

Aliso: A Journal of Systematic and Evolutionary Botany

Volume 36 | Issue 1

Article 4

2018

New Species, New Combinations and New Synonymies Towards a Treatment of Acanthaceae for the Manual de Plantas de Costa Rica

Lucinda A. McDade

Rancho Santa Ana Botanic Garden, Claremont, CA

Barry E. Hammel

Missouri Botanical Garden, St. Louis, MS

Carrie A. Kiel

Rancho Santa Ana Botanic Garden, Claremont, CA

Follow this and additional works at: <https://scholarship.claremont.edu/aliso>

 Part of the [Botany Commons](#)

Recommended Citation

McDade, Lucinda A.; Hammel, Barry E.; and Kiel, Carrie A. (2018) "New Species, New Combinations and New Synonymies Towards a Treatment of Acanthaceae for the Manual de Plantas de Costa Rica," *Aliso: A Journal of Systematic and Evolutionary Botany*: Vol. 36: Iss. 1, Article 4.

Available at: <https://scholarship.claremont.edu/aliso/vol36/iss1/4>

NEW SPECIES, NEW COMBINATIONS AND NEW SYNONYMIES TOWARDS A TREATMENT OF ACANTHACEAE
FOR THE *MANUAL DE PLANTAS DE COSTA RICA*

LUCINDA A. McDADE¹, BARRY E. HAMMEL² AND CARRIE A. KIEL^{1,3}

¹Rancho Santa Ana Botanic Garden, 1500 North College Avenue, Claremont, California 91711

²Missouri Botanical Garden, 4344 Shaw Boulevard, St. Louis, Missouri 63110

³Corresponding author (ckiel@rsabg.org)

ABSTRACT

In preparation for the publication of the *Manual de Plantas de Costa Rica*, new species, names, combinations, and synonymies are provided in six genera of Acanthaceae: *Anisacanthus*, *Chamaeranthemum*, *Dicliptera*, *Justicia*, *Ruellia* and *Stenostephanus*. The new species are **A. grace-woodiae**, **J. altior**, **J. lithophila** and **S. chavesii**. A new name at the species level, **R. leonardiana**, is provided for *R. tubiflora* var. *hirsuta*. With *Habracanthus*, *Hansteinia*, *Kalbreyeriella* and *Razisea* being subsumed within *Stenostephanus*, the new combinations **S. blepharorhachis**, **S. citrinus**, **S. leiorhachis** (= *Razisea spicata* non *S. spicatus*), **S. strictus**, **S. ventricosus**, **S. villosus** and **S. wilburii** are formalized. Seven new synonymies are presented for species of *Chamaeranthemum*, *Dicliptera*, *Justicia* and *Stenostephanus*, as well as lectotypifications in the first and latter two genera.

RESUMEN

Para facilitar la publicación del *Manual de Plantas de Costa Rica* se presentan especies nuevas, combinaciones y sinonimias en seis géneros de Acanthaceae: *Anisacanthus*, *Chamaeranthemum*, *Dicliptera*, *Justicia*, *Ruellia* y *Stenostephanus*. Las especies nuevas son **A. grace-woodiae**, **J. altior**, **J. lithophila** y **S. chavesii**. Se da un nombre nuevo a nivel de especie, **R. leonardiana**, para *R. tubiflora* var. *hirsuta*. Dado la acomodación de *Habracanthus*, *Hansteinia*, *Kalbreyeriella* y *Razisea* dentro de *Stenostephanus*, se formalizan las combinaciones nuevas **S. blepharorhachis**, **S. citrinus**, **S. leiorhachis** (= *Razisea spicata* non *S. spicatus*), **S. strictus**, **S. ventricosus**, **S. villosus** y **S. wilburii**. Siete sinonimias nuevas se presentan para especies de *Chamaeranthemum*, *Dicliptera*, *Justicia* y *Stenostephanus*, además de lectotipificaciones en el primer y los últimos dos géneros.

Key words: Acanthaceae, *Anisacanthus*, *Chamaeranthemum*, Costa Rica, *Dicliptera*, *Justicia*, *Ruellia*, *Stenostephanus*.

INTRODUCTION

Fieldwork that has supported the monumental effort to completely document the flora of Costa Rica in the form of the *Manual de Plantas de Costa Rica* (Hammel et al. 2003+) continues to reveal new species and new country records of Acanthaceae. This is true, despite the fact that the country's flora has been studied by botanists for more than 150 years, and its Acanthaceae have been treated in three major previous works (i.e., Lindau 1898; Leonard 1938; Durkee 1986). A number of new species have been discovered and described since the last countrywide treatment (e.g., Daniel 1993; Gómez-Laurito and Hammel 1994; Durkee and McDade 1996; McDade and Tripp 2007). Recently, focused effort to complete the Acanthaceae treatment for Volume IV of the *Manual de Plantas de Costa Rica* has resulted in a number of additional novelties and the need for several new combinations and synonymies.

Anisacanthus

A new species of *Anisacanthus* Nees—the first recorded for Costa Rica—has been collected from Dirí National Park on the Nicoya Peninsula, Guanacaste. This area has been the source of a number of novelties in various families (see Hammel 2012), including *Chileranthemum pyramidatum* (Lindau) T.F. Daniel (Acanthaceae), a species previously known only from Mexico and Guatemala (Daniel 1995). As discussed below, the new species of *Anisacanthus* is closely related to the two other Central American species of the genus but is quite distinct from them.

***Anisacanthus grace-woodiae* Hammel & McDade, sp. nov.** (Fig. 1–2, 8–9).—TYPE: COSTA RICA. Guanacaste: Cantón Santa Cruz. Península de Nicoya. Parque Nacional Dirí: Cerro Brujo, por el camino, cerca a las torres, 700–800 m, 19 Mar 2008, B. Hammel & I. Pérez 24533 (holotype: CR; isotypes: MO, RSA).

Similar to the other two Central American species of *Anisacanthus*, *A. nicaraguensis* Durkee and *A. tetracaulis* Leonard, plants of the new species have bright red, apparently 4-merous corollas with the stamens and style held adjacent to the middle lobe of the lower lip of the corolla at anthesis. However, they differ from both by the shorter calyx, also from *A. nicaraguensis* by the slightly shorter

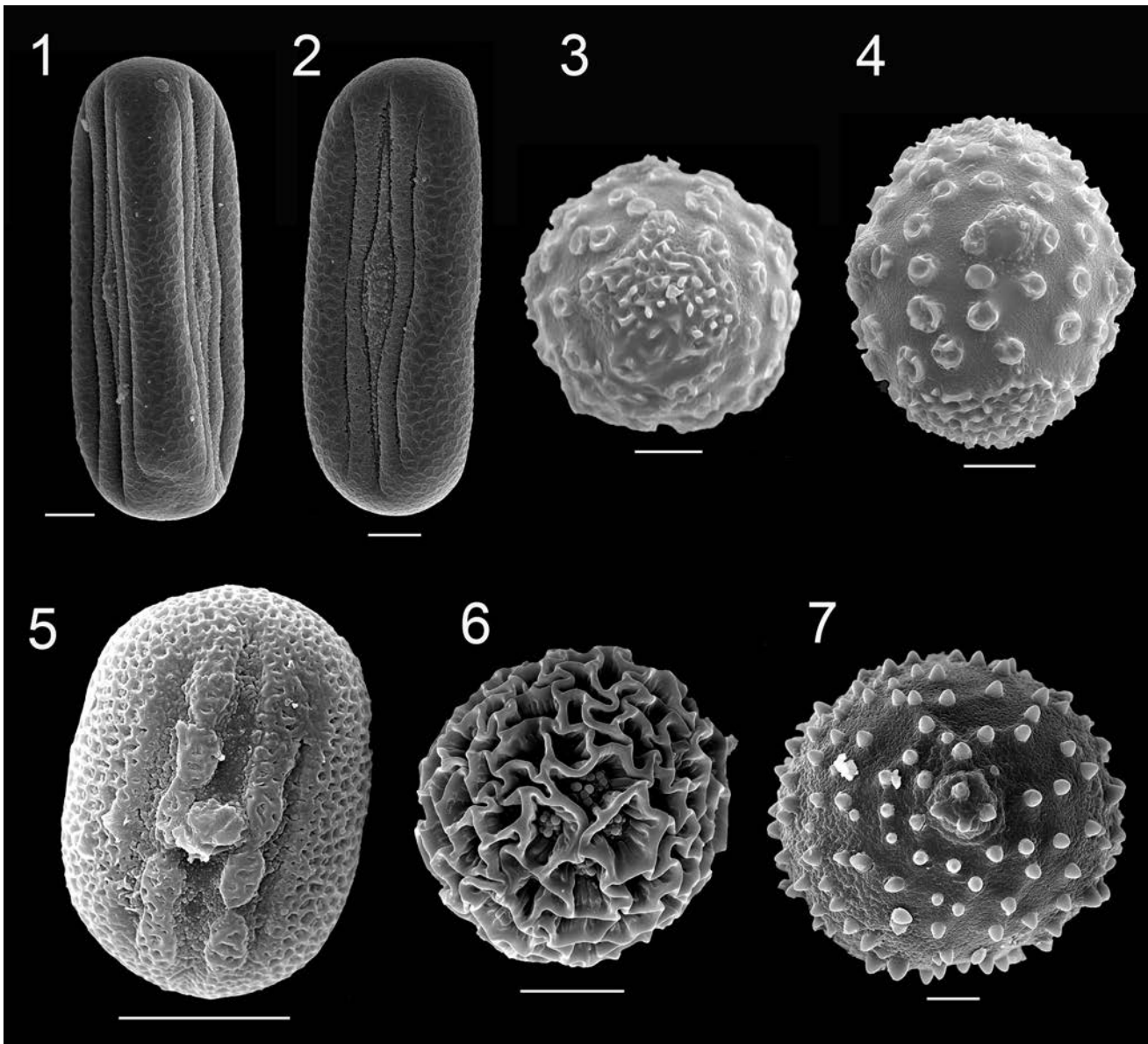


Fig. 1–7. Pollen of new species of Costa Rican Acanthaceae.—1–2. *Anisacanthus grace-woodiae*, Hammel & I. Pérez 26080 (RSA).—3–4. *Justicia altior*, Santamaría et al. 6952 (MO).—5. *Justicia lithophila*, Rivera 950 (RSA).—6. *Ruellia leonardiana* Hammel et al. 19243 (CR).—7. *Stenostephanus chavesii*, Zamora et al. 9411 (CR). (Fig. 1–7, scale bar = 10 μ m).

corolla and from *A. tetracaulis* by the lobes of the lower lip being longer and strap shaped (vs. ovate).

Erect to spreading, densely branched shrubs 0.6–1.2(–2) m tall; young stems quadrangular; cystoliths present. Leaves with the petiole 0.5–3 cm long, glabrous or with a few scattered trichomes, the blade 3–9(–10.5) \times 1.2–5 cm, basally acute to short attenuate, apically acute to acuminate, sparsely puberulent on both sides, trichomes mostly on veins. Inflorescences of terminal and axillary racemes, or panicles of racemes (sometimes with several per node, especially at distal nodes), pedunculate with peduncle 0.5–3 cm long; bracts 1.5–2 mm long, narrowly triangular, pubescent with mixed glandular and eglandular trichomes; bracteoles 1–1.2 mm long, narrowly triangular, pubescent with mixed glandular and eglandular trichomes.

Flowers one per node (bract opposite each fertile bract sterile), often secund; pedicel 1–3 mm, pubescent with mixed glandular and eglandular trichomes; calyx 5-lobed, connate basal portion ca. 0.5 mm long, the lobes equal, 3.5–4.5 mm long, pubescent with mixed glandular and eglandular trichomes; corolla lacking a styler furrow (i.e., rugula), bilabiate, red, pubescent with mixed glandular and eglandular trichomes, tube 13–15 mm long, upper lip minutely bilobed (the lobes ca. 0.5 mm long), 10–12 \times 1–2 mm, narrowly strap shaped, positioned vertically (\pm curved-patent) above throat of tube, lower lip 17–20 mm long (measured from base of upper lip), three-lobed, the lateral lobes about 10 \times 1 mm, positioned laterally (\pm curved-patent) to throat of corolla, the middle lobe 13–15 \times 1–2 mm, positioned horizontal to (i.e., continuing distal from) the tube, folded sheath-like to enclose stamens and style, all lobes strap



Fig. 8. *Anisacanthus grace-woodiae*. Photograph of living plant; insets show fruit and flower; vouchered by *Hammel 26080* (CR).



Fig. 9. *Anisacanthus grace-woodiae*. Scan of the holotype, Hammel & Pérez 24533 (CR).

shaped; stamens extending 9–12 mm beyond the middle lobe of the lower corolla lip, the anthers bithecate, the thecae equal, 3–4 mm long, evenly inserted on filament, parallel or sometimes sagitate, staminodia 0; pollen perprolate, tricolporate hexapseudocolpate, exine reticulate except granular in colpus; style exerted 0–2 mm beyond anthers, the stigma minutely bilobed. Fruits capsular (with retinacula present, persistent on capsule wall), 1.3–1.5 cm long, clavate, the stipe 0.7–0.8 cm long, seed-bearing portion discoid, 0.8–0.9 × 0.65–0.75 cm, glabrate; seeds to 4, about 5 mm in diam., flattened, minutely tuberculate.

Known only from Cerro Brujo, Parque Nacional Diríá, Santa Cruz, Guanacaste, plants of this species have been collected in flower and fruit during the dry season, January through March and in December.

Additional specimens examined.—COSTA RICA. Guanacaste: Cantón Santa Cruz. Península de Nicoya. Parque Nacional Diríá: Cerro Brujo, por el camino, cerca a las torres, 700–800 m, 4 Jan 2002, G. & D. M. Wood 2038 (CR); 2 Jan 2003, G. & D. M. Wood 3018 (CR); material cultivated from wild-collected cuttings of the type collection, established in Santo Domingo de Heredia, 24 Jan 2012, B. Hammel & I. Pérez 26080 (CR, RSA); 1 Dec 2014, Hammel 26865 (CR).

Etymology.—We are happy to name this species for Grace Wood, who first discovered this charismatic plant and whose collecting has helped make clear that the Cerro Brujo area of Costa Rica warrants considerable additional fieldwork. Grace and her husband Monty have visited Costa Rica almost annually for many years, Grace collecting plants while Monty collects flies. A gifted amateur botanist, Grace has a very good eye and it has been a joy to have her prowling the herbarium in Santo Domingo, carefully identifying her own collections, during those visits.

Among Costa Rican Acanthaceae, this species may be recognized by its densely racemose inflorescences with one flower per node, bilabiate (effectively 4-lobed), bright red flowers that are presented with the filaments clasped within the ± horizontal median lobe of the lower lip and the anthers exerted beyond that lobe, and at anthesis mostly with the lateral lobes of the lower lip held at divergent angles to the corolla tube and the minutely bilobed, vertical upper lip also held at a divergent angle to the corolla tube.

Anisacanthus grace-woodiae was included in a phylogenetic study of the *Tetramerium* lineage (Justicieae) by McDade et al. (2018), as *Anisacanthus* sp. 26865. Results showed that it is sister to the other two Central American species of *Anisacanthus*, *A. tetracaulis* and *A. nicaraguensis*; these last two are sister taxa. All three species have bright red flowers with an apparently 4-merous corolla with the stamens and style held adjacent to the middle lobe of the lower lip at anthesis. The newly described and only Costa Rican species of this genus is readily distinguished from its closest relatives by the following key:

1. Calyx 9–13 mm long; corolla 33–35 mm long; known only from Nicaragua *A. nicaraguensis*
- 1' Calyx 4–9 mm long; corolla to 30 mm long
 2. Calyx 4–5 mm long; corolla with the lower lip extending 17–20 mm beyond tube, the two lateral lobes ca. 10 × 1 mm, the middle lobe 13–15 ×

- 1–2 mm, all lobes strap shaped; known only from Costa Rica *A. grace-woodiae*
- 2' Calyx 6–9 mm long; corolla with the lower lip extending 11–14 mm beyond tube, all three lobes 3.5–6.5 × 2.5–4 mm, ovate; known from Honduras and El Salvador *A. tetracaulis*

Chamaeranthemum

Chamaeranthemum Nees, a New World genus with only four species, is very tenuously—if at all—distinct from pantropical *Pseuderanthemum* Radlk. ex Lindau. Both genera have corollas with a narrow tube that expands near the mouth and a subactinomorphic limb, two bithecate stamens and two staminodia (very rarely in Costa Rican *Chamaeranthemum*, one or both of the “staminodia” have been found fertile with the anther monothecate). Neither genus has been revised and the results of McDade et al. (2000; in progress) indicate that these genera are part of a clade referred to by these authors as the “*Pseuderanthemum* lineage,” a group that remains poorly known and requires additional phylogenetic and nomenclatural study. *Pseuderanthemum* with ca. 120 spp. is the younger, nomenclaturally. Costa Rican material of *Chamaeranthemum* may be separated from that of *Pseuderanthemum* principally by the second flowers (mostly opposite in the latter). However, whereas at least two Costa Rican species of *Pseuderanthemum* are heterostylous, all Costa Rican material of *Chamaeranthemum* we have seen appears to be homostylous. However, Lindau indicated that *C. tonduzii* Lindau had a style 15–16 mm long and a corolla with a 10 mm long tube. None of the type material, nor any other we have examined, confirms a style longer than ca. 9 mm. Lindau’s anomalous measurements are consistent with the long-styled form of a heterostylous plant, or a fairly extreme case of approach herkogamy. Neither of these seems to apply to extant Costa Rican material, but field observations are sorely lacking and more extensive collections are needed.

CHAMAERANTHEMUM TONDUZII Lindau, *Anales Inst. Fis.-Geogr. Mus. Nac. Costa Rica* 9: 184 (1896[1898]).—LECTOTYPE (chosen here): Costa Rica. Talamanca: clearings along the Río Yorkín, 50 m, Mar 1894, *Tonduz 8567*—erroneously as “8367” in the protologue—(CR; isolectotypes: BR–6943202, BR–6942496, US). Remaining syntype: Costa Rica. Dans la forêt à Terraba, 260 m, Feb 1891, *Pittier* (as *Tonduz* on the original label at CR) 3984 (BR, CR—2 sheets, both sterile).

Chamaeranthemum durandii Leonard, *Publ. Field Mus. Nat. Hist., Bot. Ser.* 18: 1208 (1938), syn. nov.—TYPE: Costa Rica. Buenos Aires: thickets along Río Ceibo, 200 m, Jan 1892, *Tonduz 6702* in part (holotype: US).

LAM has studied numerous specimens (including type material of *C. durandii*) of Costa Rican plants identified as the only two spp. known (also described) from the country, *C. durandii* and *C. tonduzii*. The former was said to be distinct from the latter by its hirsute leaves and inflorescence rachis. Indeed, one can separate specimens fairly consistently into those with glabrous leaves and a puberulous inflorescence rachis versus those with both leaves and inflorescence rachis sparsely pilose. A few specimens include material with both pubescence forms mounted on a single sheet. Also, plants of both pubescence forms rarely have

one or both of the lower stamens fertile, the anther monothe-cate. Given these patterns, we consider this to be a species with intraspecific variation in trichome and androecial features, and here synonymize *C. durandii* with the older *C. tonduzii*. The latter name had two syntypes, both here considered to belong to this one species. We have chosen *Tonduz 8567* as the lectotype because it has more known duplicates (the one at CR being the one we have studied in formulating these understandings) and with more flowers than the remaining syntype. Furthermore, the image at F of the B duplicate (presumably destroyed) has sketches on it, most likely in the hand of Lindau, showing many of the very same floral measurements used by him in the protologue. This verifies that material of the chosen lectotype was seen by Lindau, and served as an important source for his original description. As per specimens at CR and US, “*Tonduz 8367*” is actually *Cordia lucidula* I.M. Johnst. (Boraginaceae—APG Cordiaceae).

Dicliptera

Three of eight Costa Rican species of *Dicliptera* Juss. have deep magenta-purple flowers > 25 mm long, borne in long pedunculate cymes and are subtended by green, relatively small bracts: *D. iopus* Lindau, *D. skutchii* Leonard and *D. trifurca* Oerst. Study of type material of these three species indicates that *D. trifurca* and *D. iopus* are conspecific and refer to plants that are less than 1 m tall (except when supported by other plants), have corollas 33–36 mm long that are resupinate through 180° and markedly bent 4–5 mm above the base resulting in a semi-pendent presentation, and capsules 12–14 mm long. Unfortunately, for some decades, the epithet *D. trifurca* has been applied to a different species that remains unnamed pending geographically comprehensive study of this group. Plants of the undescribed species are larger in stature (to 3 m tall), have longer corollas ([4.8] 5.5–6.5 cm) that are resupinate through 360° and not bent, and capsules 18–21 mm long.

DICLIPTERA TRIFURCA Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1854: 172 (1855). *Diapedium trifurca* (Oerst.) Kuntze Revis. Gen. Pl. 2: 485 (1891) (as “trifurcatum,” but “trifurca” is correct as noun in apposition does not change according to gender of genus).—TYPE: Costa Rica. Between Cartago and Candelaria on forest edge, Jan 1845, *Oersted 10645* (holotype: C; isotype: US).

Dicliptera iopus Lindau, Anales Inst. Fis.-Geogr. Mus. Nac. Costa Rica 9: 185 (1896[1898]), syn. nov.—TYPE: Costa Rica. Forêts du Rancho Flores, 2043 m, 22 Feb 1890, *Tonduz 2136* (holotype: B; isotypes: BR, CR, US).

Because the undescribed species lacks full characterization in the literature, we provide a key to these three taxa below. In addition to the traits used in the key, LAM and CAK have observed habit differences among these three species. Plants of *D. sp. A* are self-supporting, sparsely branched shrubs to 3 m tall; those of *D. skutchii* can attain 5 m in height but are not self-supporting and must scramble on other plants. Finally, plants of *D. trifurca* rarely exceed 0.75 m in height unless sustained by other plants. Habit traits are not reliably described on herbarium specimen labels such that we do not use this trait in the key. However, we urge collectors to take note of habit when gathering specimens of these plants.

1. Leaf blades with 4–6(7) secondary veins per side; sepals connate less than 1/3 of total length; corolla usually strongly bent about 5 mm from base to become nearly pendent, tube 1.8–2.3 cm long; anther thecae about 2 mm long, displaced 0.5–1 mm *D. trifurca*
- 1' Leaf blades with 7–9 secondary veins per side; calyx connate for more than 1/3 of total length; corolla if bent then not pendent, tube > 4 cm long; anther thecae about 3 mm long, level or very slightly displaced
 2. Bracts and calyx densely glandular pubescent; flowers often bent, anthers and stigma adjacent to the lower lip as flower is presented *D. skutchii*
 - 2' Bracts and calyx lacking dense glandular pubescence (occasional glandular trichomes may be present); flowers borne erect, anthers and stigma adjacent to the upper lip as flower is presented *D. sp. A*

Justicia

The “justicioid” lineage (sensu Kiel et al. 2017) comprises the largest genus of Acanthaceae, *Justicia* L. (ca. 700 species; Daniel 2011, 2016), and at least 15 additional genera (Kiel et al. 2017). *Justicia* is globally widespread in the tropics and subtropics with species richness centered in the New World. Although the genus is highly polyphyletic, New World *Justicia* along with five smaller New World genera, *Cephalacanthus* Lindau, *Clistax* Mart., *Harpochilus* Nees, *Megaskepsma* Lindau and *Poikilacanthus* Lindau, are together monophyletic (Kiel et al. 2017, 2018). *Justicia* can be characterized by flowers with (1) a zygomorphic corolla, (2) a rugula (i.e., stilar furrow), and (3) two stamens with bithecate anthers modified in various ways (e.g., connective tissue may be expanded and thecae may be of unequal size, inserted at different levels on the filament, displaced and/or appendaged). Here, we provide descriptions for two new species and make three new synonymies. The total number of species now known from Costa Rica is 40.

JUSTICIA COSTARICANA Leonard, Publ. Field Mus. Nat. Hist. Chicago, Bot., ser. xvii. 1129 (1938).—TYPE: Costa Rica. Cartago: moist forests of El Muñeco, Río Navarro, 1400–1500 m, 6–7 Mar 1926, *Standley & Torres 51257* (holotype: US).

Justicia bitarkarae Gómez-Laur., Brenesia 33: 140–141, f. 2 (1991), syn. nov.—TYPE: Costa Rica. Limón: Reserva Biológica Hitoy Cerere, 500 m, 27 Feb 1989, *Herrera & Solís 2469*. Mixed collection, lectotype (chosen here): CR—the leafy flowering element + the detached, leafy (sterile) stem at lower right, i.e., everything but the infructescence; isolecotype: USJ—the leafy flowering element, i.e., everything but the infructescence.

Study of original material of *Justicia bitarkarae* reveals that it is a mixed collection of flowering material of *J. costaricana* and fruiting material of *Stenostephanus silvaticus* (Nees) T.F. Daniel. Lectotypification of *J. bitarkarae* is thus required. The flowering element is here chosen to lectotypify *J. bitarkarae*; in both the lectotype (CR) and the isolecotype (USJ), that element has leaves attached (the fruiting element has no leaves) and it also accounts for most of the description in the protologue. On the CR specimen at the lower right hand side there is also a piece of stem, with leaves only; that too belongs with the flowering element. Although the protologue indicates isotypes at F and

MO, no such specimen has been located at either of those institutions. Gómez-Laurito (1991) noted that long, petiolate leaves, non-imbricate bracts with glandular pubescence, five calyx segments of equal lengths and conspicuous verrucose seeds with waxy yellow projections distinguished *J. bitarkarae* from other species of *Justicia*. Excluding the seed character from the description (because it is of *S. silvaticus*), this species is indistinguishable from *J. costaricana*. *Justicia bitarkarae* thus becomes a synonym of the earlier *J. costaricana*.

JUSTICIA PITTIERI Lindau, *Anales Inst. Fis.-Geogr. Mus. Nac. Costa Rica* 9: 187 (1898).—TYPE: Costa Rica. Talamanca, Tskuinak, Haut-Zhorquin, Mar 1894, *Pittier 8642* (holotype: US).

Justicia parvibracteata Leonard, *Publ. Field Mus. Nat. Hist., Bot. Ser.* 18: 1231 (1938), syn. nov.—TYPE: Costa Rica. Cartago, wet forests in the vicinity of Pejivalle, 900 m, Feb 1926, *Standley & Valerio 47001* (holotype: US).

In his description of *Justicia parvibracteata*, Leonard (1938) mentioned affinities to *J. pittieri* but noted the former could be distinguished by bract width (1 mm wide or slightly wider vs. 2 mm, respectively). Leonard also claimed, in his key and descriptions of these two species, that the calyx lobes of the former are equal or subequal while in the latter they are distinctly unequal, with one lobe smaller than the others. On examination of the type of *J. parvibracteata* and other similar material from near the type locality, we have found the calyx to be indistinguishable from that of *J. pittieri*. It is not clear to us that Durkee studied type material of *J. parvibracteata* and *J. pittieri* when he prepared the treatment of *Justicia* for the *Flora Costaricensis* (Durkee 1986). His key brings these two out together claiming that the first has “bracts apically obtuse; leaves narrowly elliptical oblong” and the latter “bracts apically acute; leaves lanceolate elliptic.” However, even looking only at the types, it is clear that both have bracts with variably shaped apices, from acute to rounded, and both have very similarly shaped, elliptic or lanceolate elliptic leaves. His descriptions of these two don’t clearly distinguish them and he doesn’t compare them in notes after either. Durkee (1986) noted that *J. pittieri* was only known from two collections: the type, *Pittieri 8642*, from the upper Río Yorkín, Talamanca, and *Skutch 4652* from the vicinity Pejivalle in Cartago but the type of *J. parvibracteata*, *Standley & Valerio 47001*, is also from wet forests near Pejivalle. Durkee’s concept of *J. parvibracteata* (1986) was clouded by having included specimens of the species newly recognized here, *J. lithophila*, a species with features of the inflorescence and seeds more like *J. candalariae*. Our study of the type material and recent collections from all along the Atlantic slope from where the two were originally described indicates that there are no traits that unambiguously separate these two species and we here synonymize *J. parvibracteata* with the older *J. pittieri*.

JUSTICIA CANDELARIAE (Oerst.) Leonard, *Publ. Carnegie Inst. Wash.* 461: 231 (1936). *Rhytiglossa candalariae* Oerst. *Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn* 1854: 158 (1855). *Dianthera candalariae* (Oerst.) Hemsl. *Biol. cent.-amer., Bot.* 2: 517 (1882).—TYPE: Costa Rica. “In monte Candelaria,” Feb 1847, *Oersted 10683* (holotype: C; isotypes: CAS, US).

Justicia strobiloglossa V.A.W. Graham, *Kew Bull.* 43: 602 (1988). *Rhytiglossa mexicana* Oerst., *Vidensk. Meddel.*

Dansk Naturhist. Foren. Kjøbenhavn 1854: 157 (1855). *Dianthera mexicana* (Oerst.) Benth. & Hook. ex B.D. Jacks. *Index Kew.*, 1(2): 742 (1893) and 2(4): 719. 1895.—TYPE: Mexico. Veracruz, Hacienda de Jovo. May 1841, *F. Liebmann 10685* (holotype: C; isotypes: CAS, K, US), non *Justicia mexicana* Rose (1895).

Tetramerium geniculatum Brandege, *Univ. Calif. Publ. Bot.* 4: 386 (1913).—TYPE: Mexico. Veracruz, Misantla, Aug 1912, *C. Purpus 5956* (holotype: US, isotypes: F, L, MO, NY, US).

Justicia tuerckheimiana Donn. *Sm. Bot. Gaz. (Crawfordsville)* 48: 300 (1909).—TYPE: Guatemala. Alta Verapaz, Cublignitz, 350 m, Jun 1903, *H. von Tuerckheim 8726* (holotype: US).

Justicia chiapensis Brandege, *Univ. Calif. Publ. Bot.* 6: 194 (1915).—TYPE: Mexico. Chiapas, Cerro de Boquerón, Jun 1914, *C. Purpus 7285* (holotype: UC; isotypes: BM, F, US).

Justicia valerii Leonard, *Publ. Field Mus. Nat. Hist., Bot. Ser.* 18(4): 1236 (1938), syn. nov.—TYPE: Costa Rica. Guanacaste, Quebrada Serena, southeast of Tilarán, 700 m, Jan 1926, *Standley & Valerio 46147* (holotype: US).

The characters cited by Durkee (1986) to distinguish *J. candalariae* from *J. valerii* in Costa Rica included stem pubescence (pilose vs. short retrorse), shorter leaf blades (2.5–6.5 cm vs. 3.5–10 cm) and calyx pubescence (ciliolate vs. glandular-puberulous). After careful comparison of type material in addition to study of numerous specimens of both species, these traits appear to be combined in various ways. Daniel (1995) also noted that these characters varied widely among specimens of *J. candalariae* from Chiapas, Mexico. Given these patterns, we synonymize *J. valerii* with the older *J. candalariae*.

Justicia altior Kiel & Hammel, sp. nov. (Fig. 3–4, 10–11).—TYPE: COSTA RICA. Puntarenas: Cantón de Osa, entre Palmar Norte y Puerto Cortés, 9 km de la entrada a camino (Cuesta del Burro) a Fila Retinta, 800–900 m, 6 Mar 2012, *B. Hammel, C. Davidson & I. Pérez 26182* (holotype: CR; isotypes: MO, RSA).

This species is distinctive for the reddish-orange pubescence upon drying, inconspicuous cystoliths, and for its spicate inflorescences with densely imbricate bracts and light purple corollas. In those aspects it is very similar to *J. aurantiimutata* Hammel & Gómez Laur., but differs most notably by its corollas about twice as long as those of the latter.

Herb 0.3–1 m tall; stems erect, terete, densely velutinous to almost lanate (the trichomes turning reddish orange, reddish brown or tan upon drying). Leaves isophyllous, subsessile or with petioles to 0.5 cm long; blade 3–14.5 × 1.2–4 cm, lanceolate to oblanceolate, basally acute to short attenuate, apically acute to acuminate, crenulate, pilose to hirsute on both surfaces with glandular and eglandular trichomes, cystoliths inconspicuous. Inflorescences terminal and axillary, spicate, 3–8 × ca. 1 cm, the peduncle ca. 4 cm long, the rachis pilose with glandular and/or eglandular trichomes; bracts imbricate, homomorphic to slightly heteromorphic, 7–10 × 4.5–7 mm, obovate, pilose with glandular and eglandular trichomes; bracteoles 4–4.5 × 1–1.5 mm, obovate to elliptic, pubescent like the bracts. Flowers 1 per node, alternate (bract opposite each fertile bract sterile), subsecund (± in 2 rows along one side); calyx 5-lobed, the lobes subequal, 6.5–7.5 × ca. 0.3 mm, linear subulate, pubescent with



Fig. 10. ***Justicia altior***. Photograph of living plant; insets show inflorescence and flower; vouchered by *Hammel et al.* 26182 (CR).

glandular and eglandular trichomes; corolla light purple, with white nectar guides, 25–26 mm long, finely pilose distally, tube ca. 10–13 × 2 mm, the upper lip 13 mm long, the lower lip 11–13 mm long, the lobes 3–4 × 3–3.5 mm; stamens 21–22 mm long, anther thecae equal, ca. 1.5 mm long, superposed, the lower theca minutely appendaged; pollen prolate-spheroidal to subprolate, 5-porate, interapertural surfaces psilate with discrete crateriform insulae evenly distributed throughout the equatorial region and reticulate sculpturing at polar region; style 20–21.5 mm long, the stigma capitate, bilobed, lobes equal. Fruits 0.9–1 × 0.3–0.4 cm, clavate, pilose; seeds ca. 3 mm in diam., suborbicular, finely and sharply tuberculate.

Known from the Pacific slope of the eastern Cordillera de Talamanca (faldas del Cerro Amuo), Fila Costeña, in tropical wet forests, from 800–1400 m elevation, this species has been collected in flower from January to March. The pollen of *J. altior* most closely resembles that of *Poikilacanthus macranthus* Lindau (Kiel et al. 2018: Fig. 2I–J) and *P. skutchii* D.N. Gibson, which are 6- and 5-aperturate, respectively, and densely covered with insulae. However, in contrast to these, pollen of *J. altior* have insulae that are loosely spaced across the grain and are crateriform vs. planar. *Poikilacanthus macranthus* and *P. skutchii* are members of the “core *Brandegeana* lineage” which also contains four endemic Costa Rican taxa: *J. brenesii* (Leonard) D.N. Gibson, *J. densibracteata* Durkee & McDade, *J. peninsularis* Gómez-Laur. & Hammel and *J. orosiensis* Durkee. Pollen of these species is similar to that of *J. altior* with respect to aperture number > 3 (four: *J. orosiensis*, *J. densibracteata*, *J. peninsularis*; six: *J. brenesii*).

Additional specimens examined.—COSTA RICA. Puntarenas: Osa. Fila Retinto. Bosque aledaño a Torre del ICE, 860 m, 27 Apr 2016, A. Rodríguez, M. Mata & C. Vargas 14465 (CR); Osa. Fila Retinto. Approx 1.2 km north de alto Montura de Palmar, 1049 m, 14 Dec 2016, S. Lobo 3684 (CR); Coto Brus. Java River Watershed. 20 ha ribbon-shaped forest fragment approx. 1 mile west of the Las Cruces Biological Station & Wilson Botanical Garden. On a ridge of the Fila Zapote Mts. 23 Jan 2007, P. Marcum, D. Busemeyer, L. Crane, M. Feist, J. Mengelkoch, B. Molano-Flores, L. Phillippe, J. Taft, & Z. Zahawi 4528 (MO); Coto Brus. Ridge trail above La Betania where it enters primary forest. 2 Mar 1989, J. Koshear 107 (CR); Buenos Aires. P.N. La Amistad. Potrero Grande, surrounding Cerro Amuo, 1300–1600 m, 13 Jan 2012; F. González & J. Morales 3351 (CR); Buenos Aires. P.N. La Amistad. Potrero Grande, surrounding Cerro Amuo, 1300–1600 m, 13 Jan 2012; F. González & J. Morales 3352 (CR); Buenos Aires. P.N. La Amistad. Potrero Grande, surrounding Cerro Amuo, 1300–1600 m, 13 Jan 2012; F. González and J. Morales 3353 (CR); Buenos Aires. P.N. La Amistad. Potrero Grande, surrounding Cerro Amuo, 1300–1600 m, 13 Jan 2012; F. González and J. Morales 3354 (CR); Buenos Aires. Potrero Grande, La Lucha; Cerro Amuo Camino del albergue a la catarata, 1000–1100, 13 Feb 2008, D. Santamaría, F. González, W. Gamboa, C. Godínez, N. Veas Ayala, A. Rivera Cascante 6952 (CR, MO).

Etymology.—The epithet “altior” refers to this species occurring at higher elevation than the outwardly similar *Justicia aurantiimutata*.

This species is very similar to *J. aurantiimutata*; notably plants of these two species share remarkable trichomes that dry

to a reddish-orange color (see Fig. 11). However, in pollen morphology, the two species are quite different and we predict that they are not closely related among New World ‘justicioids.’ *Justicia aurantiimutata* occurs at lower elevations (0–450 m) and the two species are readily distinguished as indicated in the following key:

1. Bracts 3.5–4.5 mm wide; corolla 10–15 mm long; pollen 4-aperturate with broad reticulate bands flanking the apertures *J. aurantiimutata*
- 1' Bracts 4.5–7 mm wide; corolla 25–27 mm long; pollen 5-aperturate, psilate with crateriform insulae throughout equatorial regions and reticulate at poles ***J. altior***

Justicia lithophila Hammel & Kiel, sp. nov. (Fig. 5, 12).—
TYPE: COSTA RICA. Guanacaste: Cantón Liberia. Parque Nacional Rincón de la Vieja, Quebrada Zopilote, 1200 m, 12 Jan 1991, Gerardo Rivera 950 (holotype: CR; isotypes: MO, RSA).

This species is similar to *Justicia candelariae*, also with mostly spicate inflorescences with strongly imbricate and similarly shaped bracts, flowers with an unequally five-lobed calyx and relatively small, white or lavender corolla, and seeds with hemispherical papillae. It differs by its preference for rocks along streams; plants also have smaller bracts and smaller seeds. It is also similar to *J. pittieri*, which differs most notably by its more spicate-fasciculate inflorescences and seeds with sharply conical papillae.

Herb 0.1–0.3 m tall; stems erect (often on rocks), quadrangular, ± densely puberulous. Leaves isophyllous, the petiole 0.2–0.7 cm long; blade 1–7 × 0.3–0.8 cm, elliptic, basally attenuate, apically acuminate, entire, very sparsely puberulous (mostly along the midrib), glabrate or glabrous on both surfaces, the cystoliths visible on both surfaces. Inflorescences terminal (rarely also axillary at terminal node), spicate or spicate-fasciculate, 0.5–6 × 0.5–1 cm, subsessile or with the peduncle to 3 cm long, the rachis puberulous; bracts opposite, strongly imbricate, homomorphic, 4–6 × 1.5–2 mm, elliptic to oblanceolate, ciliate; bracteoles 3.5–5.5 × 0.5–0.8 mm, narrowly elliptic, ciliate or ciliolate. Flowers 1 or 2 per bract; calyx 5-lobed, the lobes unequal, (1.5–)3–4 × (0.1–)0.3–0.4 mm, linear or narrowly subulate, ciliolate; corolla white or lavender, the lower lip minutely red-dotted, 7–8.5 mm long, glabrous to sparsely puberulous, the tube 3.5–4.5 mm long, the upper lip 2–3 × 1 mm, the lower lip 2.5–3.5 mm long, the lobes ca. 1 × 1 mm; stamens 2 mm long, anther thecae subequal to unequal, 0.3–0.4 mm long, closely superposed, not appendaged; pollen subprolate to prolate, 2-aperturate, 4-pseudocolpate, with one row of indiscrete insulae bilaterally flanking each aperture, interapertural surfaces reticulate; style 4–4.5 mm long, the stigma oblique, lobes +/- equal. Fruits 0.45–0.5 × 0.1–0.15 cm, clavate, puberulous to glabrous; seeds ca. 0.8–1 mm in diam., ± orbicular, papillate (the papillae ± hemispherical).

Known from both slopes of the Cordillera de Guanacaste and from the Atlantic slope of the Cordillera Central, from 450–1200 m elevation; this species has been collected in flower from January to April. One collection (*Godfrey 66536*, MO), supposedly from ca. 120 m elevation on “steep forested slope, vicinity of Rincón, Península de Osa,” is so far out of range for the species that a label mix-up is suspected. In fact, Tropicos



Fig. 11. *Justicia altior*. Scan of the holotype, *Hammel et al.* 26182 (CR); note trichome color on this dried specimen.

587

INSTITUTO NACIONAL DE BIODIVERSIDAD
 CRESTADO 1997



102.057/1997

ACANTHACEAE HOLOTIPO G. Rivera 950
Justicia lithophila Hammel & Kiel
 HERBARIO NACIONAL DE COSTA RICA (CR)

FLORA DE COSTA RICA
 ACANTHACEAE dup. = 4
Justicia
 Det.

GUANACASTE: Cantón de LIBERIA
 P.N. Rincón de la Vieja
 Cordillera de Guanacaste.
 Quebrada Zopilote, a 4 Km aguas arriba
 del sendero, hacia las aguas termales.
 10°47'08"N 85°18'20"W 1200 m
 Planta con flores blancas creciendo
 sobre piedras.

INSTITUTO NACIONAL DE BIODIVERSIDAD
 ACANTHACEAE Gerardo Rivera 950
Justicia valerii Leonard

Gerardo Rivera 950 12 January 1991

INSTITUTO NACIONAL DE BIODIVERSIDAD
 EN COLABORACION CON EL MISSOURI BOTANICAL GARDEN (MO)

Identifica: J. González, IX 1996

Fig. 12. *Justicia lithophila*. Scan of the holotype, G. Rivera 950 (CR).

(www.tropicos.org) indicates that Godfrey's next number (*Godfrey 66537*) was from 700 m on "boulders...Río María Aguilar" on the Caribbean slope of Alajuela, exactly where one could expect to find *J. lithophila*. The fact that the label data indicate that *Godfrey 66537* was collected two weeks earlier than *Godfrey 66536* is further evidence of a label mix-up. On our inquiry, staff at Florida State Univ. were unable to locate the original field notes. For these reasons, we prefer to exclude *Godfrey 66536* from the formal list of specimens examined.

Additional specimens examined.—COSTA RICA. Guanacaste: Cantón de Bagaces. Río Las Flores, Hacienda Montezuma, 450 m, 25 Jan 1985, *M. Grayum, G. Herrera, O. Segura & P. Sleeper 4940* (MO); Cantón de Cañas. Camino a Nueva Guatemala, 460 m, 28 Mar 2009, *B. Hammel & I. Pérez 25114*, CR; Cantón de Liberia. Parque Nacional Rincón de la Vieja, cataratas de Río Negro, 800 m, 18 Feb 1979, *J. Gómez-Laurito 4618* (USJ); Alajuela: Cantón de Alajuela. Cerca de la unión de la Quebrada Ten Fe y Río Cariblanco, 800–950 m, 6 Mar 2003, *Kriebel 2803* (CR); Río Sarapiquí near Cariblanco, ca. 700 m, 19 Feb 1982, *W.C. Burger, J. Churchill & N. Churchill 11839* (CR); Río San Fernando, 3 km de San Miguel, ruta a Colonia Virgen del Socorro, 450 m, 28 Apr 1998, *Rodríguez, L.D. Vargas & J. González 3338* (CR, MO); Cantón de San Carlos. Río San Rafael, 2 km west of La Marina, 550 m, 21 Feb 1966, *A. Molina, L.O. Williams, W.C. Burger & B. Wallenta 17696* (MO); 500 m, 19 May 1968, *W.C. Burger & R. Stolze 5080* (CR); Cantón de Guatuso. Parque Nacional Volcán Tenorio, Estación Bijagua, El Pilón, 800–900 m, 10 Jan 2018, *E. Alfaro, I. López, & J. L. Chaves 2651* (CR, RSA); sector Los Teñideros, 700 m, 22 Mar 2005, *D. Santamaría & L. Mendez 1249* (CR).

Etymology.—The epithet refers to this species' frequent occurrence on rocks (in streams).

This species is distinctive for its plants of small stature (often growing on rocks along streams) with relatively small, narrow leaves, and for its densely bracteate, spicate or spicate-fasciculate inflorescences with one or two flowers per bract, relatively small, white or lavender flowers with an unequally 5-lobed calyx. In habit and habitat it can be very similar to plants in some populations of *J. comata* (L.) Lam. that, however, have spicate inflorescences arranged in elongate panicles, often with whorls of spikes at lower nodes, and equally 5-lobed calyces. In inflorescence and floral details the present species is more similar to *J. candelariae*. It is also somewhat similar to *J. pittieri*, which differs by its flowers in fascicles of 2–4(5) per bract, larger fruits and sharply (vs. hemispherically) papillate seeds. The new species can be distinguished from these other two as indicated in the following key:

1. Bracts spreading to weakly imbricate; flowers in fascicles of 2–4(5) per bract; fruits 0.8–1.1 × ca. 0.3 cm; seeds with sharply pointed papillae *J. pittieri*
- 1' Bracts strongly imbricate; flowers 1–(2) per bract; fruits 0.45–0.7 × 0.1–0.2 cm; seeds with hemispherical papillae
 2. Bracts 7–10 × 4–6 mm; calyx with the longest lobes 4–6 mm long; anther thecae separated by a broad connective; seeds ca. 1.5–1.6 mm in diam. *J. candelariae*
 - 2' Bracts 4–6 × 1.5–2 mm; calyx with the longest lobes 3–4 mm long; anther thecae closely superposed; seeds ca. 0.8–1 mm in diam. ***J. lithophila***

Ruellia

Genus *Ruellia* L. can be characterized by its flowers with a subactinomorphic or weakly zygomorphic and ± campanulate or funnel-shaped corolla, with four bithecate stamens, and seeds with hygroscopic trichomes. The fruits are capsular, with the retinacula persistent on the fruit wall except that species formerly treated in *Blechum* P. Browne have placentae and attached retinacula that split away from the fruit wall at dehiscence. The recent description of four new species and finding that *Blechum* (two species from Costa Rica) is nested within *Ruellia* (McDade and Tripp 2007; Tripp et al. 2009) yields a total of 22 species in Costa Rica. Here, we provide a description of an additional species, which has never been fully characterized.

Ruellia leonardiana Hammel, nom. nov. (Fig. 6, 13). Replaced synonym: *Ruellia tubiflora* Kunth var. *hirsuta* Leonard, Cont. U.S. Nat. Herb. 31: 93. 1951.—TYPE: Colombia. Meta, toward El Parrao, vicinity of Villavicencio, 500 m, 10 Nov 1938, *Cuatrecasas 4591* (holotype: US).

Herb, suffrutex or shrub 0.5–2(–3) m tall; stems erect, quadrangular, lanate. Leaves with the petiole 1–3.5 cm long; blade 10.5–19 × 4–9 cm, elliptic, cuneate to attenuate at the base, acute to (more often) acuminate at the apex, subentire to (more often) shallowly crenate, velutinous (often subappressed) on both sides, with patelliform glands ± conspicuous on the lower surface, apparently lacking on the upper. Inflorescences terminal, dense (but few-flowered), sessile or with a peduncle up to ca. 0.7 cm long, subspicate-capitate, the rachis null or up to ca. 0.3 cm long; bracts ± involucre-imbricate, 30–90 × 5–50 mm, foliaceous, elliptic, acute to acuminate at the apex, pubescent like the leaves; bracteoles not seen. Flowers sessile or subsessile with the pedicel to ca. 1 mm long, velutinous; calyx with the tube 0.5–1 mm long, the equal or subequal segments (4–)6–8 mm long, narrowly deltate to lanceolate, pilosulose and ciliate, often also with a few longer trichomes; corolla white, the tube 46–72 mm long, the proximal unexpanded part 20–37 mm long, the distal expanded part 21–35(–42) mm long, the mouth 15–18 mm wide, the lobes 8–10 × 6–10 mm, irregularly crenate-erose to emarginate, externally puberulous to tomentose; anthers included, 5.5–6 mm long; pollen spheroidal, 3-porate, surface verrucate, coarsely reticulate, reticulum homobrochate and psilate; style 31–55 mm, approximately equal in height to the anthers, the stigma to ca. 4 mm, bilobed and somewhat laminar, with one lobe smaller. Fruits ca. 1.2 cm long, ellipsoid, minutely puberulous, the placenta not fracturing; seeds potentially 6 (often only 2 develop), ca. 4 mm in diam., suborbicular, flattened, apparently glabrous.

Known from wet forest at 100–400(–800+) m elevation on the southern Pacific slope of Costa Rica (Fila Costeña and Golfo Dulce region), with flowering collections from Jan, Feb and Oct through Dec. Also known from Colombia (Meta: near Villavicencio, 500 m).

Costa Rican specimens examined.—Puntarenas: Cantón Golfito. La Gamba, alrededores de la estación, 100 m, 20 Dec 1999, *R. Aguilar 5721* (CR); Esquinas forest, 30 m, 26 Nov 1951, *Allen 6316* (MO); Parque Nacional Pedras Blancas, sendero Don Tacho, 100 m, 1 Nov 1997, *E. Fletes 517* (CR); Sector Río Esquinas, 400–500 m, 11 Feb 1991, *G. Induni 221* (CR); Sector de Esquinas, 9 Feb 1990, *R. Soto 4151* (USJ);



842

COSTA RICA INBIO
 INSTITUTO NACIONAL DE BIODIVERSIDAD
 C/10000 503179

INSTITUTO NACIONAL DE BIODIVERSIDAD
 HERBARIO (INB)

0 1 2 3 4 5 6 7 8 9 10
 cm
 copyright reserved

ACANTHACEAE U. Chavarría 495
 Ruellia leonardiana Hammel
 HERBARIO NACIONAL DE COSTA RICA (CR)

FLORA DE COSTA RICA
 ACANTHACEAE dup. = 1
 Ruellia
 Det.
 PUNTARENAS: R.N.V.S. Golfito
 Entre Golfito y Villa Briceño, 3 Km al
 NW del campo de aterrizaje. Camino norte
 Quebrada Rancho.
 8°40'20"N 83°12'10"W 400 m
 Arbusto de 1.5 m. Flor blanca.

INSTITUTO NACIONAL DE BIODIVERSIDAD
 ACANTHACEAE Uliases Chavarría 495
 Ruellia tubiflora Kunth
 Identifica: B. Hammel, July 1994

Uliases Chavarría 495 27 January 1992
 E. Bello B. Hammel A. Moreno J. Marín
 INSTITUTO NACIONAL DE BIODIVERSIDAD
 EN COLABORACION CON EL MISSOURI BOTANICAL GARDEN (MO)

Fig. 13. *Ruellia leonardiana*. Scan of a representative specimen, *Chavarría et al.* 495 (CR).

Estación Esquinas, 100 m, 21 Nov 1993, *M. Segura* 239 (CR); Bosque de los Austriacos, 150 m, 15 Jan 1998, *Huber & Weisenhofer* 839 (CR); Parcela UCR en la margen izquierda de la Quebrada la Gamba, 140 m, 10 Dec 2006, *E. Chacón et al.* 758 (USJ); Reserva Nacional de Vida Silvestre Golfito, Fila Gamba, 100 m, 24 Oct 1993, *Hammel* 19103 (CR, MO); 3 km al NW del campo de aterrizaje, 400 m, 27 Jan 1992, *U. Chavarría, E. Bello, B. Hammel, A. Moreno & J. Marín* 495 (CR); Cantón Osa. Cerro Anguciana, 800–900 m, 9 Dec 1993, *B. Hammel, R. Aguilar & M. Grayum* 19243 (CR, MO).

Etymology.—The epithet chosen is in keeping with the botanical tradition of honoring the author of a replaced name. In the case of Leonard, prolific student of New World Acanthaceae (author of more than 500 epithets in the family), the wonder is that he had yet to be so honored in *Ruellia*.

Following the taxonomy of Tripp and Luján (2018), the treatment of *Ruellia* for the *Manual de Plantas de Costa Rica* (Hammel et al. 2003+) will again recognize *Ruellia tetrastichantha* Lindau [syn. *R. tubiflora* var. *tetrastichantha* (Lindau) Leonard] at the level of species. Likewise, *R. tubiflora* var. *hirsuta* Leonard is easily recognized and we here elevate it to species level. Both of these species have pure white corollas, whereas *R. tubiflora*, not known from Costa Rica, has corollas with a purple spot in the throat (corolla lobes may also be suffused with purple). *Ruellia leonardiana* may be distinguished from *R. tetrastichantha* by its very different pubescence (leaf blades velutinous vs. glabrous or at most pilosulose in *R. tetrastichantha*), and by its consistently terminal inflorescences (vs. both terminal and axillary) with persistent bracts (vs. soon deciduous) that thus apparently do not produce the notably naked condensed rachis—cone-like in fruit—that is so characteristic of *R. tetrastichantha*. We note that extreme variation is reported in the length of the corolla tube in both of these species, as well as in the lengths of the unexpanded basal portion and the expanded distal portion (see McDade and Tripp [2007] for explanation of terms). This variation, based apparently on open flowers on herbarium specimens, merits further examination, ideally including population-level samples of fresh flowers. The new species can be confused with *R. odorata* E. Tripp & McDade, which has the leaf blades at most strigose and appressed puberulous along the principal veins, smaller bracts (10–23 × 2–5 mm), longer calyx lobes (10–14[–18] mm long), and is known only from the nearby, but biogeographically distinct, Osa Peninsula. The Costa Rican species of *Ruellia* with pure white flowers may be distinguished by the following key:

Key to the Costa Rican species of *Ruellia* with corollas uniformly white:

1. Corollas (excluding lobes) ca. 30 mm long *R. golfodulcensis* Durkee
- 1' Corollas (excluding lobes) > 45 mm long
 2. Inflorescences of dense, short spikes; bracts leaf-like (sometimes pale green to whitish), ovate to elliptic; calyx lobes < 10 mm long
 3. Leaf blades velutinous; inflorescences terminal; bracts persistent in fruit, old inflorescences not cone-like ***R. leonardiana***
 - 3' Leaf blades glabrous to sparsely strigose or puberulous on veins; inflorescences axillary and terminal; bracts deciduous soon after flowering, old in-

- florescences often appearing as scarred, cone-like stumps *R. tetrastichantha*
- 2' Inflorescences of axillary or terminal few-flowered clusters, not as above; bracts not leaf-like; calyx lobes > 15 mm long
 4. Herbaceous to woody plants to 2(–3) m tall; calyx lobes (26–)37–55 mm long; narrow, basal portion of corolla tube approximately equal to or shorter than expanded portion; anther thecae > 5 mm long; fruits > 2.5 cm long *R. praeclara* Standl.
 - 4' Herbaceous plants to 1.3 m tall; calyx lobes < 30 mm long; narrow, basal portion of the corolla tube ca. 2× longer than expanded portion; anther thecae ≤ 5 mm long; fruits < 2.5 cm long
 5. Calyx (in flower) 10–14 × 1–2 mm, vil-
lous; bracts 10–23 × 2–5 mm; fruits to 1.7
cm long; forest understory; Pacific slope, Osa
Peninsula *R. odorata*
 - 5' Calyx (in flower) 25–30 × 4–5 mm, puberu-
lous; bracts 22–40 × 0.6–2.3 mm; fruits 2–2.3
cm long; swamps and water-logged soils; At-
lantic slope, Guanacaste and Central mountain
ranges *R. palustris* Durkee

Stenostephanus

The genera *Habracanthus* Nees and *Hansteinia* Oerst., both with Costa Rican species, have been accepted on morphological grounds as synonyms of *Stenostephanus* Nees, with some new combinations already made. *Kalbreyeriella* Lindau and *Razisea* Oerst., also with Costa Rican species, have been suspected as possibly also better placed in *Stenostephanus* (see, e.g., Daniel 1999). More recent molecular phylogenetic studies (e.g., Kiel et al. 2006) have supported the inclusion of all four genera within a thus monophyletic *Stenostephanus*, characterized by bilabiate, more or less tubular corollas lacking a rugula, two stamens with monotheccate anthers, these held, with the style, adjacent to the upper lip of the corolla, staminodia lacking, and capsular fruits with the retinacula remaining attached to the fruit wall. These plants also share pollen that is banded or “girdled” (i.e., “Gürtelpollen” sensu Lindau 1895). We here provide the remaining new combinations, a few new synonymies and one new species description that are necessary to accommodate the Costa Rican species of *Stenostephanus*. Note that we use “T.F. Daniel ex” in cases where our colleague Tom Daniel has proposed the new combinations via Tropicos as well as annotations on specimens at various herbaria (e.g., K, MO, US), but the changes have not yet been published. This brings the total species known for the country to 12.

Stenostephanus blepharorrhachis (Lindau) T.F. Daniel ex Hammel, comb. nov.

Basionym: *Kolobochilus blepharorrhachis* Lindau, *Anales Inst. Fis.-Geogr. Mus. Nat. Costa Rica* 9: 189 (1896 [1898]), and in Pitt., *Prim. fl. Costaric.* 2: 309. 1900. *Hansteinia blepharorrhachis* (Lindau) Durkee, *Fieldiana, Bot.*, n.s. 18: 43 (1986).—TYPE: Costa Rica. [et Veragua (not on label)], sine loco speciali, *Warszewicz s.n.* (B—photo; F, MO). Original specimen apparently lost, neotype (chosen here): Costa Rica. Puntarenas: Monteverde Cloud Forest Reserve, along El Camino,

Sendero Brillante, and Bosque Nuboso. Cloud forest, 1550 m, 24 Feb 1992, *Daniel & Almeda 6361* (CAS; isoneotypes; CR, MO, US).

Razisea breviflora D.N. Gibson. Fieldiana, Bot. 34: 77 (1972).—TYPE: Costa Rica. Heredia, dense, wet forest, slope of Volcán Barba, 1950 m, 24 Oct 1964, *Hatheway 1270* (holotype: F).

BEH has examined numerous specimens of this Costa Rican endemic and has studied and collected material at one population in the field. The type specimen—with no known duplicates, no paratypes cited, nor other material known to have been used—is represented only in photos produced by McBride's Berlin negatives, made available online at F: http://emuweb.fieldmuseum.org/botany/search_berlin.php.

While these specimens do not themselves serve as types, they unquestionably help to understand the species. In this particular case, an illustration of floral parts (including a pollen grain!), most likely in Lindau's hand, is clearly visible and gives the very measurements used in the protologue description. One might consider that an uncited illustration that comprises part of the original material and use it as lectotype according to Article 9.12 of the Code (Turland et al. 2018). But since there is no longer any physical specimen, nor illustration, we chose a neotype. Although the protologue shows "Costa Rica et Veragua [i.e., Panama]" as the locality, the label itself says only "Costa Rica." Furthermore, the species is not otherwise known from Panama and was not treated in the *Flora of Panama* (Durkee 1978). The neotype we chose has numerous duplicates, some of which have been available to us for study and allow us to determine that it coincides with Lindau's protologue. The duplicate at US is scanned and available on the NMNH Botany Collections site: <http://n2t.net/ark:/65665/39333371c-b932-4979-963d-1342f9eeca1>.

Stenostephanus citrinus (D.N. Gibson) McDade & Hammel, comb. nov.

Basionym: *Razisea citrina* D.N. Gibson, Fieldiana, Bot. 34(6): 78 (1972).—TYPE: Costa Rica. Puntarenas: evergreen forest between Agua Buena and San Vito de Java, 1200 m, 22 Oct 1964, *Jiménez 2475*, (holotype: F; isotype: CR).

Stenostephanus leiorhachis (Lindau) Hammel, comb. nov.

Basionym: *Kolobochilus leiorhachis* Lindau, Anales Inst. Fis.-Geogr. Mus. Nac. Costa Rica 9: 188 (1896[1898]). Lectotype (chosen here): Costa Rica. [Limón:] Dans les bois à Siquirres, 100 m, *Pittier 3168* (BR-694261; isolectotypes: BR-694294, CR, US). Remaining syntypes: Costa Rica. Loco speciali non adnotato, no date, *Warszewicz s.n.* (B-photo at F); bord de la route à Carrillo, 300 m, versant atlantique, *Pittier* (as *Tonduz* on the original label at CR) *2494* (BR, CR); dans les bois à Siquirres, 100 m, *Pittier 3166* (BR, CR); forêts de Golfito, Golfo de Osa, *Pittier 9913* (BR); bois de la vallée du R. Tuis, 650 m, *Tonduz 8084* (BR); bois de la vallée du R. Tuis, 650 m, *Tonduz 8285* (BR, CR); bois de la vallée du R. Tuis, 650 m, *Tonduz 8379*—published as "8370"—(BR, CR); lieux humides à Las Delicias, llanos de Santa Clara, *Biolley 10664* (BR, CR).

Razisea spicata Oerst. Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1854(8–12): 142 (1855).—TYPE: Costa Rica. Alajuela: Bjerget Aguacate [Cerro de Aguacate], 2000 ft., Nov, *Oersted 10710* (holotype: C). Blocking name: *Stenostephanus spicatus* Wassh. & J.R.I. Wood. 2001.

Wasshausen and Wood (2001) used the enormously common epithet "spicatus" for a very rare Ecuadorian species of *Stenostephanus* with small green flowers. Lack of originality in the choice of epithets can have repercussions and we must now find a different epithet for one of southern Central America's most common and spectacular acanths. *Kolobochilus leiorhachis* has long been considered synonymous with *Razisea spicata* and no earlier contenders are known. That name had nine syntypes, all of them more or less identical and here considered to belong to this one species. The one chosen as lectotype (with good flowering material, at least at BR) is apparently the only one that has duplicates at three different herbaria.

Stenostephanus strictus (Leonard) T.F. Daniel ex Hammel, comb. nov.

Basionym: *Glockeria stricta* Leonard, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1219 (1938); *Hansteinia stricta* (Leonard) D.N. Gibson, Fieldiana, Botany 34: 63. 1972.—TYPE: Costa Rica. San José, moist forest, vicinity of Santa María de Dota, 1500–1800 m, 26 Dec 1925–3 Jan 1926, *Standley & Valerio 43311* (holotype: US; isotype: F).

Kalbreyeriella rioquebradasiana Hammel, Novon 4(4): 357, f. 5 (1994), syn. nov.—TYPE: Costa Rica. San José, Canton de Perez Zeledon: Cerro de la Muerte, carretera interamericana km 115–116, 1750 m, 4 Feb 1991, *Hammel et al. 18053* (holotype: CR; isotypes: ARIZ, CAS, F, MO, US, USJ).

Had BEH had access to relevant phylogenetic information when attempting to identify the material that he went on to describe as *Kalbreyeriella rioquebradasiana*, he would have realized the necessity of studying species then treated as *Hansteinia* (especially *H. stricta*, of which there were no named specimens at MO nor Costa Rican herbaria, at the time) as possibly relevant to his putative new taxon. The fact that some of these plants are poorly collected and not easy to capture in descriptions adds to the challenge.

Stenostephanus ventricosus (Donn. Sm.) T.F. Daniel ex Hammel & McDade, comb. nov.

Basionym: *Glockeria ventricosa* Donn. Sm., Bot. Gaz. 27: 439 (1899). *Hansteinia ventricosa* (Donn. Sm.) D.N. Gibson, Fieldiana, Bot. 34(6): 63 (1972).—TYPE: Costa Rica. Volcán de Barba, Alto de Roble, 2609 m, Jan 1891, *Pittier 3519* (lectotype [chosen by Durkee, Fl. Panama p. 203. 1978]: CR; isolectotype: US).

Stenostephanus villosus (Gómez-Laur. & Hammel) McDade, comb. nov.

Basionym: *Razisea villosa* Gómez-Laur. & Hammel, Novon 4: 357–361, f. 6, 7F (1994).—TYPE: Costa Rica. Puntarenas, Golfito, Jiménez, Dos Brazos de Rio Tigre, margen izquierda de Quebrada brailena, Fila Puriscal Rico, subiendo a Cerro Müller, 700 m, 24 Nov 1990, *Herrera & Fallas 4641* (holotype: CR; isotypes: ARIZ, CAS, F, MO, US).

Stenostephanus wilburii (McDade) McDade, comb. nov.

Basionym: *Razisea wilburii* McDade, Syst. Bot. 7: 493–496, f. 3–4 (1982).—TYPE: Costa Rica. Heredia, Finca La Selva at confluence of Ríos Sarapiquí and Puerto Viejo, near town of Puerto Viejo de Sarapiquí, 100 m, 5 Dec 1979, *Wilbur 28248* (holotype: DUKE).

STENOSTEPHANUS GRACILIS (Oerst.) T.F. Daniel, Proc. Calif. Acad. Sci., ser. 4. 48: 280 (1995). Basionym: *Hansteinia gracilis* Oerst. Vidensk. Meddel. Dansk Naturhist. Foren.

Kjøbenhavn 1854 (8–12): 143 (1855).—TYPE: Costa Rica. San José, Mt. Jaris [name not on current maps, but presumably close to the town of Jaris], Nov 1846, *Oersted 10660* (holotype: C; isotype: CAS; probable isotype: K).

Habracanthus tilaranensis Gómez-Laur., *Novon* 4: 350, f. 1 (1994), syn. nov.—TYPE: Costa Rica. Puntarenas, Esparza, Peñas Blancas Refugio de Vida Silvestre, 1000–1400 m, 30 Nov 1986, *Herrera et al. 292* (holotype: CR; isotype: MO).

On transferring *Hansteinia gracilis* to *Stenostephanus*, Daniel mentioned *G. Herrera et al. 292*, the type of *Habracanthus tilaranensis*, without making the latter a synonym, nor even mentioning the name. BEH has studied said type and other material so identified, as well as recent material collected from near the type locality of *S. gracilis*, and concluded that all material pertains to this one species.

Stenostephanus chavesii Hammel, sp. nov. (Fig. 7, 14–15).—TYPE: COSTA RICA. Guanacaste: Cantón Bagaces. Zona Protectora Miravalles, sector Caralampio, 1200–1300 m, 7 Feb 2000, *J. L. Chaves 137* (holotype: CR; isotype: MO).

This species is similar to *Stenostephanus leiorrhachis*, also with relatively large red corollas with the tube gradually expanded from the base to the mouth, but differs most notably by its leaves with the blade basally rounded to cordate (vs. cuneate and long decurrent), with the upper surface pilosulose (vs. usually glabrous).

Herb or shrub 0.5–3 m tall; stems tomentose to glabrescent. Leaves with the petiole 0.5–10 cm long, the blade 18–26 × 8–13 cm, ovate, the base rounded, often cordate, rarely obtuse, the apex acuminate, ± appressed pubescent (on the principal veins) on both sides, the surface glabrous below and pilose above, with 12–17 secondary veins per side. Inflorescences terminal and (rarely) axillary, racemose or racemose-fasciculate, dense, 13–36 × 3–8 cm (including the corollas), with the peduncle 1–7 cm long, the rachis tomentose; bracts opposite, 5–7 mm long, narrowly lanceolate, ciliate; bracteoles 3–4 mm long, narrowly lanceolate, ciliate. Flowers 1 per bract or sometimes in fascicles of 2 or 3 per bract, the pedicel 1–3 mm long; calyx 5-lobed, the lobes equal, 7–9 × 0.8–1 mm, minutely ciliate and sometimes appressed pubescent; corolla bilabiate, red, the tube (40–)45–50 mm long, gradually inflated from the base, 10–14 mm wide at the mouth, puberulous (mostly on the principal nerves and distally), the upper lip subentire, 9–13 mm long (held horizontal or curved upward), the lower lip minutely 3-lobed, barely distinct from the mouth of the tube; anthers 4–5 mm long; pollen spheroidal to prolate-spheroidal, verrucate, 2-porate, each pore surrounded by a circular psilate region separated by a poorly defined peripheral band; style 59–65 mm long, the stigma clavate and entire or minutely bilobed, lobes equal. Fruits 2–2.5 cm, glabrous; mature seeds not seen, submature seeds ca. 2.5 mm in diam., ovate to orbicular, flattened, rugose-muricate.

Known from the Atlantic slope and near the Continental divide of the Cordilleras de Guanacaste, de Tilarán and Central, this species has been collected in flower from February to May and September to November.

Additional specimens examined.—COSTA RICA. Alajuela: Cantón Upala. Volcán Tenorio, 600–700 m, 11 Sep 2000, *J.L. Chaves 814* (CR); 7 Oct 2000, *J.L. Chaves 896* (CR, MO); 11 Feb 2000, *J.L. Chaves & I. López 187* (CR); 21 Nov 2000, *A. Rodríguez 6794* (CR, MO, USJ); Parque Nacional Guanacaste,

Estación San Ramón, 550 m, 23 Nov 1995, *J. Quesada, M.M. Chavarría, C. Cano y C. Moraga 315* (CR); Estación San Gerardo, Senderos Frío y Danta, 12 Nov 2016, 796 m, *N. Zamora, J. Cai, Y. Tingshuang, Z. Ting, R. Espinoza, C. Cano, E. Araya 9411* (CR); Rincón Rain Forest, Estación Caribe, camino a Colonia Libertad, Sendero Guarumo, 368 m, 27 Nov 2017, *N. Zamora, R. Espinoza, J. Hernández, A. Córdoba, P. Umaña, C. Cano, & E. Araya 10128* (CR); Rincón Rain Forest, Sendero al cráter Volcán Rincón de la Vieja, entrando por el albergue Sensoria, 865 m, 30 Nov 2017, *N. Zamora, R. Espinoza, J. Hernández, A. Córdoba, C. Cano, E. Araya, P. Umaña, J. Pérez 10193* (CR); Cantón San Ramón. 12 km north-northwest of San Ramón by road on way to San Lorenzo, 1100 m, 25 Apr 1983, *Liesner & Judziewicz 14897* (MO); Reserva Biológica Alberto Manuel Brenes, 870–1120 m, 1 Mar 1992, *E. Schmidt 811* (CR); Guanacaste: Cantón Liberia. Parque Nacional Rincón de la Vieja, Quebrada Rancho Grande, 950 m, 28 Nov 1987, *G. Herrera 1452* (MO, USJ); Heredia: Cantón Sarapiquí. Vara Blanca de Sarapiquí, north slope of Central Cordillera, 1500–1750 m, Jul–Sep 1937, *Skutch 3326* (MO); Rara Avis, ca. 15 km al suroeste de Horquetas, 400 m, 2 Oct 1989, *O. Vargas 191* (CR); La Tirimbina, ca. 200 m, 5 Sep 2007, *J. Gonzalez 10313* (LSCR–image); 14 Oct 2008, *J. González 10419* (LSCR–image). Puntarenas: Cantón Puntarenas. Cabeceras del río Aranjuez, orillas de quebrada Socorro, 1250 m, 27 May 1996, *P. Kuss 88* (CR).

Etymology.—We name this species in honor of former parataxonomist José Luis Chaves Chaves, who made the type collection (and many others) of this new species as well as many other interesting collections from the Cordillera de Guanacaste, especially on the slopes of the Tenorio and Miravalles volcanos.

Among the *Stenostephanus* species with the corolla tube gradually expanded from the base towards the mouth and spicate to narrowly racemose (flowers short pedicellate) inflorescences, *S. chavesii* stands out for its leaves with the blade rounded to often cordate at the base, and pilosulose on the upper surface. In leaf shape, it can be very similar to *S. citrinus*, which differs markedly by its widely paniculate (vs. narrowly racemose) inflorescences and bright yellow flowers. Likewise, *S. wilburii* can also have leaf blades that are basally obtuse, if not cordate, but that species has shorter corollas. The following key will distinguish among the red-flowered species of *Stenostephanus* with a narrowly racemose inflorescence and corollas with a tube that gradually expands from the base:

1. Leaf blades cuneate and often long decurrent at the base; corolla tube 35–55 mm long ***S. leiorrhachis***
- 1' Leaf blades cuneate but not decurrent, or (more often) obtuse to rounded and sometimes cordate at the base; corolla tube 23–50 mm long
 2. Corolla tube 23–27 mm long; leaf blades glabrous on both surfaces ***S. wilburii***
 - 2' Corolla tube 30–50 mm long; leaf blades villous or pilosulose, at least on the upper surface
 3. Leaf blades cuneate at the base, villous on both surfaces, with 8–11(–16) secondary veins per side; bracts 4–5 mm long; corolla tube 30–35 mm long ***S. villosus***
 - 3' Leaf blades obtuse or, more often, rounded and sometimes cordate at the base, ± appressed pubescent on the principal veins on both surfaces, the surface

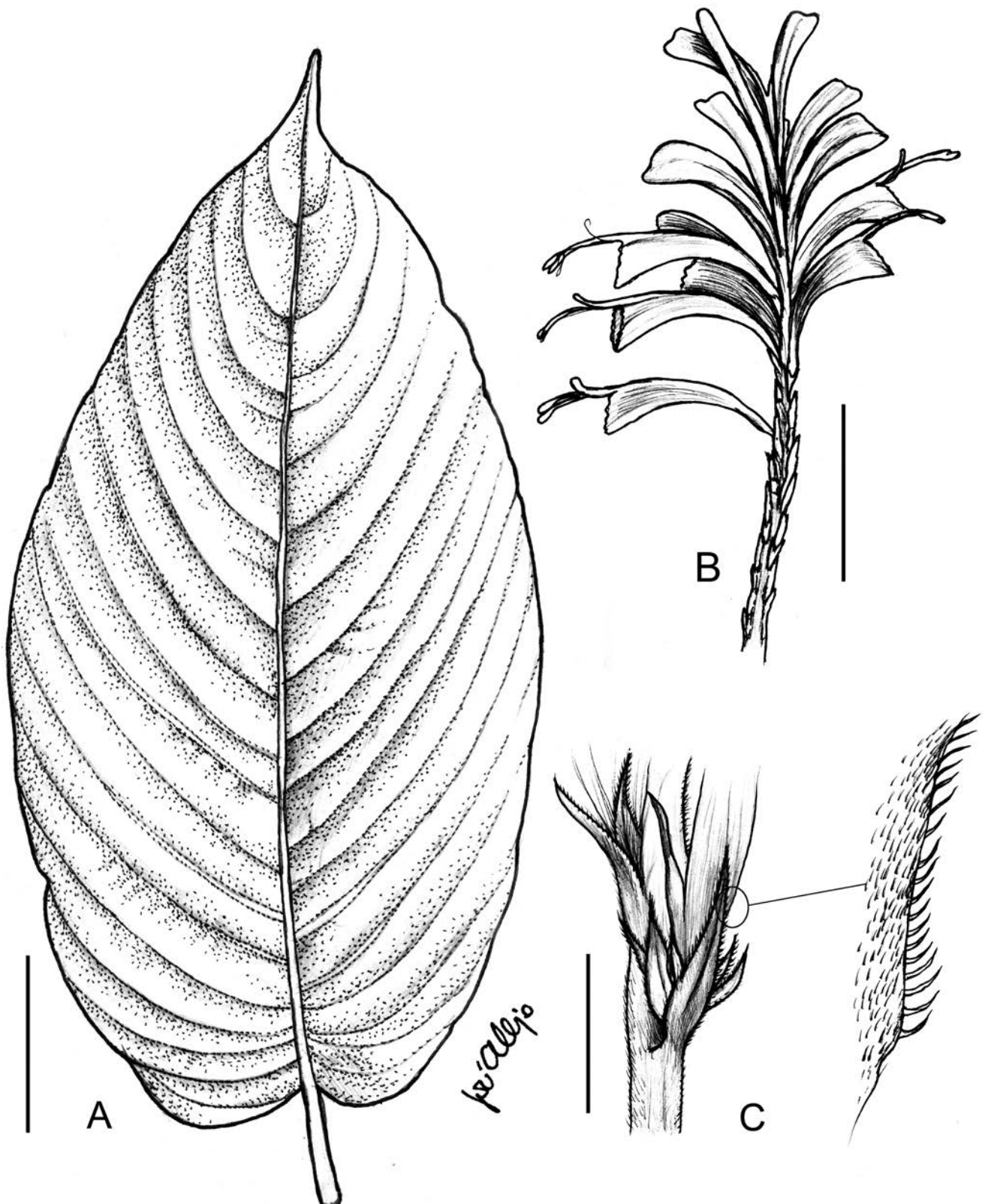
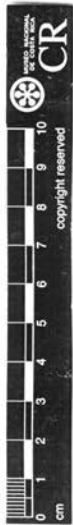


Fig. 14. *Stenostephanus chavesii*. A. Leaf; scale bar = 5 cm. B. Inflorescence; scale bar = 50 mm. C. Inflorescence bracts showing close-up of the margin of one bract; scale bar = 5 mm. *Chaves 137* (CR).

26430



ACANTHACEAE HOLOTIPO J. L. Chaves 137
 Stenostephanus chavesii Hammel
 HERBARIO NACIONAL DE COSTA RICA (CR)



Flora de Costa Rica

Acanthaceae dup. #5

Razisea citrina D. N. Gibson

Det. L. Acosta, 16/05/2001

Guanacaste: Bagaces: Z.P. Miravalles. Cuenca del Tempisque. Z.P. Miravalles, Sector Caralampio, colectando en bosque y potrero.

10:42:33.0620 N -85:07:03.6140 W 1200 a 1300 m

Hierba, flores rojas.

J. L. Chaves 137

07/02/2000

Instituto Nacional de Biodiversidad (INB)
 En colaboración con el Missouri Botanical Garden (MO)

Fig. 15. Stenostephanus chavesii. Scan of the holotype, Chaves 137 (CR).

glabrous below, pilosulose above, with 12–17 secondary veins per side; bracts 5–7 mm long; corolla tube (40–)45–50 mm long **S. chavesii**

ACKNOWLEDGEMENTS

We are grateful to Reinaldo Aguilar of Puerto Jiménez for his wealth of knowledge of plants of the Golfo Dulce region, especially the Osa Peninsula. He has been instrumental in the discovery of many new species or new country records. He assisted all three authors on one trip to the area and BEH on numerous. We are also grateful to Thomas F. Daniel for responses to numerous inquiries, to Michael Grayum for nomenclatural consultations, to illustrator José Alejandro Herrera, and to curatorial staff at CR, F, FSU, MO, RSA and USJ. We appreciate the careful work of two anonymous reviewers, which improved the manuscript. Funding from the Torrey Botanical Society (CAK) and from the U.S. National Science Foundation to LAM (DEB 9707693, DEB 0108589, DEB 0743178) and to CAK and LAM (DEB 1754845) was instrumental in accomplishing work on the Acanthaceae treatment for the *Manual de Plantas de Costa Rica*, as was the support of the Organization for Tropical Studies and Instituto Nacional de Biodiversidad (INBio).

LITERATURE CITED

- DANIEL, T. F. 1993. Taxonomic and geographic notes on Central American Acanthaceae. *Proc. Calif. Acad. Sci., ser. 4*, **48**: 119–130.
- . 1995. Flora of Chiapas, Part 4: Acanthaceae. California Academy of Sciences Press, San Francisco.
- . 1999. Revision of *Stenostephanus* (Acanthaceae) in Mexico. *Contr. Univ. Michigan Herb.* **22**: 47–93.
- . 2011. *Justicia* (Acanthaceae) in Texas. *J. Bot. Res. Inst. Texas* **5**: 595–618.
- . 2016. Vascular plants of Arizona: Acanthaceae acanthus or shrimp-plant family. *Canotia* **12**: 22–54.
- DURKEE, L. H. 1978. Acanthaceae, in Flora of Panama. *Ann. Missouri Bot. Gard.* **65**: 155–283.
- . 1986. Acanthaceae, in W. BURGER (ed.), Flora Costaricensis. *Fieldiana, Bot.* **18**: 1–87.
- AND L. A. MCDADE. 1996. Three new species of *Justicia* (Acanthaceae) from Costa Rica. *Novon* **6**: 13–21.
- GÓMEZ-LAURITO, J. 1991. Two new species from the Caribbean of Costa Rica. *Brenesia* **4**: 139–143.
- AND B. E. HAMMEL. 1994. New species of Acanthaceae of Costa Rica. *Novon* **4**: 350–361.
- HAMMEL, B. E. 2012. *Ipomoea diradactylina* (Convolvulaceae), a new species from the Nicoya Peninsula, Costa Rica. *Phytoneuron* **27**: 1–6.
- , M. H. GRAYUM, C. HERRERA AND M. ZAMORA. 2003+. Manual de Plantas de Costa Rica. Monographs in Systematic Botany from the Missouri Botanical Garden.
- KIEL, C. A., L. A. MCDADE, T. F. DANIEL AND D. CHAMPLUVIER. 2006. Phylogenetic delimitation of Isoglossinae (Acanthaceae; Justiceae) and relationships among constituent genera. *Taxon* **55**: 683–694.
- , T. F. DANIEL, I. DARBYSHIRE AND L. A. MCDADE. 2017. Unraveling relationships in the morphologically diverse and taxonomically challenging “justicioid” lineage (Acanthaceae: Justiceae). *Taxon* **66**: 645–674.
- , T. F. DANIEL AND L. A. MCDADE. 2018. Phylogenetics of New World ‘justicioids’ (Justiceae: Acanthaceae): major lineages, morphological patterns, and widespread incongruence with classification. *Syst. Bot.* **43**: 459–484.
- LEONARD, E. C. 1938. Acanthaceae. In P. C. Standley (ed.) Flora of Costa Rica. *Publ. Field Mus. Nat. Hist., Bot. Ser.* **18**: 1188–1263.
- LINDAU, G. 1895. Acanthaceae, pp. 274–354. In A. Engler and K. Prantl (eds.), Die natürlichen Pflanzenfamilien. Engelmann, Leipzig, Germany.
- . 1898. Ord. Acanthaceae. In H. Pittier (ed.), Primitiae florum costaricensis, Anales Inst. Fis.-Geogr. Mus. Nac. Costa Rica **9**: 181–189.
- MCDADE, L. A. AND E. A. TRIPP. 2007. A synopsis of Costa Rican *Ruellia* (Acanthaceae), with descriptions of four new species. *Brittonia* **59**: 199–216.
- , T. F. DANIEL AND C. A. KIEL. 2018. The *Tetramerium* lineage (Acanthaceae: Justiceae) revisited: phylogenetic relationships reveal polyphyly of many New World genera accompanied by rampant evolution of floral morphology. *Syst. Bot.* **43**: 97–116.
- , ———, S. E. MASTA AND K. M. RILEY. 2000. Phylogenetic relationships within the Tribe Justiceae: Evidence from molecular sequences, morphology, and cytology. *Ann. Missouri Bot. Gard.* **87**: 435–458.
- TRIPP, E. A. AND M. A. LUJÁN. 2018. Venezuelan *Ruellia* (Acanthaceae): a monograph. *Mem. New York Bot. Gard.* **119**: 1–76+.
- , T. F. DANIEL, J. C. LENDEMER AND L. A. MCDADE. 2009. New molecular and morphological insights prompt transfer of *Blechnum* to *Ruellia* (Acanthaceae). *Taxon* **58**: 893–906.
- TURLAND, N. J., J. H. WIERSEMA, F. R. BARRIE, W. GREUTER, D. L. HAWKSWORTH, P. S. HERENDEEN, S. KNAPP, W.-H. KUSBER, D.-Z. LI, K. MARHOLD, T. W. MAY, J. MCNEILL, A. M. MONRO, J. PRADO, M. J. PRICE AND G. F. SMITH, (eds.). 2018. International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. Regnum Vegetabile 159. Glashütten: Koeltz Botanical Books (<https://doi.org/10.12705/Code.2018>).
- WASSHAUSEN, D. C. AND J. R. I. WOOD. 2001. Further discoveries in the genus *Stenostephanus* (Acanthaceae). *Harvard Pap. Bot.* **6**: 449–454.