., Pinto R. & König K. 2009: Chilean *Bromeliaceae*: diversity, distribution and evaluation of conservation status. – *Biodivers. & Conservation* **18(9)**: 2449–2471.
- Zotz G. & Schultz S. 2008: The vascular epiphytes of a lowland forest in Panama – species composition and spatial structure. – *Pl. Ecol.* **195**: 131–141.