PhytoKeys 29: 1–15 (2013)
doi: 10.3897/phytokeys.29.5376
www.phytokeys.com

RESEARCH ARTICLE

A peer-reviewed open-access journal
PhytoKeys
Launched to accelerate biodiversity research

Lejeunea hodgsoniana, a newly described, long recognised *Lejeunea* (Jungermanniopsida, Lejeuneaceae) from lowland coastal forest habitats in New Zealand

Rodney J. Lewington[1], Peter Beveridge[2], Matt A. M. Renner[3]

1 *4 Highbury Crescent, Highbury, Wellington 6012, New Zealand* **2** *Museum of New Zealand Te Papa Tongarewa, PO Box 465, Wellington, New Zealand* **3** *Royal Botanic Gardens and Domain Trust, Mrs Macquaries Road, Sydney, NSW 2000, Australia*

Corresponding author: *Rodney J. Lewington* (rodneyjl@clear.net.nz)

Academic editor: *M. von Konrat* | Received 21 April 2013 | Accepted 21 October 2013 | Published 11 November 2013

Citation: Lewington RJ, Beveridge P, Renner MAM (2013) *Lejeunea hodgsoniana*, a newly described, long recognised *Lejeunea* (Jungermanniopsida, Lejeuneaceae) from lowland coastal forest habitats in New Zealand. PhytoKeys 29: 1–15. doi: 10.3897/phytokeys.29.5376

Abstract

Lejeunea hodgsoniana Grolle ex R.J.Lewington, P.Beveridge & M.A.M.Renner **sp. nov.**, A taxon originally recognised by Riclef Grolle in 1980, but not described, known from a number of coastal sites in the North Island, the northern extremity of the South Island, the Kermadec Islands, and the Chatham Islands of New Zealand, is described and illustrated. The species is distinctive amongst species of *Lejeunea* in the Australasian flora in the combination of complanate shoots, relatively large broadly-ovate leaf lobes, with some lobules bearing prominent multicellular triangular teeth on a base of two to four cells, the flattened perianths having a faint dorsal carina. Its publication brings the number of species recognized for New Zealand to 14, seven of which are currently considered endemic.

Keywords

Lejeunea hodgsoniana, Lejeuneaceae, Jungermanniopsida, New Zealand, new species

Introduction

The Museum of New Zealand Te Papa Tongarewa herbarium (WELT) holds five *Lejeunea* specimens bearing determinavit slips signed by the late Riclef Grolle, dated 1980 and carrying the name *Lejeunea hodgsoniana.* The specimens had been collected in 1969–1970 by B.G. Hamlin, botanist and curator of the herbarium, at that time in

the National Museum, later incorporated into Te Papa. They were loaned to Grolle, with other *Lejeunea* specimens, when he was preparing his study of the Lejeuneaceae in Tasmania (Grolle 1982). Grolle may have had the intention to describe this species. It appears, however, that the name was not published and we are unaware of any available description. In the meantime, it has become practice to refer to the species by the tag name *Lejeunea 'hodgsoniana'* Grolle ined. e.g. (Renner et al. 2010). Apart from androecia in one of the packets, the WELT collections are sterile. Recently-collected fertile material has been selected as the basis for an overdue formal description of this taxon. It is apparent that, in naming the specimens *Lejeunea hodgsoniana*, Grolle wished to recognise the contribution made to the study of New Zealand liverworts by Mrs E.A. Hodgson, 1888–1983, who during the period 1941–1972, had published a series of papers on a wide range of genera, including *Schistochila* (Hodgson 1941), *Heteroscyphus* (Hodgson 1943) and *Radula* (Hodgson 1944), but not on any member of the Lejeuneaceae (Godley 1984). Grolle had previously honoured this contribution in his naming of *Solenostoma hodgsoniae* (Grolle) J.J. Engel and *Lepidogyna hodgsoniae* (Grolle) R.M. Schust.

Most Lejeuneaceae genera in New Zealand, including *Lejeunea*, have never been the subject of comprehensive regional revision. At best they have been either studied opportunistically in response to discovery of new entities (Grolle 1973, Glenny 1996, Renner 2010, Renner and Pocs 2011, Renner and de Lange 2011, Renner et al. 2009) or included as part of studies of other regions (e.g. Grolle 1982). New Zealand appears to have a large endemic component to its Lejeuneaceae flora (Renner 2010) and this, in combination with the lack of recent study, means the family is poorly known (Renner and Pocs 2011) and several new entities await description.

Here we formally describe the longest known of these new species, Grolle's unpublished *Lejeunea 'hodgsoniana'*, and are pleased to publish the name on his behalf. Its publication brings the number of species recognized for New Zealand to 14 (based on Glenny 1998 with recent additions by Renner et al. 2010 and Renner and de Lange 2011), seven of which are currently considered endemic. Some of these fourteen species are known to be complexes requiring further investigation (i.e. *Lejeunea epiphylla* Colenso non Mitt. auct. and *Lejeunea primordialis* Taylor). Despite this, the higher than average rate of endemism for *Lejeunea* mirrors that of *Austrolejeunea*, another well-studied genus of Lejeuneaceae, and again suggests the existence of a distinct, even if not particularly diverse, southern-temperate Australasian element within this otherwise predominantly tropical family.

Taxonomic treatment

***Lejeunea hodgsoniana* Grolle ex R.J.Lewington, P.Beveridge et M.A.M.Renner, sp. nov.**
http://species-id.net/wiki/Lejeunea_hodgsoniana

Diagnosis. Differs from other antipodal Lejeunea species in its relatively large leaf and shoot size, the presence of a multicellular first lobule tooth on a base of two to four cells,

combined with complanate shoots, distant elliptic-ovate underleaves with deep sinus and narrow lobes that are usually capped by a single pointed apical cell, and an obcordate perianth with a broad flattened dorsal surface before inflation, and reduced dorsal carina.

Type. NEW ZEALAND. Porirua: Titahi Bay, Stuart Park, track to cliff edge at S end of bay: Sounds-Wellington Ecological Region, Wellington Ecological District, on trunk and branches of *Melicytus ramiflorus* in coastal thicket with *Pittosporum crassifolium* and *Coprosma repens*. Bryophyte associates, *Cololejeunea minutissima, Frullania monocera, Frullania patula, Lejeunea colensoana, Rhynchostegium muriculatum, Siphonolejeunea nudipes* and *Syntrichia papillosa,* 41°06'33"S, 174°49'43"E, ca. 15m, 19 July 2012, P. Beveridge MB-2. (Holotype: WELT [WELT H012563], isotypes AK, CHR, F, NSW).

Plants bright green, not pellucid, grey-green in herbaria, forming conspicuous more or less circular mats to 7.0 cm diameter, or more extensive mats by confluent growth. (Figure 3) Shoots 1.0–1.5 mm wide, ca. 12 mm long. Branching of the *Lejeunea*-type frequent, shoots occasionally exhibiting more or less pinnate growth patterns but more often forming diffuse complanate wefts by continued lejeuneoid branching.

Stem (Figures 1G and 2D) 90–125 μm in diameter with 7 cortical cells, walls 2–3 μm thick, and with ca.12 rows of smaller medullary cells. Ventral merophyte of two rows with cells sub-quadrate to rectangular, 22–45 μm × 22–30μm. Lateral merophytes with shared mid-dorsal row, the alternate contribution of each lateral merophyte to the row, 5–6 (8) cells long, with cells quadrate to rectangular, 22–45 μm × 17–24 μm, the contribution boundaries marked by oblique cross walls, by the antical lobe insertion of the contributing merophyte encroaching weakly onto the mid-dorsal row and by the position of a papilla.

Leaves (Figure 1F) alternate, incubous, shortly imbricate or contiguous, leaf lobes broadly ovate, on leading shoots 750–950 μm long by 550–650 μm wide , on branches 300–700 μm long × 200–600 μm wide, complanate in arrangement along the shoot and more or less flat when fresh, flat or weakly convex above when dry, at 75°–90°to the stem, margins entire, more or less straight or slightly crenulate by weakly bulging cells. Apex rounded, occasionally obtusely pointed, antical lobe margin at insertion evenly rounded or variably ampliate, projecting onto or across the stem. Postical leaf margin decurrent. Insertion 0.5 lobe width, sub-longitudinal. Two-celled leaf-free stem gutter. Lobe mid-laminal cells, (Figure 2G) hexagonal, isodiametric or slightly elongate, 17.5 × 17.5 μm to 25 × 30 μm, basal lamina cells similar, occasionally in longitudinal rows, isolated cells to 37.5 μm long, marginal cells rectangular 12.5–20 × 12.5–20 μm. Cells thin-walled in young leaves, trigones absent or weakly developed. Walls to 2 μm in older leaves. Cuticle smooth.

Mid laminal cell oil bodies in younger leaves (Figure 2G and H) (2) 4–6 (7), spherical 4–6 μm, less commonly ellipsoidal or fusiform 6–7.5 (10) μm × 4–5 (6) μm, pale grey to light brown, coarse granular to sub-botryoidal. Oil bodies in older leaves near gametangia, occasionally 14–20, then densely filling the cell (Figure 2I).

Lobules (Figure 1 A–E) polymorphic and relatively small, 0.023–0.125 of lobe area, best developed towards the apex of leading shoots, there 90–240 μm at insertion

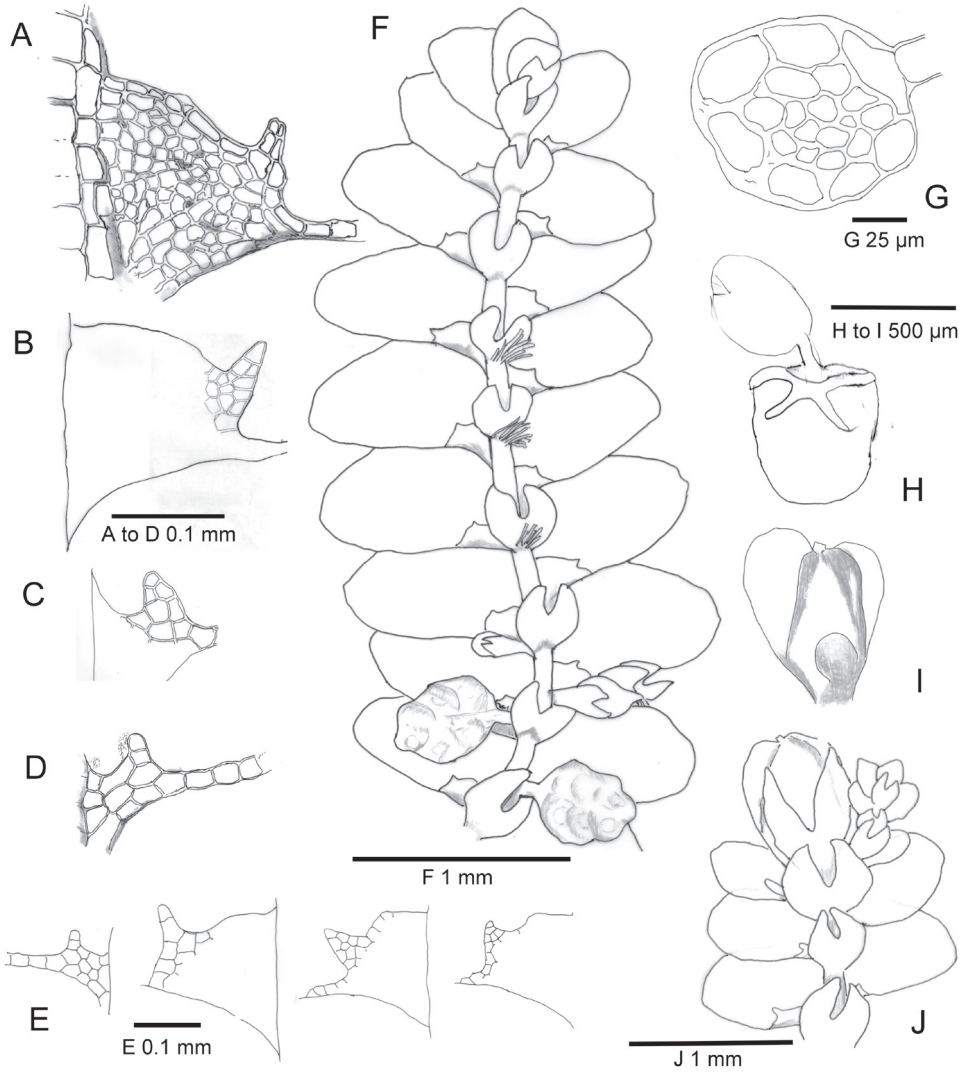

Figure 1. *Lejeunea hodgsoniana* – Morphological features. **A** and **B** Well-developed lobule **C–E** Lobules showing the variety of forms from the same stem **F** Shoot with androecia **G** Stem cross-section **H** Inflated perianth with emergent sporophyte **I** Perianth before enlargement of the sporophyte showing the lateral and ventral carinae **J** Leading shoot showing a terminal gynoecium and a subfloral innovation. (All from type.) **A–D**: lobules scale bar 0.1 mm, **E**: four lobules, scale bar 0.1 m, **F**: scale bar 1mm, **G**: scale bar 25 µm, **H–I**: scale bar is 0.5 mm and **J** scale bar 1 mm.

with a 100–300 µm carina, the free margin weakly inflated, in-rolled or not, arcuate or more or less straight, bearing a multicellular sub-triangular apical tooth, two to four cells wide at the base, up to 15 cells in total, arched or straight, usually pointing towards the stem apex. Lobule papilla proximal to the tooth and a further papilla at the free margin-stem axil. More distant from the shoot apex the lobules are explanate,

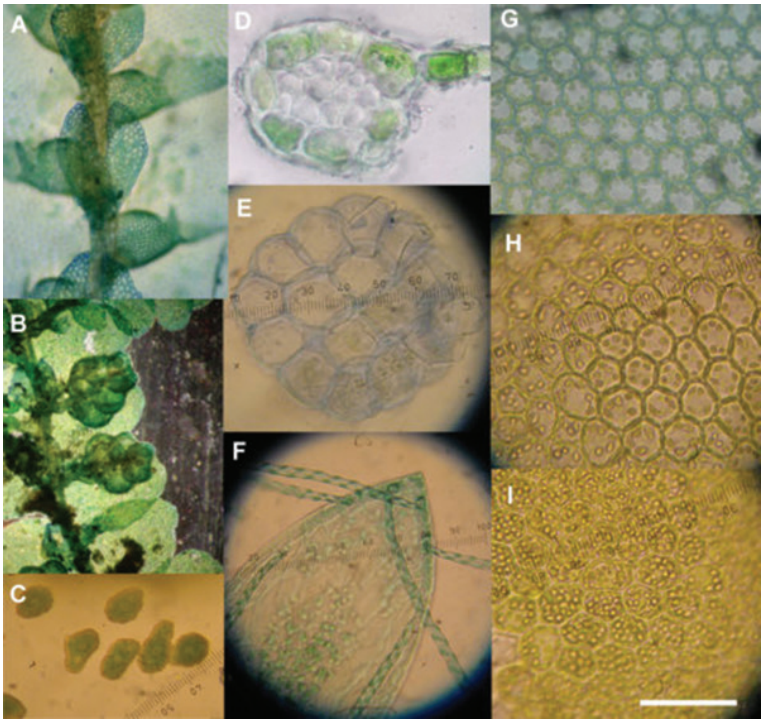

Figure 2. *Lejeunea hodgsoniana*. **A** Shoot showing the underleaf with a deep narrow sinus and long narrow lobes, and well-developed lobules **B** Androecia **C** Spores **D** Stem cross-section **E** Seta cross-section **F** Apices of a sporophyte valve showing elaters and pseudoelaters **G–I** Leaf cells showing the variation in oil body density. (**G** stained).

the tooth diminishing to three cells on a base of two cells, to two uniseriate cells, or to a single cell. Amongst and postical to the gametangia, the lobules are usually more uniformly small explanate triangular, insertion ca. 50 µm, with a single-celled tooth, carina ca. 50 µm.

Underleaves (Figures 1F and 2A) usually distant, contiguous or imbricate only at the stem apex, appressed to stem, elliptic-ovate, widest below mid leaf, in leading shoots 320–350 µm long × 260–300 µm wide, smaller to 200 × 170 µm in branch shoots, sinus 0.5–0.6, narrow U or occasionally V-shaped. Attachment transverse, occasionally to two, typically to three cortical cells. Where three, to the lateral merophyte row bearing the adjacent lobule, as well as to the two ventral merophyte rows, with or without a pair of enlarged basal marginal cells. Lobes 6–9 cells wide at base, usually ending in a single cell, occasionally two uniseriate, very occasionally two cells juxtaposed.

Rhizoids, where present, 100–200 µm long, hyaline, in fascicles arising from a cluster of basal underleaf cells forming a disk of ca. 25 rhizoid initials.

Asexual propagules not seen.

Autoicous. Androecia (Figure 1F and 2B) ca. 500 µm long × 500 µm wide, usually on short determinate achlorophyllose lateral branches, often obscured from above by

the shoot leaves, occasionally terminal on short leafy lateral shoots. One (2) proximal underleaves often connate on one side with a proximal small sterile bract. Fertile male bracts 2–4 pairs, becoming smaller distally, each bearing one or two spherical antheridia, each ca.100 μm diameter, supported by a filament of uniseriate cells.

Gynoecia (Figure 1H–J) occasionally terminal on leading shoots, subtending a single subfloral lejeuneoid innovation to continue shoot growth, more often terminal on lateral branches which may be repeated in continued lejeuneoid shoot sequences.

Female bract lobes connate, sub-symmetrical or asymmetrical, obovate-spathulate to lingulate, apices rounded or obtuse to broadly acute, spreading to squarrose, 450–750 μm long, 180–450 μm wide. Lobule ligulate, 220–450 μm long, 50–80 μm wide, erect or arching inwards from broad or narrow sinus, 0.5–0.7. A common asymmetry has a broad obovate-spathulate female bract with rounded apex and a short arched lobule paired with a narrow lingulate bract with acute apex and long erect lobule. Bracteole 300–600 μm long, 220–300 μm wide, lobes usually erect, occasionally spreading, 5–7 cells wide at the base, often with a small lateral shoulder on each outer lobe margin, sinus U shaped, usually narrow, occasionally broad, to 0.6, lobes ending in two uniseriate cells, or a single cell. Bracteole unequally biconnate to female bract bases.

Perianths (Figure 1H and I) before distortion by enlargement of the sporophyte, dorso-ventrally compressed, pentacarinate, with well-developed lateral and ventral carinae and a reduced dorsal carina. Perianth obcordate in profile, broadest below the broadly rounded apices of the lateral carinae, 500–750 μm high by ca. 80 μm wide at the base, ca. 500 μm wide at the apex, the ventral carinae before inflation as two conspicuous oblique plicae converging on the plane ventral surface below the rostrum, a short dorsal carina ca. 88 μm long as an obscure low-profile ridge immediately below the rostrum on the broad plane dorsal perianth surface, sometimes wanting. Rostrum 45 μm wide, 37.5–50 μm, two to three cells high, positioned in a variably-expressed depression between spreading apices of the lateral carinae. Estipitate.

Sporophyte capsule (Figure 1H) spherical, light brown at maturity, ca. 300 μm in diameter. Tiered seta (Figure 2E) to 1.5 mm long, usually only shortly emergent from the perianth, 150 μm wide, in cross section, 16 rows of thin-walled hyaline cells, 12 cortical and four medullary, cells isodiametric, ca. 37.5 μm wide, ca. 80 μm long. Capsule dehiscent into four erect, incompletely separated valves, the valve sinus 0.75 the valve length (Figure 2F).

Cells of the valve outer layer differentiated into three distinct areas. Firstly, in the apical part of the valve, a marginal layer of quadrate to rectangular cells with firm walls, some with a single nodular thickening on median walls or broader sheet thickening, joined by a single row of rhomboidal cells with similar thickening to a conspicuous median cluster of about 12 large, relatively thin-walled elongate-hexagonal cells without wall thickening, the largest four, ca. 62.5 × 32.5 μm. Secondly, a median basal cluster of thin-walled quadrate cells. Thirdly above the junction of adjacent valves on each side, small quadrate marginal cells with conspicuous sheet thickening on the medial walls bordering a cluster of three to four rows of rhomboidal cells with sheet and nodular thickening and variably sinuose walls. Below the valve junction a row of four

Figure 3. Type locality. Above. Regenerating native coastal bush. Below. Trunk of Melicytus ramiflorus showing the extensive mats of Lejeunea hodgsoniana resulting from confluent growth.

large quadrate-trapezoid cells extending to the hypophysis basal cell, together with the row of the adjacent valve, forming a conspicuous triangular group.

Cells of the capsule inner layer quadrate at the apex margin, otherwise rhomboidal, longer than outer layer cells with rounded ends, elliptical near valve junction, quadrate at the base.

Inner layer inner tangential walls with hyaline to light brown ornamentation in two valve regions. At the valve apex, bell and discoid thickening present at the points of attachment of the elaters and weakly extending onto adjacent cells along cell boundaries. A more extensive area of ornamentation at mid-valve with a dense array of bell and discoid thickening along axes with a more or less longitudinal orientation, not clearly related to cell boundaries, here the thickenings flare slightly onto the inner radial cell wall. The precise relationship of the thickening to inner layer cell walls could not be resolved.

Elaters and pseudoelaters on familiar pattern of 5 (2) and 4 (2), with similar opposite valve pairs, two bearing five elaters, one attached at the valve apex and two each side close to the valve apex, the other valve pairs (Figure 2F) lacking the apical elater, all valves with two pseudoelaters attached by their length to the valve inner layer. Elaters with weak unihelical thickening.

Spores, (Figure 2C) light brown ellipsoids, symmetrical or asymmetric, finely and densely papillose, 32.5–37.5 × 17.5–20 μm. Precocious germination not seen.

Distribution and habitat. *Lejeunea hodgsoniana* is known from a number of locations in New Zealand ranging from latitude 29°14'39"S in the Kermadec Islands to latitude 44° 20'S on Pitt Island in the Chatham Islands. In the northern half of the North Island, it is recorded from off-shore islands on the eastern coast from Poor Knights Island, south through the islands of the outer and inner Hauraki Gulf including the Mokohinau Islands, Hen and Chicken Group, Little Barrier Island and The Noises, and from the Mercury Islands Group and Mayor Island east of the Coromandel Peninsula. There are also a small number of northern mainland collections from North Cape south to Port Waikato and Hamilton. In the southern North Island, locations are mainly coastal in the vicinity of Wellington, including on Mana Island. On the South Island it is known from a single collection from the base of Farewell Spit. Elevation is generally less than 100 m with the altitudinal range from 1m to about 520 m, the latter in the Kermadec Islands.

Four of the collections are from shaded stream bed rock, serpentinite at North Cape, basalt or basaltic andesite elsewhere. In most of its locations, however, *Lejeunea hodgsoniana* has been corticolous in coastal forest or scrub. Species of *Melicytus, M.* aff. *ramiflorus* in the Kermadecs, *M. chathamicus* in the Chatham Islands, and *M. ramiflorus* elsewhere are the most frequently cited phorophytes or associates. Other cited phorophytes are: *Acacia dealbata*, *Agathis australis*, *Beilschmiedia tarairi*, *Brachyglottis repanda*, *Coprosma macrocarpa*, *Coprosma repens*, *Cordyline obtecta*, *Geniostoma ligustrifolium*, *Hoheria populnea*, *Kunzea spp.*, *Meryta sinclairii*, *Metrosideros excelsa*, *Metrosideros kermadecensis*, *Myrsine divaricate*, *Olearia traversiorum*, *Pittosporum umbellatum*, *Rhopalostylis sapida*, *Streblus banksii*, *Vitex lucens*, and apple tree (*Malus* x *domestica*).

Figure 4. Indicative distribution. This map shows the known distribution of *Lejeunea hodgsoniana*.

Bryophyte associates have included *Archilejeunea olivacea*, *Codonoblepharon minutus*, *Cololejeunea minutissima*, *Fabronia australis*, *Racopilum sp.*, *Frullania monocera*, *Frullania patula*, *Frullania pentapleura*, *Frullania rostellata*. *Lejeunea colensoana*, *Lejeunea helmsiana*, *Lejeunea oracola*, *Lejeunea primordialis*, *Lepidolaena taylorii*, *Lopholejeunea colensoi*, *Metalejeunea cucullata*, *Metzgeria furcata*, *Neckera hymenodonta*, *Rhynchostegium muriculatum*, *Siphonolejeunea nudipes*, *Syntrichia papillosa*, *Tetraphidopsis pusilla* and *Thuidium sparsum.*

Selected representative specimens examined. NEW ZEALAND, Kermadec Islands, North Meyer: Kermadec Islands Nature Reserve, Kermadec Ecological Region and District, on exposed roots near trunk base of a cyclone toppled *Metrosideros kermadecensis*, 29°14'39.3"S; 177°52'34"W, ca. 60m, 12 May 2011, P. J. de Lange K670 (AK 325247); **Raoul Island:** Kermadec Islands Nature Reserve, Moumoukai Track, Moumoukai, Eastern side of summit, in wet forest on damp rock lying in deep shade of very large *Metrosideros kermadecensis* and *Melicytus* aff. *ramiflorus* trees, 29°16'0"S; 177°54'0"W, ca. 520m, 8 May 2009, P. J. de Lange K278, D C Havell (AK 313726); **Te Paki:** North Cape Scientific Reserve, Eastern tributary of the Nga Whenua Stream, Te Paki Ecological Region and District, growing amongst *Frullania pentapleura* on shaded serpentinite rocks lying in ephemeral stream bed, 34°24'12"S; 173°0'10"E, ca. 80m, 16 Nov 2010, P. J. de Lange 9918 (AK 323334); **Aorangi Island:** on ridge E of Puweto Valley, Poor Knights

Ecological Region and District, epiphytic on trunk of *Cordyline obtecta*, ca. 35°28'40"S; 174°44'38"E, 28 Aug 1984, J. E. Beever s.n. (AK 291340); **Hen and Chicken Group, Whatupuke Island:** Eastern Northland Ecological Region, Taranga Ecological District, epiphytic on horizontal trunk of large *Brachyglottis repanda*, ca. 35°53'20"S; 174°45'20"E, ca. 150m, 01 Jan 1982, J. E. Beever 8-59c (AK 291283); **Hen & Chicken Group, Lady Alice Island:** Eastern Northland Ecological Region, Taranga Ecological District, on trunks of living *Meryta* trees, ca. 35°53'36"S; 174°43'27"E, 07 Jan 1982, R. E. Beever, J. E. Beever 10-22a (AK291288); **Hen & Chicken Group, Lady Alice Island:** up Kereru Stream, coastal forest, epiphytic on trunk, sloping, 25 cm diameter lacebark, ca. 35°53'S; 174°43'E, 13 Dec 1981, J. E. Beever 8-12b (AK 291289); **Mokohinau Group, Fanal Island:** head of northern valley, on *Geniostoma*, at shrub/flax margin of forest, ca. 35°56'0"S; 175°9'0"E, 04 Jan 1984, E. K. Cameron 2711b (AK 291338); **The Noises:** Auckland Ecological Region, Inner Gulf Islands Ecological District, ca. 36°41'34"S; 174°58'28"E , Mar 1948, R. C. Lloyd 12 (AK 291347); **Auckland City:** Western Springs, Auckland Zoo grounds, Motions Creek, Tamaki Ecological District, , partially submerged on basalt rock, 36°51'47"S; 174°43'15"E, ca. 2 m, 04 Jan 2008, P. J. de Lange 7500 (AK 303709); **Port Waikato:** Eric Baker Memorial Scenic Reserve, Tainui Ecological Region, Raglan Ecological District, corticolous on kauri, 37°30'10"S; 174°47'40"E, ca. 40 m, 17 Feb 2009, P. J. de Lange 9160 (AK 313163); **Little Barrier Island:** Te Titoki Flat, 5 m E of bunkhouse, Coromandel Ecological Region, Little Barrier Ecological District, on bark of *Coprosma macrocarpa*, 36°13'18"S; 175°3'31"E, ca. 5 m, 29 Jan 1980, J. E. Braggins 80/1050, J. E. Beever (AK 291998); **Middle Island:** Coromandel Ecological District, Mercury Islands Ecological District, on *Melicytus ramiflorus* bark, 36°38'24"S; 175°51'42"E, ca. 60 m, 14 Dec 1983, E. K. Cameron 2504 (AK 291336); **Tuhua (Mayor Island):** Track to Devil's Staircase, Mayor Ecological District, corticolous on puriri (*Vitex lucens*), 37°17'46"S; 176°15'46"E, ca. 180 m, 28 Jan 2012, P. J. de Lange 10600, T. J. de Lange, F. J. T. de Lange (AK 330653); **Hamilton:** Hamilton Basin, St Andrews, 9 Dover Road, Waikato Ecological Region, Hamilton Ecological District, corticolous on apple tree (*Malus* x *domestica*), 37°45'30"S; 175°15'23"E, ca. 35 m, 02 Jan 2012, P. J. de Lange 10550 (AK 330480); **Wellington:** Johnson Hill, Sounds-Wellington Ecological Region, Wellington Ecological District, on *Melicytus ramiflorus*, ca. 41°17'S; 174°44'E, 20 Apr 1969, B.G..Hamlin 1102 (WELT H000517); **Porirua:** Pauatahanui Inlet, north side, on *Melicytus ramiflorus* in small grove near shore, ca. 41°05'15"S; 174°53'12"E, 30 Apr 1969, B.G.Hamlin 1168 (WELT H000608); **Porirua:** Titahi Bay, Stuart Park, track from S end of bay, on trunk of *Melicytus ramiflorus*, 41°06'30"S, 174°49'48"E, ca. 10m, 30 Mar 2011, P. Beveridge LD-1 (WELT H012355); **Porirua:** Mitchell Stream, Spicer Botanical Park, on trunk of *Acacia dealbata* in open rank grass and weeds, S aspect, 41°09'38"S, 174°49'23"E, ca. 80m, 5 Oct 2012, P. Beveridge ME-1 (WELT H012566); **Mana Island:** lower part of Weta Valley, Cook Strait Ecological District, on lower trunk of *Coprosma repens* in lowland regenerating forest, 41°05'31"S; 174°46'52"E, ca. 15m, 10 Feb 2011, R.J..Lewington s.n. (CHR 608376); **Puponga:** Golden Bay, N.W.Nelson, on unsealed road linking Puponga and Farewell Spit, Northwest Nelson Ecological Region, West Wanganui Ecological District, growing on *Melicytus ramiflorus* bark in kanuka-dom-

Table 1. Table of Locations – representative collections of *Lejeunea hodgsoniana*.

Latitude	Longtitude	Altitude	Location	Substrate	Herbarium
29°14'39"S	177°52'34"W	ca. 60 m	Kermadec Islands northern group, North Meyer	Exposed roots of toppled *Metrosideros kermadecensis*	AK 325247
29°16'0"S	177°54'0"W	ca. 520 m	Kermadec Islands , Raoul Island, Moumoukai	Wet forest on damp rock lying in deep shade	AK 313726
34°24'12"S	173°0'10"E	ca. 80 m	Te Paki, North Cape, Eastern tributary of the Nga Whenua Stream	Shaded, serpentinite rocks lying in ephemeral stream bed	AK 323334
35°28'40"S	174°44'38"E		Poor Knights, Aorangi Island, on ridge E of Puweto Valley	Epiphytic on trunk of *Cordyline obtecta*	AK 291340
35°53'20"S	174°45'20"E	ca. 150 m	Hen and Chicken Group, Whatupuke Island	Epiphytic on horizontal trunk of large *Brachyglottis repanda*	AK 291283
35°53'36"S	174°43'27"E		Hen & Chicken Group, Lady Alice Island	Trunks of living *Meryta trees*	AK 291288
35°53'S	174°43'E		Hen & Chicken Group, Lady Alice Island, up Kereru Stream	Trunk, sloping, 25 cm diameter lacebark	AK 291289
35°56'0"S	175°9'0"E		Mokohinau Group, Fanal Island, head of northern valley	On *Geniostoma, at shrub*/flax margin of forest	AK 291338
36°41'34"S	174°58'28"E		Inner Gulf Islands Ecological District, The Noises		AK 291347
36°51'47"S	174°43'15"E	ca. 2 m	Auckland City, Auckland Zoo grounds, Motions Creek	Partially submerged on basalt rock	AK 303709
37°30'10"S	174°47'40"E	ca. 40 m	Port Waikato, Eric Baker Memorial Scenic Reserve	Corticolous on *Agathis australis*	AK 313163
36°13'18"S	175°3'31"E	ca. 5 m	Little Barrier Island, Te Titoki Flat	On bark of *Coprosma macrocarpa*	AK 291998
36°38'24"S	175°51'42"E	ca. 60 m	Mercury Islands Ecological District, Middle Island	On *Melicytus ramiflorus bark*	AK 291336
37°17'46"S	176°15'46"E	ca. 180 m	Mayor Island, Track to Devil's Staircase	Corticolous on *Vitex lucens*	AK 330653
37°45'30"S	175°15'23"E	ca. 35 m	Hamilton City, St Andrews, 9 Dover Road	Corticolous on *Malus xdomestica)*	AK 330480
41°17'S	174°44'E		Wellington, Johnsons Hill	On *Melicytus ramiflorus*	WELT H000517
41°05'15"S	174°53'12"E		Porirua, Pauatahanui Inlet, north side	On *Melicytus ramiflorus in small grove near* shore	WELT H000608
41°06'30"S	174°49'48"E	ca. 10m	Porirua, Titahi Bay, Stuart Park, track from S end of bay	On trunk of *Melicytus ramiflorus*	WELT H012355
41°06'33"S	174°49'43"E	ca. 15m	Porirua, Titahi Bay, Stuart Park, track to cliff edge at S end of bay	On trunk and branches of *Melicytus ramiflorus in coastal thicket*	WELT H012563
41°09'38"S	174°49'23"E	ca. 80m	Porirua, Mitchell Stream, Spicer Botanical Park	On trunk of *Acacia dealbata in open rank* grass and weeds	WELT H012566
41°05'31"S	174°46'52"E	ca. 15m	Mana Island, lower part of Weta Valley	Trunk of *Coprosma repens in lowland reg*enerating forest	CHR 608376
40°31'32"S	172°44'34"E	ca. 25 m	Puponga, Golden Bay, N.W.Nelson	On *Melicytus ramiflorus bark in kanuka-domi*nant scrub	WELT 012562
43°46'0"S	176°34'0"W	ca. 60 m	Chatham Islands, Nikau Bush Scenic Reserve	Corticolous on *Melicytus chathamicus*	AK 301084
44°20'04"S	176°13'40"W		Pitt Island, stream above Canister Cove	On tree root above stream	WELT H008409

inant roadside scrub, 40°31'32"S; 172°44'34"E, ca. 25 m, 24 Feb 2012, G.G. Pritchard PFP-2 (WELT H012562); **Chatham Islands, Chatham Island:** Nikau Bush Scenic Reserve, Chathams Ecological Region and District, corticolous on *Melicytus chathamicus*, 43°46'0" S; 176°34'0"W, ca. 60 m, 28 Jun 2007, P. J. de Lange CH1021 (AK 301084); **Chatham Islands, Pitt Island:** stream above Canister Cove, on tree root above stream, ca. 44°20'04"S; 176°13'40"W, 05 Jan 1970, B.G. Hamlin 1102 (WELT H008409).

Herbarium links for specimens examined. New Zealand Virtual Herbarium NZVH www.virtualherbarium.org.nz provides links to the leading New Zealand herbaria.

The Australian Virtual Museum AVH http://avh.chah.org.au/ provides links to the leading Australian herbaria.

The direct links:

for WELT is: http://collections.tepapa.govt.nz/advancedsearch.aspx?CollectionGroup=NE this provides details of bryophyte collections although no images of the specimens cited above;

for the Allan Herbarium (CHR) is: http://nzflora.landcareresearch.co.nz/default.aspx?NavControl=search&selected=CollectionSearch;

for the bryophyte collection of the Field Museum of Natural History, Chicago (F) is: http://emuweb.fieldmuseum.org/botany/search_bryo.php

Recognition. *Lejeunea hodgsoniana* is a distinctive species that can be recognized by a number of features that are unique among southern temperate Australasian *Lejeunea*: 1) the habit of shoots, with relatively large leaf-lobes closely appressed to the substrate is characteristic; 2) the multicellular, triangular first lobule tooth having a base up to four cells broad, is unique among Australasian species; 3) the elliptic-ovate, deeply divided underleaves with lobes capped (typically) by a single pointed cell are also unusual, occurring in no other *Lejeunea* from New Zealand; 4) the pentacarinate perianth with dorsal carina reduced or absent is also unusual, but not unique. The triangular, multicellular first lobule tooth, is not unique to *L. hodgsoniana* but is shared by at least two other *Lejeunea* species, *L. bidentula* Herzog and *L. kodamae* Ikegami & Inoue. However, *Lejeunea hodgsoniana* differs from both in details of the lobule and underleaf, and in the overall size of the plants. The lobule second tooth in *L. hodgsoniana* is never well developed, at best it is a broad, low and triangular with a weakly obtuse apex. Both *L. bidentula* and *L. kodamae* have a prominent, readily identifiable second lobule tooth, which is triangular in both species and has an acute to obtuse apex (Asthana and Saxena 2011). The underleaves of *L. bidentula* are shallowly bifid and broadly ovate, and those of *L. kodamae* are squat, almost rotund but for the sinus, in contrast to those borne by *L. hodgsoniana.* Both *L. bidentula* and *L. kodamae,* with shoots 0.7–0.9 mm wide, are smaller plants than *L. hodgsoniana* whose shoots frequently attain widths of 1.5 mm.

Key to species with multicellular, triangular first lobule tooth in SE Asia and Australasia

1 Underleaves ovate, 5 × stem diameter, sinus to 0.3, broadly V-shaped, underleaf lobes not capped by prominent single cell. Gynoecia usually with two

subfloral innovations, perianth pentacarinate, not dorso-ventrally flattened. Rostrum to seven cells.....***Lejeunea bidentula***

– Underleaves rotund to elliptic-ovate, 2–3 × stem diameter, sinus to 0.6, narrowly V-shaped, underleaf lobes capped by a prominent single cell. Gynoecia usually with a single subfloral innovation. Perianth pentacarinate, dorso-ventrally flattened or not. Rostrum to four cells **2**

2 Shoots to 0.9 mm wide. First lobule tooth to two cells broad at base. Squat, rotund underleaves. Perianth not compressed, obovate. Rostrum to four cells.....***Lejeunea kodamae***

– Shoots to 1.5 mm wide. First lobule tooth to four cells broad at base. Elliptic-ovate underleaves. Perianth compressed, obcordate. Rostrum to three cells... .....***Lejeunea hodgsoniana***

Conservation. *Lejeunea hodgsoniana* is widely distributed in coastal and lowland habitats in northern and southern parts of the North Island. It is abundant in mahoe dominated forests on the mainland and many offshore islands, including large areas within the conservation estate such as Hauturu and the Poor Knights Islands. The species occupies a wide range of forest habitats associated with high light environments, including forest edges, riparian vegetation, successional forest, and floodplain scrub. Within these vegetation types *L. hodgsoniana* can be found in highly disturbed remnants, as well as original stands, for instance coastal forests at Bream Tail, Northland. As a result, we consider this species to be Not Threatened according to the New Zealand Threat Classification System (Townsend et al. 2008).

Variation. Throughout its range, there appears to be little variation from the range of variability expressed in the type material. In contrast to the usual weakly bulging leaf lobe cells, those in the sample on stream basalt from Motion Creek in Auckland, AK 303709, are moderately bulging giving a moderately crenulated margin to the lobes. Variation otherwise is in the size and shape of the perianth before sporophyte enlargement. The perianths in a sample from the Spicer Botanical Park in Porirua, WELT H012566, lacked the usual distinctly obcordate profile with the rostrum borne in a depression between the rounded apices of the lateral carinae. Instead, the apex of the perianth is truncate with rounded lateral carina apices. The rostrum is longer than usual at ca. 60 μm and the apical depression absent or almost so. Perianths in the samples AK 313726 from the summit of Raoul Island in the Kermadec Islands and AK 291289 from Lady Alice Island have similar truncate apices with a small or absent depression and, in the Kermadec sample, were smaller than usual at 350 μm high × 200 μm wide.

Acknowledgements

Particular acknowledgement should be made of those, including Jessica and Ross Beever, Ewen Cameron, and John Braggins, whose dedication over the years to the

study of the botany of the northern off-shore islands has provided at AK the extensive records of their bryophyte diversity and distribution. Thanks are due also to Graham Pritchard for his recent collection, now in WELT, extending the range of the species to the South Island, and to Peter de Lange for his extensive collection of bryophytes from the Chatham and Kermadec Islands.

Our thanks are expressed to Ewen Cameron and Dhahara Ranatunga at AK for the loan of their collection of this species, to Anthony Kusabs at WELT for his facilitation of this loan, and to Jessica Beever for additional location data on some early collections. During the preparation of this paper, David Glenny, Patrick Brownsey, Leon Perrie and Carlos Lehnebach gave valuable advice and support.

Thanks are also expressed for helpful comment of the anonymous reviewer.

References

Asthana G, Saxena M (2011) *Lejeunea kodamae* Ikegami & Inoue new to India, with a note on the rediscovery of *L. bidentula* Herzog. Journal of Bryology 33–1: 89–92. http://www.ingentaconnect.com/content/maney/jbr/2011/00000033/00000001/art00016;jsessionid=2cdhvdffme6k0.alice

Glenny D (1996) *Nephelolejeunea papillosa*, a new liverwort species from New Zealand, with notes on the distribution of *Kymatolejeunea bartlettii* Grolle. New Zealand Journal of Botany 34: 195–198. http://www.tandfonline.com/doi/abs/10.1080/0028825X.1996.10410683#.UhaXZ_mN04A, doi: 10.1080/0028825X.1996.10410683

Glenny D (1998) A revised checklist of New Zealand liverworts and hornworts. Tuhinga 10: 119–149. http://collections.tepapa.govt.nz/publication.aspx?irn=3378

Godley EJ (1984) Eliza Amy Hodgson Hon. D.Sc. (Massey) F.L.S. 1888–1983. Proc. Roy. Soc. New Zealand 112: 19–25, portr.

Grolle R (1973) *Nephelolejeunea*–eine neue Gattung der Tuyamaelloideae. Journal of the Hattori Botanical Laboratory 37: 251–261.

Grolle R (1982) Ubersicht der Lejeuneaceae in Tasmanien, Wissenschaftliche Zeitschrift der Friedrich-Schiller-Universitaet Jena. Naturwissenschaftliche Reihe 31: 207–227.

Hodgson EA (1941) A Review of the New Zealand species of *Schistochila* with notes on Colenso's species. Trans. & Proc. Roy. Soc. New Zealand 71: 181–194, f. 1–33. http://rsnz.natlib.govt.nz/volume/rsnz_71/rsnz_71_03_003110.html

Hodgson EA (1943) A Review of the New Zealand species of the genus *Chiloscyphus*. Being the second of a series of papers on New Zealand Hepaticae. Trans. & Proc. Roy. Soc. New Zealand 73: 27–52, pls. 5–6. http://rsnz.natlib.govt.nz/volume/rsnz_73/rsnz_73_01_000820.html

Hodgson EA (1944) New Zealand Hepaticae (Liverworts). Part IV. A Review of the N. Z. Species of the genus *Radula*. Trans. & Proc. Roy. Soc. New Zealand 74: 273–287. http://rsnz.natlib.govt.nz/volume/rsnz_74/rsnz_74_03_003750.html

Renner MAM (2010) Another new species of *Austrolejeunea* (Lejeuneaceae) from New Zealand New Zealand's subalpine environs. The Bryologist 113: 781–787. http://www.bioone.org/

doi/abs/10.1639/0007-2745-113.4.781?journalCode=bryo#.UhPwcfmN04A, doi: 10.1639/0007-2745-113.4.781

Renner MAM, Brown EA, Wardle GM (2009) Evidence for species recognition on the basis of a single specimen: *Nephelolejeunea carcharias* sp. nov. (Lejeuneaceae: Jungermanniopsida). Systematic Botany 34: 615–624. http://www.bioone.org/doi/abs/10.1600/036364409790139754?journalCode=sbot#.UhPwAfmN04A, doi: 10.1600/036364409790139754

Renner MAM, Brown EA, Wardle GM (2010) The *Lejeunea tumida* species group (Lejeuneaceae: Jungermanniopsida) in New Zealand. Australian Systematic Botany 23: 443–462. http://www.publish.csiro.au/paper/SB10047.htm, doi: 10.1071/SB10037

Renner MAM, de Lange PJ (2011) Additions to the Lejeuneaceae flora of New Zealand: new species from the Kermadec Islands and range extensions of New Zealand species into the South Pacific. New Zealand Journal of Botany 49: 421–433. http://www.tandfonline.com/doi/pdf/10.1080/0028825X.2011.580765, doi: 10.1080/0028825X.2011.580765

Renner MAM, Pócs T (2011) *Cololejeunea grossepapillosa* (Lejeuneaceae: Jungermanniopsida), an inconspicuous species new for New Zealand. New Zealand Journal of Botany 49: 295–303. http://www.researchgate.net/publication/232956528_Cololejeunea_grossepapillosa, doi: 10.1080/0028825X.2010.548071

Townsend AJ, de Lange PJ, Norton DA, Molloy J, Miskelly C, Duffy C (2008) The New Zealand Threat Classification System Manual. Department of Conservation, Wellington. http://www.doc.govt.nz/documents/science-and-technical/sap244.pdf

PhytoKeys 29: 17–62 (2013)
doi: 10.3897/phytokeys.29.4937
www.phytokeys.com

CHECKLIST

A peer-reviewed open-access journal
PhytoKeys
Launched to accelerate biodiversity research

Diversity and levels of endemism of the Bromeliaceae of Costa Rica – an updated checklist

Daniel A. Cáceres González[1,2], Katharina Schulte[1,3,4], Marco Schmidt[1,2,3], Georg Zizka[1,2,3]

1 *Abteilung Botanik und molekulare Evolutionsforschung, Senckenberg Forschungsinstitut Frankfurt/Main, Germany* **2** *Institut Ökologie, Evolution & Diversität, Goethe-Universität Frankfurt/Main, Germany* **3** *Biodiversität und Klima Forschungszentrum (BiK-F), Frankfurt/Main, Germany* **4** *Australian Tropical Herbarium & Center for Tropical Biodiversity and Climate Change, James Cook University, Cairns, Australia*

Corresponding author: *Daniel A. Cáceres González* (consultoria.caceres@gmail.com)

Academic editor: *L. Versieux* | Received 1 March 2013 | Accepted 28 October 2013 | Published 11 November 2013

Citation: González DAC, Schulte K, Schmidt M, Zizka G (2013) Diversity and levels of endemism of the Bromeliaceae of Costa Rica – an updated checklist. PhytoKeys 29: 17–61. doi: 10.3897/phytokeys.29.4937

This paper is dedicated to the late Harry Luther, a world leader in bromeliad research.

Abstract

An updated inventory of the Bromeliaceae for Costa Rica is presented including citations of representative specimens for each species. The family comprises 18 genera and 198 species in Costa Rica, 32 species being endemic to the country. Additional 36 species are endemic to Costa Rica and Panama. Only 4 of the 8 bromeliad subfamilies occur in Costa Rica, with a strong predominance of Tillandsioideae (7 genera/150 spp.; 75.7% of all bromeliad species in Costa Rica). 124 species (62.6%) grow exclusively epiphytic, additional 59 spp. (29.8%) are facultative epiphytes. The most diverse genus is *Werauhia,* with 59 species (29.8% of the Costa Rican bromeliad flora), followed by *Tillandsia* with 40 species (20.2%) and *Guzmania* with 28 spp. (8.6%).

Resumen

Es presentada una lista de chequeo actualizada de 18 géneros y 198 especies de Bromeliaceae conocidas de Costa Rica. Por consiguiente, las bromelias endémicas de Costa Rica, ahora comprenden 32 especies. Adicionalmente, 36 especies tienen un endemismo compartido con Panamá. Sólo 4 de las 8 subfamilias actualmente reconocidas ocurren en Costa Rica con fuerte predominio de Tillandsioideae (7 géneros/150 spp.; 75.7% del total de especies de bromelias de Costa Rica). 124 especies (62.6%) crecen como epífita, 59 especies adicionales (29.8%) son epifitas facultativas. El género mejor representado es *Werauhia*, con 59 especies (29.8% de la flora de bromelias de Costa Rica), seguido por *Tillandsia* con 40 spp. (20.2%) y *Guzmania* con 28 especies (8.6%).

Keywords
Central America, epiphytism, life-form, systematic diversity

Introduction

Costa Rica is part of the hotspots of plant diversity in the Neotropics (Myers et al. 2000) with an estimated 8,249 vascular plant species (Hammel et al. 2004). Over the last century the number of scientifically documented plants for Costa Rica has increased considerably rendering the country one of the best studied in Mesoamerica. In Costa Rica, the Bromeliaceae belong to the families with highest species diversity in epiphytic habitats and thus contribute considerably to overall forest diversity.

Bromeliaceae comprise 3,172 species and 58 genera (Luther 2008), which are grouped in the 8 subfamilies Brocchinioideae, Lindmanioideae, Tillandsioideae, Hechtioideae, Navioideae, Pitcarnioideae, Puyoideae and Bromelioideae (Givnish et al. 2011). All bromeliads are restricted to the Neotropics, with the one exception of *Pitcairnia feliciana* from West Africa.

Based on the extensive revision of herbarium collections from Costa Rica, we present an updated checklist of Bromeliaceae for the country, and provide a brief analysis of systematic diversity, levels of endemism, distribution and life-form spectrum (epiphytic/terrestrial/saxicolous). Recent floristic work, in particular the revision of the diversity of Bromeliaceae of Panama (Cáceres González et al. 2011b) required the reassessment of endemicity of Costa Rican bromeliads. This led to considerable changes in the number of endemic bromeliad species recognized for Costa Rica.

Materials and methods

Herbarium collections of Bromeliaceae from 23 herbaria (B, C, CR, DUKE, F, FR, GH, INB, K, LI, MICH, MO, NY, PMA, RM, SCZ, SEL, TEX, US, USJ, UMO, WS and WU; abbreviations after Thiers 2008) were studied. Altogether 4,523 herbarium specimens of Bromeliaceae from Costa Rica were revised.

For identification and extraction of biological information, the following references were used: Smith and Downs (1974, 1977, 1979), Utley (1994), Méndez-Estrada (1995), Grant (1995a, 1995b), Luther and Kress (1996), Grant and Morales (1996), Rossi et al. (1997), Morales (1999, 2000, 2003a, 2003b, 2003c, 2005, 2009), Morales and Alfaro (2003), Luther (2003), Cascante Marín et al. (2008), and Cáceres González et al. (2011a, 2011b). Further relevant references are given under the relevant species.

All species are listed below with information on their distribution and life form. Species endemic to Costa Rica are marked with an asterisk *. The endemic species reported by Morales (2003c) are marked with a “1”. Species endemic to Costa Rica and Panama are marked with a “2”.

Type specimens are annotated (holo = holotype, iso = isotype, lecto = lectotype, para = paratype). Additionally, a maximum of five revised herbarium collections are listed for each species, except in cases where the number of available collections was less than five.

The presented checklist includes indigenous taxa and only one cultivated and naturalized taxon (*Ananas comosus* (L.) Merr.). Subspecies, varieties, and forms are not included in the list. Species erroneously reported for Costa Rica are listed separately. Synonyms (syn.) are only included if found in the recent literature.

Nomenclature, generic delimitation and total species numbers for genera follow Luther (2008) and the International Plant Names Index (IPNI 2011).

Results and discussion

Bromeliaceae diversity in Costa Rica

According to our studies, Costa Rica harbours 18 genera and 198 species of Bromeliaceae, which represents 2.4% of the total angiosperm flora of the country (see species list [Appendix] and and Table 1). Thus, species diversity of the Costa Rican Bromeliaceae is one of the richest among the Central American countries. Of the 3,172 species and 58 genera recognized for the whole family (Luther 2008), 6.2% of the species and 31% of the generic diversity are represented in Costa Rica.

The increase in species reported for Costa Rica in the recent past (e.g. Utley (1994): 169 species; Luther (1995): 192 spp.; and Morales (2003c): 195 spp) can mostly be attributed to the discovery and description of new species (Luther and Kress 1996: *Guzmania herrerae* H. Luther & W. J. Kress, *G. scandens* H. Luther & W. J. Kress; Grant and Morales 1996: *Pitcairnia calcicola* J. R. Grant & J. F. Morales; Morales 1999: *Vriesea barii* J.F. Morales, *V. simulans* J.F. Morales, *V. haberii* J.F. Morales, *V. osaensis* J.F. Morales, *V. tiquirensis* J.F. Morales, *V. vulcanicola* J.F. Morales). Nevertheless, there were several discrepancies between previous studies of the bromeliad flora for Costa Rica (e.g. Luther 1995; Morales and Alfaro 2003; Morales 2003c), which we were able to resolve. For example, Luther (1995) added *Tillandsia streptophylla* Scheidw. ex C. Morren as new for Costa Rica. Our attempt to trace the specimens on which such report was based was not successful, and perhaps for this reason, Morales (2003c) refrained from including *T. streptophylla* in his list of bromeliads of Costa Rica. Nevertheless, we were able to verify the presence of the species based on recently collected specimens revised by us, thus *T. streptophylla* is again included in our checklist (see Appendix).

According to Morales (2009), *Aechmea penduliflora* André, formerly reported for Costa Rica, does not exist in the country. Morales (2009) refers to misidentified collections (*Espinoza 94*, INB, MO; *McPherson 8533*, MO; *Rueda & Mendoza 17152*, MO), which represent *A. angustifolia* Poepp. & Endl. However, other specimens from Costa Rica revised by us represent *A. penduliflora* (see Appendix), thus we included the species in our list.

Table 1. Bromeliaceae of Costa Rica: species richness and endemism.

Subfamily & genus	Number of species	% of bromeliad flora	Number of endemic species	% of endemic species
Tillandsioideae				
Catopsis	11	5.6	1	3.1
Guzmania	28	14.1	4	12.5
Mezobromelia	1	0.5	0	0.0
Racinaea	5	2.5	0	0.0
Tillandsia	40	20.2	2	6.3
Vriesea	6	3.0	2	6.3
Werauhia	59	29.8	18	56.3
Subtotal=7	**150**	**75.7**	**27**	**84.5**
Bromelioideae				
Aechmea	17	8.6	0	0
Ananas	2	1.0	0	0
Androlepis	1	0.5	0	0
Araeococcus	1	0.5	0	0
Billbergia	1	0.5	0	0
Bromelia	3	1.5	0	0
Greigia	2	1.0	0	0
Ronnbergia	1	0.5	0	0
Subtotal=8	**28**	**14.1**	**0**	**0.0**
Pitcairnioideae				
Pepinia	1	0.5	1	3.1
Pitcairnia	17	8.6	3	9.3
Subtotal=2	**18**	**9.1**	**4**	**12.4**
Puyoideae				
Puya	2	1.0	1	3.1
Subtotal=1	**2**	**1.0**	**1**	**3.1**
TOTAL=18	**198**	**100.0**	**32**	**100.0**

Morales (2003c) included *Catopsis werckleana* Mez in the synonymy of *Catopsis nutans* (Sw.) Griseb. However, we accept *C. werckleana* as a separate species which is documented from Costa Rica and thus included in our list.

Species erroneously reported or with name unresolved for Costa Rica

The records of *Catopsis wawranea*, cited by Smith and Downs (1977), Utley (1994) and Luther (1995) are based on the collection *Werckle s.n.* (B). We determined this collection to be *C. wangerinii* Mez & Wercklé, therefore *C. wawranea* had to be excluded from the list.

Werauhia cooperiana J. F. Morales, listed and described by Morales (2003c), is based on the specimen *Morales & Soto 7700* (INB, n.v.). In this publication this spe-

cies is specified as "in press" (Morales 2003c: 360) and according to The Plant List (2010) "this name is unresolved" and not listed by Luther (2008). Since we did not study the relevant specimen, *W. cooperiana* is excluded from this checklist.

Altogether, 195 species of our list (198 spp.) are also documented in Morales (2003c), Morales (2005, 2009) and Morales and Alfaro (2003). In total, five species (*Catopsis werckleana*, *Tillandsia streptophylla, T. rhomboidea, T. guatemalensis, Werauhia anitana*) had to be added and two (*Tillandsia acostae, Guzmania mitis*) were excluded based on our revision of the herbarium material.

Taxonomic diversity

Among the four subfamilies of Bromeliaceae represented in Costa Rica, Tillandsioideae are the most diverse (7 genera/150 spp.; 75.7% of all Costa Rican bromeliad species), followed by Bromelioideae (8/28; 14.1%), Pitcairnioideae s.str. (2/18; 9.1%) and Puyoideae (1/2; 1%) (Table 1). A similar dominance of Tillandsioideae is also found in Mexico (Espejo-Serna et al. 2004), Panama (Cáceres González et al. 2011b), Colombia (Holst 1994), Ecuador (Holst 1994), Peru (Holst 1994), and Bolivia (Krömer et al. 1999).

At the generic level, *Werauhia* is the most diverse group in Costa Rica with 59 species (29.8% of the bromeliad flora). The genus has its centre of diversity in Costa Rica and Panama. Second in species richness is *Tillandsia* (40 spp., 20.2%), followed by *Guzmania* (28 spp., 14.1%), *Pitcairnia* (17 spp., 8.6%), and *Aechmea* (17 spp., 8.6%) (Table 1).

Life-form

Of the 198 bromeliad species reported for Costa Rica, 124 (62.6%) grow epiphytically (e.g. *Catopsis nutans*, *Tillandsia caput-medusae*, *Werauhia osaensis*) and 12 (6.1%) as terrestrials (e.g. *Aechmea magdalenae*, *Greigia columbiana*). Alltogether 43 spp. (21.7%) can be found growing epiphytic or terrestrial (e.g. *Guzmania plicatifolia*, *Werauhia kupperiana*), 2 species (1.0%) were found growing both, epiphytic and saxicolous (*Pitcairnia saxicola,* and *Tillandsia brachycaulos*). Only 3 species (1.5%) were found exclusively growing in soil or on rocks (*Pitcairnia calcicola, P. halophila,* and *Puya floccosa*). The number of species that can be found as epiphytes, terrestrials and/or saxicoles adds up to 14 (7.1%) (Fig. 1). The high number of epiphytes in the bromeliad flora can be explained by the dominance of different types of tropical forests in the natural vegetation of the country (Cáceres González et al. 2011b).

Endemism

Previously, 44 species were regarded to be endemic to Costa Rica (Morales 2003c), equalling 22.6% of the total bromeliad flora known at that time (195 spp.). With the

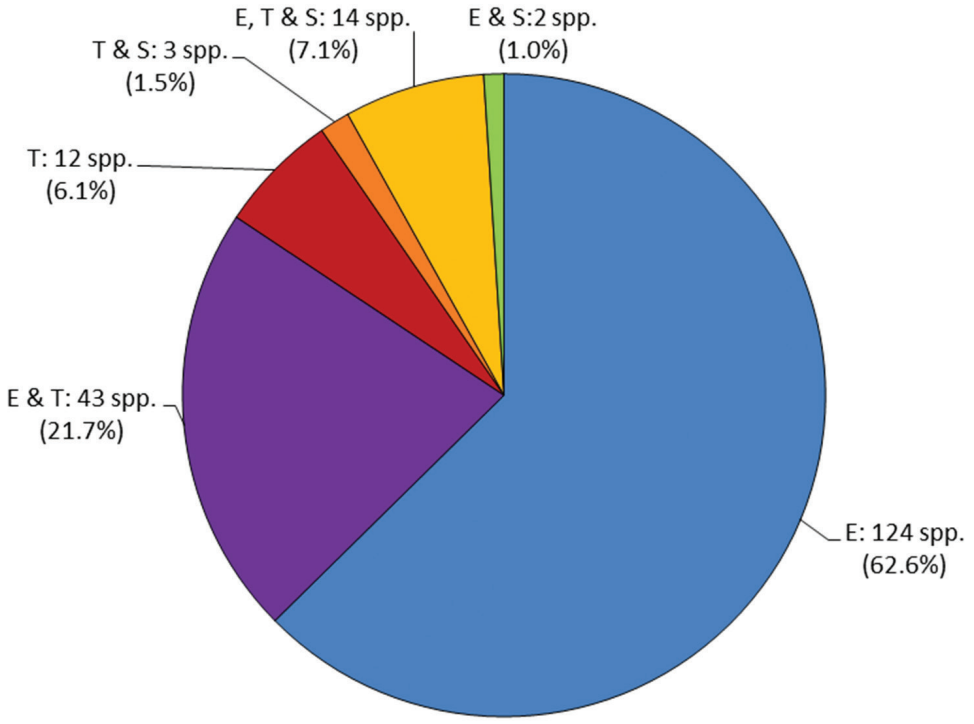

Figure 1. Bromeliaceae of Costa Rica: life form spectrum. **E**: epiphytic, **T**: terrestrial, **S**: saxicolous.

new records of bromeliad species recently reported for Panama (Cáceres González et al. 2011b) and the results presented here, the number of bromeliads endemic to Costa Rica is reduced to 32 species (16.2%). A considerable number of species previously regarded as endemic to Costa Rica is now known to occur also in Panama. In total, 36 species (18.2%) have a shared endemism with Panama (see Appendix and Table 1).

In Costa Rica, the level of endemism in the family Bromeliaceae is distributed among the subfamilies as follows: the Tillandsioideae comprise the majority of endemic species (27 species (84.5%)), followed by Pitcairnioideae with 4 species (12.4%) and Puyoideae with 1 species (3.1%) (Table 1).

Many bromeliad species with endemism shared between Panama and Costa Rica have been collected principally in the Cordillera de Talamanca of both countries.

The transborder Parque Internacional La Amistad (PILA), including nearly 1,940 km² of Costa Rica and 2,070 km² of Panama was founded in 1988 and declared a World Heritage Site in 1990. It is an important contribution to the conservation of biodiversity in this hotspot. Considering that the diversity of epiphytic bromeliads of Costa Rica and Panama is a good indicator for overall diversity in forests, additional protected areas in this mountainous region with exceptionally high geo- and biodiversity are highly desirable.

Acknowledgements

We are grateful to the curators of the herbaria B, C, CR, DUKE, F, GH, INB, K, LI, MICH, MO, NY, PMA, RM, SCZ, SEL, TEX, US, USJ, UMO, WS and WU for access to their collections. We thank colleagues and friends for important information about collections, companionship during field work, and various supports, especially Prof. Dr. Meike Piepenbring, Prof. Rafael Rincón, Harry Luther, Bruce Holst, and Alba Arbelaez.

The studies were financially supported by the German Academic Exchange Service (DAAD), Goethe Graduate Academy (GRADE), German Research Foundation (DFG Zi 557/6-2, 557/7-1), and the Hessian initiative for the development of scientific and economic excellence (LOEWE) at the Biodiversity and Climate Research Centre (BiK-F), Frankfurt/Main in Germany.

References

Cáceres González DA, Schulte K, Zizka G (2011a) Untersuchungen zur Taxonomie, Diversität und Biogeographie der Bromelien Westpanamas. Die Bromelie 2: 82–84.

Cáceres González DA, Schulte K, Schmidt M, Zizka G (2011b) A synopsis of the Bromeliaceae of Panama, including new records for the country. Willdenowia 41: 357–369. doi: 10.3372/wi.41.41216

Cascante Marín A, Wolf JHD, Oostermeijer JGB, den Nijs JCM (2008) Establishment of epiphytic bromeliads in successional tropical premontane forests in Costa Rica. Biotropica 40(4): 441–448. doi: 10.1111/j.1744-7429.2008.00403.x

Espejo-Serna A, López-Ferrari AR, Ramírez-Morillo I, Holst BK, Luther HE, Till W (2004) Checklist of Mexican Bromeliaceae with notes on species distribution and levels of endemism. Selbyana 25(1): 33–86.

Givnish TJ, Barfuss MHJ, Van Ee B, Riina R, Schulte K, Horres R, Gonsiska PA, Jabaily RS, Crayn DM, Smith JAC, Winter K, Brown GK, Evans TM, Holst BK, Luther H, Till W, Zizka G, Berry PE, Sytsma KJ (2011) Phylogeny, adaptive radiation, and historical biogeography in Bromeliaceae: Insights from an eight-locus plastid phylogeny. American Journal of Botany 98(5): 827–895. doi: 10.3732/ajb.1000059

Grant JR (1995a) The resurrection of *Alcantarea* and *Werauhia*, a new genus. Tropische und Subtropische Pflanzenwelt 91: 7–57.

Grant JR (1995b) Addendum to "The resurrection of *Alcantarea* and *Werauhia*, a new genus (Bromeliaceae: Tillandsioideae). Phytologia 78: 119–123.

Grant JR, Morales JF (1996) *Pitcairnia calcicola* (Bromeliaceae), a new species from the tropical dry forest of Costa Rica. Novon 6(4): 366–369. doi: 10.2307/3392041

Hammel BE, Grayum MH, Herrera C, Zamora N (Ed) (2004) Manual de plantas de Costa Rica 1. Introducción. Monographs in Systematic Botany from the Missouri Botanical Garden 97: 1–299.

Holst BK (1994) Checklist of Venezuelan Bromeliaceae with notes on species distribution by state and levels of endemism. Selbyana 15(1): 132–149.

International Plant Names Index (IPNI) (2011) International Plant Names Index. http://www.ipni.org/index.html [accessed February 2013]

Krömer T, Kessler M, Holst BK, Luther HE, Gouda E, Ibisch PL, Till W, Vasquez R (1999) Checklist of Bolivian Bromeliaceae with notes on species distribution and levels of endemism. Selbyana 20(2): 201–223.

Leme EMC (1997) Revision of the lithophytic *Vriesea* species from Minas Gerais state, Brazil - Part II. Journal of the Bromeliad Society 47: 168–177.

Luther HE (1995) An annotated checklist of the Bromeliaceae of Costa Rica. Selbyana 16: 230–234.

Luther HE (2003 ['2002']) Miscellaneous new taxa of Bromeliaceae (XVI). Brittonia 54: 279–285. doi: 10.1663/0007-196X(2003)54[279:MNTOBX]2.0.CO;2

Luther HE (2008) An alphabetical list of bromeliad binomials, 11th ed. Bromeliad Society International. http://www.selby.org/research/papers/alphabetical-list-bromeliad-binomials

Luther HE, Kress WJ (1996) Two overlooked species of *Guzmania* (Bromeliaceae) of the species-complex *Massangea* from Central America. Brittonia 48: 91–95. doi: 10.2307/2807668

Méndez-Estrada V (1995) Ecología de las bromelias epífitas. Repertorio Científico UNED 3(2): 20–23.

Morales JF (1999) Seis nuevas especies de *Vriesea* sect. *Xiphion* (Bromeliaceae: Tillandsoideae) para Costa Rica. Novon 9: 401–406. doi: 10.2307/3391739

Morales JF (2000) Bromelias de Costa Rica, 2da edición. Instituto Nacional de Biodiversidad, Santo Domingo de Heredia.

Morales JF (2003a) Nuevas combinaciones y un nuevo nombre en las Bromeliaceae de Costa Rica. Polibotanica 15: 109–111.

Morales JF (2003b) New combinations in *Werauhia* (Bromeliaceae) from Costa Rica. Lundiana 41(1): 65.

Morales JF (2003c) Bromeliaceae. In: Hammel BE, Grayum MH, Herrera C, Zamora N (Ed) Manual de plantas de Costa Rica 2. Gimnospermas y Monocotiledóneas (Agavaceae–Musaceae). Monographs in Systematic Botany from the Missouri Botanical Garden 92: 397–375.

Morales JF (2005) Una nueva especie de *Werauhia* (Bromeliaceae) para Costa Rica. Novon 15(2): 332–333.

Morales JF (2009) Novedades y notas misceláneas en las Bromeliaceae de Mesoamérica. Journal of the Botanical Research Institute of Texas 3(1): 113–116.

Morales JF, Alfaro E (2003) *Tillandsia guatemalensis*, un registro nuevo en la flora de Costa Rica. Lankesteriana 8: 5–6.

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403: 853–858. doi: 10.1038/35002501

Rossi MR, Mendez VH, Monge-Nájera J (1997) Distribution of Costa Rican epiphytic bromeliads and the Holdridge Life Zone System. Revista de Biología Tropical 45(3): 1021–1031.

Smith LB, Downs RJ (1974) Pitcairnioideae (Bromeliaceae). Flora Neotropica Monograph 14(1): 1–662.

Smith LB, Downs RJ (1977) Tillandsioideae (Bromeliaceae). Flora Neotropica Monograph 14(2): 663–1492.

Smith LB, Downs RJ (1979) Bromelioideae (Bromeliaceae). Flora Neotropica Monograph 14(3): 1493–2142.

The Plant List (2010) Version 1. Published on the Internet at http://www.theplantlist.org [accessed May 2012]

Thiers B (2008 [continuously updated]) Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden. http://sweetgum.nybg.org/ih/ [accessed April 2013]

Utley JF (1994) Bromeliaceae. In: Davidse G, Sousa SM, Chater AO (Ed) Flora Mesoamericana 6. Alismataceae a Cyperaceae. Universidad Nacional Autónoma de México, Missouri Botanical Garden and The Natural History Museum, 89–156.

Appendix

AECHMEA

Aechmea angustifolia Poepp. & Endl., Nov. Gen. Sp. Pl. 2: 43 (1838).

Distribution. Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Peru, Bolivia, Brazil, and Venezuela.

Representative Collections—COSTA RICA. *Pittier 9426* (B); 9 Apr 1983, *Liesner 14163* (INB, SEL); 20 Feb 1991, *Till 7053* (CR); 1 Feb 1996, *Hammel 20142* (INB); 6 May 1998, *Morales 6422* (INB).

Life form. Epiphyte.

Aechmea aquilega (Salisb.) Griseb., Fl. Brit. W. I.: 592 (1864).

Distribution. Costa Rica, Brazil, Suriname, Guianas, Venezuela, and Trinidad and Tobago.

Representative Collections—COSTA RICA. 19 Jun 1874, *Kuntze 2113* (CR, n.v.; K, n.v.).

Life form. Epiphyte.

Aechmea bracteata (Sw.) Griseb., Fl. Brit. W. I.: 592 (1864).

Distribution. Mexico, Guatemala, Belize, Honduras, Nicaragua, Costa Rica, and Panama.

Representative Collections—COSTA RICA. 25 Feb 1933, *Valerio 375* (CR); 10 Mar 1994, *Huber 355* (CR); 28 May 1995, *Grant 2348* (INB); 10 Feb 1997, *Moraga 863* (CR, INB); 11 Apr 2005, *Morales 12758* (INB).

Life form. Epiphyte.

Aechmea castelnavii Baker, Handb. Bromel.: 39 (1889).

Distribution. Costa Rica, Colombia, Bolivia, Brazil, and Venezuela.

Representative Collections—COSTA RICA. 17 Jan 1991, *Grant 91-01478* (INB); 13 May 1995, *Jiménez 1827* (INB); 5 Apr 2000, *Acosta 807* (INB); 3 Apr 1997, *Morales 6140* (INB); 4 Mar 2001, *Morales 7676* (INB).

Life form. Epiphyte.

Aechmea dactylina Baker, J. Bot. 17: 161 (1879).

Distribution. Nicaragua, Costa Rica, Panama, Colombia, and Ecuador.

Representative Collections—COSTA RICA. 4 Jan 1896, *Tonduz 9985* (CR); 1 Aug 1949, *Holm 721* (CR); 13 May 1989, *Kress 2720* (INB, SEL); 27 Jul 1995, *Lépiz 613* (INB); 21 Aug 2003, *Morales 9457* (INB).

Life form. Epiphyte.

Aechmea lingulata (L.) Baker, J. Bot. 17: 164 (1879).

Distribution. Costa Rica, Panama, Brazil, Guianas, Venezuela, Trinidad, Tobago, and Jamaica.

Representative Collections—COSTA RICA. *Oersted 24* (C, n.v.), based on Smith & Downs (1979).

Life form. Epiphyte.

Aechmea lueddemanniana (K. Koch) Brongn. ex Mez, Pflanzenr., IV, 32: 120 (1934).

Distribution. Mexico, Belize, Honduras, Nicaragua, and Costa Rica.

Representative Collections—COSTA RICA. 27 Mar 1989, *Haber 9169* (INB); 2 Jun 1990, *Varela 11* (INB); 23 Mar 1994, *Morales 2555* (INB); 29 Jan 1995, *Rivera 1005* (INB); 12 Feb 1999, *Alvarado 71* (INB).

Life form. Epiphyte.

Aechmea magdalenae (André) André ex Baker, Handb. Bromel.: 65 (1889).

Distribution. Mexico, Guatemala, Belize, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, and Venezuela.

Representative Collections—COSTA RICA. 3 Jan 1896, *Tonduz 9897* (CR); 21 Jul 1949, *Holm & Iltis 439* (NY); 24 Mar 1973, *Burger 8869* (CR); 2 Jul 1994, *Lépiz 452* (CR); 25 Jan 2000, *Acosta 280* (CR, INB).

Life form. Terrestrial.

Aechmea mariae-reginae H. Wend., Hamb. Gartenz. 19: 32 (1863).

Distribution. Nicaragua, Costa Rica, and Panama.

Representative Collections—COSTA RICA. *Wercklé 16202* (B); 8 Jun 1976, *Utley 5114* (CR); 14 Feb 1982, *Burger & Gomez 11818* (PMA); 2 Sep 1993, *Morales 1640* (INB, NY); 3 Aug 2006, *Cascante 1598* (CR).

Life form. Epiphyte (rarely terrestrial).

Aechmea mexicana Baker, J. Bot. 17: 165 (1879).

Distribution. Mexico, Guatemala, Nicaragua, Costa Rica, Panama, Colombia, and Ecuador.

Representative Collections—COSTA RICA. 3 Jan 1896, *Tonduz 10074* (CR); Mar 1947, *Buchanan 546* (NY); 19 Dec 1988, *Bello 624* (CR, INB); 21 Feb 1995, *Morales 3508* (CR, INB); 12 May 1999, *Estrada 2214* (CR).

Life form. Epiphyte.

Aechmea nudicaulis (L.) Griseb., Fl. Brit. W. I.: 593 (1864).

Distribution. Mexico, Guatemala, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Brazil, and Dominican Republic.

Representative Collections—COSTA RICA. 8 Dec 1973, *Utley 510* (CR); 25 Nov 1982, *McDowell 941* (SCZ); 3 Dec 1993, *Morales 2135* (CR, INB); 6 Mar 1998, *Vargas 37* (CR, INB); 27 Sep 2000, *Acosta 2757* (INB).

Life form. Epiphyte.

Aechmea penduliflora André, Rev. Hort. 60: 563 (1888).

Distribution. Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Peru, Bolivia, and Venezuela.

Representative Collections—COSTA RICA. 1894, *Friedrichsthal 4962* (B); Apr 1894, *J. D. Smith 4962* (US, n.v.); Mar 1924, *Standley 37556* (US, n.v.); 29 Feb 1956, *Schubert 1126* (US, n.v.); 3 Dec 1980, *Waggoner s.n.* (SEL).

Life form. Epiphyte.

[1,2]***Aechmea pittieri*** Mez, Monogr. Phan. 9: 231 (1896).

Distribution. Costa Rica and Panama.

Representative Collections—COSTA RICA. Jan 1892, *Pittier 6609* (B); Jan 1908, *Wercklé 17422* (B); 26 Jan 1967, *Burger & Matta 4673* (NY); 9 Dec 2004, *Soto 454* (INB); 27 Jan 2007, *Morales 15388* (INB).

Life form. Epiphyte (rarely terrestrial).

Aechmea pubescens Baker, J. Bot. 17: 135 (1879).

Distribution. Honduras, Nicaragua, Costa Rica, Panama, Colombia, and Venezuela.

Representative Collections—COSTA RICA. 4 Apr 1930, *Brenes 1293* (CR); 26 May 1973, *Ocampo 403* (CR); 28 May 1988, *Hammel 16870* (INB); 27 May 2003, *Holst 8654* (SEL); 14 Jan 2005, *Solano 1707* (INB).

Life form. Epiphyte (occasionally terrestrial).

Aechmea tillandsioides (Mart. ex Schult. f.) Baker, J. Bot. 17: 134 (1879).

Distribution. Mexico, Guatemala, Belize, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Peru, Bolivia, Brazil, Guianas, and Venezuela.

Representative Collections—COSTA RICA. 2 May 1951, *León 3409* (CR); 26 Apr 1973, *Burger & Gentry 9287* (NY); 10 Jul 1991, *Delprete 5199* (CR, INB, MO, NY; TEX, n.v.); 21 Mar 1997, *Morales 6126* (CR, INB); 29 Oct 2000, *Gómez-Laurito 13418* (CR).

Life form. Epiphyte.

Aechmea tonduzii Mez & Pittier ex Mez, Bull. Herb. Boissier, II, 3: 132 (1903).

Distribution. Costa Rica, Panama, Colombia, and Ecuador.

Representative Collections—COSTA RICA. Mar 1893, *Tonduz 7684* (B, holo); 24 Jan 1989, *Grayum 9292* (INB); 19 Jun 1995, *Chacón 263* (CR, USJ); 26 May 2003, *Clark 153* (SEL); 2 Mar 2005, *Morales 12277* (INB).

Life form. Epiphyte and terrestrial.

Aechmea veitchii Baker, Bot. Mag. 103: t. 6329 (1877).

Distribution. Costa Rica, Panama, Colombia, Ecuador, and Peru.

Representative Collections—COSTA RICA. 12-17 Dec 1969, *Burger & Liesner 6775* (PMA); 2 Oct 1983, *Chacón 1442* (CR); 20 Jul 1994, *Lépiz 498* (CR, INB); 23 Mar 2000, *Acosta 699* (CR, INB); 25 Oct 2007, *Santamaría 6642* (INB).
Life form. Epiphyte and terrestrial.

ANANAS

Ananas ananassoides (Baker) L. B. Sm., Bot. Mus. Leafl. 7: 79 (1939).
Distribution. Costa Rica, Panama, Colombia, Ecuador, Peru, Bolivia, Paraguay, Brazil, and Venezuela.
Representative Collections—COSTA RICA. 15 Nov 1990, *Skotak 1* (INB); 1 Feb 1991, *Skotak s.n.* (CR); 6 Feb 2000, *Aguilar 5807* (INB); 25 Aug 2001, *Hammel 22407* (INB); 25 Apr 2004, *Morales 10477* (INB).
Life form. Terrestrial.

Ananas comosus (L.) Merr., Interpr. Herb. Amboin.: 133 (1917).
Distribution. Mexico, Guatemala, Belize, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Peru, Bolivia, Brazil, Venezuela, Dominican Republic, and United States of America.
Representative Collections—COSTA RICA. 7 Jan 1992, *Grant 92-1773* (CR, INB); 25 Mar 1998, *Lépiz 255* (INB); 19 Sep 2002, *Frances 19* (CR); 25 Mar 2005, *Morales 12423* (INB); 8 Apr 2006, *Morales 13793* (INB).
Life form. Terrestrial. Cultivated and naturalized.

ANDROLEPIS

Androlepis skinneri Brongn. ex Houllet, Rev. Hort. 42: 12 (1870).
Distribution. Mexico, Guatemala, Belize, Nicaragua, and Costa Rica.
Representative Collections—COSTA RICA. 16 Oct 1933, *Dodge 4864* (INB); 7 Aug 1949, *Holm 935* (CR); 5 y 6 Jun 1967, *Burger & Matta 4214* (NY); 20 Dec 1969, *Burger 6987* (CR); 1 Dec 1988, *Robles 2194* (INB).
Life form. Epiphyte.

ARAEOCOCCUS

Araeococcus pectinatus L. B. Sm., Contr. Gray Herb. 95: 41 (1931).
Distribution. Costa Rica, Panama, and Colombia.
Representative Collections—COSTA RICA. 30 May 1950, *Allen 5558* (NY); 11 Jul 1987, *Gómez-Laurito 11577* (CR, INB); 28 May 1988, *Hammel 16873* (CR); 10 Sep 1996, *Croat 79160* (SEL); 2 Mar 2005, *Morales 12190* (INB).
Life form. Epiphyte.

BILLBERGIA

Billbergia macrolepis L. B. Sm., Contr. Gray Herb. 114: 3 (1936).

Distribution. Costa Rica, Panama, Ecuador, and Venezuela.

Representative Collections—COSTA RICA. 1 Jan 1892, *Pittier 6608* (INB); 3 Mar 2000, *Hammel 22122* (INB); 25 May 2003, *Hammel 22777* (INB); 13 Jan 2010, *Hammel 25511* (INB).

Life form. Epiphyte.

BROMELIA

Bromelia hemisphaerica Lam., Encycl. 1: 145 (1783).

Distribution. Mexico, Nicaragua, Costa Rica, and Panama.

Representative Collections—COSTA RICA. *Wercklé s.n.* (B, lecto); 9 Jun 1992, *Grant 1912* (INB); 28 May 1994, *Morales 2808* (INB, SEL); 22 Jan 1999, *Hurtado 47* (INB); 14 Sep 2003, *Morales 9876* (INB).

Life form. Terrestrial.

Bromelia karatas L., Sp. PI. 1: 285 (1753).

Syn.: *B. plumieri* (E. Morren) L.B. Sm., Phytologia 15: 173 (1967).

Distribution. Mexico, Guatemala, Belize, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Brazil, Suriname, Venezuela, and Dominican Republic.

Representative Collections—COSTA RICA. 22 Jun 1977, *Liesner 2347* (CR); 28 Jun 1991, *Hammel 18231* (CR, INB, SEL); 23 Nov 1993, *Morales 2077* (INB); 10 Mar 2000, *Hammel 22195* (INB); 24 Sep 2004, *Acosta 3470* (INB).

Life form. Terrestrial.

Bromelia pinguin L., Sp. Pl.: 285 (1753).

Distribution. Mexico, Guatemala, Belize, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Venezuela, Puerto Rico, Dominican Republic, Haiti, and Jamaica.

Representative Collections—COSTA RICA. 2 Jun 1932, *Brenes 15916* (CR); 2 Aug 1971, *Burger 7861* (CR); 13 Jul 1985, *Worthington 13541* (NY); 4 Apr 2001, *Morales 7941* (CR, INB); 18 Mar 2005, *Santamaría 1063* (INB).

Life form. Terrestrial.

CATOPSIS

Catopsis berteroniana (Schult. & Schult. f.) Mez, Monogr. Phan. 9: 621 (1896).

Distribution. Mexico, Guatemala, Belize, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Brazil, Guianas, Venezuela, Dominican Republic, Jamaica, and United States of America.

Representative Collections—COSTA RICA. 19 Jan 1994, *Morales 3341* (INB); 10 May 1995, *Morales 4095* (INB).
Life form. Epiphyte.

Catopsis hahnii Baker, J. Bot. 25: 175 (1887)
Distribution. Mexico, Guatemala, Belize, El Salvador, Honduras, Nicaragua, and Costa Rica.
Representative Collections—COSTA RICA. 1847?, *Oersted 18* (B); 11 Oct 1999, *Morales 8455* (INB); 11 feb 2005, *Morales 11984* (INB).
Life form. Epiphyte.

Catopsis juncifolia Mez & Wercklé, Bull. Herb. Boissier, II, 4: 1124 (1904).
Distribution. Nicaragua, Costa Rica, and Panama.
Representative Collections—COSTA RICA. *Wercklé 133* (B, holo); 15 Oct 1988, *Herrera 2190* (CR, INB); 17 Apr 1994, *Lépiz 289* (INB); 12 May 2005, *Morales 12961* (INB); 23 May 2007, *Zamora 3986* (INB).
Life form. Epiphyte.

Catopsis micrantha L. B. Sm., Ann. Missouri Bot. Gard. 30: 83 (1943).
Syn.: *C. pedicellata* L. B. Sm., Contr. Gray Herb. 154: 34 (1945).
Distribution. Guatemala, Costa Rica, and Panama.
Representative Collections—COSTA RICA. 19 Jan 1994, *Morales 3342* (INB); 18 Nov 2004, *Morales 11616* (INB).
Life form. Epiphyte.

Catopsis morreniana Mez, Mongr. Phan. 9: 628 (1896).
Distribution. Mexico, Guatemala, Belize, Honduras, Nicaragua, and Costa Rica.
Representative Collections—COSTA RICA. *Wercklé 135* (B); 15 Oct 1987, *Herrera 878* (CR, INB); 23 Jul 1990, *Bello 2332* (CR, INB); 30 Jun 1994, *Kress 94-4059* (CR); 23 Abr 2006, *Morales 13862* (INB).
Life form. Epiphyte.

Catopsis nitida (Hook.) Griseb., Fl. Brit. W. I.: 599 (1864).
Distribution. Guatemala, Belize, Honduras, Nicaragua, Costa Rica, Panama, and Dominican Republic.
Representative Collections—COSTA RICA. 1 Jan 1901, *Wercklé 16191* (CR; US, n.v.); 23 May 1969, *Gómez 2215* (NY); 22 Jul 1990, *Luther 2807* (CR); 13 Aug 1993, *Palaci 1206* (CR, INB); 5 Mar 2008, *Cascante 1860* (CR).
Life form. Epiphyte.

Catopsis nutans (Sw.) Griseb., Fl. Brit. W. I.: 599 (1864).
Distribution. Mexico, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Venezuela, Dominican Republic, and United States of America.

Representative Collections—COSTA RICA. 24 Jun 1943, *Quirós 1141* (CR); 16 Dec 1973, *Utley 536* (CR); 22 Feb 1990, *Grant 90-833* (CR); 18 Jan 1992, *Ramírez 94-144* (USJ); 1 Mar 2007, *Monro 5729* (INB).
Life form. Epiphyte.

Catopsis paniculata E. Morren, Phytologia 15: 179 (1967).
Distribution. Mexico, Guatemala, Honduras, Nicaragua, and Costa Rica.
Representative Collections—COSTA RICA. 19 Apr 1908, *Maxon 67* (NY); 30 Jul 1967, *Lent 1155* (CR); 22 Jun 1990, *Luther 2806* (CR, SEL); 30 Dec 1993, *Morales 2173* (INB, SEL); 22 Jul 2008, *Cascante 1983* (CR).
Life form. Epiphyte.

Catopsis sessiliflora (Ruiz & Pav.) Mez, Monogr. Phan. 9: 625 (1896).
Distribution. Mexico, Guatemala, Belize, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Peru, Bolivia, Brazil, Venezuela, and Puerto Rico.
Representative Collections—COSTA RICA. Jul 1936, *Skutch 2771* (NY); 6 Jul 1977, *Liesner 2969* (CR); 9 Sep 1996, *Hammel 20439* (CR, INB); 28 May 2005, *Santamaría 2165* (INB); 8 Mar 2008, *Morales 16251* (INB).
Life form. Epiphyte.

Catopsis wangerinii Mez & Wercklé, Bull. Herb. Boissier, II, 4: 1126 (1904).
Distribution. Guatemala, El Salvador, Nicaragua, Costa Rica, and Panama.
Representative Collections—COSTA RICA. *Wercklé 105* (B, holo); 19 Apr 1908, *Maxon 65* (NY); 30 Sep 1994, *Fernández 1387* (CR, INB); 6 Feb 1998, *Till 15001* (SEL); 26 Abr 2008, *Hammel 24723* (INB).
Life form. Epiphyte.

****Catopsis werckleana*** Mez, Bull. Herb. Boissier, II, 4: 1125 (1904).
Distribution. Costa Rica.
Representative Collections—COSTA RICA. 1 Dec 1902, *Wercklé 65* (B, holo; MO, photo); Mar 1926, *Standley & Torres 51655* (US, n.v.); Apr 1983?, *Liesner & Judziewicz 14371* (MO, n.v.) (Utley 1994: 146).
Life form. Epiphyte.

GREIGIA

Greigia columbiana L. B. Sm., Contr. Gray Herb. 98: 7 (1932).
Distribution. Costa Rica, Panama, and Colombia.
Representative Collections—COSTA RICA. 30 Jul 1962, *Lee 761* (CR); 24 Feb 1991, *Till 7105* (INB); 30 May 1995, *Grant 2335* (INB, SEL); 20 Jul 2000, *Alfaro 3235* (INB); 15 Jun 2005, *Morales 13138* (INB).
Life form. Terrestrial.

[2]***Greigia sylvicola*** Standl., J. Wash. Acad. Sci. 17: 160 (1927).
Distribution. Costa Rica and Panama.
Representative Collections—COSTA RICA. 24 Feb 1977, *Dwyer 1218* (CR); 20 Nov 1988, *Kappelle 3676* (CR); 16 Apr 1991, *Haber 10691* (INB, SEL); 23 Mar 2000, *Acosta 690* (CR, INB, NY); 15 Jun 2005, *Morales 13127* (INB).
Life form. Terrestrial.

GUZMANIA

Guzmania angustifolia (Baker) Wittm., Bot. Jahrb. Syst. 11: 62 (1889).
Distribution. Nicaragua, Costa Rica, Panama, Colombia, and Ecuador.
Representative Collections—COSTA RICA. 14 Jun 1938, *Smith 779* (NY); 6 Dec 1983, *Zamora 435* (CR); 19 Jun 1993, *Rivera 2240* (CR, SEL); 12 Feb 1994, *Herrera 6841* (USJ); 9 Mar 2008, *Morales 16323* (INB).
Life form. Epiphyte.

*[1]***Guzmania blassii*** Rauh, J. Bromeliad Soc. 33: 66 (1983).
Distribution. Costa Rica.
Representative Collections—COSTA RICA. 13 May 1989, *Kress 2722* (INB; SEL; US, n.v.); 11 Jul 1989, *Waggoner s.n.* (SEL); 3 Jun 1995, *Morales 4294* (INB); 26 May 2003, *Clark 144* (SEL); 25 Jul 2007, *Rodríguez 11309* (INB).
Life form. Epiphyte.

[2]***Guzmania circinnata*** Rauh, Trop. Subtrop. Pflanzenwelt 60: 48 (1987).
Distribution. Costa Rica and Panama.
Representative Collections—COSTA RICA. 24 Sep 1991, *Skotak s.n.* (SEL); 24 Sep 1991, *Skotak 2* (INB).
Life form. Epiphyte.

Guzmania compacta Mez, Monogr. Phan. 9: 947 (1896).
Distribution. Costa Rica and Ecuador.
Representative Collections—COSTA RICA. *Wercklé 17288* (B, lecto); 19 Jan 1991, *Rivera 998* (CR, INB); 8 Feb 1992, *Ingram 1300* (SEL); 29 Jan 1995, *Chavarría 1165* (INB); 18 Jan 2002, *Chaves 1402* (INB).
Life form. Epiphyte.

Guzmania condensata* Mez & Wercklé, Bull. Herb. Boissier, II, 3: 228 (1903).
Distribution. Costa Rica.
Representative Collections—COSTA RICA. 1 Jan 1901, *Wercklé 16198* (B, holo; CR, NY); 21 Apr 1983, *Liesner 14527* (CR, INB); 26 Jul 1990, *Luther s.n.* (SEL); 15 Mar 1994, *Morales 2490* (CR, INB); 23 Aug 2007, *Cascante 1806* (CR).
Life form. Epiphyte (rarely terrestrial).

Guzmania coriostachya (Griseb.) Mez, Monogr. Phan. 9: 914 (1896).
Distribution. Costa Rica, Panama, Colombia, Ecuador, and Venezuela.
Representative Collections—COSTA RICA. 1904, *Wercklé 78* (B, lecto); 26 May 1973, *Ocampo 401* (CR); 10 Feb 1992, *Ingram 1309* (SEL); 8 Jun 2001, *Cascante 1509* (CR); 27 Jun 2004, *Morales 10845* (INB).
Life form. Epiphyte.

Guzmania desautelsii Read & L. B. Sm., J. Brom. Soc. 33(1): 17 (1983).
Distribution. Nicaragua, Costa Rica, Panama, and Venezuela.
Representative Collections—COSTA RICA. 17 Sep 1978, *Burger 11130* (CR); 4 Mar 1991, *Rivera 1146* (CR, INB); 4 Apr 1995, *Moraga 75* (INB); 11 Feb 2000, *Mora 836* (INB); 9 Mar 2008, *Morales 16344* (INB).
Life form. Epiphyte (rarely terrestrial).

Guzmania dissitiflora (André) L. B. Sm., Contr. Gray Herb. 104: 74 (1934).
Distribution. Costa Rica, Panama, Colombia, and Ecuador.
Representative Collections—COSTA RICA. *Brenes s.n.* (NY); 27 Aug 1967, *Lent 1216* (NY); 7 Dec 1982, *Gómez 19224* (NY); 16 Jan 1991, *Bittner 277* (INB); 31 Jan 1991, *Bittner 413* (INB).
Life form. Epiphyte.

Guzmania donnellsmithii Mez ex Donn. Sm., Bot. Gaz. 35: 9 (1903).
Distribution. Nicaragua, Costa Rica, Panama, and Ecuador.
Representative Collections—COSTA RICA. Feb 1902, *Donnell-Smith 6824* (B, iso); 20 Feb 1989, *Russell 849* (CR); 18 Feb 1990, *Grant 799* (CR, SEL); 17 Oct 1996, *Moraga 769* (CR, INB); 1 Mar 2007, *Rodríguez 10930* (INB).
Life form. Epiphyte (occasionally terrestrial).

Guzmania glomerata Mez & Wercklé, Repert. Spec. Nov. Regni. Veg. 14: 256 (1916).
Distribution. Nicaragua, Costa Rica, Panama, Colombia, and Ecuador.
Representative Collections—COSTA RICA. *Wercklé s.n.* (B, holo); 20 Aug 1989, *Haber 9465* (CR, INB); 20 Aug 1993, *Palaci 1216* (INB); 27 Jul 1996, *Hammel 20312* (INB); 1 Dec 1999, *Rodríguez 5528* (INB).
Life form. Epiphyte.

*[1]***Guzmania herrerae*** H. Luther & W. J. Kress, Brittonia 48: 91 (1996).
Distribution. Costa Rica.
Representative Collections—COSTA RICA. 16 Nov 1987, *Herrera 1322* (CR, holo; MO, iso); 8 Jul 1988, *Herrera 2014* (INB); 12 Oct 1995, *Cascante 787* (CR); 20 Sep 2003, *Kriebel 3838* (INB); 27 Oct 2007, *Solano 4755* (INB).
Life form. Epiphyte.

Guzmania lingulata (L.) Mez, Monogr. Phan. 9: 899 (1896).

Distribution. Mexico, Guatemala, Belize, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Peru, Bolivia, Brazil, Suriname, Guianas, Venezuela, Trinidad and Tobago, and Dominican Republic.

Representative Collections—COSTA RICA. 20 Aug 1964, *Lent 233* (CR); 21 Sep 1986, *Davidse 31521* (CR); 31 May 1990, *Herrera 3938* (INB, SEL); 28 Jun 1994, *Kress 94-4055* (CR, USJ); 11 Jun 2003, *Alfaro 4488* (INB).

Life form. Epiphyte.

Guzmania monostachia (L.) Rusby ex Mez, Monogr. Phan. 9: 905 (1896).

Distribution. Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Peru, Bolivia, Venezuela, Trinidad and Tobago, Puerto Rico, Dominican Republic, Haiti, Jamaica, and United States of America.

Representative Collections—COSTA RICA. 1 May 1913, *Tonduz s.n.* (CR); 1 Aug 1949, *Holm 782* (CR); 10 Aug 1967, *Taylor 4276* (NY); 7 Jan 1992, *Grant 92-1761* (CR, INB, SEL); 28 May 2003, *Clark 268* (SEL).

Life form. Epiphyte.

Guzmania musaica (Linden & André) Mez, Monogr. Phan. 9: 898 (1896).

Distribution. Costa Rica, Panama, Colombia, Ecuador, and Venezuela.

Representative Collections—COSTA RICA. 7 Jul 1989, *Hammel 17600* (CR, INB); 9 Jul 1989, *Chacón 138* (INB); 25 Jul 1989, *Chacón 278* (INB).

Life form. Epiphyte.

Guzmania nicaraguensis Mez & C. F. Baker ex Mez, Bull. Torrey Bot. Club 30: 436 (1903).

Distribution. Mexico, Guatemala, Belize, Honduras, Nicaragua, Costa Rica, Panama, and Ecuador.

Representative Collections—COSTA RICA. 20 Jan 1939, *Smith 1529* (NY); 7 Feb 1940, *Brenes 23012* (NY); 17 Feb 1992, *Ingram 1350* (SEL); 26 Apr 2001, *Mora 1994* (NY; CR; INB; MO, n.v.); 22 Aug 2007, *Morales 15497* (INB).

Life form. Epiphyte.

Guzmania obtusiloba L. B. Sm., Contr. Gray Herb. 104: 74 (1934).

Distribution. Costa Rica, Panama, and Colombia.

Representative Collections—COSTA RICA. 15 Aug 1933, *Valerio 702* (CR); 28 Nov 1971, *Lent 2254* (CR, n.v.; NY; PMA); 20 Feb 1990, *Grant 814* (CR, SEL); 25 Aug 2000, *Homeier & Vora 496* (USJ); 27 Oct 2007, *Monro 5847* (INB).

Life form. Epiphyte (rarely terrestrial).

Guzmania patula Mez & Wercklé, Repert. Sp. Nov. Regni. Veg. 14: 255 (1916).

Distribution. Costa Rica, Panama, Colombia, Ecuador, and Venezuela.

Representative Collections—COSTA RICA. *Wercklé s.n.* (B, holo; US, iso, n.v.); 23 Oct 1964, *Jiménez 2490* (SCZ); 1 Jul 1976, *Ocampo 1356* (CR); 8 Jul 1997, *Estrada 946* (CR); 8 Aug 2007, *Soto 1644* (INB, NY).
Life form. Epiphyte.

[2]***Guzmania plicatifolia*** L. B. Sm., Contr. Gray Herb. 102 68: 146 (1933).
Distribution. Costa Rica and Panama.
Representative Collections—COSTA RICA. 10 Jun 1925, *Brenes 7473* (CR); 22 May 1977, *Dwyer 1365* (CR); 17 Feb 1992, *Ingram 1340* (INB, SEL); 21 Jul 1994, *Lépiz 501* (CR, INB); 8 Jun 2000, *Chaves 568* (INB).
Life form. Epiphyte and terrestrial.

Guzmania polycephala Mez & Wercklé ex Mez, Repert. Spec. Nov. Regni. Veg. 14: 254 (1916).
Distribution. Costa Rica, Panama, and Colombia.
Representative Collections—COSTA RICA. *Wercklé s.n.* (B, holo); Apr 1989, *Hall s.n.* (SEL); 3 Jun 2001, *Morales 8176* (CR, INB); 3 Aug 2006, *Cascante 1597* (CR); 6 Mar 2007, *Solano 4204* (INB).
Life form. Epiphyte.

Guzmania sanguinea (André) André ex Mez, Monogr. Phan. 9: 901 (1896).
Distribution. Costa Rica, Panama, Colombia, and Ecuador.
Representative Collections—COSTA RICA. *Wercklé 84* (B, lecto); 1 Mar 1970, *Gómez 3272* (CR); 8 Mar 1994, *Morales 2460* (INB, SEL); 22 Jun 1997, *Rojas 3656* (CR, INB); 30 Aug 2001, *Cascante 1545* (CR).
Life form. Epiphyte.

[2]***Guzmania scandens*** H. Luther & W. J. Kress, Brittonia 48: 93 (1996).
Distribution. Costa Rica and Panama.
Representative Collections—COSTA RICA. 15 Aug 1933, *Valerio 721* (CR); 10 Jun 1968, *Burger 5743* (CR); 28 Jul 1990, *Luther 2816* (CR; SEL, holo); 2 Jun 1994, *Lépiz 321* (CR, INB); 28 Oct 2007, *Santamaría 6684* (INB).
Life form. Epiphyte (rarely terrestrial or saxicolous).

Guzmania scherzeriana Mez, Monogr. Phan. 9: 949 (1896).
Distribution. Guatemala, Belize, Honduras, Nicaragua, Costa Rica, Panama, Colombia, and Ecuador.
Representative Collections—COSTA RICA. 12-15 Aug 1971, *Burger & Burger 8084* (NY, PMA); 20 Aug 1989, *Haber 9470* (CR, INB); 1 Aug 1994, *Alverson 3209* (CR, USJ); 28 May 2005, *Solano 2458* (INB); 2 Jul 2008, *Vargas 3399* (INB).
Life form. Epiphyte.

*[1]***Guzmania skotakii** H. Luther, Selbyana 12: 68 (1991).
Distribution. Costa Rica.
Representative Collections—COSTA RICA. 23 Jul 1990, *Luther 2810* (CR; SEL, holo); 28 Jul 1990, *Luther 2817* (SEL); 17 Jan 1991, *Grant 1510* (INB, SEL); 22 Jul 1994, *Morales 3073* (INB).
Life form. Epiphyte.

[1]***Guzmania spectabilis*** (Mez & Wercklé) Utley, Phytologia 40(1): 55 (1978).
Distribution. Costa Rica and Ecuador.
Representative Collections—COSTA RICA. *Wercklé s.n.* (B, holo); 6 Mar 1992, *Bittner 1438* (INB); 22 Jun 1998, *Valverde 1005* (CR); 23 Sep 1998, *Estrada 1745* (CR); 25 Feb 2001, *Morales 7618* (INB).
Life form. Epiphyte.

Guzmania sprucei (André) L. B. Sm, Contr. Gray Herb. 104: 75 (1934).
Distribution. Costa Rica, Panama, and Colombia.
Representative Collections—COSTA RICA. 19 Apr 1988, *Kress 2406* (SEL); 10 Oct 1989, *Vargas 225* (CR, INB); 8 Sep 1990, *Solomon 19255* (CR); 24 Sep 1994, *Gallardo 301* (CR, INB); 2 Nov 2007, *Rodríguez 11675* (INB).
Life form. Epiphyte.

[2]***Guzmania stenostachya*** L. B. Sm., Contr. Gray Herb. 117: 9 (1937).
Distribution. Costa Rica and Panama.
Representative Collections—COSTA RICA. 4 May 1975, *Utley 2371* (CR); 14 May 1983, *Liesner 15559* (CR, SEL); 12 Jul 1992, *Kress 3487* (INB, SEL); 28 May 2005, *Morales 13106* (INB); 8 Aug 2007, *Soto 1647* (INB, NY).
Life form. Epiphyte (occasionally terrestrial).

Guzmania subcorymbosa L. B. Sm., Contr. Gray Herb. 117: 10 (1937).
Distribution. Costa Rica, Panama, and Colombia.
Representative Collections—COSTA RICA. 15 Oct 1987, *Herrera 874* (CR, INB); 18 Feb 1990, *Grant 800* (INB, SEL); 14 Apr 1995, *Moraga 126* (CR, INB); 7 Dec 1996, *Moraga 843* (INB); 8 Jan 2000, *Morales 7234* (INB).
Life form. Epiphyte.

Guzmania zahnii (Hooker f.) Mez, Monogr. Phan. 9: 940 (1896).
Distribution. Nicaragua, Costa Rica, and Panama.
Representative Collections—COSTA RICA. 5 Aug 1980, *Meerow 2020* (CR, SEL); Aug 1991, *Luther s.n.* (SEL); 30 Aug 2001, *Cascante 1546* (CR); 7 Apr 2005, *Morales 12670* (INB); 19 Jun 2007, *de Melo & Moran 8032* (NY).
Life form. Epiphyte.

MEZOBROMELIA

Mezobromelia pleiosticha (Griseb.) Utley & H. Luther, Ann. Missouri Bot. Gard. 78: 270 (1991).

Distribution. Costa Rica, Panama, Colombia, Ecuador, Peru, Bolivia, and Venezuela.
Representative Collections—COSTA RICA. Feb 1969, *Lankester s.n.* (SEL); 22 Jul 1994, *Morales 3072* (CR, INB); 21 Jun 1995, *Herrera 8020* (CR); 21 Aug 2002, *Estrada 3328* (CR); 17 Jun 2005, *Morales 13196* (INB).
Life form. Epiphyte.

PEPINIA

*[1]***Pepinia beachiae*** (Utley & Burt-Utley) H. Luther, Phytologia 74: 449 (1993).

Syn.: *Pitcairnia beachiae* Utley & Burt-Utley, Ann. Missouri Bot. Gard. 78: 266 (1991).
Distribution. Costa Rica.
Representative Collections—COSTA RICA. 24 Jul 1974, *Beach 74-25* (SEL); 27 Jul 1990, *Luther s.n.* (SEL); 21 May 1992, *Luther s.n.* (SEL).
Life form. Epiphyte and terrestrial.

PITCAIRNIA

Pitcairnia arcuata (André) André, Rev. Hort. 60: 565 (1888).

Distribution. Costa Rica, Panama, and Colombia.
Representative Collections—COSTA RICA. 16 Apr 1983, *Liesner 14378* (CR); 22 Jun 1990, *Luther 2800* (MO, SEL); 5 Mar 1994, *Boyle 2877* (CR, INB, SEL); 17 Nov 1999, *Acosta 132* (CR, INB); 14 May 2006, *Cascante 1565* (CR).
Life form. Epiphyte and terrestrial.

Pitcairnia atrorubens (Beer) Baker, J. Bot. 19: 307 (1881).

Distribution. Guatemala, Honduras, Costa Rica, Panama, and Colombia.
Representative Collections—COSTA RICA. 9 Aug 1898, *Tonduz 12532* (CR); 19–20 Dec 1966, *Burger & Ramirez 4011* (CR, NY); 22 Feb 1990, *Grant 846* (CR, SEL); 6 Sep 1995, *Jiménez 1909* (CR, INB); 27 Jul 2007, *Bridgewater 4221* (INB).
Life form. Epiphyte and terrestrial.

Pitcairnia brittoniana Mez, Monogr. Phan. 9: 451 (1896).

Distribution. Belize, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, and Venezuela.
Representative Collections—COSTA RICA. *Wercklé 108* (B, holo);7 Jul 1964, *Jiménez 2014* (CR, NY); 14 May 1983, *Liesner 15466* (CR, SEL); 27 Jul 2004, *Solano 1205* (INB); 5 Mar 2008, *Morales 15976* (INB).
Life form. Epiphyte and terrestrial.

*[1]***Pitcairnia calcicola** J. R. Grant & J. F. Morales, Novon 6: 366 (1996).
Distribution. Costa Rica.
Representative Collections—COSTA RICA. 17 Jul 1992, *Grant 92-2008* (CR, SEL); 3 May 1995, *Espinoza 1276* (CR, INB); 27 Jan 2000, *Rodríguez 5640* (INB); 17 Nov 2004, *Morales 11589* (INB); 20 Nov 2005, *Hammel 23887* (INB).
Life form. Terrestrial and saxicolous.

*[1]***Pitcairnia funkiae** M. A. Spencer & L. B. Sm., J. Bromeliad Soc. 41: 214 (1991).
Distribution. Costa Rica.
Representative Collections—COSTA RICA. 16 Jul 1992, *Grant 1982* (CR, SEL); 27 Jul 1991, *Rivera 1478* (INB); 15 Jan 1992, *Grant 1887* (INB); 26 May 2003, *Holst 8553* (SEL); 30 Apr 2004, *Rodríguez 8775* (INB).
Life form. Epiphyte and terrestrial.

Pitcairnia guzmanioides L. B. Sm., Contr. U.S. Natl. Herb. 29: 306 (1949).
Distribution. Costa Rica, Colombia, Ecuador, and Peru.
Representative Collections—COSTA RICA. 22 May 1994, *Morales 3365* (INB); 22 Jun 1994, *Morales 3343* (INB); 21 Jul 1994, *Lépiz 509* (INB); 17 Jun 2005, *Morales 13207* (INB); 8 Jul 2005, *Solano 2592* (INB).
Life form. Terrestrial (rarely epiphyte).

*[1,2]***Pitcairnia halophila** L. B. Sm., Phytologia 10: 32 (1964).
Distribution. Costa Rica and Panama.
Representative Collections—COSTA RICA. 24 Jul 1985, *Soto 2348* (CR); 21 Jan 1987, *Grayum 7979* (CR, INB); 18 Dec 1989, *Merz 565* (CR); 21 Dec 1998, *Morales 6879* (CR, INB); 28 Nov 2004, *Hammel 23446* (INB).
Life form. Terrestrial and saxicolous.

Pitcairnia heterophylla (Lindl.) Beer, Fam. Bromel.: 68 (1856).
Distribution. Mexico, Guatemala, Belize, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Peru, and Venezuela.
Representative Collections—COSTA RICA. Dec 1899, *Tonduz 13645* (B); Dec 1936, *Skutch 3105* (NY); 4 Oct 1987, *Herrera 769* (CR, INB); 11 Feb 1995, *Haber 11900* (CR, INB); 19 Jun 2003, *Moran & Noguera 6446* (NY).
Life form. Epiphyte, terrestrial, and saxicolous.

Pitcairnia kalbreyeri Baker, J. Bot. 19: 273 (1881).
Distribution. Costa Rica, Panama, Colombia, Ecuador, and Peru.
Representative Collections—COSTA RICA. 14 Apr 1975, *Utley 2116* (CR); 11 Feb 1986, *Gómez-Laurito 11050* (CR); 14 Mar 1990, *Haber 9807* (CR, INB); 21 May 2005, *Morales 13014* (INB); 18 Feb 2007, *Santamaría 5703* (INB).
Life form. Terrestrial (rarely epiphyte).

[2]***Pitcairnia lymansmithiana*** H. Luther, J. Bromeliad Soc. 37: 212 (1987).
Distribution. Costa Rica and Panama.
Representative Collections—COSTA RICA. Jul 1992, *Hidalgo s.n.* (SEL); 2 Jun 1994, *Lépiz 325* (INB); 22 Jul 1994, *Lépiz 516* (INB).
Life form. Terrestrial.

Pitcairnia maidifolia (C. Morren) Decne., Fl. Serres Jard. Eur. 9: 151 (1854).
Distribution. Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Peru, and Venezuela.
Representative Collections—COSTA RICA. 14 Nov 1985, *Gómez-Laurito 10692* (CR); 5 Dec 1990, *Herrera 4708* (CR, INB); 22 Feb 1991, *Till 7072* (CR); 25 Nov 1994, *Jiménez 1669* (CR, INB, MO, NY); 9 Dec 2004, *Solano 1610* (INB).
Life form. Epiphyte, terrestrial, and saxicolous.

Pitcairnia megasepala Baker, J. Bot. 19: 229 (1881).
Distribution. Costa Rica, Panama, and Colombia.
Representative Collections—COSTA RICA. Mar 1892, *Tonduz 6868* (B, iso; NY); 1 Nov 1978, *Ocampo 2264* (CR); 5 Jan 1992, *Grant 1739* (CR, INB, SEL); 14 Nov 2000, *Acosta 2931* (INB); 20 Oct 2005, *Morales 13415* (INB).
Life form. Epiphyte and terrestrial (rarely saxicolous).

*[1]***Pitcairnia membranifolia*** Baker, Handb. Bromel.: 109 (1889).
Distribution. Costa Rica.
Representative Collections—COSTA RICA. 23 May 1981, *Gómez-Laurito 6721* (CR); 23 May 1981, *Gómez-Laurito 6722* (INB); May 1986, *Skotak s.n.* (SEL); 22 Aug 1998, *Morales 6470* (INB); 16 Oct 2000, *Morales 7384* (INB).
Life form. Terrestrial, saxicolous, very rarely epiphytic.

Pitcairnia quesnelioides L. B. Sm., Contr. U. S. Natl. Herb. 29: 313 (1949).
Distribution. Costa Rica and Colombia.
Representative Collections—COSTA RICA. 3 Aug 1990, *Herrera 4113* (INB); 24 Apr 2004, *Morales 10447* (INB); 16 Aug 2005, *Morales 13266* (INB).
Life form. Terrestrial.

Pitcairnia saxicola L. B. Sm., Contr. Gray Herb. 117: 29 (1937).
Distribution. Mexico, Honduras, Costa Rica, and Panama.
Representative Collections—COSTA RICA. 6 Jan 1994, *Grant 94-2301* (CR); 2 Jan 1997, *Morales 5980* (INB); 18 Oct 2001, *Lobo 422* (CR); 12 Dec 2001, *Bustamante 227* (INB).
Life form. Saxicolous (rarely epiphyte).

[2]***Pitcairnia valerioi*** Standl., J. Wash. Acad. Sci. 17: 246 (1927).
Distribution. Costa Rica and Panama.
Representative Collections—COSTA RICA. 29 Jun 1925, *Brenes 4261* (CR); 3 Feb 1986, *Grayum 6333* (CR); 19 Apr 1988, *Kress 88-2415* (SEL); 20 Apr 1988, *Hammel 16702* (CR, INB); 26 Oct 2007, *Solano 4733* (INB).
Life form. Terrestrial and epiphyte (rarelly saxicolous).

Pitcairnia wendlandii Baker, J. Bot. 19: 306 (1881).
Distribution. Mexico, Guatemala, Belize, Costa Rica, and Panama.
Representative Collections—COSTA RICA. 20-22 Dec 1969, *Burger 6985* (NY); 1 Jul 1974, *Ocampo 688* (CR); 31 May 1991, *Bittner 1043* (CR, INB); 5 Sep 1993, *Herrera 6509* (CR); 2 Mar 2000, *Acosta 513* (INB).
Life form. Terrestrial and epiphyte.

PUYA

*[1]***Puya dasylirioides*** Standl., J. Wash. Acad. Sci. 17: 159 (1927).
Distribution. Costa Rica.
Representative Collections—COSTA RICA. 30 Jul 1962, *Lee 760* (CR); 23 Jan 1965, *Lems 5186* (NY); 8 Jul 1986, *Atwood 27* (SEL); 8 Apr 1995, *Aguilar 4006* (CR, INB); 15 Jun 2005, *Morales 13139* (INB).
Life form. Terrestrial.

Puya floccosa (Linden) E. Morren ex Mez, Monogr. Phan. 9: 478 (1896).
Distribution. Costa Rica, Colombia, and Venezuela.
Representative Collections—COSTA RICA. 12 Mar 1993, *Fernández 612* (INB); 9 Sep 1995, *Jiménez 1998* (INB); 22 Nov 2005, *Solano 2877* (INB); 30 May 2006, *González 4184* (CR); 15 Jun 2006, *Santamaría 4569* (INB).
Life form. Terrestrial (rarely saxicolous).

RACINAEA

Racinaea adpressa (André) J. R. Grant, Novon 4(4): 362 (1994).
Distribution. Costa Rica, Panama, Ecuador, Peru, Bolivia, and Guianas.
Representative Collections—COSTA RICA. 3 Jan 1990, *Bello 1656* (INB); 10 Jan 1992, *Bello 4310* (CR, INB); 25 Mar 1993, *Fernández 830* (INB); 3 Apr 1994, *Morales 2626* (INB, SEL); 29 Jul 1996, *Gamboa 519* (INB).
Life form. Epiphyte.

Racinaea contorta (Mez) M. A. Spencer & L. B. Sm., Phytologia 74: 153 (1993).
Distribution. Nicaragua, Costa Rica, Panama, Colombia, and Ecuador.
Representative Collections—COSTA RICA. 26 May 1973, *Ocampo 405* (CR); 3 May 1984, *Gómez 21195* (INB, SEL); Jul 1985, *Cathcart s.n.* (SEL); 10 Apr 1991, *Smith 10853* (CR); 23 Aug 2000, *Moraga 1121* (INB).
Life form. Epiphyte.

Racinaea rothschuhiana (Mez) M. A. Spencer & L. B. Sm., Phytologia 74: 157 (1993).
Distribution. Mexico, Guatemala, Honduras, Nicaragua, and Costa Rica.
Representative Collections—COSTA RICA. Jul 1985, *Cathcart s.n.* (SEL); 6 Apr 1994, *Morales 2655* (INB); 20 May 1996, *Morales 5365* (INB); 16 Feb 2005, *Morales 11993* (INB); 11 May 2005, *Morales 12927* (INB).
Life form. Epiphyte.

Racinaea schumanniana (Wittm.) J. R. Grant, Novon 4: 363 (1994).
Distribution. Costa Rica, Panama, Colombia, Ecuador, Peru, Bolivia, and Venezuela.
Representative Collections—COSTA RICA. 11 Jan 1896, *Tonduz 12670* (CR); 22 Jul 1990, *Luther 2804* (CR, SEL); 2 Dec 1993, *Lépiz 640* (INB, MO, NY); 19 Jul 2000, *Rodríguez 5986* (CR, INB); 10 May 2005, *Morales 12878* (INB).
Life form. Epiphyte.

Racinaea spiculosa (Griseb.) M. A. Spencer & L. B. Sm., Phytologia 74: 157 (1993).
Distribution. Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Peru, Bolivia, Brazil, Suriname, Guianas, Venezuela, and Dominican Republic.
Representative Collections—COSTA RICA. 1 Jan 1901, *Wercklé 16175* (CR); Jan 1964, *Lankester s.n.* (SEL); 14 Jan 1992, *Grant 92-1867* (CR); 11 Mar 2001, *Cascante 1501* (CR); 20 Jun 2004, *Morales 10808* (INB).
Life form. Epiphyte.

RONNBERGIA

Ronnbergia hathewayi L. B. Sm., Phytologia 15: 196 (1967).
Distribution. Costa Rica, Panama, and Colombia.
Representative Collections—COSTA RICA. 13 Feb 1984, *Gómez. 21065* (CR); 19 Apr 1988, *Kress 88-2405* (INB, SEL); 12 Jul 1995, *Morales 4858* (INB); 6 Mar 2001, *Mora 1838* (CR, INB); 28 Oct 2007, *Monro 5861* (INB).
Life form. Epiphyte and terrestrial.

TILLANDSIA

*[1]***Tillandsia abdita** L. B. Sm., Phytologia 8: 10 (1961).
Distribution. Costa Rica.
Representative Collections—COSTA RICA. 31 Jul 1935, *Solís 314* (CR, NY); 25 Jun 1995, *Morales 4614* (INB); 16 Apr 1994, *Morales 2692* (INB); 22 Jul 2000, *Morales 7332* (INB).
Life form. Epiphyte.

Tillandsia anceps Lodd., Bot. Cab. 8: t. 771 (1823).
Distribution. Guatemala, Belize, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Brazil, Guianas, and Venezuela.
Representative Collections—COSTA RICA. 1 Apr 1913, *Tonduz s.n.* (CR); 29 Sep 1985, *Atwood 8516* (SEL); 14 Jul 1989, *Herrera 3289* (CR, INB); 30 Jul 2001, *Acosta 3129* (CR, INB); 28 May 2005, *Morales 13112* (INB).
Life form. Epiphyte.

Tillandsia balbisiana Schult. f., Syst. Veg. 7(2): 1212 (1830).
Distribution. Mexico, Guatemala, Belize, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Venezuela, Dominican Republic, Jamaica, Cuba, and United States of America.
Representative Collections—COSTA RICA. 1 Aug 1949, *Holm 781* (CR); 8 Jul 1987, *Zamora 1348* (CR, INB); 6 Jan 1992, *Grant 1756* (CR, INB, SEL); 23 Aug 1995, *Sanders 17699* (CR, SEL); 26 Sep 2000, *Acosta 2743* (CR, INB).
Life form. Epiphyte.

Tillandsia biflora Ruiz & Pav., Fl. Peruv. 3: 41 (1802).
Distribution. Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Peru, Bolivia, and Venezuela.
Representative Collections—COSTA RICA. 18 Aug 1995, *Picado 286* (CR, INB); 18 Sep 1996, *Morales 5804* (CR, INB); 10 Jul 1998, *Boyle 5433* (CR); 20 Sep 2003, *Alfaro 5207* (INB); 25 Jun 2006, *Morales 13988* (INB).
Life form. Epiphyte.

Tillandsia brachycaulos Schltdl., Linnaea 18: 422 (1845).
Distribution. Mexico, Guatemala, Belize, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, and Venezuela.
Representative Collections—COSTA RICA. 7 Jan 1890, *Pittier 2927* (CR); 30 May 1932, *Brenes 15614* (NY); 1 Jul 1964, *Gilmartin 931* (SEL); 19 Aug 2000, *Acosta 2504* (CR, INB); 15 Dec 2004, *Hammel 23488* (INB).
Life form. Epiphyte (rarely saxicolous).

Tillandsia bulbosa Hook., Exot. Fl.: t. 173 (1826).

Distribution. Mexico, Guatemala, Belize, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Guianas, Venezuela, Dominican Republic, and Jamaica.

Representative Collections—COSTA RICA. 22 Jun 1966, *Jiménez 4031* (CR); 9 Apr 1983, *Liesner 14151* (CR); 27 Mar 1995, *Herrera 7593* (CR); 29 May 2003, *Clark 301* (SEL); 7 Apr 2005, *Solano 2094* (INB).

Life form. Epiphyte.

Tillandsia butzii Mez, Pflanzenr., IV, 32: 636 (1935).

Distribution. Mexico, Guatemala, Belize, El Salvador, Honduras, Nicaragua, Costa Rica, and Panama.

Representative Collections—COSTA RICA. 5 Jan 1890, *Pittier 2615* (CR); 12 Dec 1976, *Lent 3957* (NY); 16 Jan 1991, *Grant 1467* (CR, SEL); 27 Jan 1998, *Rodríguez 2938* (INB, MO, NY); 6 Aug 2008, *Cascante 2006* (CR).

Life form. Epiphyte.

Tillandsia caput-medusae E. Morren, Ann. Bot. Hort. 30: 90 (1880).

Distribution. Mexico, Guatemala, Belize, El Salvador, Honduras, Nicaragua, Costa Rica, and Panama.

Representative Collections—COSTA RICA. 21 Dec 1974, *Taylor 17383* (NY); 24 Apr 1988, *Kress 2446* (SEL); 7 Jan 1990, *Merz 570* (CR); 26 Jul 1994, *Estrada 103* (CR, INB); 23 Apr 2005, *Morales 12807* (INB).

Life form. Epiphyte.

*[1]***Tillandsia cauliflora*** Mez & Wercklé, Bull. Herb. Boissier, II, 5: 100 (1905).

Distribution. Costa Rica.

Representative Collections—COSTA RICA. *Wercklé 68* (B, holo; NY, photo); Feb 1984, *Waggoner s.n.* (SEL); Jun 1990, *Tristram s.n.* (SEL); 20 Jul 1995, *Morales 4597* (CR, INB, MO).

Life form. Epiphyte.

Tillandsia complanata Benth., Bot. Voy. Sulphur: 173 (1846).

Distribution. Costa Rica, Panama, Colombia, Ecuador, Peru, Bolivia, Venezuela, and Jamaica.

Representative Collections—COSTA RICA. 10 Jul 1962, *Lee 671* (CR); 19-20 Dec 1966, *Burger 4023* (CR, NY); 27 Feb 1990, *Grant 898* (SEL); 6 Apr 1994, *Morales 2639* (CR, INB); 19 Jul 2007, *Cascante 1788* (CR).

Life form. Epiphyte.

*[1,2]***Tillandsia dexteri*** H. Luther, Selbyana 11: 54 (1989).

Distribution. Costa Rica and Panama.

Representative Collections—COSTA RICA. 24 Feb 1988, *Dexter s.n.* (SEL, holo); 28 Jul 1988, *Skotak s.n.* (SEL); 30 Sep 1995, *Tust s.n.* (SEL).

Life form. Epiphyte.

Tillandsia elongata Kunth, Nov. Gen. Sp. 1: 293 (1816).
Distribution. Nicaragua, Costa Rica, Panama, and Colombia.
Representative Collections—COSTA RICA. 22 Aug 2005, Morales 13326 (INB).
Life form. Epiphyte.

Tillandsia excelsa Griseb., Fl. Brit. W. I.: 597 (1864).
Distribution. Mexico, Guatemala, Belize, Honduras, Nicaragua, Costa Rica, Panama, and Jamaica.
Representative Collections—COSTA RICA. Nov 1897, *Tonduz 11375* (B, lecto); 9 Aug 1967, *Taylor 4195* (NY); 3 Sep 1989, *Hammel 17683* (CR, INB); 22 Jul 1990, *Luther 2807* (SEL); 22 Feb 2008, *Rodríguez 11835* (INB).
Life form. Epiphyte.

Tillandsia fasciculata Sw., Prod. Veg. Ind. Occ.: 56 (1788).
Distribution. Mexico, Guatemala, Belize, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Brazil, Guianas, Venezuela, Virgin Islands, Puerto Rico, Dominican Republic, Haiti, Jamaica, and United States of America.
Representative Collections—COSTA RICA. 5 Jan 1890, *Pittier 2616* (CR); 1 Aug 1949, *Holm 772* (CR); 18 Feb 1991, *Till 7026* (CR); 11 Oct 1995, *Jiménez 2044* (CR, INB); 5 Feb 2008, *Cascante 1840* (CR).
Life form. Epiphyte.

Tillandsia festucoides Brongn. ex Mez, Monogr. Phan. 9: 678 (1896).
Distribution. Mexico, Guatemala, Belize, Honduras, Nicaragua, Costa Rica, Panama, Dominican Republic, and Jamaica.
Representative Collections—COSTA RICA. 24-26 Apr 1906, *Maxon 166* (NY); 20-22 Dec 1969, *Burger 6875* (CR, PMA); 14 Apr 1994, *Gallardo 138* (CR, INB, NY); 18 Jan 2002, *Ferrufino & González 180* (USJ); 23 Apr 2006, *Morales 13858* (INB).
Life form. Epiphyte.

Tillandsia filifolia Schltdl. & Cham., Linnaea 6: 53 (1831).
Distribution. Mexico, Belize, Honduras, Nicaragua, and Costa Rica.
Representative Collections—COSTA RICA. 24 Jul 1972, *Ocampo 716* (CR); 6 Jul 1983, *Gómez-Laurito 9556* (CR); 5 May 1983, *Liesner 15289* (INB); 14 Apr 1994, *Gallardo 128* (INB); 23 Apr 2006, *Morales 13857* (INB).
Life form. Epiphyte.

Tillandsia flexuosa Sw., Prod. Veg. Ind. Occ.: 56 (1788).
Distribution. Costa Rica, Panama, Colombia, Bolivia, Brazil, Venezuela, Trinidad and Tobago, Dominican Republic, Haiti, Cuba, and United States of America.
Representative Collections—COSTA RICA. 27 Jul 1990, *Luther s.n.* (SEL); 20 Oct 1993, *Quesada 769* (INB); 22 Oct 1993, *Morales 1932.1* (INB); 14 Sep 1999, *Takizawa 99-f* (SEL).
Life form. Epiphyte.

Tillandsia guatemalensis L. B. Sm., Contr. U. S. Natl. Herb. 29: 281 (1949).
Distribution. Mexico, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, and Panama.
Representative Collections—COSTA RICA. 16 May 2000, *Alfaro 3159* (INB).
Life form. Epiphyte.

Tillandsia ionantha Planch., Fl. Serres Jard. Eur. 10: 101 (1855).
Distribution. Mexico, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, and Peru.
Representative Collections—COSTA RICA. 22 Nov 1973, *Solomon s.n.* (CR); 17 Dec 1986, *Soto 3300* (CR); 18 Mar 1992, *Skotak s.n.* (SEL); 13 Sep 1995, *Sanders 17882* (SEL); 25 Apr 2001, *Acosta 3052* (INB).
Life form. Epiphyte.

Tillandsia juncea Poir., Encycl., Suppl. 5: 309 (1817).
Distribution. Mexico, Guatemala, Belize, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Peru, Bolivia, Venezuela, Dominican Republic, and Haiti.
Representative Collections—COSTA RICA. 5 Jan 1890, *Pittier 2617* (CR); 18 Feb 1991, *Till 7030* (CR); 10 Jan 1992, *Grant 92-1828* (CR, INB, NY, SEL); 10 May 2003, *Alfaro 4374* (CR, INB); 6 Aug 2008, *Cascante 2008* (CR).
Life form. Epiphyte.

Tillandsia lampropoda L. B. Sm., Publ. Field Mus. Nat. Hist., Bot. Ser. 17: 320 (1938).
Distribution. Mexico, Guatemala, El Salvador, Honduras, Nicaragua, and Costa Rica.
Representative Collections—COSTA RICA. 22 Jan 1994, *Morales 2298* (INB); 23 Dec 1997, *Morales 6341* (INB); 11 May 2005, *Morales 12926* (INB).
Life form. Epiphyte.

Tillandsia leiboldiana Schltdl., Linnaea 18: 414 (1844).
Distribution. Mexico, Belize, Honduras, Nicaragua, Costa Rica, and Panama.
Representative Collections—COSTA RICA. 1 Jan 1901, *Wercklé 16177* (B, CR); 25 Aug 1975, *Utley & Utley 2981* (NY); 19 May 1989, *Kress 89-2813* (CR, INB, SEL); 18 Nov 1992, *Ingram 1742* (SEL); 20 Feb 2008, *Santamaría 7016* (INB).
Life form. Epiphyte.

Tillandsia longifolia Baker, Handb. Bromel.: 185 (1889).
Distribution. Costa Rica, Panama, Peru, Bolivia, and Venezuela.
Representative Collections—COSTA RICA. 5 Apr 1974, *Utley 791* (CR); 19 Aug 1983, *Herrera 21625* (CR); 23 Jan 1996, *Morales 5106* (CR, INB); 13 Nov 2000, *Acosta 2912* (INB); 24 Feb 2008, *Santamaría 7140* (INB).
Life form. Epiphyte.

Tillandsia makoyana Baker, Handb. Bromel.: 189 (1889).

Distribution. Mexico, Guatemala, El Salvador, Honduras, Nicaragua, and Costa Rica.

Representative Collections—COSTA RICA. 15 Jul 1992, *Grant 1972* (INB, MO, SEL); 9 Nov 1996, *Oconnor 70* (INB); 16 Mar 2002, *Arauz 3144* (CR); 2 Sep 2003, *Morales 9737* (INB); 16 Mar 2005, *Rodríguez 9511* (INB).

Life form. Epiphyte.

Tillandsia monadelpha (E. Morren) Baker, J. Bot. 25: 281 (1887).

Distribution. Guatemala, Belize, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Suriname, Guianas, and Venezuela.

Representative Collections—COSTA RICA. 16 Apr 1983, *Liesner 14312* (CR); 21 Apr 1988, *Kress 2425* (SEL); 30 May 1995, *Grant 95-2350* (CR, INB, SEL); 22 Oct 1998, *Estrada 1838* (CR); 28 Feb 2005, *Morales 12072* (INB).

Life form. Epiphyte.

Tillandsia multicaulis Steud., Nomencl. Bot., ed. 2, 2: 688 (1841).

Distribution. Mexico, Guatemala, Belize, El Salvador, Honduras, Nicaragua, Costa Rica, and Panama.

Representative Collections—COSTA RICA. 19 Apr 1906, *Maxon 66* (NY); 21 Apr 1983, *Liesner 14528* (CR); 27 Feb 1990, *Grant 897* (SEL); 25 May 1997, *Rodríguez 2220* (CR, INB); 5 Mar 2008, *Cascante 1865* (CR).

Life form. Epiphyte.

[2]***Tillandsia oerstediana*** L. B. Sm., Phytologia 13: 141 (1966).

Distribution. Costa Rica and Panama.

Representative Collections—COSTA RICA. 1 Dec 1945, *Echeverría 221* (CR); 20 Aug 1975, *Utley & Utley 2990* (CR, SCZ); 22 Jul 1990, *Luther 2818* (SEL); 8 Jan 1992, *Grant & Rundell 92-1793* (CR, INB, NY); 30 Nov 2004, *Morales 11691* (INB).

Life form. Epiphyte.

Tillandsia paucifolia Baker, Gard. Chron., II, 10: 748 (1878).

Distribution. Mexico, El Salvador, Honduras, Nicaragua, Costa Rica, Venezuela, and United States of America.

Representative Collections—COSTA RICA. 28 Jun 1977, *Liesner 2660* (CR); 15 Jul 1992, *Grant 1975* (INB, SEL); 15 Feb 1994, *Quesada 93* (CR, INB); 15 Mar 2005, *Morales 12325* (CR, INB); 20 Feb 2007, *Vargas 2209* (INB).

Life form. Epiphyte.

Tillandsia pruinosa Sw., Fl. Ind. Occid. 1: 594 (1797).

Distribution. Mexico, Guatemala, Belize, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Venezuela, Dominican Republic, Cuba, and United States of America.

Representative Collections—COSTA RICA. 7 Feb 1926, *Standley 47294* (INB); 1 Jul 1974, *Ocampo 680* (CR); 1 Oct 1985, *Atwood 60* (SEL); 9 Mar 1994, *Morales 2482* (CR, INB); 23 Apr 2006, *Morales 13859* (INB).
Life form. Epiphyte.

Tillandsia punctulata Schltdl. & Cham., Linnaea 6: 53 (1831).
Distribution. Mexico, Guatemala, Belize, El Salvador, Honduras, Nicaragua, Costa Rica, and Panama.
Representative Collections—COSTA RICA. 19 Apr 1906, *Maxon 63* (NY); 19-22 Jan 1970, *Burger & Liesner 7505* (CR, NY); 29 Sep 1989, *Herrera 3599* (CR, INB); 30 Nov 1999, *Estrada 2262* (CR); 24 Feb 2008, *Santamaría 7207* (INB).
Life form. Epiphyte.

Tillandsia rhomboidea André, Énum. Bromél.: 6 (1888).
Syn.: *T. acostae* Mez & Tonduz, Repert. Spec. Nov. Regni. Veg. 14: 252 (1916).
Distribution. Honduras, Costa Rica, Colombia, Ecuador, Peru, and Bolivia.
Representative Collections—COSTA RICA. 13 May 1913, *Tonduz 17891* (B, holo; CR); 3 May 1988, *Hammel 16821* (INB); Oct 1991, *Hidalgo 2* (SEL); 16 Jul 1992, *Grant 92-1983* (CR); 28 Jun 2000, *Acosta 1937* (CR, INB); 21 Aug 2005, *Morales 13321* (INB).
Life form. Epiphyte.

Tillandsia schiedeana Steud., Nomencl. Bot., ed. 2, 2: 688 (1841).
Distribution. Mexico, Guatemala, Belize, El Salvador, Honduras, Nicaragua, Costa Rica, Colombia, Venezuela, Dominican Republic, Haiti, Jamaica, and Cuba.
Representative Collections—COSTA RICA. 1 May 1970, *Charles 1139* (NY); 12 May 1989, *Kress 2706* (SEL); 11 Oct 1995, *Jiménez 2043* (CR, INB); 15 Dec 2004, *Hammel 23489* (INB); 23 Apr 2006, *Morales 13854* (INB).
Life form. Epiphyte.

Tillandsia singularis Mez & Wercklé, Bull. Herb. Boissier, II, 5: 103 (1905).
Distribution. Costa Rica, Panama, and Ecuador.
Representative Collections—COSTA RICA. 1908, *Wercklé 17424* (B); 11 May 1938, *Smith 572* (NY); 19 Feb 1989, *Russell 819* (CR); 18 Jan 1994, *Lépiz 127* (CR, INB); 23 Apr 2006, *Morales 13860* (INB).
Life form. Epiphyte.

Tillandsia streptophylla Scheidw. ex C. Morren, Hort. Belge 3: 252 (1836).
Distribution. Mexico, Guatemala, Belize, Honduras, Nicaragua, and Costa Rica.
Representative Collections—COSTA RICA. 25 Mar 2005, *Morales 12453* (INB); 25 Mar 2005, *Morales 12464* (INB).
Life form. Epiphyte.

Tillandsia subulifera Mez, Repert. Spec. Nov. Regni Veg. 16: 74 (1919).
Distribution. Nicaragua, Costa Rica, Panama, Colombia, and Venezuela.
Representative Collections—COSTA RICA. 10 Apr 1988, *Herrera 1753* (INB); 11 Dec 1990, *Herrera 4755* (INB); 7 Jan 1992, *Grant & Rundell 92-1760* (CR; INB; NY; SEL; US, n.v.); 19 Oct 1993, *Morales 1897* (INB); 19 Dec 1998, *Morales 8490* (CR, INB).
Life form. Epiphyte.

Tillandsia tricolor Schltdl. & Cham., Linnaea 6: 54 (1831).
Distribution. Mexico, Guatemala, Belize, Honduras, Nicaragua, Costa Rica, and Panama.
Representative Collections—COSTA RICA. 15 Nov 1987, *Grayum 8453* (CR, INB); 8 Jan 1992, *Grant 92-1794* (CR; INB; NY; US, n.v.); 15 Aug 1993, *Palaci 1208* (CR, INB); 17 Jun 2002, *Boyle 6344* (CR); 5 Mar 2008, *Cascante 1858* (CR).
Life form. Epiphyte.

Tillandsia usneoides (L.) L., Sp. Pl. ed. 2: 411 (1762).
Distribution. Mexico, Guatemala, Belize, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Peru, Bolivia, Chile, Argentina, Uruguay, Paraguay, Brazil, Venezuela, Trinidad and Tobago, Puerto Rico, Dominican Republic, Jamaica, Cuba, and United States of America.
Representative Collections—COSTA RICA. 11 Jan 1893, *Tonduz 8246* (CR); 9 Sep 1978, *Burger 10982* (CR, PMA); 17 Jan 1991, *Grant 1479* (CR, INB, SEL); 18 Jan 1997, *Rodríguez 1922* (CR, INB); 27 Feb 2007, *Monro 5668* (INB).
Life form. Epiphyte.

Tillandsia utriculata L., Sp. Pl.: 286 (1753).
Distribution. Mexico, Guatemala, Belize, Honduras, Nicaragua, Costa Rica, Panama, Trinidad and Tobago, Virgin Islands, Puerto Rico, Dominican Republic, Haiti, Jamaica, and United States of America.
Representative Collections—COSTA RICA. 16 Jul 1949, *Holm & Iltis 436* (NY); 12 Jul 1992, *Grant & Rundell 92-1937* (CR; INB; MO; NY; SEL; US, n.v.); 6 Apr 1994, *Morales 2658* (CR, INB, SEL); 14 Oct 1997, *Jiménez 2337* (CR, INB); 23 Apr 2006, *Morales 13861* (INB).
Life form. Epiphyte.

Tillandsia variabilis Schltdl., Linnaea 18: 418 (1844).
Distribution. Mexico, Guatemala, Belize, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Bolivia, Venezuela, Puerto Rico, Cuba, and United States of America.
Representative Collections—COSTA RICA. 13 Jul 1962, *Lee 706* (CR); 31 May 1984, *Hernández 8* (CR); 18 Feb 1991, *Till 7027* (CR); 3 Jun 1999, *Vargas 211* (INB); 23 Apr 2006, *Morales 13853* (INB).
Life form. Epiphyte.

Tillandsia venusta Mez & Wercklé, Bull. Herb. Boissier, II, 5: 108 (1905).
Distribution. Costa Rica, Panama, and Ecuador.
Representative Collections—COSTA RICA. 30 Sep 1985, *Atwood 52* (SEL); 15 Jan 1987, *Haber 6585* (INB); 11 Mar 1991, *Richardson 82* (SEL); 4 Jun 1995, *Wilbur 64365* (CR); 16 Feb 2005, *Morales 11989* (INB).
Life form. Epiphyte.

VRIESEA

*[1]***Vriesea castaneobulbosa*** (Mez & Wercklé) J. R. Grant, J. Bromeliad Soc. 42: 14 (1992).
Distribution. Costa Rica.
Representative Collections—COSTA RICA. 23 Jul 1962, *Lee 742* (CR); Jan 1990, *Merz 659* (CR); 12 Jan 1991, *Grant 91-1363* (SEL); 8 Aug 1998, *Morales 6939* (INB); 11 Feb 2005, *Morales 11983* (INB).
Life form. Epiphyte.

Vriesea chontalensis (Baker) L. B. Sm., Contr. U.S. Natl. Herb. 29: 518 (1951).
Distribution. Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Peru, and Bolivia.
Representative Collections—COSTA RICA. *Wercklé s.n.* (B, holo; US, iso, n.v.); 1 Jan 1976, *Ocampo 1158* (CR); 6 Apr 1994, *Morales 2650* (CR, INB); 26 Apr 2001, *Mora 2011* (CR, INB); 20 Feb 2008, *Rodríguez 11767* (INB).
Life form. Epiphyte.

Vriesea heliconioides Lindl., Ann. Bot. Syst. 3: 623 (1852).
Distribution. Mexico, Guatemala, Belize, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Peru, Bolivia, Brazil, Suriname, and Venezuela.
Representative Collections—COSTA RICA. 6 Jul 1977, *Liesner 2993* (CR); 4 Aug 1994, *Alverson 3222* (CR, USJ); 3 Dec 1999, *Estrada 2285* (CR); 28 May 2003, *Clark 266* (SEL); 27 Jan 2007, *Morales 15366* (INB).
Life form. Epiphyte.

Vriesea incurva (Griseb.) Read, Phytologia 16: 458 (1968).
Distribution. Costa Rica, Panama, Colombia, Ecuador, Peru, Bolivia, Brazil, Venezuela, and Dominican Republic.
Representative Collections—COSTA RICA. 1901, *Wercklé 16189* (B, holo); 6 Feb 1965, *William et al. 28940* (SCZ); Apr 1982, *Gómez-Laurito 8146* (CR); 30 May 2006, *Rodríguez 10280* (INB); 7 Mar 2008, *Morales 16118* (INB).
Life form. Epiphyte.

*[1]***Vriesea lutheriana*** J. R. Grant, J. Bromeliad Soc. 42: 114 (1992).
Distribution. Costa Rica.

Representative Collections—COSTA RICA. 16 Jan 1991, *Grant 1475* (CR; SEL, iso); 12 Jun 2002, *Luther s.n.* (SEL).
Life form. Epiphyte.

Vriesea monstrum (Mez) L. B. Sm., Phytologia 16: 81 (1968).
Distribution. Nicaragua, Costa Rica, Panama, Colombia, and Ecuador.
Representative Collections—COSTA RICA. 18 Jun 1977, *Dwyer 1495* (CR); 13 Jun 1987, *Hammel 16043* (CR); 24 Sep 1994, *Gallardo 288* (INB); 13 Oct 1995, *Cascante 824* (CR); 7 Jun 2003, *Morales 9344* (INB).
Life form. Epiphyte.

WERAUHIA

[2]***Werauhia acuminata*** (Mez & Wercklé) J. R. Grant, Trop. Subtrop. Pflanzenwelt 91: 30 (1995).
Distribution. Costa Rica and Panama.
Representative Collections—COSTA RICA. *Wercklé 117* (B, holo); 16 Mar 1992, *Herrera 5363* (INB); 12 May 2005, *Morales 12980* (INB); 1 Mar 2007, *Solano 4104* (INB); 7 Oct 2008, *Cascante 2027* (CR).
Life form. Epiphyte and terrestrial.

*[1]***Werauhia ampla*** (L. B. Sm.) J. R. Grant, Trop. Subtrop. Pflanzenwelt 91: 30 (1995).
Distribution. Costa Rica.
Representative Collections—COSTA RICA. 2 Jan 1991, *Moraga 273* (INB); 6 Aug 1994, *Morales 3081* (INB, SEL); 1 Mar 1997, *Gamboa 1146* (INB); 26 Apr 2008, *Hammel 24735* (INB); 8 Jul 2008, *Cascante 1977* (CR).
Life form. Epiphyte and terrestrial.

****Werauhia anitana*** J. F. Morales, Novon 15: 332 (2005).
Distribution. Costa Rica.
Representative Collections—COSTA RICA. 2 Nov 2002, *Morales & Abarca 9074* (INB, holo, n.v.); 12 Dec 2002, *Morales 8919* (INB, para, n.v.); 10 Jun. 2003, *Morales & ldarraga 9432* (INB, para, n.v.).
Life form. Epiphyte.

*[1]***Werauhia apiculata*** (L. B. Sm.) J. R. Grant, Trop. Subtrop. Pflanzenwelt 91: 30 (1995).
Distribution. Costa Rica.
Representative Collections—COSTA RICA. 8 Apr 1992, *Marin 453* (INB); 17 Jul 1994, *Jiménez 1592* (CR, INB); 26 Aug 2000, *Luther s.n.* (SEL); 23 Apr 2006, *Morales 13856* (INB).
Life form. Epiphyte.

[2] ***Werauhia attenuata*** (L. B. Sm. & Pittendr.) J. R. Grant, Trop. Subtrop. Pflanzenwelt 91: 39 (1995).

Distribution. Costa Rica and Panama.

Representative Collections—COSTA RICA. 30 Apr 1980, *Meerow 1103* (SEL); 19 Apr 1988, *Kress 2408* (SEL); 6 Nov 1993, *Herrera 6642* (INB); 12 Feb 1994, *Herrera 6849* (INB).

Life form. Epiphyte.

*[1] ***Werauhia balanophora*** (Mez) J. R. Grant, Trop. Subtrop. Pflanzenwelt 91: 39 (1995).

Distribution. Costa Rica.

Representative Collections—COSTA RICA. 1901, *Wercklé 16207* (B, holo); 12 Jul 1996, *Morales 5466* (INB, NY); 6 Mar 1997, *Navarro 687* (INB); 5 Aug 2004, *Azofeifa 111* (INB); 18 Feb 2007, *Santamaría 5710* (INB).

Life form. Epiphyte and terrestrial.

*[1] ***Werauhia barii*** (J. F. Morales) J. F. Morales, Polibotanica 15: 110 (2003).

Distribution. Costa Rica.

Representative Collections—COSTA RICA. 5 Apr 1993, *Fernández 1052* (INB); 18 Apr 1994, *Morales 3329* (INB); 12 Jun 1996, *Morales 5387* (INB); 28 May 2005, *Morales 13105* (INB); 6 Sep 2006, *Vargas 1629* (INB).

Life form. Epiphyte.

[1,2] ***Werauhia bicolor*** (L. B. Sm.) J. R. Grant, Subtrop. Pflanzenwelt 91: 30 (1995).

Distribution. Costa Rica and Panama.

Representative Collections—COSTA RICA. 20 Mar 1994, *Morales 2519* (INB); 26 Jan 1996, *Morales 5103* (INB); 30 jan 2001, *Ramírez 744* (INB); 21 May 2005, *Morales 13009* (INB); 19 May 2006, *Cascante 1575* (CR).

Life form. Epiphyte.

[1,2] ***Werauhia bracteosa*** (Mez & Wercklé) J. R. Grant, Trop. Subtrop. Pflanzenwelt 91: 40 (1995).

Distribution. Costa Rica and Panama.

Representative Collections—COSTA RICA. 31 Mar 1995, *Morales 4898* (INB); 18 Jul 1997, *Morales 6197* (INB); 5 May 2001, *Cardelús 1383* (CR); 15 Jun 2005, *Morales 13126* (INB); 7 Sep 2005, *Acosta 3623* (INB).

Life form. Epiphyte.

[1,2] ***Werauhia brunei*** (Mez & Wercklé) J. R. Grant, Trop. Subtrop. Pflanzenwelt 91: 31 (1995).

Distribution. Costa Rica and Panama.

Representative Collections—COSTA RICA. 6 Apr 1993, *Herrera 6218* (INB); 18 Apr 1994, *Morales 3325* (INB); 20 Nov 1997, *Gamboa 1981* (INB); 18 Jun 2004, *Morales 10724* (INB); 22 Jun 2004, *Morales 10830* (INB).

Life form. Epiphyte (rarely terrestrial).

[2]***Werauhia burgeri*** (L. B. Sm.) J. R. Grant, Phytologia 78: 121 (1995).
Distribution. Costa Rica and Panama.
Representative Collections—COSTA RICA. 23 Jan 1983, *Davidse 23227* (INB); Apr 1989, *Ferenczi 1* (SEL); 31 Mar 1996, *Alfaro 526* (INB); 3 Feb 1999, *Rodríguez 4386* (INB); 5 Mar 2008, *Morales 15982* (INB).
Life form. Epiphyte (rarely terrestrial).

[1,2]***Werauhia camptoclada*** (Mez & Wercklé) J. F. Morales, Monogr. Syst. Bot. Missouri Bot. Gard. 92: 360 (2003).
Distribution. Costa Rica and Panama.
Representative Collections—COSTA RICA. Oct 1908, *Wercklé 17292* (B, holo); 14 Oct 1995, *Morales 4902* (INB); 19 Oct 2003, *Morales 10034* (INB); 28 May 2006, *Cascante 1584* (CR); 11 Nov 2008, *Cascante 2050* (CR).
Life form. Epiphyte.

[2]***Werauhia capitata*** (Mez & Wercklé) J. R. Grant, Trop. Subtrop. Pflanzenwelt 91: 40 (1995).
Distribution. Costa Rica and Panama.
Representative Collections—COSTA RICA. *Wercklé 86* (B, holo); 6 Apr 1994, *Morales 2645* (INB); 20 May 1996, *Morales 5369* (INB); 7 Nov 1996, *Oconnor 30* (INB); 7 Nov 1996, *Oconnor 34* (INB).
Life form. Epiphyte.

[2]***Werauhia comata*** (Mez & Wercklé) J. R. Grant, Trop. Subtrop. Pflanzenwelt 91: 40 (1995).
Distribution. Costa Rica and Panama.
Representative Collections—COSTA RICA. *Wercklé s.n.* (B, holo); 10 Feb 1992, *Ingram 1305* (INB, SEL); 19 Jul 1994, *Morales 3027* (CR, INB); 22 Jul 1994, *Quesada 128* (CR, INB); 20 Sep 2003, *Kriebel 3902* (INB).
Life form. Epiphyte, terrestrial, and saxicolous.

*[1]***Werauhia dodsonii*** (L. B. Sm.) J. R. Grant, Phytologia 79(3): 255 (1995).
Distribution. Costa Rica.
Representative Collections—COSTA RICA. 26 Mar 1995, *Morales 3769* (INB); 5 Jan 1996, *Morales 5048* (INB); 11 Jul 2004, *Morales 10910* (INB); 28 May 2005, *Morales 13110* (INB); 6 Mar 2008, *Morales 16047* (INB).
Life form. Epiphyte.

Werauhia gladioliflora (H. Wendl.) J. R. Grant, Trop. Subtrop. Pflanzenwelt 91: 31 (1995).
Distribution. Mexico, Belize, Nicaragua, Costa Rica, Panama, Colombia, and Ecuador.
Representative Collections—COSTA RICA. 27 May 1968, *Burger 5391* (CR, NY); 25 Feb 1991, *Till 7110* (CR); 8 Jan 1992, *Grant 1774* (CR, INB, SEL); 27 Jun 2001, *Chaves 1214* (INB); 6 Mar 2008, *Morales 16057* (INB).
Life form. Epiphyte and terrestrial (rarely saxicolous).

Werauhia graminifolia (Mez & Wercklé) J. R. Grant, Trop. Subtrop. Pflanzenwelt 91: 32 (1995).

Distribution. Nicaragua, Costa Rica, Panama, and Ecuador.

Representative Collections—COSTA RICA. 29 Dec 1974, *Taylor 17733* (SCZ); 14 Jan 1984, *Gómez 20792* (CR); 18 Feb 1990, *Grant 793* (INB); 1 Apr 1997, *Rodríguez 2079* (INB); 10 Jan 2000, *Alfaro 2659* (INB).

Life form. Epiphyte (rarely terrestrial).

Werauhia greenbergii (Utley) J. R. Grant, Trop. Subtrop. Pflanzenwelt 91: 42 (1995).

Distribution. Costa Rica, Panama, and Ecuador.

Representative Collections—COSTA RICA. 27 Jan 1976, *Utley 3741* (CR); 10 Nov 1993, *Bello 5405* (CR, INB); 17 Apr 1994, *Morales 2699* (CR, INB); 18 Feb 1995, *Morales 4884* (INB); 20 Mar 2005, *Santamaría 1152* (INB).

Life form. Epiphyte, terrestrial, and saxicolous.

*[1]***Werauhia haberi*** (J. F. Morales) J. F. Morales, Polibotanica 15: 110 (2003).

Distribution. Costa Rica.

Representative Collections—COSTA RICA. 23 Dec 1988, *Haber 8947* (INB).

Life form. Epiphyte.

*[1]***Werauhia hainesiorum*** (L. B. Sm.) J. R. Grant, Trop. Subtrop. Pflanzenwelt 91: 42 (1995).

Distribution. Costa Rica.

Representative Collections—COSTA RICA. 20 Feb 1994, *Morales 3337* (INB); 18 Apr 1994, *Morales 3330* (INB); 22 May 1994, *Morales 3363* (INB).

Life form. Epiphyte.

Werauhia hygrometrica (André) J. R. Grant, Trop. Subtrop. Pflanzenwelt 91: 42 (1995).

Distribution. Guatemala, Honduras, Nicaragua, Costa Rica, Panama, Colombia, and Ecuador.

Representative Collections—COSTA RICA. Apr 1975, *Velick 1* (SEL); 27 Sep 1988, *Ingram 252* (SEL, CR, NY); 22 Jul 1994, *Lépiz 510* (CR, INB); 6 Apr 2005, *Soto 695* (INB, NY); 22 Feb 2007, *Rodríguez 10692* (INB).

Life form. Epiphyte, terrestrial, and saxicolous.

*[2]***Werauhia insignis*** (Mez) W. Till, Barfuss & M. R. Samuel, J. Bromeliad Soc. 54: 13 (2004).

Syn.: *Tillandsia insignis* (Mez) L. B. Sm. & Pittendr., J. Wash. Acad. Sci. 43: 402 (1953).

Distribution. Costa Rica and Panama.

Representative Collections—COSTA RICA. 1 Jan 1922, *Brenes 3595* (CR); 20 Mar 1959, *Charles 89* (NY); 20 Dec 1982, *Zuchowski 608* (SEL); 10 Mar 2001, *Mora 1901* (CR, INB, NY); 16 Jun 2005, *Morales 13169* (INB).

Life form. Epiphyte, terrestrial, and saxicolous.

[1,2] ***Werauhia kathyae*** (Utley) J. R. Grant, Trop. Subtrop. Pflanzenwelt 91: 42 (1995).
Distribution. Costa Rica and Panama.
Representative Collections—COSTA RICA. 24 Apr 1983, *Liesner 14676* (INB); 22 Feb 1990, *Grant 824* (INB, SEL); 21 Jul 1994, *Morales 3055* (CR, INB); 20 Feb 1999, *Vargas 157* (INB); 17 Jun 2005, *Morales 13220* (INB).
Life form. Epiphyte (rarely terrestrial).

Werauhia kupperiana (Suess.) J. R. Grant, Trop. Subtrop. Pflanzenwelt 91: 32 (1995).
Distribution. Nicaragua, Costa Rica, Panama, Colombia, and Ecuador.
Representative Collections—COSTA RICA. 15 Sep 1986, *Davidse 31283* (INB); 19 Oct 1989, *Funk 10599* (INB); 3 Dec 1993, *Morales 2127* (CR, INB, SEL); 17 Apr 1994, *Morales 2703* (CR, INB, SEL); 18 Nov 1996, *Oconnor 202* (INB).
Life form. Epiphyte and terrestrial.

[2] ***Werauhia latissima*** (Mez & Wercklé) J. R. Grant, Trop. Subtrop. Pflanzenwelt 91: 43 (1995).
Distribution. Costa Rica and Panama.
Representative Collections—COSTA RICA. *Wercklé s.n.* (B, holo, n.v); *Wercklé 82* (B, n.v.); *Wercklé 8* (US, n.v.); 10 Apr 2005, *Soto 773* (INB).
Life form. Epiphyte (rarely terrestrial).

[2] ***Werauhia laxa*** (Mez & Wercklé) J. R. Grant, Trop. Subtrop. Pflanzenwelt 91: 43 (1995).
Distribution. Costa Rica and Panama.
Representative Collections—COSTA RICA. *Wercklé 90* (B, holo); 26 Feb 1975, *Utley 1857* (CR, INB, NY); 12 Feb 1992, *Ingram 1325* (INB, SEL); 20 Jul 1996, *Morales 5533* (INB); 16 Apr 2004, *Solano 978* (INB).
Life form. Epiphyte, terrestrial, and saxicolous.

[2] ***Werauhia leucophylla*** (L. B. Sm.) J. R. Grant, Trop. Subtrop. Pflanzenwelt 91: 43 (1995).
Distribution. Costa Rica and Panama.
Representative Collections—COSTA RICA. 29 Jun 1972, *Utley 401* (CR); 13 Sep 1978, *Burger & Antonio 11024* (CR, SCZ); 22 Jul 1990, *Luther 2804* (SEL); 20 Mar 1994, *Morales 2520* (INB); 25 Sep 2005, *Solano 2705* (INB).
Life form. Epiphyte (occasionally terrestrial).

*[1] ***Werauhia luis-gomezii*** (Utley) J. R. Grant, Trop. Subtrop. Pflanzenwelt 91: 43 (1995).
Distribution. Costa Rica.
Representative Collections—COSTA RICA. 11 Jul 1996, *Morales 5460* (INB); 1 Apr 1997, *Quesada 1965* (CR, INB); 21 May 2005, *Morales 13008* (INB); 15 Jun 2005, *Morales 13133* (INB).
Life form. Epiphyte (occasionally terrestrial).

*[1]***Werauhia lyman-smithii** (Utley) J. R. Grant, Trop. Subtrop. Pflanzenwelt 91: 43 (1995).
Distribution. Costa Rica.
Representative Collections—COSTA RICA. 3 Oct 1993, *Morales 1825* (INB); 29 Mar 1994, *Morales 2614* (INB); 21 Feb 1995, *Morales 3492* (INB); 19 Mar 1996, *Morales 5330* (INB); 7 Dec 2004, *Morales 11742* (INB).
Life form. Epiphyte.

[1,2]***Werauhia macrantha*** (Mez & Wercklé) J. R. Grant, Phytologia 78: 121 (1995).
Distribution. Costa Rica and Panama.
Representative Collections—COSTA RICA. *Wercklé s.n.* (B, holo); 31 Mar 1995, *Morales 3824* (INB); 28 Jan 1996, *Morales 5201* (INB).
Life form. Epiphyte.

[1,2]***Werauhia macrochlamys*** (Mez & Wercklé) J. F. Morales, Lundiana 4(1): 65 (2003).
Distribution. Costa Rica and Panama.
Representative Collections—COSTA RICA. *Wercklé 115* (B, holo); 21 Jul 1994, *Morales 3047* (INB); 17 Oct 1996, *Moraga 775* (CR, INB); 22 Nov 2004, *Soto 346* (INB); 27 Jul 2005, *Acosta 3524* (INB).
Life form. Epiphyte (occasionally terrestrial).

[2]***Werauhia marnier-lapostollei*** (L. B. Sm.) J. R. Grant, Trop. Subtrop. Pflanzenwelt 91: 33 (1995).
Distribution. Costa Rica and Panama.
Representative Collections—COSTA RICA. 21 Apr 1994, *Lépiz 305* (INB); 20 Apr 1995, *Morales 3881* (INB); 3 Apr 1997, *Morales 6159* (INB); 4 Apr 2002, *Arauz 3250* (CR); 7 Apr 2005, *Morales 12782* (INB).
Life form. Epiphyte.

Werauhia moralesii* H. Luther, Brittonia 54(4): 281 (2002 publ. 2003).
Syn.: *Werauhia clandestina* J.F. Morales, Polibotanica 15: 110 (2003).
Distribution. Costa Rica.
Representative Collections—COSTA RICA. 22 Jul 1990, *Luther 2801* (MO, SEL); 17 Apr 1994, *Morales 2704* (INB).
Life form. Epiphyte, terrestrial, and saxicolous.
Note. According to The Plant List (www.theplantlist.org) "this name is unresolved". The species was originally described as *Vriesea simulans* J.F. Morales in Novon 9: 404 (1999), which is a homonym of *Vriesea simulans* Leme in J. Bromeliad Soc. 47(4): 169 (1997).

Werauhia nephrolepis (L. B. Sm. & Pittendr.) J. R. Grant, Trop. Subtrop. Pflanzenwelt 91: 44 (1995).
Distribution. Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, and Panama.

Representative Collections—COSTA RICA. 1901, *Wercklé 16201* (B); 27 Feb 1987, *Grayum 8097* (INB); 19 Sep 1997, *Rodríguez 2479* (INB); 6 Apr 2005, *Soto 694* (INB, NY); 5 Feb 2008, *Cascante 1842* (CR).
Life form. Epiphyte (occasionally terrestrial).

[1,2]***Werauhia notata*** (L. B. Sm. & Pittendr.) J. R. Grant, Trop. Subtrop. Pflanzenwelt 91: 44 (1995).
Distribution. Costa Rica and Panama.
Representative Collections—COSTA RICA. 4 Oct 1898, *Tonduz 12526* (B, holo; CR); 14 Jan 1992, *Grant 1870* (CR, INB); 26 Mar 1995, *Morales 3771* (INB); 8 Mar 2000, *Acosta 557* (CR, INB); 7 Oct 2008, *Cascante 2022* (CR).
Life form. Epiphyte and terrestrial.

Werauhia ororiensis (Mez) J. R. Grant, Trop. Subtrop. Pflanzenwelt 91: 44 (1995).
Distribution. Costa Rica, Panama, and Ecuador.
Representative Collections—COSTA RICA. 2 Jun 1890, *Tonduz 2159* (B, CR); 14 Apr 1968, *Rodríguez & Sevilla 1143* (USJ); 5 Mar 1976, *Utley & Utley 4238* (SCZ); 12 Jan 1992, *Grant 1842* (INB, SEL); 16 Jun 2005, *Morales 13186* (INB).
Life form. Epiphyte and terrestrial.

*[1]***Werauhia osaensis*** (J. F. Morales) J. F. Morales, Polibotanica 15: 110 (2003).
Distribution. Costa Rica.
Representative Collections—COSTA RICA. 26 Aug 1990, *Herrera 4144* (INB); 4 Sep 1993, *Aguilar 2227* (INB); 15 Mar 1995, *Mora 83* (INB); 13 May 2001, *Morales 8069* (INB); 28 Feb 2005, *Morales 12071* (INB).
Life form. Epiphyte.

[1,2]***Werauhia paniculata*** (Mez & Wercklé) J. R. Grant, Trop. Subtrop. Pflanzenwelt 91: 45 (1995).
Distribution. Costa Rica and Panama.
Representative Collections—COSTA RICA. *Wercklé 55* (B, lecto); 25 Jun 1976, *Utley 5196* (CR); 17 Jun 1994, *Morales 2937* (INB); 30 Jul 2001, *Acosta 3127* (INB); 17 Jun 2005, *Morales 13216* (INB).
Life form. Epiphyte (occasionally terrestrial).

Werauhia pedicellata (Mez & Wercklé) J. R. Grant, Trop. Subtrop. Pflanzenwelt 91: 47 (1995).
Distribution. Honduras, Nicaragua, Costa Rica, and Panama.
Representative Collections—COSTA RICA. *Wercklé 116* (B, holo; GH, iso, n.v.); 28 Apr 1980, *Meerow 1037* (SEL); 6 Apr 1994, *Morales 2641* (CR, INB, SEL); 15 May 2004, *Kriebel 4641* (INB); 10 Mar 2008, *Cascante 1883* (CR).
Life form. Epiphyte (occasionally terrestrial).

[2] ***Werauhia picta*** (Mez & Wercklé) J. R. Grant, Trop. Subtrop. Pflanzenwelt 91: 47 (1995).
Distribution. Costa Rica and Panama.
Representative Collections—COSTA RICA. *Wercklé 119* (B, lecto); May- Jun 1976, *Utley & Utley 4979* (CR).
Life form. Epiphyte.

[2] ***Werauhia pittieri*** (Mez) J. R. Grant, Trop. Subtrop. Pflanzenwelt 91: 33 (1995).
Distribution. Costa Rica and Panama.
Representative Collections—COSTA RICA. Apr 1898, *Tonduz 12229* (B, holo, n.v.; US, iso, n.v.); 6 Apr 1995, *Aguilar 3884* (INB); 24 Jul 1997, *Rodríguez 2410* (INB); 5 Jul 2000, *Morales 7288* (CR, INB); 9 Dec 2004, *Morales 11873* (INB).
Life form. Epiphyte.

Werauhia ringens (Griseb.) J. R. Grant, Trop. Subtrop. Pflanzenwelt 91: 35 (1995).
Distribution. Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Dominican Republic, and Haiti.
Representative Collections—COSTA RICA. 12 Mar 1993, *Luther s.n.* (SEL); 23 Nov 1994, *Morales 3224* (CR, INB); 17 May 1995, *Morales 4210* (INB); 15 Mar 2004, *Morales 10320* (INB).
Life form. Epiphyte.

[2] ***Werauhia rubra*** (Mez & Wercklé) J. R. Grant, Trop. Subtrop. Pflanzenwelt 91: 47 (1995).
Distribution. Costa Rica and Panama.
Representative Collections—COSTA RICA. *Wercklé 100* (B, lecto); 11 May 1975, *Utley 2486* (CR); 8 Sep 1984, *Davidse 28704* (CR); 21 Feb 1995, *Morales 3493* (CR, INB, NY); 29 Aug 2000, *Rodríguez 6346* (INB).
Life form. Epiphyte and terrestrial.

*[1] ***Werauhia rugosa*** (Mez & Wercklé) J. R. Grant, Phytologia 79(3): 255 (1995).
Distribution. Costa Rica.
Representative Collections—COSTA RICA. *Wercklé s.n.* (B); 29 Apr 1980, *Meerow et al. 1073* (SEL); 6 Aug 1994, *Morales 3077* (INB).
Life form. Epiphyte (rarely terrestrial).

Werauhia sanguinolenta (Linden ex Cogn. & Marchal) J. R. Grant, Trop. Subtrop. Pflanzenwelt 91: 35 (1995).
Distribution. Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Peru, Bolivia, Brazil, Venezuela, Dominican Republic, and Jamaica.
Representative Collections—COSTA RICA. 5 Jan 1992, *Grant 1729* (CR, INB, SEL); 3 Dec 1993, *Morales 2136* (CR, INB, SEL); 27 Jul 1995, *Lépiz 612* (CR, INB); 13 Nov 1998, *Estrada 1933* (CR); 11 Apr 2005, *Morales 12752* (INB).
Life form. Epiphyte (occasionally terrestrial and saxicolous).

[1,2]***Werauhia singuliflora*** (Mez & Wercklé) J. R. Grant, Trop. Subtrop. Pflanzenwelt 91: 48 (1995).
Distribution. Costa Rica and Panama.
Representative Collections—COSTA RICA. *Wercklé 89* (B, holo); 31 Jul 1982, *Gómez-Laurito 8914* (INB); 31 Mar 1995, *Morales 4899* (INB); 19 Mar 1996, *Morales 5336* (INB); 12 May 2005, *Morales 12959* (INB).
Life form. Epiphyte.

[2]***Werauhia stenophylla*** (Mez & Wercklé) J. R. Grant
Trop. Subtrop. Pflanzenwelt 91: 48 (1995).
Distribution. Costa Rica and Panama.
Representative Collections—COSTA RICA. *Wercklé 112* (B, holo); 12-17 Dec 1969, *Burger & Liesner 6734* (SCZ); 22 Feb 1990, *Grant 844* (INB); 12 Feb 1992, *Ingram 1323* (SEL).
Life form. Epiphyte (occasionally terrestrial).

Werauhia subsecunda (Wittm.) J. R. Grant, Trop. Subtrop. Pflanzenwelt 91: 35 (1995).
Distribution. Costa Rica, Panama, and Colombia.
Representative Collections—COSTA RICA. *Wercklé 118* (B, holo); 27 Apr 1980, *Meerow 1010* (SEL); 14 Jan 1992, *Grant 1869* (CR, INB); 9 Dec 2004, *Morales 11911* (INB); 23 Apr 2008, *Cascante 1923* (CR).
Life form. Epiphyte.

*[1]***Werauhia tiquirensis*** (J. F. Morales) J. F. Morales, Polibotanica 15: 110 (2003).
Distribution. Costa Rica.
Representative Collections—COSTA RICA. 22 Apr 1995, *Morales 3984* (INB); 23 Jun 1995, *Morales 4462* (INB); 13 May 2001, *Morales 8024* (INB); 6 Apr 2005, *Morales 12506* (INB).
Life form. Epiphyte and terrestrial.

*[1]***Werauhia tonduziana*** (L. B. Sm.) J. R. Grant, Trop. Subtrop. Pflanzenwelt 91: 35 (1995).
Distribution. Costa Rica.
Representative Collections—COSTA RICA. 15 Jan 1991, *Grant 1438* (INB); 9 Nov 1992, *Ingram 1701* (CR, SEL); 10 May 2005, *Morales 12873* (INB); 19 May 2006, *Cascante 1574* (CR); 26 May 2008, *Hammel 24778* (INB).
Life form. Epiphyte (rarely terrestrial).

Werauhia umbrosa (L. B. Sm.) J. R. Grant, Trop. Subtrop. Pflanzenwelt 91: 48 (1995).
Distribution. Costa Rica, Panama, and Colombia.
Representative Collections—COSTA RICA. 20 Apr 1993, *Ingram 1845* (INB, SEL); 5 Jan 1997, *González 1495* (INB); 13 Apr 2005, *Santamaría 1654* (INB); 11 May 2005, *Morales 12904* (INB); 9 Aug 2007, *Soto 1697* (INB).
Life form. Epiphyte and terrestrial.

*[1]***Werauhia uxoris** (Utley) J. R. Grant, Trop. Subtrop. Pflanzenwelt 91: 48 (1995).
Distribution. Costa Rica.
Representative Collections—COSTA RICA. 1 May 1994, *Morales 3333* (INB); 11 Jul 1996, *Morales 5457* (INB); 5 Sep 1996, *Morales 5790* (INB); 21 May 2005, *Morales 13031* (INB); 16 Jun 2005, *Morales 13185* (INB).
Life form. Epiphyte.

*[1]***Werauhia vietoris** (Utley) J. R. Grant, Trop. Subtrop. Pflanzenwelt 91: 48 (1995).
Distribution. Costa Rica.
Representative Collections—COSTA RICA. 5 Mar 1980, *Meerow 1117* (SEL); 28 Mar 1994, *Morales 2598* (INB); 10 Apr 1994, *Morales 2674* (INB); 19 Jul 2000, *Rodríguez 5981* (INB).
Life form. Epiphyte.

Werauhia viridiflora (Regel) J. R. Grant, Trop. Subtrop. Pflanzenwelt 91: 38 (1995).
Distribution. Mexico, Guatemala, Belize, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, and Venezuela.
Representative Collections—COSTA RICA. *Wercklé 66* (B, lecto); 15 Feb 1990, *Grant 90-766* (SEL); 16 Jul 1992, *Ingram 1539* (CR, SEL); 28 Mar 2003, *Morales 9265* (INB); 23 Feb 2008, *Rodríguez 11907* (INB).
Life form. Epiphyte.

*[1,2]***Werauhia viridis** (Mez & Wercklé) J. R. Grant, Trop. Subtrop. Pflanzenwelt 91: 49 (1995).
Distribution. Costa Rica and Panama.
Representative Collections—COSTA RICA. *Wercklé s.n.* (B, holo; US, iso, n.v.); 1 Apr 1976, *Utley 4421* (INB); 29 Mar 1994, *Morales 2613* (INB); 3 Feb 1995, *Morales 3434* (INB); 19 Mar 1996, *Morales 5326* (INB).
Life form. Epiphyte.

Werauhia vittata (Mez & Wercklé) J. R. Grant, Trop. Subtrop. Pflanzenwelt 91: 38 (1995).
Distribution. Belize, Nicaragua, Costa Rica, Panama, and Ecuador.
Representative Collections—COSTA RICA. *Wercklé 79* (B, holo); 12 Jan 1981, *Waggoner s.n.* (SEL); 22 Feb 1990, *Grant 848* (INB); 10 May 1995, *Morales 4077* (INB); 1 May 2004, *Morales 10567* (INB).
Life form. Epiphyte.

*[1]***Werauhia vulcanicola** (J. F. Morales) J. F. Morales, Polibotanica 15: 110 (2003).
Distribution. Costa Rica.
Representative Collections—COSTA RICA. 9 Jan 1993, *Morales 2237* (INB); 15 Aug 1996, *Morales 5704* (INB); 12 Apr 2005, *Morales 12780* (INB).
Life form. Terrestrial.

Werauhia werckleana (Mez) J. R. Grant, Trop. Subtrop. Pflanzenwelt 91: 38 (1995).
Distribution. Mexico, Guatemala, Belize, El Salvador, Honduras, Nicaragua, Costa Rica, and Panama.
Representative Collections—COSTA RICA. 1 Jan 1901, *Wercklé 16210* (B, holo; US, iso, n.v.); 14 Jan 1992, *Grant 92-1865* (CR, INB, SEL); 22 Jan 1994, *Morales 2287* (INB, NY, SEL); 8 Jan 1996, *Penneys 982* (CR, INB); 26 Apr 2008, *Hammel 24736* (INB).
Life form. Epiphyte (occasionally terrestrial).

Werauhia williamsii (L. B. Sm.) J. R. Grant, Trop. Subtrop. Pflanzenwelt 91: 49 (1995).
Distribution. Nicaragua, Costa Rica, and Panama.
Representative Collections—COSTA RICA. 9 Aug 1971, *Burger & Burger 7950* (SCZ); 5 May 1980, *Meerow 1177* (SEL); 11 Jul 1996, *Morales 5459* (INB); 7 Jun 2003, *Alfaro 4446* (INB); 7 Sep 2006, *Vargas 1634* (INB).
Life form. Epiphyte (occasionally terrestrial).

PhytoKeys 29: 63–74 (2013)
doi: 10.3897/phytokeys.29.6103
www.phytokeys.com

SHORT COMMUNICATION

A peer-reviewed open-access journal
PhytoKeys
Launched to accelerate biodiversity research

Correct names for some of the closest relatives of *Carica papaya*: A review of the Mexican/ Guatemalan genera *Jarilla* and *Horovitzia*

Fernanda Antunes Carvalho[1], Susanne S. Renner[2]

1 *Systematic Botany and Mycology, Ludwig-Maximilians-Universität München, Menzinger Strasse 67, D-80638 Munich, Germany*

Corresponding author: *Fernanda Antunes Carvalho* (antunesfc@gmail.com)

Academic editor: *K. Marhold* | Received 14 August 2013 | Accepted 7 November 2013 | Published 19 November 2013

Citation: Carvalho FA, Renner SS (2013) Correct names for some of the closest relatives of *Carica papaya*: A review of the Mexican/Guatemalan genera *Jarilla* and *Horovitzia*. PhytoKeys 29: 63–74. doi: 10.3897/phytokeys.29.6103

Abstract

Using molecular data, we recently showed that *Carica papaya* L. is sister to a Mexican/Guatemalan clade of two genera, *Jarilla* Rusby with three species and *Horovitzia* V.M. Badillo with one. These species are herbs or thin-stemmed trees and may be of interest for future genomics-enabled papaya breeding. Here we clarify the correct names of *J. heterophylla* (Cerv. ex La Llave) Rusby and *J. caudata* (Brandegee) Standl., which were confused in a recent systematic treatment of *Jarilla* (McVaugh 2001). We designate epitypes for both, provide weblinks to type specimens, a key to the species of *Jarilla* and *Horovitzia*, and notes on their habitats and distribution.

Keywords

Caricaceae, nomenclature, epitypification, papaya sister clade

Introduction

The family Caricaceae Dumort. comprises 34 species and one formally named hybrid in currently six genera. A molecular phylogeny that included all species revealed that *Carica papaya* L. (the only species in the genus *Carica*) is sister to a clade of four species endemic to Mexico and Guatemala (Carvalho and Renner 2012). The discovery that the closest relatives of *C. papaya* are three herbs in the genus *Jarilla* Rusby and

a thin stemmed tree, *Horovitzia cnidoscoloides* (Lorence & R. Torres) V. M. Badillo, has implications for plant breeders, who have so far tried in vain to cross papaya with tree species in the genus *Vasconcellea* A. St.-Hil., known as the highlands papayas. To facilitate communication among researchers from different fields, and since full-genome sequencing of the species of *Jarilla* and *Horovitzia* is ongoing (R. Ming, Urbana-Champaign, personal communication, Aug. 2013), we here provide a conspectus of the four species that are the closest relatives of papaya and clean up a nomenclatural confusion involving two names in the genus *Jarilla*.

We start with the nomenclatural issues, then provide a key to the four species, and end with brief comments on the range and habitat of each species.

Nomenclature of *Jarilla*

Pablo de La Llave (1832), a director of the National Museum of Natural History of Mexico, was the first to describe one of the unusual herbaceous Caricaceae that are today placed in *Jarilla*. He had access to fruiting specimens only and based his description of the flowers on notes made by Vicent Cervantes, a professor of botany in Mexico City and one of the founders of that city's botanical garden in 1788. La Lave gave his new species the epithet *"heterophilla"* [sic] to refer to its variably shaped leaves. To mark the distinctness of the new species, he placed it in a separate genus, *Mocinna*, honoring the Mexican naturalist José Mariano Mociño. Unfortunately, this overlooked that Lagasca in 1816 had already described an Asteraceae genus by that name. Soon thereafter, George Bentham (1839) described the same species as *Carica nana*, based on an unnumbered Hartweg specimen (Fig. 1) collected in 1836 in Léon (Guanajuato, Mexico). The holotype at K (Fig. 1) bears the number *288* on its label, a number corresponding to the page of *Plantae Hartwegianae* on which *C. nana* was described. Diaz-Luna and Lomeli-Sención (1992), in their revision of *Jarilla*, cite this collection as *Hartweg 255* (K), probably due to a misreading of 288 for 255.

The second herbaceous Caricaceae species was named in March 1894 by Townshend S. Brandegee, who described *Carica caudata* from the Cape region of Baja California, Mexico, based on a plant he collected the year before (Fig. 2). In August of the same year, José Ramírez, unaware of Brandegee's publication, described a new variety of the first herbaceous Caricaceae, *M. heterophylla* La Llave, naming it varietas *sesseana*, based on living plants from Guanajuato and Jalisco. Unfortunately, he appears to have made no herbarium specimens, but only two beautiful plates showing the typical variety and var. *sesseana* (Fig. 3). Comparison of the plate of var. *sesseana* and the holotype of *C. caudata* leaves no doubt that these names refer to the same species, and we therefore agree with previous assessments (Diaz-Luna and Lomeli-Sención 1992, Badillo 1993) that they are synonyms.

Realizing that *Mocinna* La Llave was a younger homonym of *Mocinna* Lag., Henry Hurd Rusby (1921) proposed the substitute name *Jarilla*, derived from the Spanish vernacular name Jarrila, for *M. heterophylla*. He also up-ranked var. *sesseana* as a separate species, *Jarilla sesseana* (Ramírez) Rusby. We agree with Diaz-Luna and Lomeli-Sención

(1992) and McVaugh (2001) that Rusby's publication of the substitute name *Jarilla* meets the requirement for valid publication and that Ivan M. Johnston's (1924) slightly later publication of the name *Jarrilla* (the correct Spanish spelling) to replace *Mocinna* is a superfluous name. At around the same time, Standley (1924) realized that *Carica caudata* Brandegee belonged in *Jarilla* and was in fact an older name for *J. heterophylla* var. *sesseana* Ramírez (= *Jarilla sesseana* (Ramírez) Rusby), and he accordingly changed the name to *J. caudata*. He also described a third herbaceous species of Caricaceae, *Jarilla chocola* Standley, based on two collections made in 1935 from Sonora, Mexico (Standley 1937).

Thus, by 1937 it was clear there were three species of *Jarilla* and also what their correct names were. In their revision of the genus, Diaz-Luna and Lomeli-Sención (1992) designated plate II of Ramírez (1894; our Fig. 3 left-hand plate) as the lectotype of *J. heterophylla* var. *sesseana* and plate V as the neotype of var. *heterophylla* (our Fig. 3 right-hand plate). Unfortunately, the most recent study of *Jarilla*, that of Rogers McVaugh (2001), synonymized the two taxa distinguished by Ramírez. This error is surprising given the different leaves and fruits of Ramírez's two varieties (our Fig. 3), and indeed McVaugh seems to have been aware he might be making a mistake because he writes (2001: 469), "In the following I have drawn heavily upon the work of Diaz-Luna and Lomelí-Sención, whose personal observations of these interesting species greatly increased our knowledge of them, and have indeed provided almost all the available information about the living plants. Errors introduced here, as a result of faulty translation or interpretation of the work of these authors, or otherwise, are solely my responsibility."

We agree with Diaz-Luna and Lomeli-Sención (1992) and the earlier workers cited above that *Jarilla heterophylla* var. *heterophylla* is the oldest name for Bentham's *Carica nana*, while var. *sesseana* is a younger synonym of *Carica caudata.* We have accordingly up-dated the names of our previous *Jarilla heterophylla* and *J. nana* sequences in GenBank (Carvalho and Renner 2012; all of which are vouchered). Together, the descriptions of Ramírez (1894), Brandegee (1894), Rusby (1921), Johnson (1924), Standley (1924), and Diaz-Luna and Lomeli-Sención (1992) provide a clear idea of the morphological distinctions of the two species: *Jarilla caudata* has rounded to ovate or deltoid (never hastate) leaves, c. 1 cm (rarely longer) male flowers, and 10 cm long fruits that are narrowed at the base with five horn-like appendages, each 3–6 cm long (Fig. 4). *Jarilla heterophylla* has hastate leaves, 0.5 cm long male flowers, and c. 3 cm long fruits with short and thick appendages as shown in Fig. 5.

To fix the usage of the two names more reliably, we below designate epitypes to serve as interpretative specimens for plates II and V of Ramírez (1894), following Art. 9.8 of the Melbourne Code (McNeill et al. 2012). The plates published by Ramírez fail to include staminate and pistillate flowers for both species and therefore do not precisely fix the application of the names of these dioecious species. In addition, physical specimens also can help in evolutionary studies because they can yield DNA that may be used in future comparisons. We chose as epitypes complete male and female specimens from the same population. The epitypes are deposited in M. Isoepitypes of *Mocinna heterophylla* Cerv. ex La Llave var. *sesseana* (=*Jarilla caudata* (Brandegee)

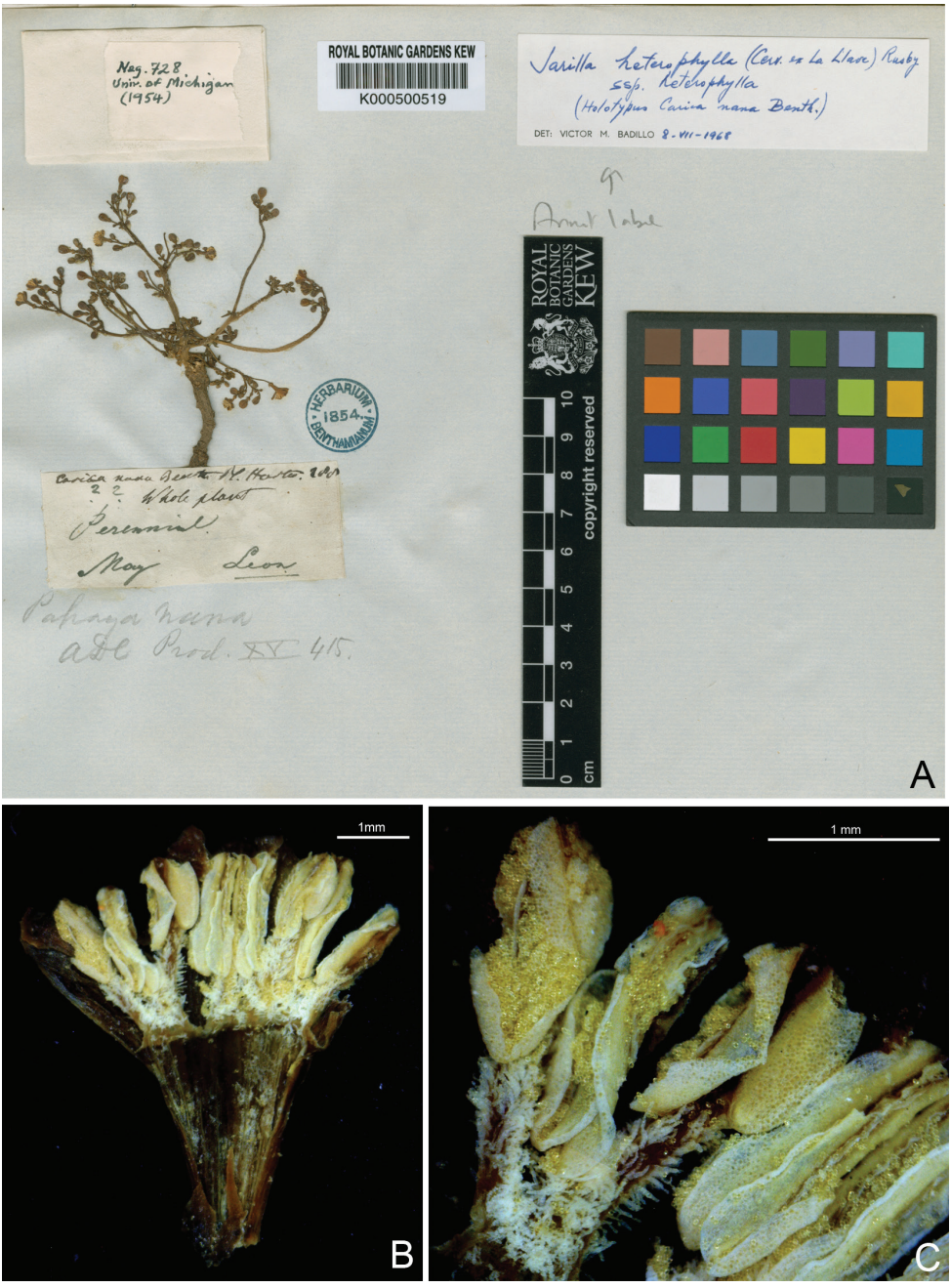

Figure 1. Holotype of *Carica nana* Benth. **A** Specimen in K (http://www.kew.org/herbcatimg/202388.jpg) **B** Photo of an opened flower showing the arrangement of the anthers and the pistillode (arrow) **C** Close-up of the anthers. Filaments are densely covered by moniliform trichomes. **B** and **C** were taken by the first author in K.

Figure 2. Holotype of *Carica caudata* Brandegee (http://ucjeps.berkeley.edu/new_images/UC108333.jpg)

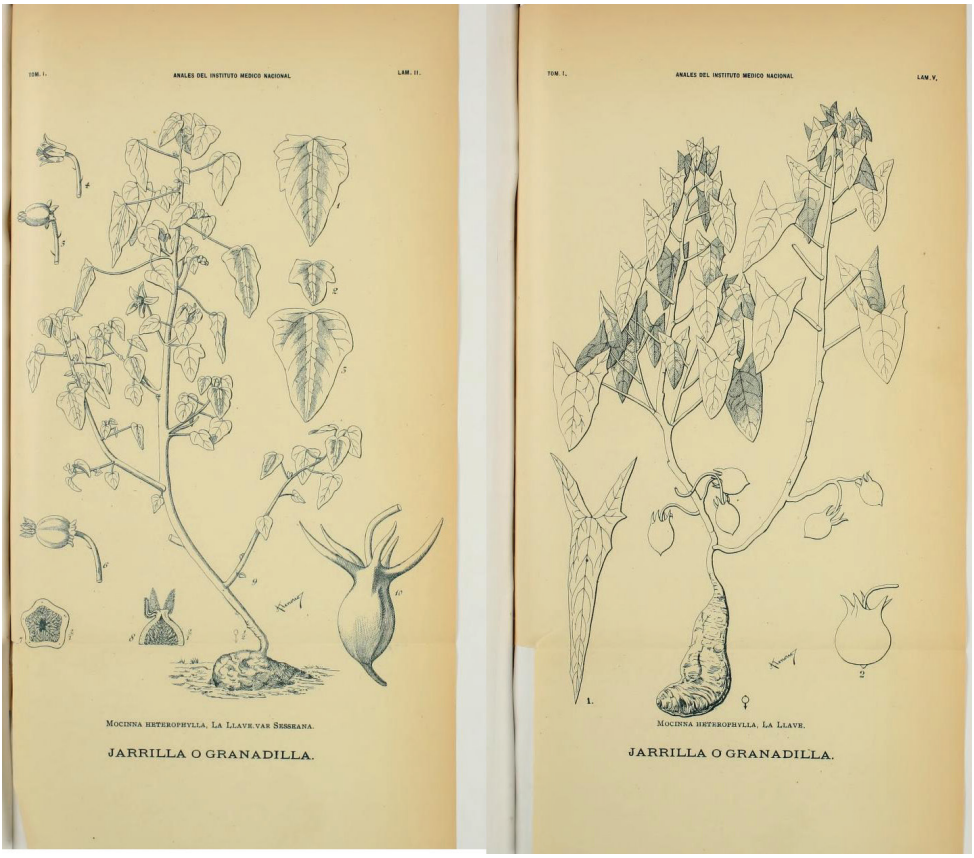

Figure 3. The two varieties of *Mocinna heterophylla* La Llave. **Left plate** shows the lectotype of *Mocinna heterophylla* var. *sesseana* Ramírez. **Right plate** shows the neotype of *Mocinna heterophylla* var. *heterophylla*, both designated by Díaz and Lomeli-Sención (1992). Plates reproduced from Ramírez (1894).

Standl.) are in MEXU and NY. Isoepitypes of *Mocinna heterophylla* Cerv. ex La Llave (= *Jarilla heterophylla* (Cerv. ex La Llave) Rusby) are in MEXU, NY and K.

The four species in the *Jarilla*/*Horovitzia* clade can be distinguished from all other Caricaceae and from each other, using a combination of the plastid markers *trnL-trnF* and *psbA-trnH* (Carvalho and Renner 2012; GenBank accessions JX091966, JX091977, JX091975, JX091978, JX092054, JX092064, JX092065, JX092066).

Key to the species of *Jarilla* and *Horovitzia*

1a Small tree, completely covered by stinging hairs...***Horovitzia cnidoscoloides***
1b Herb, glabrous or pubescent, but never with stinging hairs.....**2**

2a Erect herb. Leaves lobate, rarely entire. Ovary and mature fruits with 5 longitudinal wings. Female flowers 7–9 mm long. Male flowers 5–9 mm long ..... ***Jarilla chocola***

2b Procumbent herb, sometimes using understory plants for support. Leaves entire, rarely lobed. Ovary and young fruits with 5 basal appendages, but not winged. Female flowers 5–15 mm long. Male flowers 4-12 mm long..... **3**

3a Mature fruits 6–30 cm long with 5 horn-like basal appendages 3–6 cm long. Seeds black, 4–5.5 mm long. Male flowers in general >1 cm (1–1.7 cm) ..... ***Jarilla caudata***

3b Mature fruits 2–4 cm long with 5 curved basal appendages 0.5–2 cm long. Seeds light brown, 2.5–3.5 mm long. Male flowers in general <1 cm (0.3–0.8 cm)..... ***Jarila heterophylla***

Epitypification and comments on morphology and habitats

Horovitzia cnidoscoloides **(Lorence & R. Torres) V.M. Badillo, Rev. Fac. Agron. (Maracay) 43: 104. 1993.**
http://species-id.net/wiki/Horovitzia_cnidoscoloides

Carica cnidoscoloides Lorence & R. Torres, Syst. Bot. 13(1): 107–109, f.1. 1988.

Type: Mexico. Oaxaca: Ixtlan, Sierra de Juárez, 9 March 1986, *R. Torres & P. Teonorio 8168* (holotype: MEXU, a photo in GUADA; isotypes: BM, MO [MO-193213], NY[00112155]). Mexico. Oaxaca. Type locality, 25 May 1883, *T. Cedillo & Lorence 2347* (paratype: MEXU, a photo in GUADA, a duplicate in MO); 4 Ago 1985, *Lorence et al. 4733* (paratype: MEXU, a duplicate in BM); 9 Mar 1985, *C. Torres & L. Tenorio 8167* (paratype: MEXU); 27 Ago 1986, *C. Torres & L. Tenorio 8760* (paratype: MEXU).

Horovitzia cnidoscoloides is a small tree, 0.5–4 m tall endemic to Sierra de Juarez in Oaxaca, Mexico. It occurs in cloud forests from 800 to 1600 m above sea level. Unusual features are subcapitate stigma, and stinging hairs covering the entire plant.

Jarilla chocola **Standl. Publ. Field Mus. Nat. Hist., Bot. Ser. 17: 200. 1937.**
http://species-id.net/wiki/Jarilla_chocola

Type. Mexico. Sonora: Chihuahua, Guasarema, Rio Mayo, 10 August 1936, *H. S. Gentry 2366* (holotype: F; isotypes: GUADA photo, K [K000500520], S [S-G-3434]). Mexico. Sonora: San Bernardo, Rio Mayo, 14 August 1935, *H. S. Gentry 1624* (paratype: F, duplicates in MEXU and K [000500521], a photo in GUADA).

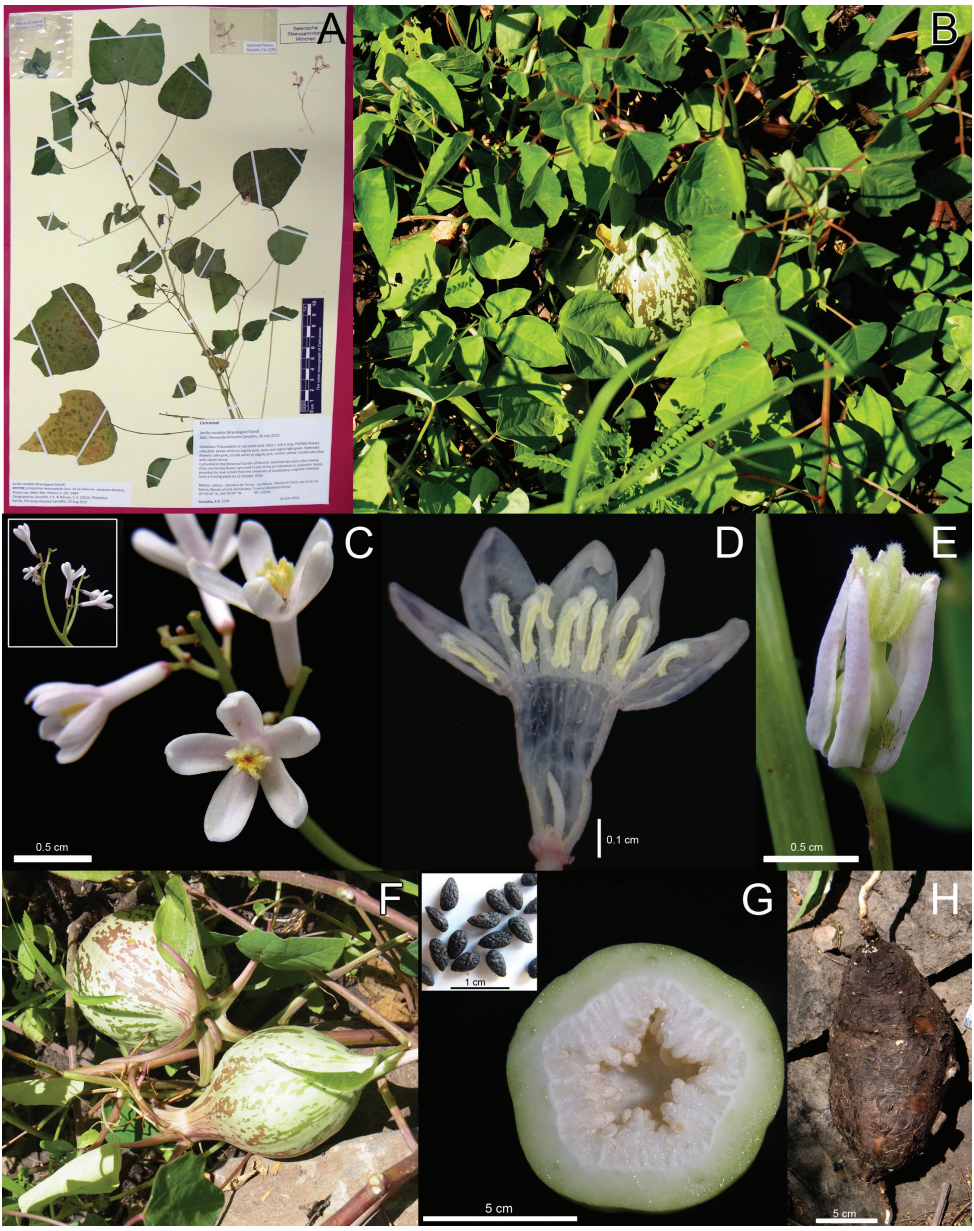

Figure 4. *Jarilla caudata* (Brandegee) Standl. **A** Epitype of *Mocinna heterophylla* La Llave (*F.A. Carvalho 2240*, M) **B** Habit **C** Male inflorescence **D** Staminate flower. **E** Pistillate flower **F** Fruits **G** Ovary unilocular and seeds **H** Tuber.

Jarilla chocola is an erect herb, with mostly lobate leaves and fruits with 5 longitudinal wings. The species occurs at low altitudes (100–1300 m) along the Pacific Coast from Sonora to El Salvador.

***Jarilla caudata* (Brandegee) Standl., Contr. U.S. Natl. Herb. 23(4): 853. 1924.**
http://species-id.net/wiki/Jarilla_caudata
Fig. 4

Carica caudata Brandegee, Zoe 4: 401. 1894.
Type: Mexico. Baja California Sur: Corral de Piedra, September 1893, *Brandegee s.n.* (holotype: UC[UC108333]).
Mocinna heterophylla var. *sesseana* Ramírez, Anales Inst. Med.-Nac. Mexico 1: 207. 1894.
Type: Plate II of Ramírez, 1894 (lectotype designated by Diaz-Luna and Lomeli-Sención 1992: 81). Mexico, Jalisco, Zacoalco de Torres, Las Moras, 5 June 2013, *F. A. Carvalho 2239* (epitype, designated here: M; isoepitypes: MEXU, NY).
Jarilla sesseana (Ramírez) Rusby, Torreya 21: 47. 1921.

Remarks. *Jarilla caudata* is morphologically and phylogenetically closely related to *J. heterophylla.* Their main distinguishing features are the fruits, which in *J. caudata* can attain a length of 30 cm, having a smooth surface and 5 long, horn-like appendages (3–6 cm long). Other differences are given in the key. The species occurs in deciduous forests and fields of Baja California and central Mexico from 1500 to 1800 m above sea level.

***Jarilla heterophylla* (Cerv. ex La Llave) Rusby, Torreya 21(3): 50. 1921.**
http://species-id.net/wiki/Jarilla_heterophylla
Fig. 5

Mocinna heterophylla Cerv. ex La Llave, Reg. Trim. 1(3): 351. 1832.
Type: Plate V of Ramírez, 1894 (neotype, designated by Diaz-Luna and Lomeli-Sención 1992: 88). Mexico, Jalisco, Zacoalco de Torres, Las Moras, 5 June 2013, *F. A. Carvalho 2240* (epitype, designated here: M; isoepitypes: MEXU, NY, K).
Carica nana Benth., Pl. Hartw. 288. 1849.
Type: Mexico. Guanajuato, Leon, *K. T. Hartweg s.n.* (holotype K [K000500519]; isotype: G-DC n.v.).
Papaya nana (Benth.) A. DC., Prodr. 15(1): 415. 1864.
Jarilla nana (Benth.) McVaugh, Fl. Novo-Galiciana 3: 475. 2001.

Remarks. For differences from *Jarilla caudata* see under that species and in the key. *Jarilla heterophylla* occurs in oak forests, deciduous forests, and abandoned fields of central Mexico at 1500 to 2700 m above sea level.

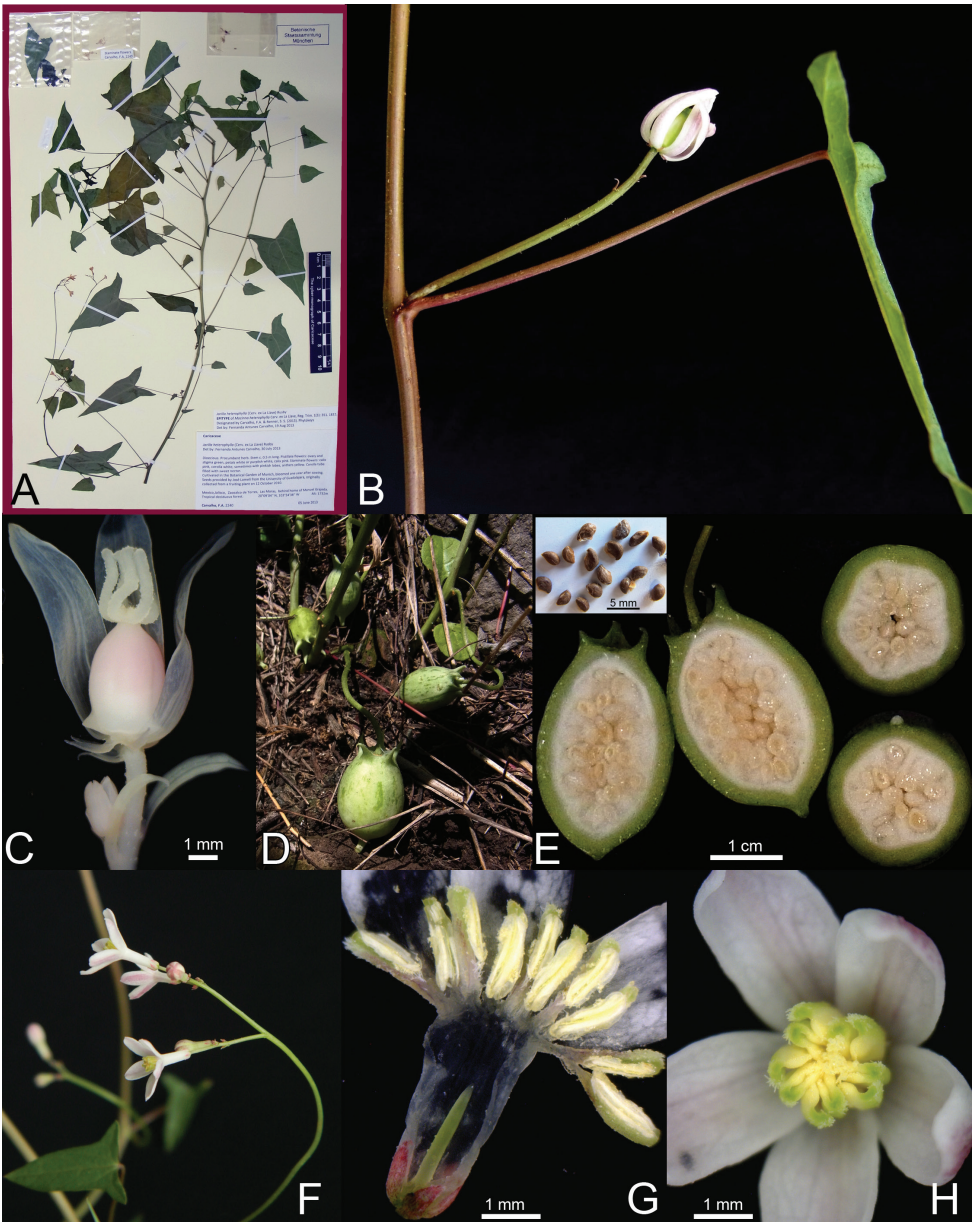

Figure 5. *Jarilla heterophylla* (Cerv. ex La Llave) Rusby. **A** Epitype of *Mocinna heterophylla* La Llave var. *sesseana* Ramírez (*F.A. Carvalho 2239*, M) **B** Female inflorescence (uniflora). **C** Female flower showing the short appendages at the base of the ovary **D–E** Fruits and seeds **F** male inflorescence **G–H** Staminate flowers.

Weblinks to type specimens

Carica caudata Brandegee, holotype:
http://ucjeps.berkeley.edu/new_images/UC108333.jpg [accessed 30.07.2013]
Carica cnidoscoloides Lorence & R. Torres, isotypes:
http://www.tropicos.org/Image/11116 [accessed 11.08.2013]
http://sweetgum.nybg.org/vh/specimen.php?irn=707429 [accessed 11.08.2013]
Carica nana Benth., holotype: http://www.kew.org/herbcatimg/202388.jpg [accessed 30.07.2013]
Jarilla chocola Standl., isotypes:
http://apps.kew.org/herbcat/getImage.do?imageBarcode=K000500520 [accessed 11.08.2013]
http://andor.nrm.se/kryptos/fbo/kryptobase/large/S-G-003001/S-G-3434.jpg [accessed 11.08.2013]
Mocinna heterophylla Cerv. ex La Llave, epitype:
http://herbaria.plants.ox.ac.uk/bol/caricaceae [accessed 11.10.2013]
Mocinna heterophylla var. *sesseana* Ramírez, epitype:
http://herbaria.plants.ox.ac.uk/bol/caricaceae [accessed 11.10.2013]

Acknowledgements

We thank J. F. Barêa Pastore for discussion of the nomenclature of *Jarilla*, and the herbaria K, MO, NY, S, and UC for providing open access to type images. The first author is supported by a fellowship from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq 290009/2009-0), and additional funding came from the German Research Foundation (DFG RE 603/13).

References

Badillo VM (1993) Caricaceae, segundo esquema. Revista de la Faculdad de Agronomia de la Universidad Central de Venezuela 43: 1–111.

Bentham G (1839) Plantae Hartwegianae. London, Facsimile edition: Lehre J. Cramer 1970. http://www.biodiversitylibrary.org/page/796739#page/288/mode/1up [accessed 30.07.2013]

Brandegee TS (1894) Additions to the flora of the Cape region of Baja California. II. Zoe 4(4): 398–407. http://www.biodiversitylibrary.org/page/568039#page/97/mode/1up [accessed 30.07.2013]

Carvalho FA, Renner SS (2012) A dated phylogeny of the papaya family (Caricaceae) reveals the crop's closest relatives and the family's biogeographic history. Molecular Phylogenetics and Evolution 65(1): 46–53. doi: 10.1016/j.ympev.2012.05.019

Diaz-Luna CL, Lomelí-Sención JA (1992) Revisión del género *Jarilla* Rusby (Caricaceae). Acta Botánica Mexicana 20: 77–99. http://www.redalyc.org/pdf/574/57402010.pdf [accessed 30.07.2013]

Johnston IM (1924) Taxonomic notes concerning the American Spermatophytes. New or otherwise noteworthy plants. Contributions from the Gray Herbarium of Harvard University 70: 69–87. http://www.biodiversitylibrary.org/page/39944720#page/77/mode/1up [accessed 30.07.2013]

Kyndt T, Van Droogenbroeck B, Romeijn-Peeters E, Romero-Motochi JP, Scheldeman X, Goetghebeur P, Van Damme P, Gheysen G (2005) Molecular phylogeny and evolution of Caricaceae based on rDNA internal transcribed spacers and chloroplast sequence data. Molecular Phylogenetics and Evolution 37(2): 442–59. doi: 10.1016/j.ympev.2005.06.017

La Llave P (1832) Descripcion de alguns géneros y especies nuevas de vegetales. Registro Trimestre ó Coleccion de Memorias de Historia, Literatura, Ciencias y Artes1(3): 345–358. http://www.biodiversitylibrary.org/page/14631797#page/373/mode/1up [accessed 30.07.2013]

Lorence DH, Colín RT (1988) *Carica cnidoscoloides* (sp. nov.) and sect. *Holostigma* (sect. nov) of Caricaceae from Southern Mexico. Systematic Botany 13(1): 107–110. doi: 10.2307/2419246

McNeill J, Barrie FR, Buck WR, Demoulin V, Greuter W, Hawksworth DL, Herendeen PS, Knapp S, Marhold K, Prado J, Prud'homme van Reine WF, Smith JF, Wiersema JH, Turland NJ (2012) International Code of Nomenclature for Algae, Fungi, and Plants (Melbourne Code): adopted by the Eighteenth International Botanical Congress Melbourne, Australia, July 2011. Regnum Vegetabile 154. Koeltz Scientific Books. http://www.iapt-taxon.org/nomen/main.php [accessed 30.07.2013]

McVaugh R (2001) Caricaceae. In: Anderson WR (Ed) Flora Novo-Galiciana. A descriptive account of the vascular plants of Western Mexico. Vol. 3 Ochnaceae to Losaceae. The University of Michigan Press, Ann Arbor, 461–477.

Ramírez J (1894) La *Mocinna heterophylla.* Nuevo género de las papayáceas. Anales del Instituto Médico Nacional 1(5): 205–212, pl. II–V. http://archive.org/stream/analesdelinstitu01inst#page/206/mode/2up [accessed 30.07.2013]

Rusby HH (1921) A strange fruit. Torreya 21(3): 47–50. http://www.biodiversitylibrary.org/item/100133#page/243/mode/1up [accessed 30.07.2013]

Standley PC (1924) Caricaceae. In: Standley PC (Ed) Tree and shrubs of Mexico (Passifloraceae-Schrofulariaceae). Contributions from the United States National Herbarium 23(4): 849–853. http://www.biodiversitylibrary.org/page/375754#page/939/mode/1up [accessed 30.07.2013]

Standley PC (1937) Caricaceae. In: Standley PC (Ed) Studies of American Plants–VII. Publications of the Field Museum of Natural History, Botanical Series 17(2): 200–202.

PhytoKeys 29: 75–87 (2013)
doi: 10.3897/phytokeys.29.6004
www.phytokeys.com

RESEARCH ARTICLE

A peer-reviewed open-access journal
PhytoKeys
Launched to accelerate biodiversity research

A synopsis of the New World species of *Drypetes* section *Drypetes* (Putranjivaceae) with asymmetrical fruits, including description of a new species

Geoffrey A. Levin[1]

1 *Illinois Natural History Survey, Prairie Research Institute, University of Illinois at Urbana-Champaign, 1816 South Oak Street, Champaign, Illinois 61820*

Corresponding author: *Geoffrey A. Levin* (levin1@illinois.edu)

Academic editor: *Lyubomir Penev* | Received 23 July 2013 | Accepted 14 November 2013 | Published 22 November 2013

Citation: Levin GA (2013) A synopsis of the New World species of *Drypetes* section *Drypetes* (Putranjivaceae) with asymmetrical fruits, including description of a new species. PhytoKeys 29: 75–87. doi: 10.3897/phytokeys.29.6004

Abstract

A synopsis of the New World species of *Drypetes* (Putranjivaceae) with asymmetrical drupes is presented. The group consists of three species: *D. alba*, with two varieties, from the West Indies, *D. gentryi* from Mexico, and the newly described *D. asymmetricarpa* from Costa Rica. The new species can be distinguished from both its relatives by its longer fruiting pedicels. In addition, the new species differs from *D. alba* by its larger fruits, and from *D. gentryi* by having shorter staminate pedicels and stigmas borne on styles (rather than sessile). Lectotypes are designated for *D. alba* var. *latifolia* and *D. incurva*.

Keywords

Costa Rica, *Drypetes*, Mexico, Putranjivaceae, West Indies

Introduction

The genus *Drypetes* Vahl (Putranjivaceae) contains about 220 species of dioecious trees and shrubs, mostly of the Old World tropics. About 17 known species are found in the Americas, with the greatest diversity in the West Indies. However the Amazonian species are poorly studied and further research undoubtedly will yield many new species. In the classification of Pax and Hoffmann (1922), the most recent comprehensive

treatment available for the genus, all but three of the American species belong to the pantropical section *Drypetes* based on their pistil consisting of a single carpel [although Pax and Hoffmann named this section *Hemicyclia* (Wight & Arn.) Pax & K. Hoffm., it contains *D. glauca* Vahl, the type of the genus, and therefore must be called *Drypetes*, as was pointed out by Airy Shaw (1969)]. The other three species have 2-carpellate pistils and belong to section *Oligandrae* Pax & K. Hoffm. with 3–4(–7) stamens [*D. lateriflora* (Sw.) Krug & Urb.] or section *Sphragidia* (Thwaites) Pax & K. Hoffm. with 8–12(–50) stamens (*D. brownii* Standl. and *D. guatemalensis* Lundell); both of these sections also are pantropical. It is worth noting *Drypetes* has not been examined phylogenetically and the classification by Pax and Hoffmann (1922) may not reflect evolutionary relationships (Levin 1986).

Although no formal groups below the sectional level have been recognized among New World members of section *Drypetes*, there is a distinctive group of species with strongly asymmetrical drupes. In these species, the young ovary is symmetrical, as in other members of section *Drypetes*, but as the fruit develops the ovary grows faster on one side than the other, resulting in an oblique fruit apex with the stigma shifted to one side (Fig. 1B). As many as four species commonly have been recognized in this group. Here these are reduced to two species, one with two varieties, and a new species is described. The south Asian species *Drypetes gardneri* (Thwaites) Pax & K. Hoffm., *D. lanceolata* (Thwaites) Pax & K. Hoffm., and *D. venusta* (Wight) Pax & K. Hoffm. have somewhat similar fruits but differ significantly from the American species in foliar and floral characters and probably are not closely related.

Methods

The study was based on the examination of specimens from the following herbaria: A, ARIZ, BM, CAS, CM, CR, DAV, F, G, G-DC, GH, GOET, HAJB, ILLS, K, LL, MEXU, MICH, MO, NY, P, SD, TEX, U, UC, UCR, and US. All cited specimens were seen by the author unless otherwise indicated. Identifications were made by comparison with the original descriptions and, when available, with the type material or photographs of types. Details of the flowers and fruits were examined under a stereoscopic microscope. All descriptions and data on flowering times, habitats, and distribution are based on the herbarium material examined. Countries in the Selected Specimens sections are listed alphabetically.

Taxonomic treatment

Key to the New World asymmetrical-fruited *Drypetes*

1 Fruiting pedicels (8–)10–15 mm long; Costa Rica.....**2. *D. asymmetricarpa***
– Fruiting pedicels 4–10 mm long; Mexico and West Indies

2 Staminate pedicels 7–14 mm long; drupes 12–15 mm long; Mexico .... **3. *D. gentryi***

– Staminate pedicels 3–6 mm long; drupes 9–10(–13) mm long; West Indies . ..... [1. ***D. alba***]

3 Stigmas sessile; Hispaniola, Puerto Rico, U.S. Virgin Islands .... **1a. *D. alba* var. *alba***

– Stigmas borne on style 1 mm long; Cuba, Jamaica, Lesser Antilles..... ..... **1b. *D. alba* var. *latifolia***

1a. *Drypetes alba* Poit., Mém. Mus. Hist. Nat. 1: 157, t. 7. 1815; var. *alba*

Liparena alba (Poit.) Poit. ex Baill., Étude Euphorb. 608. 1858.
Type: Based on *Drypetes alba* Poit.

Drypetes sessiliflora Baill., Étude Euphorb., Atlas: 45. 1858, nom. illeg.
Type: Based on *Drypetes alba* Poit.

Drypetes alba var. *genuina* Müll. Arg. in DC., Prodr. 455. 1866, nom. inval.
Type: Based on *Drypetes alba* Poit.

Guatteria berteriana Spreng., Syst. Veg. (ed. 16) 2: 635. 1825.
Type: Puerto Rico, s.d., *C. G. L. Bertero s.n.* (holotype: B†, isotype: TO n.v.).

Guatteria prinoides Spreng., Syst. Veg. (ed. 16) 2: 635. 1825.
Type: Haiti, s.d., *C. G. L. Bertero s.n.* (holotype: B†, isotypes: MO, TO n.v.).

Drypetes alba var. *brevipes* Müll. Arg. in DC., Prodr. 455. 1866.
Type: Puerto Rico, s.d., collector unidentified (holotype: G-DC).

Type. [Haiti.] Île de Tortue, s.d., *A. Poiteau s.n.* (holotype: P; isotype: G-DC).

Distribution. Haiti, Dominican Republic, Puerto Rico, and U.S. Virgin Islands.

Ecology. Forests from sea level to 1000 m, primarily on calcareous soils, but in Puerto Rico also on serpentine-derived soils.

Phenology. Flowering primarily January to April, rarely as early as November. Fruiting February to August.

Conservation status. Least concern. *Drypetes alba* var. *alba* is widespread and likely secure in the Dominican Republic, Puerto Rico, and U.S. Virgin Islands. It may be vulnerable or endangered in Haiti due to extensive deforestation there; I have seen no specimens from Haiti collected later than 1929.

Selected specimens examined. HAITI. Southeast of St. Louis du Nord, 3 Apr 1928 (♂ fl), *Leonard & Leonard 14268* (CM, K, UC, US).

Dominican Republic. Loma Mala, near arroyo Guayabal, Maimón, 300–500 m, 16 Feb 1974 (fr), *Liogier 21293* (F, K, MO).

Puerto Rico. Maricao Afuera, along Maricao River upstream from the fish hatchery, 18°10'11"N, 66°59'10"W, 460–580 m, 11 Jan 1996 (♀ fl), *Acevedo-Rodríguez et al. 7724* (K, US).

United States Virgin Islands. Saint Croix: Salt River bluffs, 6 Jul 1896 (♂ fl), *Ricksecker 462* (P). **Saint John:** Coral Bay Quarter, Bordeaux Mtn., east side, 11 Jan

1992 (bud), *Acevedo-Rodríguez & Siaca 4710* (MO, US). **Saint Thomas:** s.d. (fr), *Riedlé s.n.* (F, P).

1b. *Drypetes alba* Poit. var. *latifolia* Griseb., Nachr. Königl. Ges. Wiss. Georg-Augusts-Univ. 1: 165. 1865.

Drypetes crocea Poit. var. *latifolia* (Griseb.) Müll. Arg., in A. P. de Candolle, Prodr. 15(2): 456. 1866.

Type: Based on *Drypetes alba* Poit. var. *latifolia* Griseb.

Drypetes latifolia (Griseb.) C.Wright, Anales Acad. Ci. Méd. Habana 7: 151. 1870.

Type: Based on *Drypetes alba* Poit. var. *latifolia* Griseb.

Koelera? *serrata* Maycock, Fl. Barbad. 38. 1830.

Type: No specimens cited or located [according to Stafleu and Cowan (1981), Maycock probably made no herbarium; no type has ever been cited for this name].

Drypetes serrata (Maycock) Krug & Urb., Bot. Jahrb. Syst. 15: 354. 1892.

Type: Based on *Koelera serrata* Maycock.

Drypetes serrulata Pax & K.Hoffm. in H.G.A.Engler, Pflanzenr., IV, 147, XV: 267. 1922, nom. superfl.

Type: Based on *Koelera serrata* Maycock.

Drypetes glomerata Griseb., Abh. Königl. Ges. Wiss. Göttingen 7: 75. 1857.

Type: Guadeloupe. n.d., *E. P. Duchassaing s.n.* (holotype: GOET, photo plants.jstor.org/specimen/goet006390).

Drypetes glomerata Griseb. var. *genuina* Müll.Arg. in A.P.de Candolle, Prodr. 15(2): 454. 1866, nom. inval.

Type: Based on *Drypetes glomerata* Griseb.

Drypetes incurva Müll. Arg., Linnaea 32: 82. 1863.

Type: Cuba, prope Havana, 1833 (fr), *R. de la Sagra 607* (lectotype, designated here: G-DC, duplicate: K).

Drypetes glomerata Griseb. var. *olivacea* Müll. Arg. in DC., Prodr. (DC.) 15(2): 454. 1866.

Type: Cuba, 1860–1864, *C. Wright 1929* (holotype: G-DC, isotypes: BM, F, GH, K, MO, NY).

Drypetes serrata (Maycock) Krug & Urb.var. *olivacea* (Müll. Arg.) Krug & Urb., Bot. Jahrb. Syst. 15: 355. 1892.

Type: Based on *Drypetes glomerata* Griseb. var. *olivacea* Müll. Arg.

Type. Cuba, occ., 1863 (fr), *Wright 1927* (lectotype, designated here: GOET003380, photo plants.jstor.org/specimen/goet003380; duplicates: GH pro parte, K pro parte, MO pro parte, NY pro parte).

Distribution. Cuba, Jamaica, and the Lesser Antilles (Antigua, Guadeloupe, Martinique, Barbados).

Ecology. Forests on limestone and schist, from sea level to 1100 m.

Phenology. Flowering October to March. Fruiting December to July.

Conservation status. Least concern. *Drypetes alba* var. *latifolia* is widespread and probably secure in Cuba and Jamaica. Its status in the Lesser Antilles is difficult to assess because of a paucity of specimens.

Discussion. The plants I include in *Drypetes alba* have been segregated into species or varieties in various ways since the middle of the 19th century (Grisebach 1857; 1865; Howard 1989; León and Alain 1953; Müller 1863; 1866; Pax and Hoffmann 1922). Characters that have been used include those of the leaves (petiole length and blade color, shape, and degree of marginal serration), staminate flowers (size, pedicel length, and stamen exsertion), and pistillate flowers/fruits (pedicel length relative to fruit length, style presence/absence, and fruit size). Most of the distinctions were based on observations of the one or two specimens available to earlier workers and these disappear when more specimens are examined. For example, Grisebach (1857), Müller (1866), and León and Alain (1953) distinguished *D. alba* (equivalent to var. *alba* is this treatment) from *D. glomerata* or its synonym *D. serrata* (here synonyms of var. *latifolia*) on the basis of the former having staminate flowers that are more than 1 mm long borne on longer pedicels and with exserted stamens in contrast to the latter having staminate flowers that are about 1 mm long borne on short pedicels and with included stamens. These differences appear to be an artifact of flower age: specimens with immature flowers, generally with the anthers indehiscent, were called *D. glomerata* or *D. serrata*, whereas those bearing fully mature flowers with dehiscent anthers were called *D. alba*. Pax and Hoffmann (1922) separated the same taxa using petiole length: 5–8 mm for *D. alba* vs. about 1 cm for *D. serrulata*, the superfluous name they used for what Grisebach and Müller called *D. glomerata*. In their concept, *D. serrulata* is restricted to the Lesser Antilles whereas *D. alba* is found throughout the Greater Antilles. Measurement of specimens shows that plants from the Lesser Antilles have slightly longer petioles (7–12 mm vs. 5–10 mm) than those from farther west, but clearly the variation is great and broadly overlapping. As I treat them, the two varieties have completely overlapping petiole lengths (6–10 mm long for var. *alba* vs. 5–12 mm for var. *latifolia*). Howard (1989) reported that *D. serrata*, which he considered to be restricted to the Lesser Antilles, had larger fruits than *D. alba* of the Greater Antilles, but he did not provide comparative measurements. Although mature fruits of *D. alba* are rarely found on herbarium specimens, those I have seen are about 12–13 mm long throughout its range. Differences in leaf color, shape, and degree of marginal serration, alone or in combination, were used by Grisebach (1865) and Müller (1866) to describe new varieties based on single specimens, but these characters have been ignored by subsequent authors, presumably because they found, as I have, that these characters vary considerably even within individuals and certainly do not show consistent patterns.

The only character that seems consistently to differentiate *Drypetes alba* var. *alba* from var. *latifolia* is the presence of a style about 1 mm long in the former and its absence in the latter, the stigma being sessile. This character was first observed by Müller (1863) when he described *D. incurva* having a sessile stigma; he later noted the same condition in *D. glomerata* (Müller, 1866). I have found that all specimens from an

individual island show the same condition and I have seen no intermediate specimens. Although this character is consistent geographically, in the absence of additional differences it seems too minor to support more than a varietal distinction. The distribution of the varieties is curious, with var. *latifolia* found both east and west of var. *alba*. DNA sequence data might elucidate this interesting distribution and clarify the evolutionary history of *D. alba.*

Grisebach (1865) based *Drypetes alba* var. *latifolia* on *Wright 1927*. It has long been recognized that this collection, like many of Wright's *Drypetes* collections, is a mixture of two species, in this case *D. alba* and *D. lateriflora* (Krug and Urban 1892; Pax and Hoffmann 1922). The material at GOET includes two sheets, both from the Grisebach Herbarium, and therefore presumably is the original material studied by Grisebach. These have the additional numbers 46 and 47 on the labels. The sheet labeled 46 (GOET 7917) consists of staminate and pistillate flowering branches of *D. lateriflora* and the sheet labeled 47 (GOET 3380) consists of a fruiting specimen of *D. alba* var. *latifolia*. Grisebach briefly described the leaves, staminate flowers, and fruits ("drupa"), thus he must have considered both sheets to be his new variety. In deciding which material best matches the protologue, the staminate flowers argue for GOET 7917 (*D. lateriflora*) and the fruits argue for GOET 3380 (*D. alba* var. *latifolia*). However Grisebach described the leaves as being subentire. The leaves of *D. lateriflora* on GOET 7917 are completely entire, whereas the leaves of *D. alba* var. *latifolia* on GOET 3380 are very shallowly crenulate-serrulate. The latter sheet thus better matches the protologue of D. *alba* var. *latifolia* and therefore I designate it as the lectotype.

Müller (1863) based *Drypetes incurva* on two collections, *de la Sagra 607* and *Wright 593*, pro parte [this collection number includes material of *D. incurva* (= *D. alba* var. *latifolia*) and *D. lateriflora*]. Later, Müller (1866) cited only *de la Sagra 607* under *D. incurva*, placing *Wright 593* under *D. crocea* Poit., a synonym of *D. lateriflora.* Based on the protologue of *D. incurva*, either sheet at G-DC could be chosen as the lectotype, but because it is not a mixed collection and therefore minimizes the potential for confusion, I designate *de la Sagra 607* as the lectotype.

Selected specimens examined. CUBA. Camagüey: Banao, 300–500 m, Nov 1975 (♂ fl), *Alvarez et al. 28778* (HAJB). **Guantánamo:** San Antonia del Sur, Puriales de Caujeri, Sierra de Purial cerca de Arroyo, 800 m, 30 May 1982 (fr), *Bisse et al. 47259* (HAJB). **Holguín:** Sierra de Nipe, prope Río Piloto, 350 m, 16 Dec 1915 (♂ fl), *Ekman 6694* (F, K, NY, U, US). **Isla de la Juventud:** Caleta Cocodrilos, 8 Mar 1916 (fr), *Britton et al. 15305* (CM, F, NY, US). **Matanzas:** Cienega, Peninsula de Zapata, montes al norte de Sto. Tomás, 19 Apr 1977 (fr), *Bisse et al. 34469* (HAJB). **Pinar del Río:** La Guásima, Rangel, Jan 1950 (♀ fl), *Liogier 1261* (GH, US). **Sancti Spíritus:** Trinidad Mountains, Arroyo Grande, 650–750 m, 11–12 Mar 1910 (fr), *Britton &Wilson 5459* (F, NY). **Santiago de Cuba:** Bayate, 20 Feb 1917 (fr), *Ekman 8544* (F, K, LL, NY, U, US).

Jamaica. Trelawny: Boothe district, ca. 3 mi. north of Troy, 1600 m, 14 Mar 1955 (♀ fl, fr), *Proctor 9956* (NY, US).

Antigua and Barbuda. Antigua: environs de St. Jean, Dec 1902 (♂ fl), *Duss 80* (NY).

Guadeloupe. Marie-Galante, bois de Folle-Anse, 1896 (fr), *Duss 3628* (F, MO pro parte, NY, US pro parte).

Martinique. Morne Saint-Martin, pied de la montagne Pelée, 1878 (♂ fl), *Duss 50* (NY).

2. *Drypetes asymmetricarpa* G. A. Levin, sp. nov.
urn:lsid:ipni.org:names:77134216-1
http://species-id.net/wiki/Drypetes_asymmetricarpa
Figure 1

Diagnosis. Differs from the other New World *Drypetes* species with asymmetrical fruits by its longer fruiting pedicels [(8–)10–15 mm vs. 4–10 mm]; also differs from *D. alba* by its larger fruits [12–18 mm vs. 9–10(–13) mm], and from *D. gentryi* by having shorter staminate pedicels (5–8 mm vs. 7–14 mm) and stigmas borne on styles (vs. being sessile).

Type. Costa Rica. Puntarenas: Cove at NE base of peninsula, Punta Quepos (3 km S of Puerto Quepos), 9°24'N, 84°10'W, 0 m, 8 Mar 1986 (fr), *M. H. Grayum 6614* (holotype: MO, isotypes: CR n.v., F).

Description. Trees 6–20 m, to 35 cm dbh; bark with longitudinal fissures; branches brown when young, becoming gray, glabrous or sparsely minutely puberulent with spreading hairs. Leaves: stipules 0.5 × 0.5 mm, deltate, puberulent; petiole 3–10 × 0.3–1 mm, glabrous; blade elliptic to lanceolate, straight or somewhat curved, 4–12 × 1.5–4.5 cm, base asymmetrical, acute, margins entire or minutely crenulate-serrulate, often undulate, apex attenuate, surfaces glabrous, 2° veins 6–9/side. Inflorescences axillary fascicles; staminate 25–40-flowered, bracts 0.5 mm, puberulent, pedicels 5–8 × 0.2 mm, glabrous; pistillate (known only in fruit) 2–6-flowered, bracts 0.25 × 0.25 mm, deltate, puberulent, pedicels (8–)10–15 × 0.4–0.8 mm, glabrous. Staminate flowers: sepals 5–6, narrowly triangular to narrowly lanceolate, 1 × 0.3 mm, spreading and slightly incurved at apex, apex acute, margins ciliate, abaxial surface glabrous except puberulent at apex, adaxial surface densely to sparsely puberulent; stamens 5(–6), irregularly alternate and opposite sepals, filaments 1.5–2 mm × 0.1 mm, glabrous, anthers 0.4–0.5 × 0.4–0.5 mm, glabrous, latrorse; disc lobed between stamens, densely puberulent. Pistillate flowers unknown, but remnant sepals (below fruits) ovate-elliptic, 1.5 × 0.6 mm, apex acute and slightly incurved, abaxial surface glabrous, adaxial surface densely puberulent; disc annular, densely puberulent; ovary unknown; style becoming subapical during fruit development, 0.5 mm; stigma subreniform, 0.5 × 1 mm, glabrous. Drupes (immature) green, 1-carpellate, ovoid-globose, 12–18 × 7–10 × 6–8 mm, apex strongly asymmetrical, sparsely to densely puberulent with very short hairs (0.1 mm). Seed 1.

Etymology. The specific epithet refers to the strongly asymmetrical drupes, which are unique among Central American *Drypetes*.

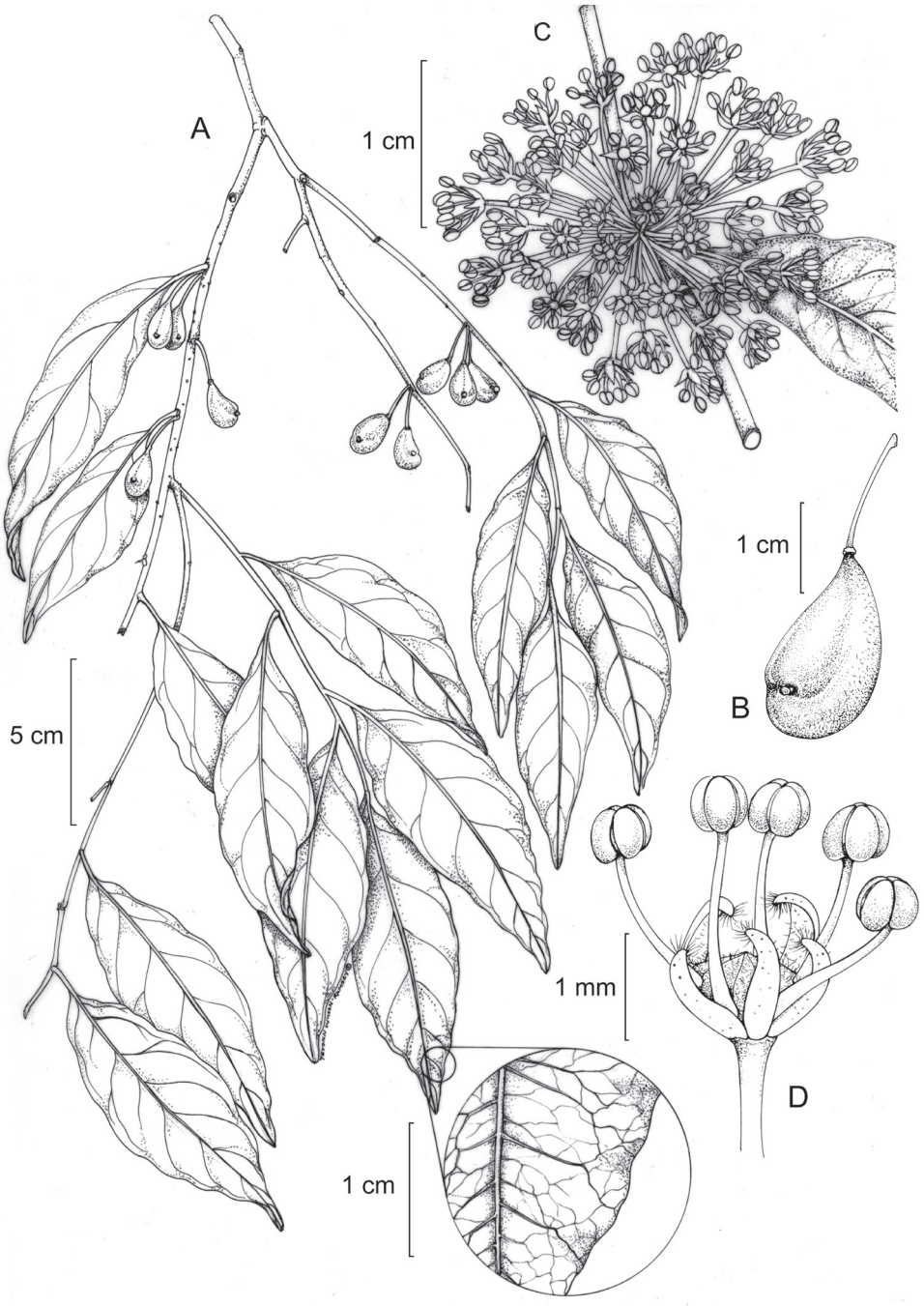

Figure 1. *Drypetes asymmetricarpa*. **A** Fruiting branch (detail of venation) **B** Immature fruit **C** Staminate inflorescence **D** Staminate flower. (**A–B** from *Grayum 6614*, MO; **C–D** from *Harmon 41*, MO).

Distribution. Known only from Costa Rica, where it is found from the north central part of the country to the central west coast. It may also be expected in extreme southern Nicaragua.

Ecology. Forests at elevations from sea level to 750 m.

Phenology. Flowering January (possibly longer, but only a single flowering specimen known). Fruiting March to June (possibly longer as only immature fruits are known).

Conservation status. Probably of Least Concern. The range of *Drypetes asymmetricarpa* spans at least 200 km. Although its habitat is highly fragmented, the species is found in Manuel Antonio National Park and near both Guanacaste and Rincón de la Vieja national parks.

Discussion. *Drypetes asymmetricarpa* was listed by Burger and Huft (1995) as *D.* sp. aff. *D. alba* and by González (2010) as *Drypetes* sp. 1 and sp. 2.

All the pistillate specimens studied have immature fruits, so their full size and color at maturity are unknown. The label on *Hammel & Trainer 17046*, with fruits 9–11 × 7–8 × 6–7 mm, says "fruits ca. 1/3 full size," but based on my experience with other species I suspect this overestimates the mature size.

Specimens examined. COSTA RICA. Alajuela: Cantón de Upala, Distrito Dos Ríos, 7.5 km NE of town, between La Jabalina and the Río Cucaracho, 10°56'N, 85°19'W, 325 m, 4 Apr 1988 (fr), *Herrera 1693* (F, ILLS, MO); **Puntarenas:** Cantón de Puntarenas, Distrito Monteverde, San Luis, finca de Chepe Rojas, al oeste del pueblo, 10°16'N, 84°50'W, 750 m, 24 Jun 1988 (fr), *Bello et al. 35* (F, ILLS, MO), *Bello et al. 58* (F, ILLS, MO); Monteverde area from Santa Elena to San Luis, 10°16'N, 84°50'W, 700 m, 16 Jun 1988 (fr), *Hammel & Trainer 17046* (F, ILLS, MO); Parque Nacional Manuel Antonio, Playa Espadilla Sur. 9°24'N, 84°10'W, 1–100 m. 2 Jan 1990 (♂ fl), *Harmon 41* (MO).

3. *Drypetes gentryi* Monach., Phytologia 3: 32. 1948, as "gentryii"

http://species-id.net/wiki/Drypetes_gentryi

Type. Mexico. Sinaloa: Capadero, Sierra Tacuichamona, rocky canyon under basaltic rim, 3500 ft., 13 Feb 1940 (fr), *H. S. Gentry 5597* (holotype: NY, isotypes: ARIZ, MICH, MO).

Distribution. Western Mexico, in the Sierra Madre Occidental from near 27° N in Chihuahua and Sonora to about 19° N in Colima.

Ecology. Tropical deciduous forests at about 100–1100m.

Phenology. Flowering December–February. Fruiting December–June.

Conservation status. Least Concern. *Drypetes gentryi* is widespread in the lower elevations of the Sierra Madre Occidental.

Discussion. When Monachino (1948) described *Drypetes gentryi*, he examined only a single specimen. No other descriptions of the species have been published, so I provide here an expanded description:

Trees 8–25 m, often with multiple trunks from near base, to 20–100 cm dbh; bark scaled and with longitudinal fissures; branches brown when young, becoming gray, minutely puberulent with spreading hairs, becoming glabrous. Leaves: stipules 0.5–0.6 × 0.7–1 mm, deltate, puberulent; petiole 6–12 × 0.7–1 mm, puberulent with spreading hairs or glabrous; blade elliptic to lanceolate, straight or somewhat curved, 4–15 × 1.5–4 cm, base asymmetrical, acute to narrowly obtuse, margins subentire to crenulate-serrulate, often undulate, apex attenuate, surfaces glabrous or very sparsely pubescent with appressed hairs especially near base, 2° veins 6–9/side. Inflorescences axillary fascicles; staminate 20–40-flowered, bracts 0.5 × 0.5 mm, deltate, puberulent, pedicels 7–14 × 0.2 mm, glabrous; pistillate 1–6-flowered, bracts 0.5 x0.5 mm, deltate, puberulent, pedicels 3–10 × 0.4–0.5 mm, puberulent when young, becoming glabrous. Staminate flowers: sepals 5(–6), linear to narrowly triangular, 1.2 × 0.4 mm, spreading and slightly incurved at apex, apex bluntly acute, margins ciliate, abaxial surface glabrous except puberulent at apex, adaxial surface puberulent; stamens 5(–6), mostly opposite sepals, filaments 1.6–2.2 mm × 0.1 mm, glabrous, anthers 0.8–1 × 0.5–0.6 mm, glabrous, latrorse; disc lobed between stamens, densely puberulent. Pistillate flowers: sepals 5, narrowly triangular to linear, 1–1.2 × 0.3–0.4 mm, spreading, entire, apex bluntly acute, abaxial surface glabrous to sparsely puberulent but densely puberulent at apex, adaxial surface densely puberulent; disc annular, densely puberulent; ovary densely puberulent; style absent; stigma apical at anthesis, becoming subapical during fruit development, subreniform, 0.8 × 1.2 mm, glabrous. Drupes (immature) green, 1-carpellate, obovoid, 12–15 × 7–9 × 6–8 mm, apex strongly asymmetrical, densely puberulent with very short hairs (0.1 mm). Seed 1.

The mature fruits are described as white (*Bye 6066*) or yellow (*Bye et al. 12847*), with the mesocarp juicy and both sweet and astringent (*Bye et al. 12847*). Spanish vernacular names include *cortopico* (*Gentry 5597*), *palo masiso* (*Bye 9707*), and *tempisque* (*Bye 3401*, *Bye et al. 12847*); in Tarahumara it is called *bapible* (*Bye 3401*) or *kafe* (*Bye et al. 12847*), and in Guarijio *joyarí* (*Felger et al. 94-56*).

Selected specimens examined. MEXICO. Chihuahua: Mpio. Batopilas, north side of Barranca de Batopilas, along arroyo Samachique between Rio Batopilas and Tarahuamara village of Wimivo, 27°09'N, 107°38'W, 900–1000 m, 30 May 1980 (fr), *Bye 9707* (ARIZ, DAV, F, GH, ILLS, MEXU, MICH, MO, NY, SD, TEX, UCR, US); **Colima:** canyon near Rio Marabasco (Cihuatlan) bridge on road to Chacala, north of Santiago, 19°17'N, 104°19'W, 200–250 m, 21 Jan 1988 (fr), *Levin & Dice 1975* (MO, SD); **Jalisco:** canyon east of Highway 200 ca. 2 km east-southeast of Boca de Tomatlan, at bridge, 20°03'N, 105°18'W, 100–200 m, 25 Jan 1988 (♂), *Levin & Dice 2001* (MO, SD); **Sonora:** Arroyo Gochico ca. 8 km E of San Bernardo, 27°02'04"N, 108°04'07"W, 300 m, 31 Jan 1988 (♀ fl, fr) *Levin et al. 2015* (MO, SD).

Acknowledgements

I thank Jochen Heinrichs for providing high-resolution scans of specimens at GOET, and the staff of the other herbaria listed for providing access to the specimens in their care. Lynn Gillespie and three anonymous reviewers provided helpful comments on the manuscript. Figure 1 was prepared by Yevonn Wilson-Ramsey.

References

Airy Shaw HK (1969) Notes on Malesian and other Asiatic Euphorbiaceae. CII. New or noteworthy species of *Drypetes* Vahl. Kew Bulletin 23: 55–62. http://www.jstor.org/stable/4117000

Burger W, Huft M (1995) Flora Costaricensis, Family #113. Euphorbiaceae. Fieldiana, Botany, ns 36: 1–169. http://www.biodiversitylibrary.org/item/20358

González J (2010) Euphorbiaceae. In: Hammel BE, Grayum MH, Herrera C, Zamora N (Eds) Manual de Plantas de Costa Rica, vol. V. Dicotiledoneas (Clusiaceae - Gunneraceae). Monographs in Systematic Botany from Missouri Botanical Garden 119: 290–394.

Grisebach AHR (1857) Systematische Untersuchungen Über die Vegetation der Karaiben, insbesondere Insel Guadeloupe. Abhandlungen der Königlichen Gesellschaft der Wissenschaften zu Göttingen 7: 151–286. http://www.biodiversitylibrary.org/item/109580

Grisebach AHR (1865) Diagnosen neuer Euphorbiaceen aus Cuba. Nachrichten von der Königlichen Gesellschaft der Wissenschaften und von der Georg-Augusts-Universität 1: 161–181. http://www.digizeitschriften.de/dms/resolveppn/?PPN=GDZPPN002510227

Howard RA (1989) Flora of the Lesser Antilles, Dicotyledoneae–part 2. Arnold Arboretum, Harvard Univ., Jamaica Plain, Massachusetts, 1–604.

Krug CWL, Urban I (1892) Additamenta ad cognitionem florae Indiae occidentalis. Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 15: 286–437. http://www.biodiversitylibrary.org/item/674

León H, Alain H (1953) Flora de Cuba. Fernandez, Havana, 1–556.

Levin GA (1986) Systematic foliar morphology of Phyllanthoideae (Euphorbiaceae) III. Cladistic analysis. Systematic Botany 11: 515–530. doi: 10.2307/2419031

Monachino JV (1948) Three new species of *Drypetes*. Phytologia 3: 32–35. http://www.biodiversitylibrary.org/item/46705

Müller J (1863) Euphorbiaceae. Vorläufige Mittheilungen aus dem für DeCandolle's Prodromus bestimmten Manuscript über diese Familie. Linnaea 32: 1–126. http://www.biodiversitylibrary.org/item/10877

Müller J (1866) Euphorbiaceae. In: de Candolle AP (Ed) Prodromus systematis naturalis regni vegetabilis, vol. 15(2). Masson, Paris, 1–1286. http://www.biodiversitylibrary.org/item/7166

Pax F, Hoffmann K (1922) Euphorbiaceae-Phyllanthoideae-Phyllantheae. In: Engler A (Ed) Das Pflanzenreich, IV, 147 XV (Heft 81). 1–349. http://www.biodiversitylibrary.org/item/61957

Stafleu FA, Cowan RS (1981) Taxonomic literature, ed. 2, vol. III: Lh–O. Bohn, Scheltema, & Holkema, Utrecht, Netherlands, 1–980. http://www.biodiversitylibrary.org/item/104137

Index to numbered collections

Abbott, W.L. 2571, 2932 (alba var. alba)
Acevedo-Rodríguez, P. 4710, 4781, 7724 (alba var. alba)
Alvarez, A. 28778, 45576 (alba var. latifolia)
Areces, A. 25812 (alba var. latifolia)
Bello, E. 35, 58 (asymmetricarpa)
Bisse, J. 16899, 22625, 26478, 34469, 46192, 47203, 47259, 53290 (alba var. latifolia)
Britton, E.G. 5154 (alba var. alba)
Britton, N.L. 2457, 2748, 4128, 4208 (alba var. alba); 5459 (alba var. latifolia); 8104, 9676 (alba var. alba); 15305 (alba var. latifolia)
Bye, R.A. 3401, 3557, 3558, 3958, 6066, 9707, 12847 (gentryi)
Duke, J.A. 7350 (alba var. alba)
Duss, A. 50, 80 (alba var. latifolia); 3628 (alba var. latifolia and Drypetes glauca Vahl); 4142 (alba var. latifolia)
Eggers, H.F.A. 2612 (alba var. alba)
Ekman, E.L. 4146 (alba var. latifolia); 4179 (alba var. alba); 4543, 4568, 4838, 5006 (alba var. latifolia); 5528 (alba var. alba); 6694, 8544, 9764, 9913 (alba var. latifolia); 12160 (alba var. alba); 12462, 18213 (alba var. latifolia); H.3512, H.3870, H.4178, H.4179, H.5134, H.5528, H.6061, H.9614, H.12160 (alba var. alba)
Felger, R.S. 94-56, 97-118 (gentryi)
Gentry, A.H. 50716 (alba var. alba)
Gentry, H.S. 3618, 5597 (gentryi)
Grayum, M.H. 6614 (asymmetricarpa)
Haenke, T. 1605 (gentryi)
Hammel, B.E. 17046 (asymmetricarpa)
Harmon, W.E. (asymmetricarpa)
Harris, W. 7098 (alba var. latifolia)
Herrera, G. 1693 (asymmetricarpa)
Holdridge, L.R. 149 (alba var. alba)
Jack, J.G. 7809 (alba var. latifolia)
Jiménez Almonte, J. de J. 1981, 4360, 5058 (alba var. alba)
León, Bro. 6081, 11800 (alba var. latifolia)
Leonard, E.C. 11589, 14257, 14268, 15686 (alba var. alba)
Lesueur, D.H. 1419 (gentryi)
Levin, G.A. 1973, 1975, 2001, 2014, 2015 (gentryi)
Liogier, A.H. 1017, 1261, 1275, 2997, 5719 (alba var. latifolia); 10466, 10714, 10779, 14325, 15661, 20858, 21293, 21600, 22628, 24490, 24537, 25846, 26463, 26835 (alba var. alba)
Little, E.L., Jr. 13297, 13366 (alba var. alba)
Luna, A. 15 (alba var. latifolia)
McVaugh, R. 1647, 25404 (gentryi)

Pérez J., L.A. 413 (gentryi)
Proctor, G.R. 9956 (alba var. latifolia)
Ricksecker, A.E. 462 (alba var. alba)
Sagra, R. de la 607 (alba var. latifolia)
Sanders, A.C. 1096 (gentryi)
Schiffino, J. 15 (alba var. alba)
Shafer, J.A. 3693, 4403 (alba var. latifolia)
Sintenis, P.E.E. 1502 (alba var. alba)
Stehlé, H. 416 (alba var. latifolia)
Valeur, E.J. 837 (alba var. alba)
Van Devender, T.R. 93-1381 (gentryi)
Wilson, P. 9287 (alba var. latifolia)
Wright, C. 498, 501 (alba var. alba and Drypetes lateriflora (Sw.) Krug & Urb.); 593 (alba var. latifolia and D. lateriflora); 1112 (alba var. latifolia); 1927 (alba var. latifolia and D. lateriflora); 1928, 1929, 1929, 593b (alba var. latifolia)
Zanoni, T.A. 36401 (alba var. alba)