

A New Bernardia (Euphorbiaceae) with Stellate Trichomes from the Brazilian Cerrado

Authors: Carrión, Juan F., Cordeiro, Inês, and Amorim, André M.

Source: Systematic Botany, 44(4): 826-831

Published By: The American Society of Plant Taxonomists

URL: https://doi.org/10.1600/036364419X15710776741431

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

A New Bernardia (Euphorbiaceae) with Stellate Trichomes from the Brazilian Cerrado

Juan F. Carrión, 1,5 Inês Cordeiro, and André M. Amorim 1,3,4

¹Programa de Pós-Graduação em Botânica, Universidade Estadual de Feira de Santana, Avenida Transnordestina s/n, Novo Horizonte, 44036-900, Feira de Santana, Bahia, Brazil; carrionjf@gmail.com

²Instituto de Botânica, Secretaria do Meio Ambiente, Avenida Miguel Stéfano, 3687, 04301-902, São Paulo, São Paulo, Brazil; isandona@uol.com.br

³Departamento de Ciências Biológicas, Universidade Estadual de Santa Cruz, Km 16 Rodovia Ilhéus–Itabuna, 45600-970, Ilhéus, Bahia, Brazil; amorim.uesc@gmail.com

⁴Herbário Centro de Pesquisas do Cacau, CEPEC, Km 22 Rodovia Ilhéus–Itabuna, 45650-000, Ilhéus, Bahia, Brazil

⁵Author for correspondence (carrionjf@gmail.com)

Communicating Editor: Luciano Paganucci Queiroz

Abstract—A new species of *Bernardia* with stellate trichomes from the Brazilian Cerrado is described and illustrated. **Bernardia allemii** is most similar to *B. gardneri*, but differs by its multi-stemmed, subshrub habit, broader leaf blades, tomentose old branches, staminate bracteoles that are usually reniform to flabellate, and larger sepals and bracts in the pistillate flowers. Photographs, a distribution map, information about the conservation status of the new species, and a key to the species with stellate trichomes in Brazil are also provided.

Keywords—Brazilian savanna vegetation, tribe Bernardieae, Bernardia sect. Alevia.

Bernardia Houst. ex Mill. is an American genus of Euphorbiaceae with approximately 70 species (Radcliffe-Smith 2001) distributed from the southern United States to Uruguay and northern Argentina, including the West Indies, with centers of diversity in Mexico and Brazil. Species of the genus occur in a wide range of habitats, such as rain forests, xerophytic vegetation, dry forests, savanna vegetation, and on rocky outcrops.

Webster (1975) created the tribe Bernardieae (subfamily Acalyphoideae) that included, besides *Bernardia*, the African genera *Discocleidion* (Müll.Arg.) Pax & K.Hoffm., *Necepsia* Prain, and *Neopalissya* Pax. In the second version of his classification of the family Euphorbiaceae (Webster 1994), the American genus *Adenophaedra* (Müll.Arg.) Müll.Arg. and the African genus *Paranecepsia* Radcl.-Sm. were added to the tribe and *Neopalissya* was synonymized under *Necepsia*. In 2001, Radcliffe-Smith included the African genus *Amyrea* Leandri in the tribe.

Based on a phylogenetic study, Wurdack et al. (2005) found that Acalyphoideae s. s. contains two strongly supported lineages: the "core acalyphoids" and the "alchorneoids." The core acalyphoids are in eight clades named A1 to A8. Bernardia, Adenophaedra, and Caryodendron (tribe Caryodendreae, sensu Webster 1994) emerged in clade A7. The remaining Bernardieae (sensu Webster 1994 and Radcliffe-Smith 2001) are further removed, with Discocleidion nested in clade A4, and Amyrea, Necepsia, and Paranecepsia in the alchorneoids lineage. Subsequent molecular studies (Jestrow et al. 2008; Cervantes et al. 2016) corroborated the affinities between Adenophaedra, Bernardia, and Caryodendron.

Species of *Bernardia* are dioecious or monoecious shrubs, subshrubs, trees, or rarely herbs. They have the following features: indumentum of simple or/and stellate trichomes; serrate or crenate leaf margins with glandular teeth and glands on the leaf blade; small, apetalous flowers in unisexual inflorescences; staminate flowers that usually have entire or segmented nectary(ies) intermixed with the stamens, four-locellate basifixed anthers with an emarginate to enlarged connective and and articulate pedicel; pistillate flowers with an annular or dissected membranous disk, bifid to lacerate-laciniate styles; and ecarunculate seeds (Cervantes 2006; Webster 2014; Carrión et al. 2017).

In the latest taxonomic treatment of Bernardia (Pax and Hoffmann 1914), seven sections were recognized for the genus: Bernardia sect. Alevia (Baill.) Müll.Arg., Bernardia sect. Crassifoliae Pax & K.Hoffm., Bernardia sect. Phyllopassaea Müll.Arg., Bernardia sect. Polyboea (Klotzsch) Müll.Arg., Bernardia sect. Passaea (Baill.) Müll.Arg., Bernardia sect. Traganthus (Klotzsch) Müll.Arg., and Bernardia sect. Tyria (Klotzsch) Müll.Arg. [= Bernardia sect. Bernardia]. These are based on habit, indumentum, venation patterns, presence or absence of a pistillate disk, and style morphology. Allem (1979) and Cervantes (2006) mentioned the artificial nature of this classification. In addition, *B.* sect. *Traganthus* and *B.* sect. Passaea were suggested as candidates for exclusion from Bernardia (Webster 1994, 2014; Radcliffe-Smith 2001). Considering these problems, a phylogenetic analysis including the seven sections of Bernardia and the other lineages of clade A7 (Bernardieae s. s.) is needed to test the monophyly of Bernardia and to evaluate the current infrageneric classification of the genus. As part of a study of Bernardia developed by the first author, here we describe a new species of Bernardia with stellate trichomes from the Cerrado of central Brazil, which is the largest (2 million km²) and most species-rich area of savanna in the Neotropics (Simon and Pennington 2012). We also provide a key to the species of Bernardia with stellate trichomes in Brazil.

Materials and Methods

Natural populations of the new species were visited in the municipality of Niquelândia (state of Goiás, Brazil) in April 2017, and we studied Bernardia collections deposited in the following herbaria: A, ALCB, BHCB, CEN, CEPEC, F, GH, HAS, HUCS, HUEFS, HURB, ICN, MBML, MO, NY, PACA, R, RB, SP, SPF, UB, UFG, US, and VIC (acronyms according to Thiers 2017). Material preserved in alcohol and dried specimens were analyzed under a stereomicroscope. To micromorphologically study the leaf blade surface using scanning electron microscopy (SEM), ca. 10 mm² fragments from the central portion of a dry leaf blade were removed and glued to stubs. SEM analyses were conducted using a FEI Quanta 250 microscope, with xT Microscope Control software to take images, in the Electronic Microscopy Center (CME) at the State University of Santa Cruz. Morphological terminology follows Radford et al. (1974) and Beentje (2016). An informal conservation status was assessed based on the range size (criterion B) established by the IUCN (2017). The extent of occurrence (EOO) and

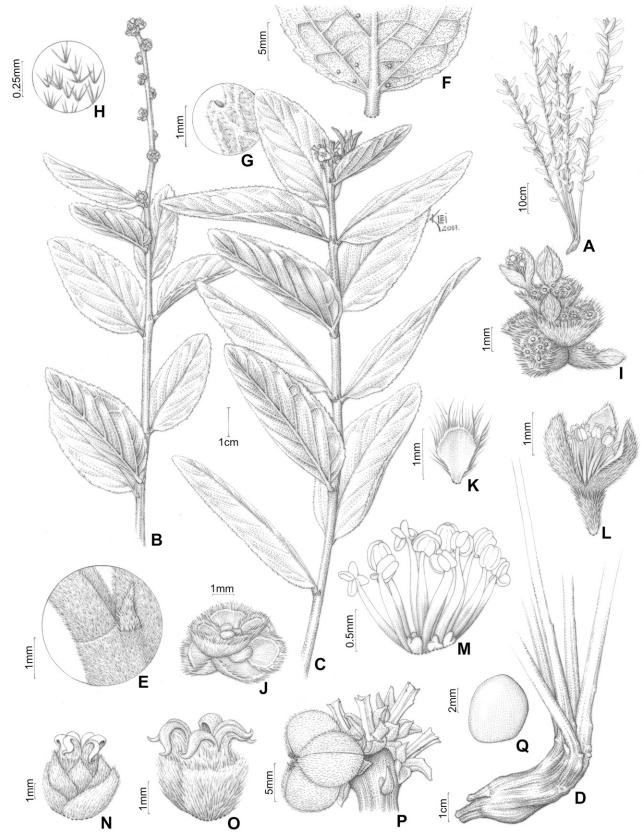


Fig. 1. Bernardia allemii J.F.Carrión. A. Habit. B. Staminate branch. C. Pistillate branch. D. Detail of stems growing from xylopodium. E. Detail of petiole and stipules. F. Abaxial leaf surface with circular glands. G. Detail of leaf margin with glandular teeth. H. Detail of stellate trichomes on the blade. I. Staminate inflorescence. J. Staminate bracts. K. Staminate bracteole. L. Staminate flower. M. Detail of androecium showing basal nectaries. N. Pistillate flower. O. Gynoecium. P. Fruit and persistent columellas. Q. Seed in lateral view. Drawings by Klei Sousa. F, E, H, and staminate characters based on J.F. Carrión 1827; and A, D, and pistillate characters based on J.F. Carrión 1828.

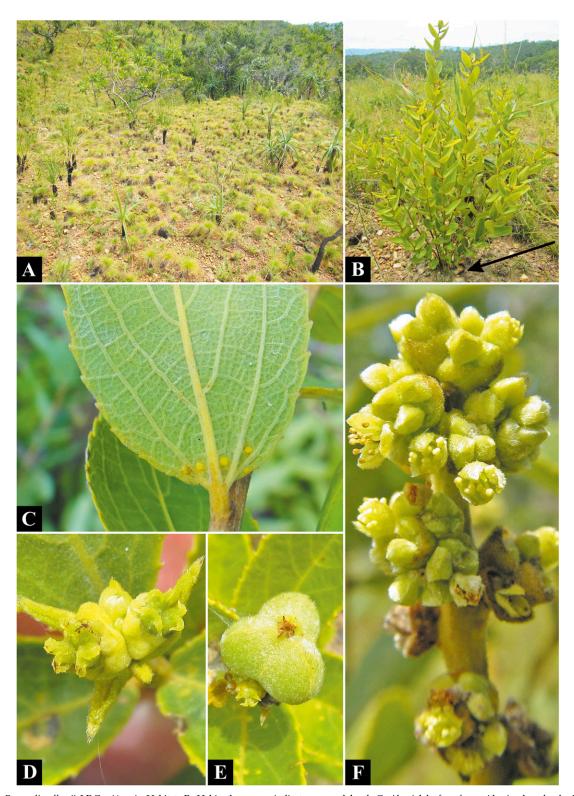


Fig. 2. Bernardia allemii J.F.Carrión. A. Habitat. B. Habit, the arrow indicates ground level. C. Abaxial leaf surface with circular glands. D. Pistillate inflorescence. E. Fruit. F. Staminate inflorescence.

area of occupancy (AOO) were calculated using the GeoCAT tool (Bachman et al. 2011).

TAXONOMIC TREATMENT

Bernardia allemii J.F.Carrión, sp. nov. Type: Brazil. Goiás. Niquelândia, aprox. 4 km do povoado de Muquém em direção a Niquelândia na rodovia GO-237, 14°31′15.4″S, 48°9′9.8″W,

545 m, 14 Apr 2017 (& fl.), *J.F. Carrión & G.A. Reis-Silva 1827* (holotype: HUEFS 234598!; isotypes: CEN, RB 778800!).

Bernardia allemii resembles *B. gardneri* Müll.Arg. by the indumentum of stellate trichomes, staminate inflorescences subglobose, sessile, and compound, with congested cymules

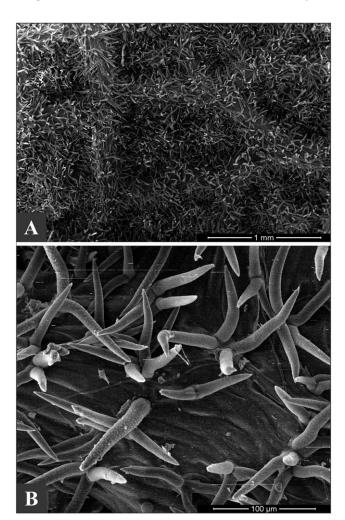


Fig. 3. Scanning electron microscopy image of the abaxial leaf blade surface of *Bernardia allemii* J.F.Carrión. A. Indumentum. B. Detail of trichomes. From *J.F. Carrión 1827*.

along the axis, pistillate flowers in glomeruliform cymes, and coriaceous leaves, but differs by its multi-stemmed, subshrub habit (vs. single-stemmed, shrub habit), broader leaf blades, 2.2–4.5 cm wide (vs. narrower leaf blades, 0.5–2 cm wide), old branches densely tomentose (vs. glabrous to puberulous), staminate bracteoles usually reniform to flabellate (vs. usually linear to oblanceolate), and larger pistillate bracts and sepals, 2.5–4.5 \times 2.2–3.8 and 2.6–3.5 \times 1.6–2.8 mm, respectively (vs. smaller pistillate bracts and sepals, 1–2 \times 1–2.5 and 0.8–1.7 \times 0.8–1.5 mm, respectively).

Dioecious, multi-stemmed subshrub, 0.4–1.3 m tall, growing from xylopodium; branches sulcate, covered by a tomentose indumentum of sessile, stellate trichomes, with 2–7 arms, 0.05–0.5 mm long; bark mustard-pale yellow. Leaves alternate; covered by sessile, stellate trichomes, with 2–7 arms, 0.05–0.6 mm long; stipules 0.7– 1.4×0.2 –0.4 mm, lanceolate-falcate, attenuate, rigid, thickened, covered by simple trichomes, persistent after the leaf falls; petiole 1–3 mm long, densely tomentose with stellate trichomes; blade coriaceous, usually ovate to lanceolate, discolor, 2.5– 8.2×2.2 –4.5 cm; base rounded; margin serrate, with glandular teeth; apex rounded to obtuse; abaxial surface densely tomentose, adaxial surface tomentose when young and puberulous-glabrescent when old; circular glands 2–14, on the abaxial surface, raised when

young to embedded when old, yellow, usually aggregated close to the blade base, on both sides of the midvein, and sometimes near the apex; venation palmati-pinnate, secondary veins in 5-8 pairs, intersecondary veins reticulate, dense, and prominent. Staminate inflorescence subglobose, axillary and terminal, sessile, with 2–6 cymules of 3–8 flowers, congested and spiraled along the axis, subtended by fleshy bracts, these $1-2 \times$ 0.5–3.5 mm, reniform to flabellate, ciliate, pubescent on the outer surface, glabrous on the inner surface; bracteoles very unequal in size and shape, usually reniform to flabellate, 0.8–1.8 imes0.4–2.5 mm, ciliolate, pubescent on the outer surface, glabrous on the inner surface. Staminate flowers shortly pedicellate, articulate near the calyx, 0.7–2 mm long, densely pubescent; sepals 3(4), valvate, ovate to lanceolate, $1.8-2.3 \times 0.8-1.5$ mm, slightly hyphodromous, outer surface densely covered by stellate trichomes, inner surface sparsely covered by stellate trichomes, denser in the central area, margin ciliate; stamens 7-11; filaments 1.3-2 mm long, alternating with 7-12 shortly stalked nectaries; anthers 0.1– 0.2×0.2 –0.3 mm, basifixed, 4locellate, dehiscent through longitudinal slits, connective emarginate. Pistillate inflorescence a sessile glomeruliform cyme, terminal. Pistillate flowers sessile; each one subtended by 3 fleshy bracts, these ovate, ciliate, concave, unequal in size and shape, $2.5-4.5 \times 2.2-3.8$ mm, one bract conspicuously larger with attenuate to acuminate apex, the remaining two smaller bracts with acute apex, densely pubescent on the outer surface, glabrous on the inner surface; sepals 5, ovate, persistent, $2.6-3.5 \times 1.6-2.8$ mm, inconspicuously hyphodromous, outer surface densely pubescent with stellate trichomes, inner surface glabrous; disk dissected; ovary globose, densely pubescent; styles 3(-4), bifid, recurved, 1.5-2 mm long, branches to 3 mm, entire, stigmatic surface smooth to verrucose, covered by sparse simple trichomes. Fruits globose, trilobed, $8-10 \times 11-12$ mm, green when mature, pubescent to tomentose, with persistent styles, bracts and accrescent calyx; sometimes pedicellate, pedicel 2–8 mm long; mericarps 2-valved, splitting septicidally then loculicidally; columella 5–7 mm long, trilobed, persistent. Seeds rounded, slightly carinate, cordiform in ventral view, smooth, shiny, buff, sometimes brown-marbled, 5–7 (long) \times 4-6 (deep) \times 4-5 (wide) mm, ecarunculate, micropyle at the apex, ventral surface longitudinally traversed by the raphe, with the hilum in the center. Figures 1, 2, 3.

Distribution, Habitat, and Conservation—Bernardia allemii occurs in the Cerrado phytogeographic domain in the Brazilian states of Goiás and Tocantins, in campo sujo (shrub savanna), campo limpo (grassland), campo cerrado (wooded savanna), and cerrado sensu stricto (woodland) vegetation, between 350-1000 m elevation, on rocky-gravelly, sandy soils, serpentine soils, and quarzitic outcrops (Fig. 4). Burned vegetation and soil were observed at the type locality, as well as some live individuals of B. allemii that had burned stems, which were evidence of survival/regeneration after a recent fire. The multiple stems growing from a xylopodium suggest the new species is adapted to resist fire and/or grow in nutrient-poor soils, which are characteristic features of the Cerrado (Eiten 1972; Simon and Pennington 2012). The thickened leaf texture, dense network of veins, and dense indumentum of this species are also evidence of adaptations to the xeromorphic conditions of the Cerrado (Eiten 1972).

Bernardia allemii was recorded at twelve locations, among which only one is in a protected area (Chapada dos Veadeiros National Park, Goiás State). Also, several of the collection localities are within or near mining areas and dams and,

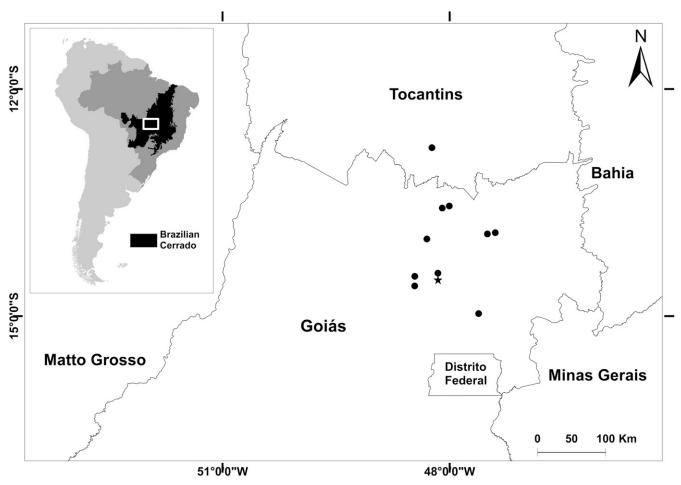


Fig. 4. Geographical distribution of Bernardia allemii J.F.Carrión (black symbols) in the Brazilian Cerrado (area in black); the black star indicates the type locality.

therefore, populations of the new species are subjected to disturbance and habitat deterioration. Thus, following the IUCN red list categories and criteria (IUCN 2017), the extent of occurrence (EOO) of 16,762,438 km² and area of occupancy (AOO; grid cell area of 2 km²) of 44,000 km² we believe that if a formal assessment were prepared *Bernardia allemii* would probably be classified as Endangered (EN B2 ab[ii,iii,iv]).

Etymology—The specific epithet honors Brazilian botanist Antônio Costa Allem, who has greatly contributed to the systematics of Brazilian Euphorbiaceae, including contributions to the taxonomy of *Bernardia*. He also collected some of the paratypes.

Notes—Several herbarium collections of Bernardia allemii and B. gardneri have been misidentified as B. crassifolia or B. similis; however, the latter two species have an indumentum of only simple trichomes (vs. stellate and simple trichomes in B. allemii and B. gardneri). According to the treatment of Pax and Hoffmann (1914), the only Bernardia sections that include species with an indumentum of stellate trichomes are B. sect. Alevia and B. sect. Bernardia, but these sections only contain shrubby tree species (vs. the subshrub habit of B. allemii). The only section in this treatment that includes subshrubs is B. sect. Phyllophassaea, but species in this section have an indumentum of simple trichomes (vs. stellate and simple trichomes in B. allemii). Despite not fitting

TABLE 1. Distinctive morphological features of B. allemii and B. gardneri.

Characters	B. allemii	B. gardneri
Habit	Multi-stemmed subshrub, usually with leaves near the base of the stem	Single-stemmed shrub, without leaves near the base of the stem
Old branches (indumentum)	Densely tomentose	Glabrous to puberulous
Leaf size (cm)	$2.5 - 8.2 \times 2.2 - 4.5$	$1-4.2 \times 0.5-2$
Venation	Palmati-pinnate	Pinnate to palmati-pinnate
Gland number and position on leaves	Always present (2–14), usually aggregated close to the blade base, sometimes near the apex	Sometimes absent or with 1–2(3) glands near the blade base
Bracteole shape	Usually reniform to flabellate	Usually linear to oblanceolate
Stamen number	7–11	5–8
Filament length (mm)	1.3–2	0.6–1.2
Pistillate bract size (mm)	$2.5-4.5 \times 2.2-3.8$	$1-2 \times 1-2.5$
Pistillate sepal size (mm)	$2.6-3.5 \times 1.6-2.8$	$0.8-1.7 \times 0.8-1.5$

appropriately into any of the sections, *B. allemii* resembles *B. gardneri* by the characteristics mentioned in the diagnosis and can be separated from this species by the morphological differences summarized in Table 1. *Bernardia gardneri* was placed in *Bernardia* sect. *Alevia* by Pax and Hoffmann (1914). However, they were unsure about its systematic position, perhaps because the pistillate flowers were unknown for *B. gardneri* at that time. We place the new species, at least provisionally, in *Bernardia* sect. *Alevia* due to the presence of stellate trichomes and bifid styles. Future phylogenetic studies will prove the validity of the morphological characters used by Pax and Hoffmann (1914) to delimit the current infrageneric classification of *Bernardia*.

Additional Specimens Examined—Brazil.—Goias: Cavalcante, 18 km ao sul de Cavalcante rumo a Alto Paraiso, 13°55′S, 47°30′W, 1020 m, 22 Nov 1984 (♂ fl.), Allem et al. 3095 (CEN); ibid. (♀ fl. and fr.), Allem et al. 3096 (CEN); Cavalcante, Balsa do Rio Tocantins (Serra Branca), para Serra Branca km 2, 13°34′26″S, 48°05′48″W, 410 m, 23 May 2001, (♀ fl. and fr.), G. Pereira-Silva et al. 5076 (CEN, HUEFS); Cavalcante, cerca de 4 km da Vila Veneno, na direção do Rio São Félix, cerca de 12 km da Balsa da Coterra,

13°32′49"S, 48°0′15"W, 390 m, 25 Jan 2001 (& fl.), B.M.T. Walter et al. 4813 (CEN); Niquelândia, nas margens do Rio Tocantinzinho, 13°59'S, 48°18'W, 400 m, 22 Jul 1995 (9 fl. and fr.), T.B. Cavalcanti et al. 1599 (CEN, SP); Niquelândia, Fazenda Engenho, ca. de 11 km de Niquelândia/Dois Irmãos, 14°36′03″S, 48°27′40″W, 585 m, 13 Aug 1997 (9 fl. and fr.), M.L. Fonseca et al. 1515 (SP); Niquelândia, estrada para Colinas do Sul, ca. 36km de Niquelândia, 14°25′56″S, 48°9′16″W, 490 m, 7 May 1998 (9 fl. and fr.), D. Alvarenga et al. 1183 (SP); Niquelândia, 4km do povoado de Muquém em direção a Niquelândia, 14°31′14″S, 48°9′8″W, 495 m, 8 May 1998 (9 fl. and. fr), M.A. da Silva et al. 3805 (SP); Niquelândia, margem esquerda do lago da Serra da Mesa, 28 Apr 1999 (9 fl. and fr.), M.M.R. Cunha et al. 12 (CEN); Niquelândia, aprox. 4 km do povoado de Muquém em direção a Niquelândia na rodovia GO-237, 14°31′15.4″S, 48°9′9.8″W, 545 m, 14 Apr 2017 (9 fl. and. fr), J.F. Carrión & G.A. Reis-Silva 1828 (CEN, CEPEC, HUEFS, RB); São João D' Aliança, 31 km de São João D' Aliança ao longo da rodovia GO-118 rumo a São Gabriel km 54 da rodovia, 14°58'S, 47°37W, 1170 m, 07 Mar 1986 (9 fl. and fr.), Allem & Werneck 3498 (CEN); Teresina de Goiás, Fazenda Hotel Ecológico Alpes Goianos, rodovia GO-118 km 202, 13°53′59.1″S, 47°23′48.9″W, 31 Jul 2000 (& fl.), V.C. Souza et al. 24779 (SP); Tocantins, Paraná (a leste do canteiro de obra do AHES. Salvador), 12°46′32″S, 48°13′59″W, 490 m, 4 Jul 2002 (\$\partial and \$\partial and \$ ∂ fl. and fr.), G. Pereira-Silva et al. 6553 (CEN, HUEFS).

KEY TO THE BRAZILIAN BERNARDIA SPECIES WITH STELLATE TRICHOMES (B. SECT. ALEVIA)

ACKNOWLEDGMENTS

Thanks to the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for providing the Ph.D. fellowship to JFC (grant # 141302/2016-0) and research productivity fellowships to AMA (grant # 312404/2018-2) and IC (grant # 309917/2015-8). We also thank SISBIO/ICMBio for permission to collect in Chapada dos Veadeiros National Park, Dr. Taciana B. Cavalcanti (CEN Herbaria, Embrapa Genetic Resources and Biotechnology), Genilson Alves for the logistical support during fieldwork, Klei Sousa for the line drawings, and Nathan Smith for the English revision.

AUTHOR CONTRIBUTIONS

JFC conducted fieldwork (made field observations, collected some of the types, and photographed live specimens), analyzed herbarium specimens, wrote the manuscript, and prepared the distribution maps and figures. AMA and IC supervised the first author's Ph.D. study and reviewed the manuscript. All authors discussed the results and contributed to the final version of the manuscript.

LITERATURE CITED

- Allem, A. C. 1979. Discussão taxonômica sobre as seções Polyboea e Phyllopassaea (gênero Bernardia, Euphorbiaceae). Revista Brasileira de Biologia 39: 529–544.
- Bachman, S., J. Moat, A. W. Hill, J. de la Torre, and B. Scott. 2011. Supporting red list threat assessments with GeoCAT: Geospatial conservation assessment tool. *ZooKeys* 150: 117–126.
- Beentje, H. J. 2016. The Kew Plant Glossary: An Illustrated Dictionary of Plant Terms, ed. 2. Kew: Royal Botanic Gardens.
- Carrión, J. F., I. Cordeiro, and A. M. Amorim. 2017. A new species of *Bernardia* (Euphorbiaceae) from the Chapada Diamantina, Bahia State, Brazil. *Phytotaxa* 317: 69–75.
- Cervantes, A. 2006. Sistemática de Bernardia sección Tyria (Euphorbiaceae). Doctoral thesis. México City: Universidad Nacional Autónoma de México.

- Cervantes, A., S. Fuentes, J. Gutiérrez, S. Magallón, and T. Borsch. 2016. Successive arrivals since the Miocene shaped the diversity of the Caribbean Acalyphoideae (Euphorbiaceae). *Journal of Biogeography* 43: 1773–1785.
- Eiten, G. 1972. The cerrado vegetation of Brazil. *Botanical Review* 38: 201–341
- IUCN. 2017. Guidelines for using the IUCN red list categories and criteria. Version 13. Prepared by the Standards and Petitions Subcommittee. Gland, Switzerland and Cambridge, UK: IUCN. http://www.iucnredlist.org/documents/RedListGuidelines.pdf (accessed 1 March 2018).
- Jestrow, B., G. Proctor, and J. Francisco-Ortega. 2008. Lasiocroton trelawniensis (Euphorbiaceae), a critically endangered species from the Cockpit Country of Jamaica, belongs to Bernardia (Euphorbiaceae). Botanical Review 74: 166–177.
- Radcliffe-Smith, A. 2001. Genera Euphorbiacearum. Kew: Royal Botanic Gardens.Radford, A. E., W. C. Dickison, J. R. Massey, and C. R. Bell. 1974. Vascular Plant Systematics. New York: Harper and Row Publishers.
- Pax, F. and K. Hoffmann. 1914. Euphorbiaceae—Acalypheae—Mercurialinae. Pp. 21–45 in *Das Pflanzenreich* IV.147.vii, ed. A. Engler. Leipzig: Wilhelm Engelmann.
- Simon, M. F. and T. Pennington. 2012. Evidence for adaptation to fire regimes in the tropical savannas of the Brazilian Cerrado. *International Journal of Plant Sciences* 173: 711–723.
- Thiers, B. 2017 [continuously updated]. Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. http://sweetgum.nybg.org/science/ih/ (Last accessed March 2018).
- Webster, G. L. 1975. Conspectus of a new classification of the Euphorbiaceae. *Taxon* 24: 593–601.
- Webster, G. L. 1994. Synopsis of the genera and suprageneric taxa of Euphorbiaceae. *Annals of the Missouri Botanical Garden* 81: 33–144.
- Webster, G. L. 2014. Euphorbiaceae. Pp. 51–216 in *The Families and Genera of Vascular Plants*, vol. 11, ed. K. Kubitzki. Berlin: Springer.
- Wurdack, K. J., P. Hoffmann, and M. Chase. 2005. Molecular phylogenetic analysis of uniovulate Euphorbiaceae (Euphorbiaceae sensu stricto) using plastid rbcL and trnL-F DNA sequences. American Journal of Botany 92: 1397–1420.