



<https://doi.org/10.11646/phytotaxa.579.3.1>

## Two noteworthy *Calea* (Asteraceae: Neurolaeneae) from contact areas of the Atlantic Forest and Cerrado of Brazil

VINICIUS R. BUENO<sup>1,6</sup>, A. P. V. CASSOL<sup>2</sup>, C. J. LEROY<sup>3</sup>, M. L. BUENO<sup>4</sup> & GUSTAVO HEIDEN<sup>5</sup>

<sup>1</sup>Universidade Federal do Rio Grande do Sul, Programa de Pós-graduação em Botânica, Laboratório de Sistemática Vascular, Prédio 43432, sala 107, Porto Alegre, RS 91501-970, Brazil

✉ [vrbueno@outlook.com](mailto:vrbueno@outlook.com); ✉ [vnrbueno@gmail.com](mailto:vnrbueno@gmail.com); <https://orcid.org/0000-0001-9834-1951>

<sup>2</sup>Universidade Federal do Rio Grande do Sul, Programa de Pós-graduação em Botânica, Laboratório de Ficologia, Museu de Ciências Naturais - Sema/RS, Porto Alegre, RS 90690-000, Brazil

✉ [anapvcassol@gmail.com](mailto:anapvcassol@gmail.com); <https://orcid.org/0000-0003-3662-9372>

<sup>3</sup>Centro Universitário Una, Belo Horizonte, MG, Brazil

✉ [carolinajleroy@gmail.com](mailto:carolinajleroy@gmail.com); <https://orcid.org/0000-0002-7436-7126>

<sup>4</sup>Universidade Estadual de Mato Grosso do Sul, Laboratório de Macroecologia & Evolução (LAMEV), BR-163, Mundo Novo, MS, Brazil, 79980-000, Brazil

✉ [buenotanica@gmail.com](mailto:buenotanica@gmail.com); <https://orcid.org/0000-0001-6146-1618>

<sup>5</sup>Embrapa Clima Temperado, Rodovia BR 392, km 78, Caixa Postal 403, Pelotas, RS 96010-971, Brazil

✉ [gustavo.heiden@embrapa.com.br](mailto:gustavo.heiden@embrapa.com.br); <https://orcid.org/0000-0002-0046-6500>

<sup>6</sup>Author for correspondence: ✉ [vrbueno@outlook.com](mailto:vrbueno@outlook.com); ✉ [vnrbueno@gmail.com](mailto:vnrbueno@gmail.com)

### Abstract

Systematic studies in the *Calea myrtifolia* complex have revealed two noteworthy new taxa from the contact, relict and transitional areas of the Atlantic Forest and Cerrado domains in Brazil: *Calea grandiflora* and *Calea* × *parviantha*, both having been treated as *C. myrtifolia*, now considered endemic to Minas Gerais state, Brazil. Thus, we herein provide morphological descriptions, illustrations, geographical distribution maps and discuss their taxonomic affinities. Moreover, their potential distributions are predicted. *Calea grandiflora* is related to *C. arachnoidea* and is recognized by the basal acrodromous venation (vs. semicraspedodromous), outer phyllary series 12.2–20 × 4.2–10.6 mm long (vs. 9–12 × 3–5 mm), and ray floret corolla 16.9–31 mm long (vs. 10–12 mm). *Calea* × *parviantha* is a new nothospecies, supported by a unique set of character states partially shared with the parental species *C. parvifolia* and *C. triantha*. The new hybrid species has intermediate morphology, as demonstrated by a multivariate analysis. It differs from *C. parvifolia* by the hispid, hispidulous or glabrous stems (vs. puberulous or puberulent) and coriaceous leaves (vs. chartaceous leaves), and from *C. triantha* by the rounded leaf base, sometimes subcordate (vs. cordate) and pappus scales 1.1–2.7 mm long (vs. 0.8–1.3 mm). Furthermore, we provide a taxonomic key for *Calea* in the states of São Paulo and Paraná.

**Keywords:** Compositae, Heliantheae *s.l.*, Hibridization, *Meyeria*, Systematics

### Introduction

Neurolaeneae Rydberg (1927: 303) is one of the 50 tribes of Asteraceae Berchtold & Presl (1820: 254) (Susanna *et al.* 2020), reinstated by Panero and Funk (2002). The tribe comprises five genera and 182 species (Bueno *et al.* 2021). *Calea* Linnaeus (1763: 1179) is the largest genus, with 157 species (Bueno *et al.* 2022, Bueno & Heiden 2021, Bueno & Heiden 2022a, 2022b). Species of *Calea* are usually characterized by herbaceous or shrubby habit, opposite leaves, radiate capitula, sometimes discoid, 2–6-seriate involucrem, pappus of 6–30 scales (Bueno *et al.* 2021). The *Calea myrtifolia* complex has 18 species (Pruski 2005, Reis-Silva & Nakajima 2021, Bueno & Heiden 2021, 2022a, 2022b), defined by the ovate leaves, cymose capitulescence, involucrem with at least four foliaceous phyllaries in the outer series, and pappus usually 1 to 2.5 mm long (Bueno & Heiden 2022b).

The number of species of Neurolaeneae has continuously increased in the last two decades, with 20 new species described: one new species of *Neurolaena* Brown (1817: 120) (Turner 2014) and 18 new species of *Calea* (Deble 2011, Pruski 2011, 2013, Diaz-Piedrahita & Rodriguez-Cabeza 2012, Pozo & Hind 2013, Silva *et al.* 2016, Reis-Silva & Nakajima 2020, 2021, Bueno *et al.* 2022, Bueno & Heiden 2021, 2022a, b). Brazil is the richest country in

number of species of Neurolaeneae (Bueno *et al.* 2021), and from these 19 recently described species of *Calea*, eleven are Brazilian endemic (Pruski 2005, Reis-Silva *et al.* 2022). In the *Calea myrtifolia* complex specifically, five new Brazilian species were described in the meantime (Bueno & Heiden 2021, 2022a, b, Reis-Silva & Nakajima 2021).

Hybridization is defined as crossing between species or genetically distinct populations of the same species, and is responsible for a significant portion of speciation events in plants (Soltis & Soltis 2009, Peruzzi *et al.* 2012). It has been recognized as an important process in plant evolution, being associated with diversification, radiation, extinction, and invasion (Mitchell *et al.* 2019). Countless phylogenies provide evidence on the impact of hybridization in the appearance of new species, merging or assimilation of some taxa and on the nature of reticulate evolution processes occurring in the deep past or present (Alvarez & Wendel 2003, Schilling 2011, Wang *et al.* 2014, Loeuille *et al.* 2015, Gruenstaudl *et al.* 2017, Nauheimer *et al.* 2019, Shipunov *et al.* 2019).

In Asteraceae, several authors described or provided discussions on the nature of hybrids over the past decade (Peruzzi *et al.* 2012, Garrison *et al.* 2013, İlçim *et al.* 2013, Lipman *et al.* 2013, Mameli *et al.* 2013, Filigheddu *et al.* 2014, Yu *et al.* 2014, Li *et al.* 2015, Loeuille *et al.* 2015, Smissen *et al.* 2015, Sears *et al.* 2015, Desjardins *et al.* 2016, Semple 2016, Gemenholzer *et al.* 2017; Gruenstaudl *et al.* 2017, Zhang *et al.* 2017, Jazwa *et al.* 2018, Pliszko & Kostrakiewicz-Gieralt 2018, Wang & Wang 2018, Smith & Figueiredo 2020, Cardo & Melgar 2021, Semíz *et al.* 2021). Most of these studies document events from the northern hemisphere (Eurasia and North America), with only four studies focusing on the southern hemisphere (Africa, Oceania, and South America). Given the high diversity of Asteraceae in the southern hemisphere, it is highly likely that natural hybrids are underreported.

The aforementioned studies and Funk *et al.* (2009) indicate that at least 14 Asteraceae tribes have hybrid species, with Cichorieae Lamarck & Candolle (1806: 255), Cardueae Cassini (1819: 155–157), and Gnaphalieae Cassini ex Lecoq & Juill. (1831: 296) as most representative. Neurolaeneae is not listed in these studies, although Malme (1933) found morphological evidence of hybridization between *Calea parvifolia* (DC.) Baker (1884: 259–260) and *C. longifolia* (DC.) Baker (1884: 260), currently a synonym of *C. marginata* S.F. Blake (1937: 387). Besides, Turner (1982, 2014) reported hybrids in *Neurolaena* between the widespread *N. lobata* Brown (1817: 120–121) and its congeners, without further evidence.

Pruski (2005) pointed out that *C. myrtifolia* (DC.) Baker (1884: 260) occurs from the state of Minas Gerais to Rio Grande do Sul in Brazil. Nevertheless, ongoing study supports that specimens from the states of Rio Grande do Sul and Santa Catarina previously labeled as *C. myrtifolia* in fact belong to *C. phyllolepis* Baker (1884: 260–261) (Roque *et al.* 2022). Recent progress on the circumscription of taxa belonging to *C. myrtifolia* complex led to the discovery that geographically isolated specimens previously determined as *C. myrtifolia* occurring in the Atlantic Forest from the states of São Paulo and Paraná, disjunct from the rest of the distribution, have unusual characteristics and the detailed analyses of these specimens evidenced they were two new taxa of *Calea*, hereby described.

## Material and methods

All the available literature for *Calea* was revised (Baker 1884, Barroso 1975, Bueno *et al.* 2021, Bueno *et al.* 2022, Bueno & Heiden 2021, Bueno & Heiden 2022a, b, Malme 1933, Pozo & Hind 2013, Pruski 1983, 1984, 1997, 1998, 2005, 2011, 2013, Pruski & Hind 1998, Pruski & Robinson 2018, Pruski & Urbatsch 1987, 1988, Reis-Silva 2019, Reis-Silva & Nakajima 2020, 2021, Robinson 1975, 1979, Roque & Carvalho 2011, Silva 2016, Silva *et al.* 2016, Urbatsch *et al.* 1986, Wussow *et al.* 1985). The general morphological terminology follows Beentje (2010), Ellis *et al.* (2009), and Hickey (1973). The specialized terminology on Compositae follows Funk *et al.* (2009) and the specific terminology about receptacle and pappus follows Bueno *et al.* (2022) and Bueno & Heiden (2022a), respectively.

Several collections were studied from the herbaria BHCB, BHZB, BM, CEN, CESJ, DIAM, ECT, EFC, ESA, ESAL, FLOR, FUEL, FURB, G, HAS, HEPH, HUCP, HUFJSJ, HUFU, ICN, IPA, K, MBM, MO, NYBG, P, PACA, PAMG, PEL, R, RB, RFA, S, SP, SPF, U, UB, UEC, UEPG, UNIP, UPCB, and U (acronyms according to Thiers 2022, continuously updated). About 500 specimens were studied in person for the elaboration of this manuscript.

Morphological descriptions were based on vegetative and reproductive material from herbarium specimens, using a stereomicroscope to perform measurements with a caliper rule. Vegetative structures were described from dried material, whereas reproductive structures were described after rehydration, immersing the structure in warm water (ca. 80°C) for about one minute. Measurement outliers were based on calculation of medians, quartiles, and interquartile deviations. “Rarely” is used for characters that occur in up to 10% of the specimens studied, “sometimes” is applied for features that occur in between 10.01% and 25% of the analyzed specimens and “often” is adopted for characters

that occur between 25.01% and 40% of the specimens studied. “Or” is adopted for traits that occur between 40% and 60% of the specimens.

Distribution maps were prepared in Quantum GIS v. 3.0 (QGIS Development Team 2015). The GeoCAT analysis (Bachman *et al.* 2011) and IUCN guidelines (2019) were used to define a preliminary conservation status assessment.

Statistical analyses to study hybrids (Brochmann 1987, Gruenstaeudl *et al.* 2017, Pliszko *et al.* 2018, Semple *et al.* 2016) were adopted to verify whether multivariate analyses would corroborate the nothospecies hypothesis. A PCA (Principal Components Analysis) was used to verify whether the morphological data allowed to test specimen placement in groups: *C. parvifolia*, *C. triantha* (Vell.) Pruski (2005: 2) and the hypothesized nothospecies. For the analysis, 48 characters were measured in six different specimens per group, chosen from distinct geographical sites to represent the whole geographic distribution of taxa. In all, 8 vegetative and 40 reproductive characters were studied, from this set, 22 were quantitative and 36 were qualitative (matrix available in the supplementary files—Tab. 2). The statistical analyses were performed using R (version 4.1.1; R Development Core Team, 2022; [www.r-project.org/](http://www.r-project.org/)), the R package ‘vegan’ (Oksanen *et al.* 2020) and visualized with the R package ‘ggplot2’ (Wickham *et al.* 2020).

Environmental predictors consisted of bioclimatic variables interpolated from climate data between 1970 and 2000, obtained from the WorldClim dataset v.2.1 (Fick & Hijmans 2017; <http://www.worldclim.org>). The 19 standard variables at 30s (approximately 1 km) resolution reflect various aspects of temperature, precipitation, and seasonality, which are likely to be important in determining species distributions. We used a stepwise procedure implemented in the R package usdm (Naimi & Araújo 2016) to test the issue of multicollinearity among environmental variables by estimating the variance inflation factor (VIF) and retained only the variables with VIF < 10 (Graham 2003). This reduced our number of environmental predictors to five (BIO2 = Mean Diurnal Range, BIO3 = Isothermality, BIO9 = Mean Temperature of Driest Quarter, BIO13 = Precipitation of Wettest Month, BIO14 = Precipitation of Driest Month).

We fitted ENMs (Ecological niche models) for each analyzed *Calea* taxon using four modelling algorithms implemented in the R package sdm (Naimi & Araújo 2016). These were maximum entropy (MaxEnt) (Phillips *et al.* 2006), random forests (rf) (Breiman 2001), generalized linear models (glm) (McCullagh & Nelder 1989) and bioclimatic variables (bioclim) (Hijmans *et al.* 2006). These methods were used to link the current environmental conditions to taxon presence and absence data, and subsequently, to predict and map the spatial distribution of the taxa for the current and paleoclimatic projections. All models were calibrated with presence only data combined with 10,000 randomly selected pseudo-absence records for each species across the study area, generated with the R package sdm (Naimi & Araújo 2016). Rather than relying on individual modelling algorithm approaches, we built ensemble models combining multiple replicates of several different modelling algorithms to represent alternate possible states of the system being modelled (Araújo & New 2007). Due to their combined power, ensemble models are widely accepted to provide more accurate results than single models (Forester *et al.* 2013).

## Taxonomic treatment

### *Calea grandiflora* V.R.Bueno & G.Heiden, **sp. nov.** (Fig.1)

Type:—BRAZIL. São Paulo, Santo André, Paranapiacaba Biological Station, about 30 km north of Santos, 02 December 1977, L.R. Landrum 2761 (holotype: SP!).

*Calea grandiflora* resembles *C. arachnoidea* but differs by the basal acrodromous venation (vs. semicraspedodromous), outer phyllaries 12.2–20 × 4.2–10.6 mm long (9–12 × 3–5 mm), ray floret corolla 16.9–31 mm long (vs. 10–12 mm), and monolength pappus scales (vs. polylength).

**Shrubs**, 0.5–2 m tall, **stems** castaneous, cylindrical, striate, glabrous to puberulous or sparsely sericeous, internodes 9.1–34.5 mm long. **Leaves** decussate, petiole 2.2–4.3 mm long; blades discolorous, abaxial surface olivaceous, adaxial surface dark green, coriaceous, 1.58–6.86 × 0.84–2.63 cm, elliptic or narrow elliptic, sometimes narrow ovate, base attenuate, apex acute, sometimes attenuate, venation basal acrodromous, margins slightly revolute or revolute, entire or pauciserrate, 0–9 teeth, 0.1–0.8 (–1.1) mm long, from the middle to apex, abaxial surface sparsely glandular-punctate, veins glabrous, adaxial surface glabrous, glands absent. **Capitulescence** cymose dichasial, slightly branched, axis 0–25.57 cm long, branching to 2<sup>nd</sup> order ramifications, 2–8 secondary stems; peduncle 1.35–4.28 cm long, puberulous to pilose or pilose, glandular-punctate to densely glandular-punctate. **Capitulum** heterogamous, radiate, involucrem

campanulate, 8.9–14.65 × 12.44–15.46 mm, 5-seriate; **phyllaries** conspicuously striated; two outermost series of phyllaries olivaceous, foliaceous, margins entire, flat; first series 5–8 striate, blades 12.2–20 × 4.2–10.6 mm, narrow elliptic to wide elliptic or wide ovate, apex acute or obtuse, abaxial surface glabrous or sparsely puberulous to glabrous, wholly glandular-punctate or only at apex; second series 8–12 striate, blades 13–18.1 × 6.1–7.8 mm, elliptic, apex acute or cuneate, abaxial surface glabrous to sparsely puberulous, sparsely glandular-punctate; third series yellowish green to olivaceous, foliaceous or scarious at apex, blades 10–13.8 × 4.5–8.1 mm, wide elliptic or narrow ovate or ovate to oblong, margins entire, apex obtuse or acute, revolute or flat, abaxial surface glabrous, glandular-punctate at apex; innermost series yellowish green to light yellow, scarious, 9–12 striate, margins entire, abaxial surface glabrous, fourth series blades 7–12.7 × 4.3–5.9 mm, oblong to elliptic, sometimes ovate, apex obtuse; fifth series blades 8.4–14.5 × 4.3–5.9 mm, obovate or elliptic, apex rounded, sometimes obtuse; **receptacle** slightly convex, holopaleaceous; paleae light yellow, conduplicate, 7.7–9.8 mm long, narrow elliptic, apex acute or long acuminate. **Ray florets** 10–18, 19–33.2 mm long, pistillate, corolla liguliform, 16.9–31 mm long, yellow, tube 4–5 mm long, limb 12.9–26 × 3.2–3.5 mm, narrow oblong, sometimes narrow obovate, apex 3-lobulate or rounded or obtuse or bifid, 5–8 veins, surface abaxial glandular-punctate, surface adaxial glabrous; style arms yellow, 0.5–1.1 mm long. **Disc florets** 45–50, 7.8–8.5 mm long, bisexual, corolla tubular, 5.9–6.5 mm long, yellow, tube 1.6–2.2 mm long, lobes 1.4–1.5 mm long, glabrous; anthers light yellow, 2.1–2.9 mm long, apical anther appendages ovate; style arms yellow, 1–1.1 mm long, linear. **Cypselae** blackish, 2.5–3.2 mm long, prismatic, ray cypselae 3-angled, disc cypselae 4-angled, glabrous, ribs sparsely pilose; **pappus** monotypic, scales monolength, 10–12, free, 0.9–1.5 mm long, oblanceolate, sometimes oblong, apex obtuse, sometimes rounded, margins entire.

**Distribution, Habitat and Predicted Area of Occurrence:**—*Calea grandiflora* occurs in two municipalities from São Paulo state and the occurrence points are 50 km away. Probably, it occurs in other hilltops of the Serra do Mar mountain range (Fig. 2), displaying similar environmental conditions. The new species occurs on rocks outcrops amidst the dominant Atlantic Rainforest (Aguiar *et al.* 2003), characterized by the high elevation tropical grasslands which harbor distinct floras within the main surrounding vegetation matrix and bears strong past floristic connections with the cerrado (tropical savanna) and campos rupestres floras (high altitude tropical grasslands) typical of Brazilian hinterland mountains (Stafford 2001, Simon 2009).

According to the predicted area of occurrence (Fig. 3), the new species has higher suitability in Serra do Mar mountains from São Paulo, where it occurs, and other scattered spots: Itatiaia National Park in the triple border of the states of Minas Gerais, Rio de Janeiro, and São Paulo; Lagamar de Cananeia State Park and Guaraqueçaba Ambiental Protection Area at the border of the states of São Paulo and Paraná; the area nearby Campos do Quiriri, São Joaquim National Park highlands and the coastal promontory of Serra do Tabuleiro State Park in the state of Santa Catarina; the Aparados da Serra highlands escarpment area of Serra Geral close to the ocean in northeastern Rio Grande do Sul. Although all the modeled area is not likely occupied by *C. grandiflora* due the land discontinuity of the sky island distribution of rock outcrops on mountaintops, for example, in the flora of Itatiaia (Moreira *et al.* 2021) this species was not found. Our modeling shows that these areas bear suitable habitats for the new species and could harbor other *Calea* species with habitat requirements similar to those of *C. grandiflora*. Besides *C. grandiflora*, only *C. subintegerrima* (Malme 1933: 94) V.R.Bueno & G.Heiden (Bueno & Heiden 2022a) and *C. ilienii* Malme (1933: 94–95), from the *C. myrtifolia* complex, have occurrence records along the Serra do Mar range.

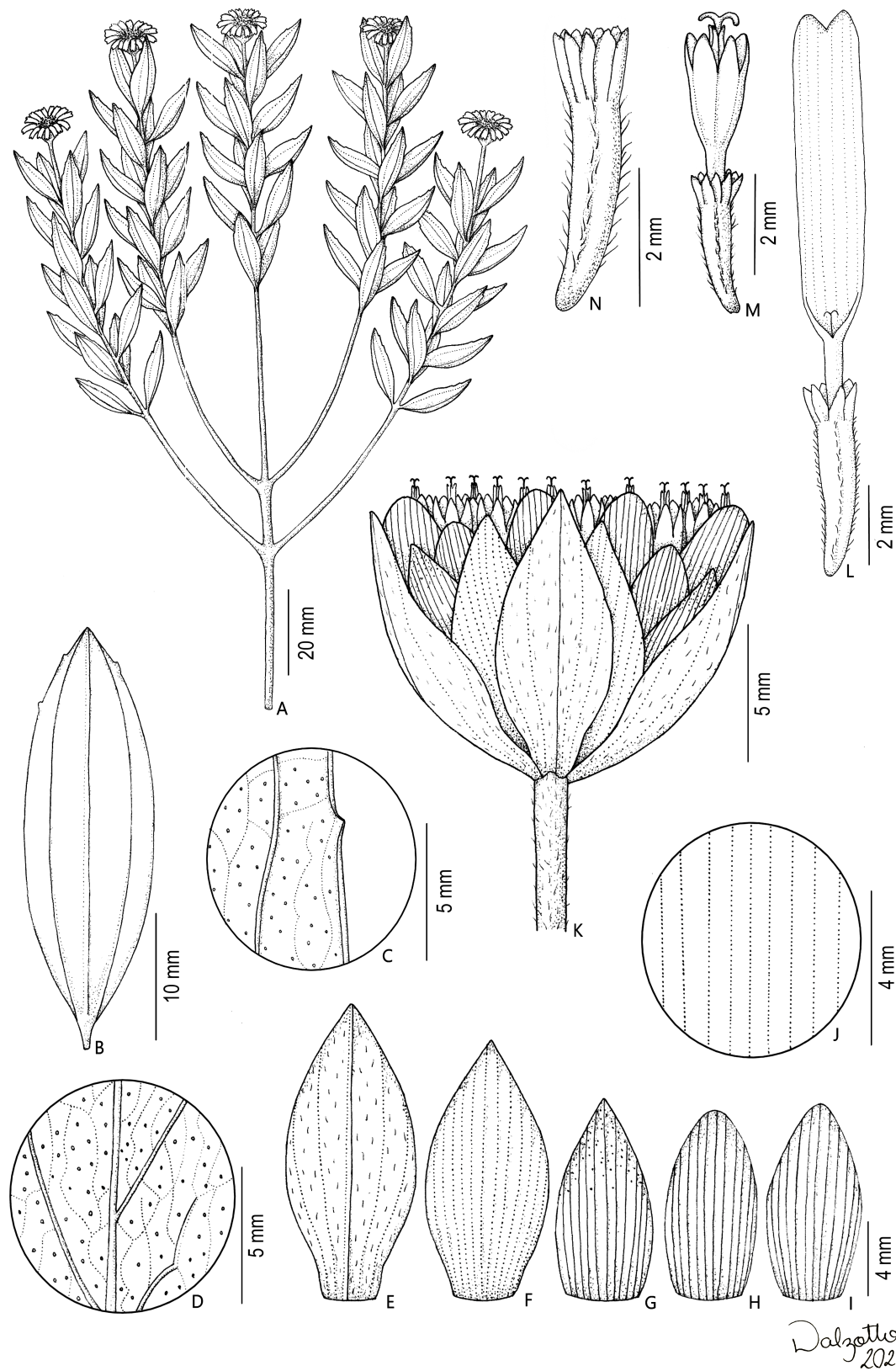
**Informal Conservation Status:**—*Calea grandiflora* could be considered Critically Endangered (CR). The analyses through GeoCAT (Bachman *et al.* 2011) generated only an AOO (8.0 km<sup>2</sup>), due the limited distribution records known so far (only two points). According to the IUCN (2019) criteria, this new species complies with several requirements of the CR status: B1B2; C2(i); D, mainly because the new species was found in only two locations. The scarce records, in agreement with the condition b<sup>a</sup> (IUCN 2019), suggest that this species is Endangered. Despite the apparent contradiction, when two distinct statuses are confronted, the most restrictive one is preferred according to the IUCN (2019) guidelines.

*Calea grandiflora* occurs in two protected areas: Paranapiacaba Biological Station and Sabesp Forest Reserve. These areas are in one of the four centers of endemism of the Atlantic Forest (Aguiar *et al.* 2003). Due to the apparent rarity, the AOO value, the adopted IUCN criteria and conditions, and because the last collection is from 1991, the status CR is warranted for *C. grandiflora*.

**Etymology:**—The epithet “grandiflora” refers to the ray florets, which are larger than those found in other species of the *Calea myrtifolia* complex.

**Phenology:**—The collected specimens were flowering and fruiting in December and March.





**FIGURE 1.** *Calea grandiflora* sp. nov. (Neurolaeneae, Asteraceae) A. Flowering branch. B. Leaf with pauciserrate margins, adaxial surface. C. Margin with small teeth. D. Abaxial surface indumentum. E. Phyllary of first series. F. Phyllary of second series. G. Phyllary of third series. H. Phyllary of fourth series. I. Phyllary of fifth series. J. Striate surface of scarious phyllaries. K. Capitulum with ray florets removed to show involucre, paleae and disc floret arrangements. L. Ray floret. M. Disc floret with monolength pappus scales. N. Cypsela with monolength pappus scales. A–N drawn from *L. R. Landrum 2761* (SP); A–M: millimeter scale. Illustration by Débora Dalzotto.

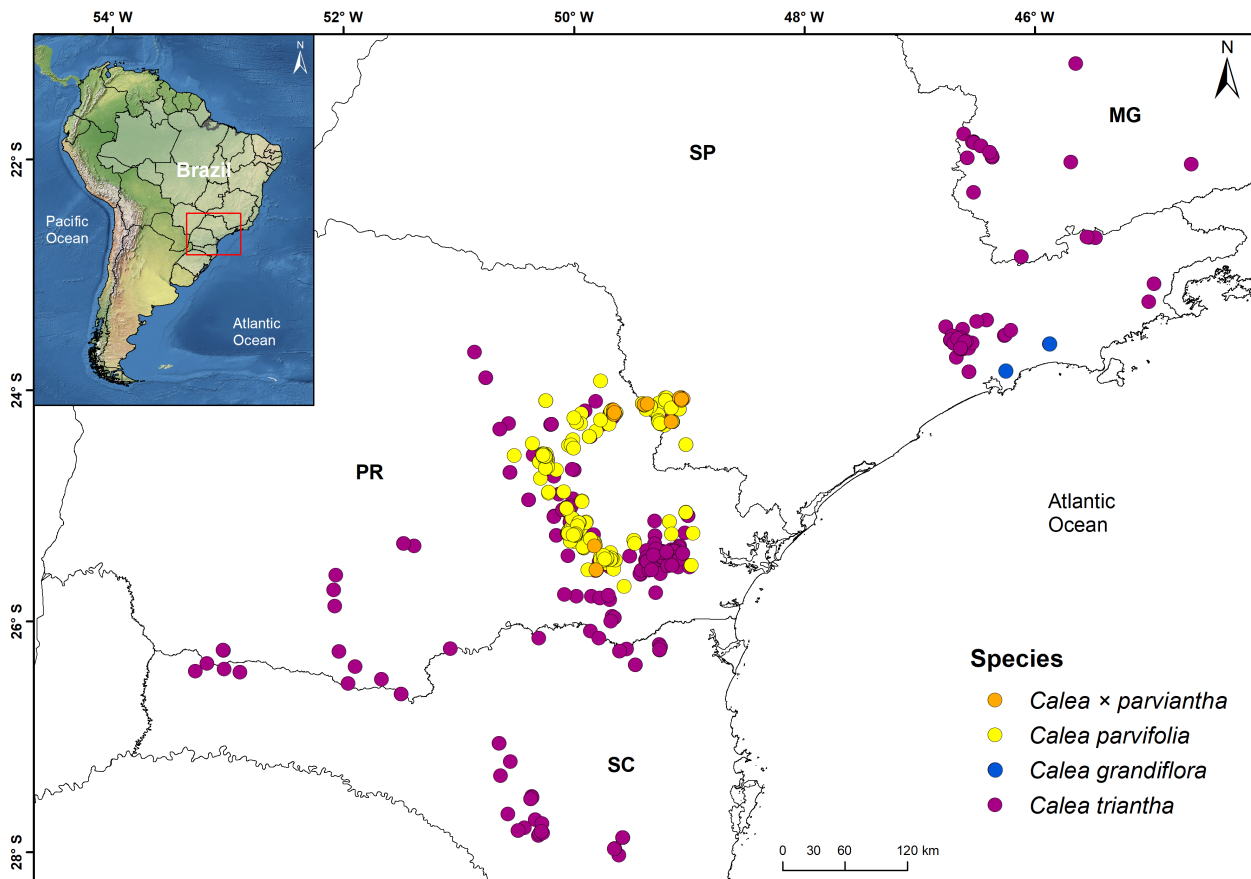


FIGURE 2. Occurrence map of *Calea grandiflora*, *C. parvifolia*, *C. × parviantha*, and *C. triantha* (Neurolaeneae, Asteraceae) in Brazil. MG—Minas Gerais, SP—São Paulo, PR—Paraná, SC—Santa Catarina. Figure by: Marcelo L. Bueno.

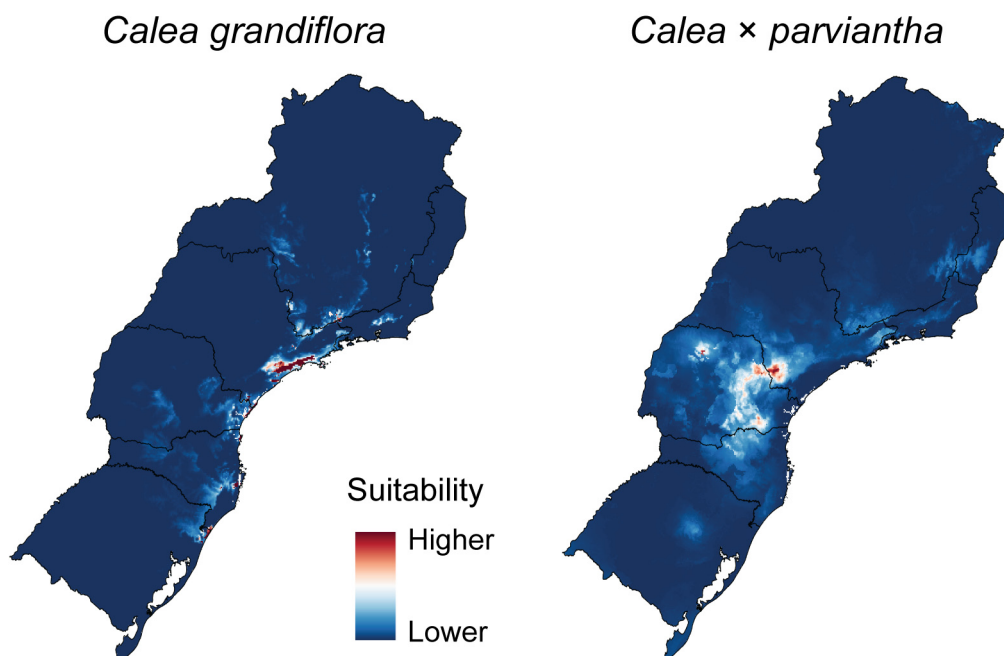


FIGURE 3. Prediction occurrence map of suitable ecological niche modelling for *Calea grandiflora* and *C. × parviantha* (Neurolaeneae, Asteraceae). Figure by: Marcelo L. Bueno.

**Taxonomic comments:**—One of the two specimens of *Calea grandiflora* was initially identified as *C. myrtifolia*, probably due to the glabrous leaves, acrodromous venation, and involucre with foliaceous outer phyllaries. These features together with shrubby habit, cymose dichasial capitulescence, and the pappus shorter than the cypsela place it

in the *Calea myrtifolia* complex. These two species can be distinguished by elliptic blade leaf (vs. ovate or lanceolate), attenuate base leaf (vs. rounded), outer series of phyllaries 12.2–20 mm long (vs. 4.9–11.3 mm), ray floret tube 4–5 mm long (vs. 2.1–3.1 mm), disc corolla lobes 1.4–1.5 mm long (vs. 0.8–1.2 mm).

The elliptic and longer leaves, the capitulum with longer outer phyllaries and ray floret corolla, and the uncommon occurrence in the Serra do Mar corroborate that this is a new species, resembling the previously described *Calea arachnoidea* Reis-Silva & Nakajima (2021: 130–131).

Both *Calea grandiflora* and *C. arachnoidea* have shrubby habit, elliptic leaves up to 6.8 cm long, slightly branched cymose dichasial capitulescence, glandular-punctate peduncle, involucre 10.8–20 mm long, and similar habitat associated with rock outcrops in the Atlantic Rainforest. These species can be differentiated by the striate stems (vs. conspicuously furrowed), discoloured leaf blades (vs. concolorous), venation basal (vs. semicraspedodromous); peduncle 1.35–4.28 cm long (vs. 0.3–0.8 cm), puberulous to pilose or pilose indumentum (vs. arachnoid, rarely glabrous), outer series of phyllaries 12.2–20 × 4.2–10.6 mm long (9–14.1 × 2.9–6.1 mm); paleae 7.7–9.8 mm long (9.8–13.2 mm); ray florets 10–18 (vs. 3–8), corolla 16.9–31 mm long (vs. 8.1–12 mm); and monolength pappus scales (vs. polylength).

**Paratype:**—BRAZIL. SÃO PAULO: Salesópolis, Reserva Florestal da Sabesp, adjacente à Estação Biológica da Boraceia, 22 March 1991, *M. Kirizawa* 2432 (SP).

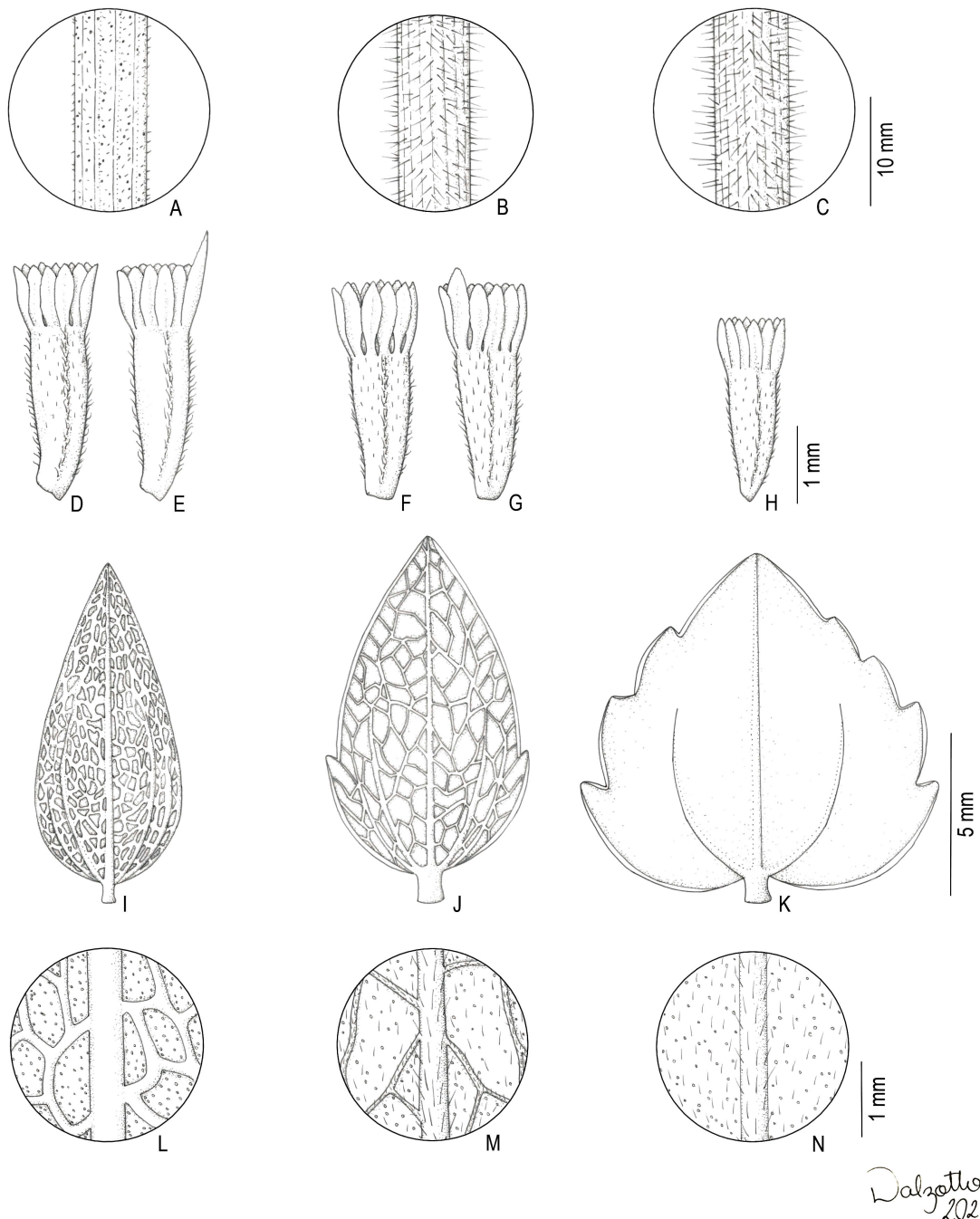
***Calea* × *parviantha*** V.R.Bueno & G.Heiden, **nothosp. nov.** (Fig. 4, 5)

*Calea* × *parviantha* differs from *C. parvifolia* by the striate stems (vs. corrugate stems), hispid or hispidulous or glabrous stems (vs. puberulous or puberulent), and coriaceous leaves (vs. chartaceous leaves); and from *C. triantha* by the rounded base leaf, sometimes subcordate (vs. cordate), concave paleae (vs. conduplicate), and pappus scales 1.1–2.7 mm long (vs. 0.8–1.3 mm).

Type:—BRAZIL. Paraná, Jaguariaíva, campo próximo à ponte do Rio das Mortes, PR-151, 16 December 1991, *A.C. Cervi et al.* 3546 (holotype: MBM!, isotypes: CGMS!, CPAP!, UPCB!).

**Shrubs**, 0.2–1.2 m tall, **stems** castaneous, cylindrical, striate, hispid, often sparsely hispid, rarely densely hispid or hispidulous or glabrous, rarely glandular-punctate, internodes 5.4–32.7 mm long. **Leaves** decussate, petiole 0.5–2.2 mm long; blades olivaceous or dark green adaxially, concolorous, sometimes slightly discoloured or discoloured, coriaceous, 0.78–2.57 × 0.42–1.59 cm, ovate or narrow ovate, rarely wide ovate, base rounded, sometimes subcordate, apex acute, rarely attenuate or obtuse, venation basal acrodromous and reticulate or basal acrodromous, margins revolute, often slightly revolute, entire or pauciserrate, sometimes serrate, 0–12 (–13–14) teeth, 0.3–1.8 mm long, from the base to middle, sometimes absent or just in the middle, rarely along the margins, abaxial surface hispidulous, often glabrous, sometimes hispid, veins hispid to hispidulous or hispidulous, sometimes glabrous, densely glandular-punctate, often glandular-punctate, adaxial surface scabridulous, often sparsely scabridulous with margin scabridulous, sometimes glabrous to scabridulous, glands absent. **Capitulescence** cymose dichasial, sometimes capitulum solitary, profusely branched or branched, axis 0–14.56 (–30.3) cm long, branching to 2–3<sup>rd</sup> ramifications, rarely 4–5<sup>th</sup> ramifications, 2–18 secondary stems, peduncle 0.08–3.55 (–3.9–4.16) cm long, hispid, rarely glandular-punctate. **Capitulum** heterogamous, radiate, involucre campanulate, 5.8–9.7 × 6.8–13.6 mm, 5-seriate; **phyllaries** conspicuously or inconspicuously striated; two outermost series of phyllaries olivaceous, sometimes olivaceous with base yellowish green, foliaceous, sometimes foliaceous with base scarious, margins entire, sometimes serrate, abaxial surface hispid to hispidulous, sometimes glabrous or hispidulous, densely glandular-punctate or glandular-punctate; first series 4–6 striate, blades 6.6–10.2 × (3–3.3–) 3.9–4.7 (–5.5–5.7) mm, wide elliptic or narrow obovate, sometimes elliptic, rarely oblanceolate, apex acute or obtuse, half revolute, often revolute; second series 4–8 striate; blades 7–10.4 × 3.1–5.7 (–7.5) mm, obovate or wide elliptic or panduriform, apex obtuse, often acute, revolute, rarely half revolute; third series yellowish green to olivaceous, apex foliaceous, sometimes scarious, 6–10 striate, blades 5.5–9.7 × 2.7–4.8 mm, oblong or narrow ovate, sometimes narrow obovate, margins entire, apex obtuse, sometimes rounded, rarely acuminate, revolute or flat; abaxial surface sparsely hispid at apex or pilose at apex, sometimes glabrous, densely to moderately glandular-punctate at apex, sparsely to densely glandular-punctate; two innermost series yellowish green to light yellow or yellowish green, scarious, glabrous, sometimes glandular-punctate at apex, fourth series 8–15 striate, blades 7.2–9.9 × 3.3–4.3 mm, oblong, sometimes narrow obovate, margins entire, sometimes erose at apex, apex rounded; fifth series 10–15 striate, blades 7.4–10.9 × 2.3–3.9 mm, narrow oblong or oblanceolate, sometimes narrow elliptic, margins entire, apex rounded, sometimes obtuse; **receptacle** slightly convex, holopaleaceous; paleae light yellow, concave, 7–9 mm long, narrow elliptic or narrow oblong, sometimes oblanceolate, apex long acuminate. **Ray florets** 8–15, (10.2–) 12–15.7 (–19.8) mm long, pistillate, corolla liguliform, (8.3–) 9.3–14.2 (–16.4) mm long, yellow, tube 1.5–3.8 mm long, limb 5.9–12.6 × (1.8–2.3–) 3.2–4.6 mm, narrow obovate, often narrow elliptic or narrow oblong or oblanceolate

or elliptic, apex rounded, sometimes 2–4 lobulate, rarely obtuse, 5–7 veins, abaxial surface densely glandular-punctate, sometimes glandular-punctate, adaxial surface glabrous; style arms yellow, 0.7–1.5 mm long. **Disc florets** 30–55, 7–10 mm long, bisexual, corolla tubular, 4.4–7 mm long, yellow, tube 1.3–2.6 mm long, lobes 1–1.7 (–2.1) mm long, sparsely glandular-punctate or glands absent, rarely glandular-punctate; anthers light yellow, (2.3–) 2.5–2.9 mm long, apical appendages ovate; style arms yellow, 0.8–1.2 mm long, linear. **Cypselae** blackish, 2.2–3.2 (–3.6) mm long, prismatic, ray cypselae 3-angled, disc cypselae 4-angled, glabrous to pilose or densely pilose or sparsely pilose to pilose, ribs densely pilose, often pilose; **pappus** monotypic, often bitypic, scales monolength, sometimes bilength, 8–15 (1–2 distinctly longer, when present), free, 1.1–2.2 mm long, longer scales 1.6–3 mm long, when present, oblong or oblanceolate, sometimes narrow elliptic, apex obtuse or rounded, margins entire, erose at apex.

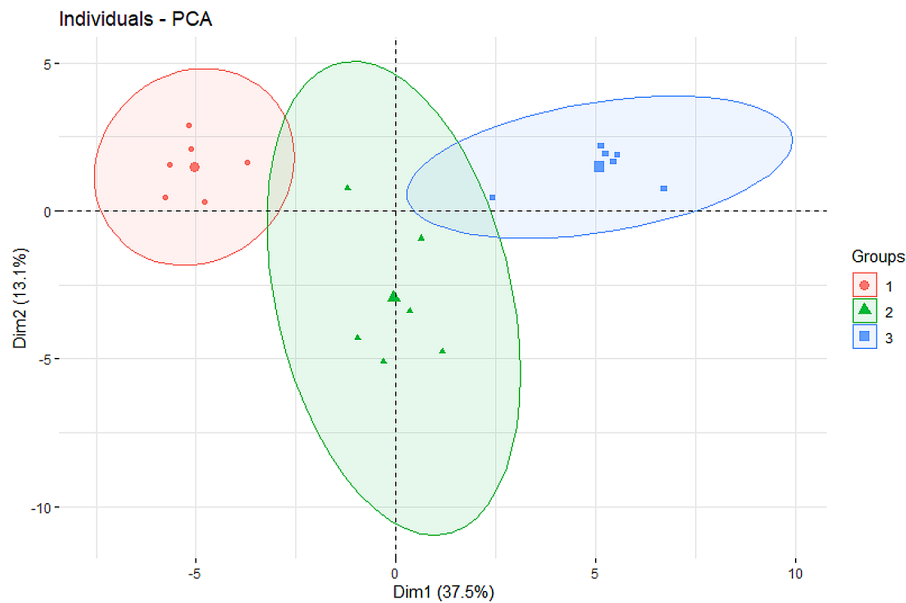


**FIGURE 4.** Comparative illustration of informative structures to recognize the new nothospecies *Calea* × *parviantha* in comparison to its parental species *C. parvifolia* and *C. triantha* (Neurolaeneae, Asteraceae) A–C. Indumentum of stems. D–H. Cypselae with pappus scales. I–K. Leaves, abaxial surface with venation. L–N Abaxial surface with vein and indumentum in detail. A, D, E, I and L: *Calea parvifolia* drawn from *M. L. Brotto et al.* 3175 (MBM). B, F, G, J and M: *Calea* × *parviantha* nothospecies nov. drawn from *A. C. Cervi* 3546 (MBM). C, H, K and N: *Calea triantha* drawn from *G. Heiden et al.* 2312 (ECT); A–M: millimeter scale. Illustration by Débora Dalzotto.





**FIGURE 5.** *Calea* × *parviantha* nothospecies nov. (Neurolaeneae, Asteraceae) in tropical high elevation grasslands in the contact zone of the Atlantic Forest and Cerrado domains at Porto Amazonas, Paraná, Brazil. A. Leaf abaxial surfaces and phyllaries of involucre. B. Radiate capitulum. Photos by R. T. Dall’Agnol.



**FIGURE 6.** Principal Component Analysis performed with the informative morphological characters of *C. × parviantha* and its parents: *C. parvifolia* and *C. triantha*. 1. *Calea triantha*. 2. *Calea × parviantha*. 3. *Calea parvifolia*. Figure by Marcelo L. Bueno.

**Distribution, Habitat and Predicted Area of Occurrence:**—*Calea × parviantha* occurs in two Brazilian states: São Paulo and Paraná (Fig. 2). A total of eight municipalities have occurrences of this new nothospecies, two in São Paulo and six in Paraná. In addition, Ponta Grossa (municipality in Paraná) has an occurrence only recorded by photos (Pricila Just, pers. comm.). The new nothospecies occurs in areas of grasslands with rocks outcrops and riverine vegetation along the contact zones of high elevation tropical grasslands of the Atlantic Forest domain and the southernmost limits of open grasslands and savannas from the Cerrado domain. In the Jaguariaíva sites, *C. × parviantha* is more commonly found than its parental taxa (Fig. 2), suggesting that hybrid populations are probably replacing them in this area.

According to the niche modelling, the new nothospecies potentially occurs in open areas where the two parental species are allopatric from the center-south of São Paulo to the south of Paraná (Fig. 3). However, due to its hybrid nature, it is more likely that the distribution of the nothospecies is restricted from Itararé, São Paulo, to Lapa, Paraná, where the parental species co-occurrence is likely and the contacts between Atlantic Forest and Cerrado are more common (Fig. 2).

**Informal Conservation Status:**—*Calea × parviantha* could be considered Endangered (EN). Traditionally, hybrids are not evaluated for their conservation status, but as this hybrid has different collections over almost a century, it is probably a stable hybrid and therefore this status was evaluated. The GeoCAT (Bachman *et al.* 2011) analyses generated an EOO of 5,000 km<sup>2</sup> and AOO of 48 km<sup>2</sup>, both values suggesting EN status. *C. × parviantha* also can be considered EN due the criteria (IUCN 2019): B1B2; C2(i); D. The new nothospecies mostly occurs out of protected areas, except for three occurrences in Ecologic Station of Itapeva (Itapeva, São Paulo), Ecological Park of Barreira (Itararé, São Paulo) and probable occurrence in Cerrado State Park (Jaguariaíva, Paraná). The few records in protected areas, the AOO and EOO values and the above-mentioned IUCN criteria are strong subsidies for classifying *Calea × parviantha* as Endangered.

**Etymology:**—The nothospecific epithet “parviantha” is proposed based on the merging of the specific epithets of the putative parental species: *Calea parvifolia* and *C. triantha*.

**Phenology:**—Most of the collected specimens were found flowering and fruiting from December to April, with one outlier record flowering in August.

**Taxonomic comments and support analysis:**—Most of the specimens of *Calea × parviantha* were misidentified as *C. myrtifolia*, mainly due to the ovate leaves bigger than the leaves of *C. parvifolia*. Studies of specimens labeled as *C. myrtifolia* from São Paulo and Paraná evidenced that some specimens were the hereby described *C. grandiflora* and the remaining a putative hybrid between *C. parvifolia* and *C. triantha*. The main morphological characteristics that indicated these specimens as a new hybrid species were the combination of reticulate venation and hispid indumentum—features absent in *C. myrtifolia*, but present in *C. parvifolia* and *C. triantha*, respectively. Therefore,

based on the evaluation of all the available specimens previously labeled as *C. myrtifolia* we can currently confirm that this species is endemic to the state of Minas Gerais in Southeastern Brazil.

*Calea* × *parviantha* shares with *C. parvifolia* the rounded leaf base, occasionally subcordate, elliptic blade of first series of phyllaries, concave paleae of receptacle, tube of disc floret 1.3–2.6 mm long, most of cypselae with glabrous to pilose face and densely pilose ribs, and pappus monotypic, often bitypic in the same plant. They can be distinguished by the striate stems (vs. furrowed stems), hispid or hispidulous or glabrous stems (vs. puberulous or puberulent), glands absent in stems, rarely glandular-punctate (vs. densely glandular-punctate, sometimes glandular-punctate), coriaceous leaves (vs. chartaceous), revolute margin, sometimes slightly revolute (vs. flat), commonly hispidulous abaxial surface (vs. commonly glabrous), revolute apex in second series of phyllaries (vs. flat), and always entire margin in third series of phyllaries (vs. mostly serrate, rarely entire).

*Calea* × *parviantha* has striate stems and coriaceous leaves in common with *C. triantha*. In addition, these species commonly have hispid and eglandular stems, hispid peduncle, hispid to hispidulous outer phyllaries, and rounded apex of ray florets. The nothospecies differs from this parental species by the commonly ovate or narrow ovate leaves (vs. very wide ovate, sometimes wide ovate, rarely ovate), rounded base leaf, sometimes subcordate (vs. cordate), usually acute apex (vs. usually obtuse apex), concave paleae (vs. conduplicate), pappus monotypic, often bitypic (vs. always monotypic), monolength pappus scales, often monolength and bilength (vs. only monolength), and pappus scales 1.1–2.7 mm long (vs. 0.8–1.3 mm).

The characteristics that the nothospecies presents that are intermediate or that overlap with those of the parental species are listed in Table 1. The PCA results corroborate the hypothesis on the hybrid origin of *C. × parviantha*, all characters listed in Table 2 contributed to the separation of taxa in the PCA analysis. The multivariate analyses plot (Fig. 6) evidences that the morphological data groups the specimens in distinct groups of parental species and the nothospecies with intermediate values.

**TABLE 1.** Vegetative and reproductive informative characteristics measured for the Principal Component Analysis performed with *Calea* × *parviantha* and its parental species *C. parvifolia* and *C. triantha* (Neurolaeneae, Asteraceae).

	<i>C. parvifolia</i>	<i>C. × parviantha</i>	<i>C. triantha</i>
<b>Venation</b>	reticulate	basal acrodromous and reticulate or basal acrodromous	basal acrodromous
<b>Leaf margin</b>	entire	entire or pauciserrate, rarely serrate	serrate
<b>Glands in peduncle</b>	densely punctate	eglandular, rarely glandular-punctate	eglandular
<b>Margin of outer phyllaries</b>	pauciserrate, rarely entire	entire, sometimes pauciserrate	entire
<b>Third series of phyllaries (mm)</b>	8.8–10.3	5.5–9.7	5.1–7.9
<b>Fifth series of phyllaries (mm)</b>	(8.1) 9–10.2	7.4–10.9	6.6–8.2 (9.3)
<b>Paleae</b>	narrow elliptic	narrow elliptic or narrow oblong, sometimes oblanceolate	oblong
<b>Disc floret length (mm)</b>	8.5–11.6	7–10	6.1–8.4
<b>Glands on disk floret corolla</b>	glandular-punctate	sparsely glandular-punctate or eglandular, rarely glandular-punctate	eglandular
<b>Length of pappus scales</b>	monotypic, often bitypic	monotypic, often bitypic	monotypic
<b>Length of pappus scales</b>	monolength or bilength	monolength, sometimes bilength	monolength

Examining all the specimens, a gradation of characters was seen in the different populations, but within these, some morphological standardization is seen among the specimens, mainly in those found in the municipality of Jaguariaíva and region, Paraná state. All hybrid populations are in contact with populations of the parental species, the nothospecies populations further south of the distribution are more than the Jaguariaíva populations (north of the nothospecies distribution). We believe that due to all the evidence presented here it is a nothospecies; however, more molecular studies would be needed to corroborate this hybrid status.

**TABLE 2.** Intermediate or overlapped morphological features of *Calea* × *parviantha* and its parents: *C. parvifolia* and *C. triantha* (Neurolaeneae, Asteraceae).

Informative Characters			
Vegetative	Internodes	Measurement	Length
	Petiole	Measurement	Length
	Leaf	Measurement	Length
		Measurement	Wide
		Characterization	Shape of apex
	Peduncle	Characterization	Types of venation
		Characterization	Types of margins
		Measurement	Length
	Involucre	Measurement	Length
		Measurement	Wide
	Striate phyllaries	Characterization	Stripes conspicuous or inconspicuous
		Counting	Number
	Second order of phyllaries	Characterization	Shape
		Measurement	Length
	Third order of phyllaries	Measurement	Wide
		Characterization	Shape
		Characterization	Apex
		Characterization	Glandular or eglandular
		Characterization	Margins
	Fourth order of phyllaries	Measurement	Length
		Measurement	Wide
		Characterization	Glandular or eglandular
	Fifth order of phyllaries	Measurement	Length
Measurement		Wide	
Paleae	Measurement	Length	
	Characterization	Apex	
Reproductive	Ray florets	Counting	Number
		Measurement	Length of corolla
	Ray florets	Measurement	Length of limb
		Characterization	Shape of apex
		Counting	Veins in corolla
		Characterization	Glandular or eglandular
		Measurement	Length of style
	Disc florets	Measurement	Length
		Measurement	Length of Corolla
		Measurement	Length of Tube
		Measurement	Length of Limb
	Anthers	Characterization	Glandular or eglandular
		Measurement	Length
		Measurement	Length
	Style	Measurement	Length
		Measurement	Length
	Cypselae	Measurement	Length
Characterization		Indumentum of surface	
Pappus scales	Measurement	Length	
	Characterization	Shape	
		Characterization	Apex



**Paratypes:**—BRAZIL. Paraná: Balsa nova, Ponte dos Arcos, 07 December 2005, *C. Kozera 2688* (MBM); Jaguariaíva, campo próximo à ponte do Rio das Mortes - PR 151, 16 December 1991, *C. Kozera & O. P. Kozera 2688* (MBM); Castro, entre Castro e Ponta Grossa, 1950, *J. Vidal 3-151* (R); Jaguariaíva, campos, 05 February 1910, *P. Dusén 9187* (S); campos, 26 December 1914, *P. Dusén 16195* (MO, US); rio das Mortes, 02 February 1995, *J.R. Stehmann & J. Semir 2169* (BHCB, UEC); montanha, 07 April 2007, *F. Bueno s.n.* (RB); Palmeira, fazenda Santa Rita, 24 January 1990, *L. T. Dombrowski et al. 14258* (MBM); Sengés, mata ciliar na margem esquerda do Rio Funil, 08 April 1995, *Ribeiro Jr. et al. 04* (FUEL, SP, UEC); Tibagi, Parque Estadual Canyon Guartelá, 10 February 1997, *V. F. Kinupp et al. 273* (FUEL, UEPG). São Paulo: Itapeva, Estação Ecológica de Itapeva, 18 August 1995, *V.C. Souza et al. 8732* (ESA, SP, SPF); 27 January 2009, *J. B. Baitello & C. R. Lima 2236* (MBM, SPSF); Estação Ecológica de Itapeva, trilha da Vila, 26 March 2008, *J. B. Baitello et al. 2051* (SPSF, UEC); Itararé, Gruta da Barreira, 04 December 1984, *C. Muller et al. 5994* (FUEL, UEC); próximo à entrada da Fazenda São Nicolau, 21 April 1993, *V. C. Souza et al. 3981* (ESA).

**Additional specimens examined:**—*Calea parvifolia*—BRAZIL. Paraná: Arapoti, Estrada para Ventania na Barra do Rio Perdizes com o Rio das Cinzas, beira da estrada, 03 March 2003, *M. A. G. Magenta 558* (MO, SPF); Balsa Nova, Ponte dos Arcos, afloramento rochoso próximo a Mata de Pinus, 02 April 2019, *A. L. Christ et al. 646* (ICN); Bocaiúva do Sul, Serra da Bocaina, 20 April 1998, *J. M. Silva et al. 2331* (MBM); Ponta Grossa, Furnas de Itaiacoca, 20 August 2014, *J. Cordeiro et al. 4705* (MBM); Tibagi, Parque Estadual do Guartelá, Rio Iapó, 01 September, *S. R. Ziller 1578* (MBM). São Paulo: Itapeva, Estação Experimental, 03 November 2009, *R. Cielo-Filho et al. 896* (SPSF).

*Calea triantha*—BRAZIL. Minas Gerais: Poços de Caldas, Campo do Saco, 12 Feb 1965, *M. Emmerich 2381* (RB). Paraná, Campo Largo, fazenda Thalia, 08 March 1998, *W. Amaral 22* (MBM); Ventania, fazenda Santa Inês, 11 February 2005, *D. A. Estevan et al. 531* (HUFU). Santa Catarina, Lages, salto Caveira, 29 January 2015, *R. Mello-Silva 3765* (SPF); Rio Negrinho, salto do rio Antinha, 23 December 2018, *C. Ribeiro et al. 313* (ICN). São Paulo, Campos do Jordão, vale do rio Coxim, areal, 17 March 1964, *J. Correa Gomes Jr. 1620* (SP).

### Key to the species of *Calea* from the states of Paraná and São Paulo, Brazil

1. Discoid capitulum.....2.
- Radiate capitulum.....5.
2. Outer phyllaries scarious.....3.
- Outer phyllaries foliaceous.....4.
3. Capitulescences umbelliform; pappus scales 1.8–4.2 mm long..... *C. lantanoides*
- Capitulescences cymose; pappus scales 0.2–1.1 mm long..... *C. polycephala*
4. Venation acrodromous basal; pappus scales 4–5 mm long..... *C. gentianoides*
- Venation hypodromous; pappus scales 0.2–0.3 mm long..... *C. senecioides*
5. Leaf margins thickened and white.....6.
- Leaf margins slender and green.....7.
6. Leaves discolorous, abaxial surface glandular-punctate; cypselae 2–2.5 mm..... *C. ilieni*
- Leaves concolorous, abaxial surface eglandular; cypselae 3.2–3.6 mm..... *C. monocephala*
7. Capitulescence umbelliform.....8.
- Capitulescence cymose dichasial or capitula solitary.....10.
8. Leaves whorled.....9.
- Leaves decussate.....11.
9. Leaf limb elliptic; receptacle conic..... *C. mediterranea*
- Leaf limb obovate or oblanceolate or rhombic; receptacle convex.....10.
10. Leaves crowded in a basal rosette; ray floret corolla 9.8–11 mm long..... *C. acaulis*
- Leaves evenly distributed along the stems; ray floret corolla 11.3–14.7 mm long..... *C. cymosa*
11. Leaves serrate; capitulescence congest..... *C. serrata*
- Leaves crenate; capitulescence lax..... *C. pinnatifida*
12. Habit herbaceous.....13.
- Habit shrubby.....18.
13. Leaves 0.04–0.1 cm wide, linear; involucre 8.4–13.4 mm long, receptacle oligopaleaceous..... *C. graminifolia*
- Leaves 0.6–4.5 cm wide, ovate to lanceolate or elliptic or obovate to orbiculate; involucre 14.1–25 mm long, receptacle holopaleaceous.....14.
14. Leaf blade ovate; peduncle strigose to scabrous or tomentose.....15.
- Leaf blade elliptic or obovate to orbiculate; peduncle velutinous or hirsute.....16.
15. Receptacle convex, paleae 9–13 mm long; tube of ray florets 3–5 mm long..... *C. uniflora*
- Receptacle conic, paleae 14–20 mm long; tube of ray florets 6–7.5 mm long..... *C. verticillata*
16. Leaf limb elliptic, apex acute; peduncle hirsute; receptacle convex..... *C. clauseniana*
- Leaf limb obovate to orbiculate, apex rounded; peduncle velutinous; receptacle conic.....17.
17. Outermost series of phyllaries longer than the second and third series..... *C. pohliana*
- Outermost series of phyllaries shorter than the second and third series..... *C. cuneifolia*

18. Leaves sessile, limb linear, venation hypodromous; disc florets 5–10; pappus scales 0.2–0.5 mm long ..... *C. hymenolepis*  
 - Leaves petiolate, limb ovate or lanceolate or elliptic or deltate, venation acrodromous basal or reticulate or eucamptodromous; disc florets 15–75; pappus scales 0.7–3.0 mm long..... 19.
19. Leaf base attenuate; two outermost series of phyllaries 12.2–20 mm long; corolla of ray florets 16.9–31 mm long .....  
 ..... *C. grandiflora*  
 - Leaf base rounded or cordate or truncate; two outermost series of phyllaries 3.3–11.2 mm long; corolla of ray florets 7.4–16.5 mm long ..... *C. marginata*
20. Stems corrugated, puberulous or puberulent; leaves chartaceous, margins flat ..... *C. parvifolia*  
 - Stems striated, hispid to hispidulous, strigose, rarely glabrous; leaves coriaceous, margins revolute..... 21.
21. Second series of phyllaries pubescent to puberulous; ray floret corolla 15.3–17 mm long, limb 12.5–13.5 mm long .....  
 ..... *C. pruskiana*  
 - Second series of phyllaries strigose or glabrous or hispid; ray floret corolla 7.4–14.2 mm long, limb 5.9–10.5 mm long ..... 22.
22. Leaf abaxial surface glabrous; cypselas angles hirsute ..... *C. subintegerrima*  
 - Leaf abaxial surface sparsely scabridous or scabridulous; cypselas angles pilose ..... 23.
23. Leaf base cordate; third series of phyllaries glandular; receptacle paleae conduplicate ..... *C. triantha*  
 - Leaf base rounded or subcordate; third series of phyllaries glandular-punctate; receptacle paleae concave ..... *C. × parviantha*

## Acknowledgements

VRB acknowledges CNPq (141645/2018-0) for the fellowship granted, CAPES/PROAP for research support, the Harold E. Robinson and Vicki A. Funk 2020 Award, the IAPT Research Grants 2021, and the Mini-ARTS Awards 2021. GH acknowledges CNPq (314590/2020-0) for the research productivity grant. The authors are grateful to the staff of all herbaria visited; the six different photographers who recorded this species in the wild, represented here by P. Just and R. T. Dall’Agnol; Débora Dalzotto, who prepared the beautiful botanical illustrations; and João Iganci for the useful advice on the improvement of the fine line drawings. We are also grateful for the important contributions of two anonymous reviewers.

## References

- Aguiar, A.P., Chiarello, A.G., Mendes, S.L. & Matos, E.N. (2003) The Central and Serra do Mar Corridors in the Brazilian Atlantic Forest. *In: Galindo-Leal, C. & Câmara, I.G. (Eds.) The Atlantic Forest of South America: biodiversity status, threats, and outlook*. Island Press, Washington, pp. 118–132.
- Alvarez, I. & Wendel, J.F. (2003) Ribosomal ITS sequences and plant phylogenetic inference. *Molecular Phylogenetics and Evolution* 29 (3): 417–434.  
[https://doi.org/10.1016/S1055-7903\(03\)00208-2](https://doi.org/10.1016/S1055-7903(03)00208-2)
- Bachman, S., Moat, J., Hill, A.W., Torre, J. & Scott, B. (2011) Supporting Red List threat assessments with GeoCAT: Geospatial conservation assessment tool. *ZooKeys* 150: 117–126.  
<https://doi.org/10.3897/zookeys.150.2109>
- Baker, J.G. (1884) Compositae: Helianthoideae. *In: Martius, C.F.P. & von Eichler, A.W. (Eds.) Flora brasiliensis*. Oldenbough, Munchen and Leipzig, pp. 251–258.
- Barroso, G.M. (1975) De Compositarum Novitatibus. *Sellowia* 26: 102–118.
- Beentje, H. (2010) *The Kew Plant Glossary an Illustrated Dictionary of Plant Terms*. Kew Publishing, Richmond, 160 pp.
- Berchtold, F.W. & Presl, J.S. (1820) *O Prirozenosti Rostlin*. Krala Wiljma Endersa, Prague, 322 pp.
- Blake, S.F. (1937) Eleven new Asteraceae from North and South America. *Journal of the Washington Academy of Sciences* 27: 374–391.
- Breiman, L. (2001) Random forests. *Machine Learning* 45: 5–32.  
<https://doi.org/10.1023/A:1010933404324>
- Brochmann, C. (1987) Evaluation of some methods for hybrid analysis, exemplified by hybridization in *Argyranthemum* (Asteraceae). *Nordic Journal of Botany* 7: 609–630.  
<https://doi.org/10.1111/j.1756-1051.1987.tb02030.x>
- Brown, R. (1817) *Observations on the Natural Family of Plants called Compositae*. London, pp. 75–142.  
<https://doi.org/10.5962/bhl.title.140190>
- Bueno, V.R. & Heiden, G. (2021) *Calea funkiana* (Compositae, Neurolaeneae), a new species endemic from Serra do Cipó, Minas Gerais, Brazil. *Systematic Botany* 46 (2): 470–475.

<https://doi.org/10.1600/036364421X16231782047497>

- Bueno, V.R. & Heiden, G. (2022a) Novelty in *Calea* sect. *Meyeria* (Asteraceae, Neurolaeneae) from Brazil. *Systematic Botany* 47 (2): 575–585.  
<https://doi.org/10.1600/036364422X16512564801632>
- Bueno, V.R. & Heiden, G. (2022b) *Calea sessilifolia* (Asteraceae, Neurolaeneae), an unusual new species from the Diamantina Plateau, Minas Gerais, Brazil. *Systematic Botany* 47 (2): 586–592.  
<https://doi.org/10.1600/036364422X16512564801687>
- Bueno, V.R., Gostel, M.R. & Heiden, G. (2021) An overview of Neurolaeneae (Compositae). *Capitulum* 1: 36–43.  
<https://doi.org/10.53875/capitulum.01.1.03>
- Bueno, V.R., Gostel, M.R. & Heiden, G. (2022) *Calea repanda* (Asteraceae, Neurolaeneae), a new species of *Calea* and new taxonomic implications for the genus. *Phytotaxa* 544 (3): 280–288.  
<https://doi.org/10.11646/phytotaxa.544.3.2>
- Cardo, O.G. & Melgar, I.S. (2021) *Achillea* × *keuperi*, nothospecies nov. (sect. *Achillea*, Asteraceae). *Flora Montiberica* 79: 113–115.
- Cassini, A.H.G. (1819) Suite du sixième mémoire sur la famille des Synanthérées, contenant les caractères des tribus. *Journal de Physique, de Chimie, d'Historie Naturelle et des Arts* 88: 189–204.
- Deble, L.P. & Oliveira-Deble, A.S. (2011) Novelty to Compositae Family in Rio Grande do Sul State Flora. *Balduinia* 29: 1–8.  
<https://doi.org/10.5902/2358198014131>
- Desjardins, S.D., Hoare, A.G. & Stace, C.A. (2016) A new natural hybrid in the genus *Petasites*: *P. japonicus* × *P. pyreinaeus* (Asteraceae). *New Journal of Botany* 6: 2–3.  
<https://doi.org/10.1080/20423489.2016.1271383>
- Diaz-Piedrahita, S. & Rodríguez-Cabeza, B.V. (2012) Novedades em Asteráceas Colombianas II. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales* 36 (141): 501–515.
- Ellis, B., Daly, D.C., Hickey, L.J., Johnson, K.R., Mitchell, J.D., Wilf, P. & Wing, S.L. (2009) *Manual of Leaf Architecture*. The New York Botanical Garden Press, New York, 190 pp.  
<https://doi.org/10.1079/9781845935849.0000>
- Fick, S.E. & Hijmans, R.J. (2017) WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* 37 (12): 4302–4315.  
<https://doi.org/10.1002/joc.5086>
- Filigheddu, R., Farris, E., Pisanu, S., Urbani, M. & Susanna, A. (2014) Validation of the name *Centaurea* × *forsythiana* Levier (Asteraceae). *Phytotaxa* 166 (4): 297–300.  
<https://doi.org/10.11646/phytotaxa.166.4.6>
- Forester, B.R., De Chainé, E.G. & Bunn, A.G. (2013) Integrating ensemble species distribution modelling and statistical phylogeography to inform projections of climate change impacts on species distributions. *Diversity and Distributions* 19: 1480–1495.  
<https://doi.org/10.1111/ddi.12098>
- Funk, V.A., Susanna, A., Stuessy, T.F. & Robinson, H. (2009) *Systematics, Evolution and Biogeography of Compositae*. International Association for Plant Taxonomy, Vienna, 965 pp.
- Garrison, H., Shultz, L.M. & McArthur, D. (2013) Studies of a New Hybrid Taxon in the *Artemisia tridentata* (Asteraceae: Anthemideae) Complex. *Western North American* 73 (1): 1–19.  
<https://doi.org/10.3398/064.073.0101>
- Gemenholzer, B., Granica, S., Moura, M., Teufel, L. & Zidorn, C. (2017) *Leontodon* × *grassiorum* (Asteraceae, Cichorieae), a newly discovered hybrid between an Azorean and a mainland taxon: morphology, molecular characteristics, and phytochemistry. *Biochemical Systematics and Ecology* 72: 32–39.  
<https://doi.org/10.1016/j.bse.2017.04.001>
- Graham, M.H. (2003) Confronting multicollinearity in ecological multiple regression. *Ecology* 84: 2809–2815.  
<https://doi.org/10.1890/02-3114>
- Gruenstaudl, M., Carstens, B.C., Santos-Guerra, A. & Jansen, R.K. (2017) Statistical hybrid detection and the inference of ancestral distribution in *Tolpis* (Asteraceae). *Biological Journal of the Linnean Society* 121: 133–149.  
<https://doi.org/10.1093/biolinnean/blw014>
- Hickey, L.J. (1973) Classification of the architecture of dicotyledonous leaves. *American Journal of Botany* 60: 17–33.  
<https://doi.org/10.1002/j.1537-2197.1973.tb10192.x>
- Hijmans, R.J. & Graham, C.H. (2006) Testing the ability of climate envelope models to predict the effect of climate change on species distributions. *Global Change Biology* 12: 2272–2281.  
<https://doi.org/10.1111/j.1365-2486.2006.01256.x>
- Ilçim, A., Özçelik, H. & Çenet, M. (2013) A new natural hybrid of *Cousinia* Cass. (Asteraceae) from Türkiye. *Biological Diversity and*

- IUCN (2019) *Guidelines for using the IUCN red list categories and criteria*, version 13. Prepared by the Standards and Petitions Committee, Cambridge U.K. Available from: <http://www.iucnredlist.org/documents/RedListGuidelines.pdf> (accessed 13 January 2022)
- Jazwa, M., Jedrzejczak, E., Klichowska, E. & Pliszko, A. (2018) Predicting the potential distribution area of *Solidago × niededereri* (Asteraceae). *Turkish Journal of Botany* 42: 51–56.
- Lamarck, J.B.A.P.M. & Candolle, A.P. (1806) *Synopsis plantarum in Flora Gallica Descriptarum*. Pritzel, Geneve, 432 pp.  
<https://doi.org/10.5962/bhl.title.6624>
- Lecoq, H. & Juillet, J. (1831) *Dictionnaire raisonné des termes de botanique et des familles naturelles*. J. B. Baillière, Paris, 719 pp.
- Li, H., Ren, C., Yang, Q. & Yuan, Q. (2015) A new natural hybrid of *Sphagneticola* (Asteraceae, Heliantheae) from Guangdong, China. *Phytotaxa* 221 (1): 71–76.  
<https://doi.org/10.11646/phytotaxa.221.1.7>
- Linnaeus, C. von. (1763) *Species plantarum*, ed. 2, vol. 2. L. Salvius, Stockholm, pp. 785–1684.
- Lipman, M.J., Chester, M., Soltis, P.S. & Soltis, D.E. (2013) Natural hybrids between *Tragopogon mirus* and *T. miscellus* (Asteraceae): A new perspective on karyotypic changes following hybridization at the polyploid level. *American Journal of Botany* 100 (10): 2016–2022.  
<https://doi.org/10.3732/ajb.1300036>
- Loeuille, B., Semir, J., Lohmann, L.G. & Pirani, J.R. (2015) A phylogenetic analysis of Lyncophorinae (Asteraceae: Vernoniae) based on molecular and morphological data. *Systematic Botany* 40 (1): 299–315.  
<https://doi.org/10.1600/036364415X686585>
- Malmé, G.O.A. (1933) Compositae paranenses. *Kongliga Svenska Vetenskaps Akademiens Handlingar* 12 (2): 1–122.
- Mameli, G., López-Alvarado, J., Farris, E., Susanna, A., Filigheddu, R. & Garcia-Jacas, N. (2013) The role of parental and hybrid species in multiple introgression events: evidence of homoploid hybrid speciation in *Centaurea* (Cardueae, Asteraceae). *Botanical Journal of the Linnean Society* 175: 453–467.  
<https://doi.org/10.1111/boj.12177>
- McCullagh, P. & Nelder, J.A. (1989) *Generalized Linear Models*. Chapman and Hall, London, 510 pp.  
<https://doi.org/10.1007/978-1-4899-3242-6>
- Mitchell, N., Campbell, L.G., Ahern, J.R., Paine, K.C., Giroldo, A.B. & Whitney, K.D. (2019) Correlates of hybridization in plants. *Evolution Letters* 3–6: 570–585.  
<https://doi.org/10.1002/evl3.146>
- Moreira, M.M., Carrijo, T.T., Alves-Araújo, A., Amorim, A.M.A., Rapini, A., da Silva, A.V.S. Cosenza, B.A.P., Lopes, C.R., Delgado, C.N., Kameyama, C., Couto, D.R., Barbosa, D.E.F., Monteiro, D., Gonzaga, D.R., Dalcin, E.C., Guimarães, E.F., de Lirio, E.J., Matos, F.B., Salimena, F.R.G., Oliveira, F.A., Heiden, G., Lanna, J.M., Baumgratz, J.F., Pastore, J.F.B., Oliveira, J.R.P.M., Barcelos, L.B., Sylvestre, L.S., Freitas, L., Giacomini, L.L., Pederneiras, L., Meireles, L.D., Lohmann, L.G., Pereira, L.C., Silva, L.A.E., Neto, L.M., Souza, M.C., Trovó, M., Sobral, M.E.G., Garbin, M.L., Gomes, M., Morim, M.P., Mota, M.C.A., Labiak, P.H., Viana, P.L., de Moraes, P.L.R., Goldenberg, R., Coelho, R.L.G., Furtado, S.G., da Silva-Neto, S.J., Flores, T.B., Dutra, V.F., Bueno, V.R. & Forzza, R.C. (2020) Using online databases to produce comprehensive accounts of the vascular plants from the Brazilian protected areas: The Parque Nacional do Itatiaia as a case study. *Biodiversity Data Journal* 8: e50837.  
<https://doi.org/10.3897/BDJ.8.e50837>
- Mundell, A.R.G. (2016) The genus *Conyza* in Britain and a name for the hybrid between *Erigeron acris* and *Conyza floribunda* (Asteraceae). *New Journal of Botany* 6 (1): 16–20.  
<https://doi.org/10.1080/20423489.2016.1173806>
- Naimi, B. & Araújo, M.B. (2016) Sdm: a reproducible and extensible R platform for 643 species distribution modelling. *Ecography* 39: 368–375.  
<https://doi.org/10.1111/ecog.01881>
- Naimi, B., Hamm, N.A., Groen, T.A., Skidmore, A.K. & Toxopeus, A.G. (2014) Where is positional uncertainty a problem for species distribution modelling? *Ecography* 37: 191–203.  
<https://doi.org/10.1111/j.1600-0587.2013.00205.x>
- Nauheimer, L., Cui, L., Clarke, C., Crayn, D.M., Bourke, G. & Nargaret, K. (2019) Genome skimming provides well resolved plastid and nuclear phylogenies, showing patterns of deep reticulate evolution in the tropical carnivorous plant genus *Nepenthes* (Caryophyllales). *Australian Systematic Botany* 32: 243–254.  
<https://doi.org/10.1071/SB18057>
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGinn, D., Minchin, P.R., O’Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E. & Wagner, H. (2020) *Vegan: Community Ecology Package* (Version 2.5-6) [Software]. [<https://CRAN.R-project.org/package=vegan>]



- Panero, J. & Funk, V.A. (2002) Toward a phylogenetic subfamilial classification for the Compositae (Asteraceae). *Proceedings of the Biological Society of Washington* 115 (4): 909–922.
- Peruzzi, L., Bedini, G. & Andreucci, A. (2011) Homoploid hybrid speciation in *Doronicum* L. (Asteraceae)? Morphological, karyological and molecular evidences. *Plant Biosystems* 146 (4): 867–877.  
<https://doi.org/10.1080/11263504.2011.634445>
- Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190: 231–259.  
<https://doi.org/10.1016/j.ecolmodel.2005.03.026>
- Pliszko, A. & Kostrakiewicz-Gieralt, K. (2018) The morphological intermediacy of *Erigeron* × *huelsenii* (Asteraceae), a hybrid between *E. acris* and *E. canadensis*. *Turkish Journal of Botany* 42: 543–550.  
<https://doi.org/10.3906/bot-1711-27>
- Pozo, P. & Hind, D.J.N. (2013) A new species of *Calea* sect. *Meyeria* (Compositae: Heliantheae: Neurolaeninae). *Calea woodi*, from Santa Cruz, Bolivia. *Kew Bulletin* 68: 1–5.  
<https://doi.org/10.1007/s12225-013-9463-z>
- Pruski, J.F. & Hind, D.J.N. (1998) Two new species of *Calea* (Compositae: Heliantheae) from Serra do Grão Mogol and Vicinity, Minas Gerais, Brazil. *Kew Bulletin* 53: 695–701.  
<https://doi.org/10.2307/4110488>
- Pruski, J.F. & Robinson, H.E. (2018) Asteraceae In: Davidse, G., Sánchez, M.S., Knapp, S. & Cabrera, F.C. (Eds.) *Flora Mesoamericana*. Missouri Botanical Garden, Saint Louis, pp. 1–608.
- Pruski, J.F. & Urbastch, L.E. (1988) Five new species of *Calea* (Compositae: Heliantheae) from Planaltine Brazil. *Brittonia* 40: 341–356.  
<https://doi.org/10.2307/2807644>
- Pruski, J.F. & Urbastch, L.E. (1987) *Calea dalyi* (Compositae: Heliantheae), a new species from the Serranía de Santiago, Bolivia. *Brittonia* 39: 201–204.  
<https://doi.org/10.2307/2807375>
- Pruski, J.F. (1983) *Calea bucaremagensis* (Asteraceae), a new species from the Colombian Andes. *Systematic Botany* 8 (1): 93–95.  
<https://doi.org/10.2307/2418567>
- Pruski, J.F. (1984) *Calea brittoniana* and *Calea kristinia*: Two New Compositae from Brazil. *Brittonia* 36: 98–103.  
<https://doi.org/10.2307/2806617>
- Pruski, J.F. (1997) *Calea* L. In: Steyermark, J.A., Berry, P.E. & Holst, B.K. (Eds.) *Flora of the Venezuelan Guayana*. Missouri Botanical Garden, St. Louis, pp. 221–236.
- Pruski, J.F. (1998) Novelties in *Calea* (Compositae: Heliantheae) from South America. *Kew Bulletin* 53: 683–693.  
<https://doi.org/10.2307/4110487>
- Pruski, J.F. (2005) Studies of Neotropical Compositae–I. Novelties in *Calea*, *Clibadium*, *Conyza*, *Llerasia*, and *Pluchea*. *Sida* 21: 2023–2037.
- Pruski, J.F. (2011) Compositae of the Guayana Highland–XIV. Four new species of *Calea* (Neurolaeneae) from Tepui summits in Venezuela. *Phytoneuron* 52: 1–9.
- Pruski, J.F. (2013) Studies of Neotropical Compositae–IX. Four new species of *Calea* (Neurolaeneae) from Bolivia, Brazil and Paraguay. *Phytoneuron* 72: 1–4.
- QGIS Development Team (2015) *QGIS Geographic Information System, Open Source Geospatial Foundation Project*. Available from: <http://qgis.osgeo.org> (accessed 10 December 2020)
- R Core Team (2022) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. [<https://www.R-project.org/>]
- Reis-Silva, G.A. & Nakajima, J.N. (2020) A new species of *Calea* (Neurolaeneae, Asteraceae) from the Espinhaço Range, Minas Gerais, Brazil. *Phytotaxa* 432 (2): 199–205.  
<https://doi.org/10.11646/phytotaxa.432.2.9>
- Reis-Silva, G.A. & Nakajima, J.N. (2021) A new species of *Calea* (Neurolaeneae, Asteraceae) from the Atlantic Forest, Minas Gerais, southeastern Brazil. *Phytotaxa* 490 (1): 129–136.  
<https://doi.org/10.11646/phytotaxa.494.1.9>
- Reis-Silva, G.A. (2019) *The Genera Calea L. (Neurolaeneae, Asteraceae) in Minas Gerais, Brazil*. Universidade Federal de Viçosa, Viçosa, 181 pp.
- Robinson, H. (1975) Studies in the Heliantheae (Asteraceae). VI. Additions to the genus *Calea*. *Phytologia* 32 (5): 426–430.
- Robinson, H. (1979) Studies in the Heliantheae (Asteraceae). XIX. Four new species of *Calea* from Brasil. *Phytologia* 44 (4): 270–276.
- Roque, N. & Carvalho, V.C. (2011) Estudos taxonômicos do gênero *Calea* (Asteraceae, Neurolaeneae) no estado da Bahia, Brasil.

*Rodriguésia* 62: 547–561.

<https://doi.org/10.1590/2175-7860201162308>

- Roque, N., Reis-Silva, G.A., Silva, G.H.L. & Bueno, V.R. (2022) *Calea* in Flora do Brasil 2020 em construção. Jardim Botânico do Rio de Janeiro. Available from: <http://floradobrasil.jbrj.gov.br/reflora/floradobrasil/FB103751> (accessed 13 January 2022)
- Rydberg, A. (1927) (Carduales) *Carduaceae*, *Liabeae*, *Neurolaeneae*, *Senecioneae*. *New York Botanical Garden* 34 (4): 289–360.
- Safford, H.D. (2001) Brazilian Páramos. III. Patterns and rates of postfire regeneration in the Campos de Altitude. *Biotropica* 33 (2): 282–302.  
<https://doi.org/10.1111/j.1744-7429.2001.tb00179.x>
- Schilling, E.E. (2011) Hybrid genera in *Liatrinae* (Asteraceae: Eupatorieae). *Molecular Phylogenetics and Evolution* 59: 158–167.  
<https://doi.org/10.1016/j.ympev.2011.01.011>
- Semíz, G., Şenol, S.G., Günel, B., Çiçek, M. & Eroğlu, V. (2021) *Helichysum ×kani-isikii* (Asteraceae), a new nothospecies from Turkey. *Phytotaxa* 507 (4): 283–292.  
<https://doi.org/10.11646/phytotaxa.507.4.2>
- Semple, J.C. (2016) Documenting a *Solidago bicolor* × *S. brendiae* hybrid (Asteraceae: Astereae) from Nova Scotia. *Phytoneuron* 2016 (23): 1–10.
- Shipunov, A., Gladkova, S., Timoshina, P., Lee, H.-J., Choi, J.-H., Despiegelaere, S. & Connolly, B. (2019) Mysterious chokeberries: new data on the diversity and phylogeny of *Aronia* Medik. (Rosaceae). *European Journal of Taxonomy* 570: 1–14.  
<https://doi.org/10.5852/ejt.2019.570>
- Silva, G.H.L. (2016) *Estudos Taxonômicos do Gênero Calea L. (Asteraceae: Neurolaeneae) na região Centro-Oeste do Brasil*. Universidade Federal de Goiás, Goiânia, 165 pp.
- Silva, G.H.L., Bringel, J.B. & Teles, A.M. (2016) A new species of *Calea* (Asteraceae–Neurolaeneae) from Goiás State, Brazil. *Phytotaxa* 265 (3): 279–284.  
<https://doi.org/10.11646/phytotaxa.265.3.9>
- Simon, M.F., Grether, R., Queiroz, L.P., Skema, C., Pennington, R.T. & Hugues, C.E. (2009) Recent assembly of the Cerrado, a neotropical plant diversity hotspot, by in situ evolution of adaptations to fire. *Proceeding of the National Academy of Sciences* 106 (48): 20359–20364.  
<https://doi.org/10.1073/pnas.0903410106>
- Smissen, R.D., Thorsen, M.J., Breitwieser, I. & Ward, J.M. (2015) DNA sequence analysis confirms the identity of the intergeneric hybrid *Argyrotegium mackayi* × *Leucogenes leontopodium* (Asteraceae, Gnaphalieae). *New Zealand Journal of Botany* 53 (4): 210–215.  
<https://doi.org/10.1080/0028825X.2015.1093000>
- Smith, G.F. & Figueiredo, E. (2020) × *Bacurio*, a new nothogenus for the hybrid × *B. delphinatifolius* (*Baculellum articulatum* × *Curio rowleyanus*), with notes on the nomenclature of *Kleinia* × *peregrina*, *Senecio peregrinus*, *S. × peregrinus*, and *Curio × peregrinus* (Asteraceae: Asteroideae: Senecioneae). *Phytotaxa* 458 (1): 1–28.  
<https://doi.org/10.11646/phytotaxa.458.1.8>
- Soltis, P.S. & Soltis, D.E. (2009) The role of hybridization in plant speciation. *Annual Review Plant Biology* 60: 561–588.  
<https://doi.org/10.1146/annurev.arplant.043008.092039>
- Susanna, A., Baldwin, B.G., Bayer, R.J., Bonifacino, J.M., Garcia-Jacas, N., Keeley, S.C., Mandel, J.R., Ortiz, S., Robinson, H. & Stuessy, T.F. (2020) The classification of the Compositae: A tribute to Vicki Ann Funk (1947–2019). *Taxon* 69: 807–814.  
<https://doi.org/10.1002/tax.12235>
- Thiers, B. (2022) [continuously updated] *Index Herbariorum: A global directory of public herbaria and associated staff*. New York Botanical Garden’s Virtual Herbarium, New York U.S.A. Available from: <http://sweetgum.nybg.org/science/ih/> (accessed 17 Jan 2022)
- Turner, B.L. (1982) Taxonomy of *Neurolaena* (Asteraceae–Heliantheae). *Plant Systematics and Evolution* 140: 119–139.  
<https://doi.org/10.1007/BF02407293>
- Turner, B.L. (2014) The comps of Mexico, A systematic account of the family Asteraceae, Chapter 14, Tribe: Neurolaeneae. Tribe: Heliantheae: subtribes: Ambrosiinae, Chromolepidinae and Dugesiinae. *Phytologia Memoirs* 19: 1–21.
- Urbatsch, L.E., Zlotzky, A. & Pruski, J.F. (1986) Revision of *Calea* sect. *Lemmatium* (Asteraceae: Heliantheae) from Brazil. *Systematic Botany* 11 (4): 501–514.  
<https://doi.org/10.2307/2419029>
- Wang, J. & Wang, J. (2018) Emerging natural hybrid between Invasive Species and Native Congener of *Emilia* (Asteraceae) Found in Northern Taiwan. *Phytotaxa* 382 (2): 204–212.  
<https://doi.org/10.11646/phytotaxa.382.2>
- Wang, Z., Du, S., Dayanandan, S., Wang, D., Zeng, Y. & Zhang, J. (2014) Phylogeny Reconstruction and Hybrid Analysis of *Populus* (Salicaceae) Based on Nucleotide Sequences of Multiple Single-Copy Nuclear Genes and Plastid Fragments. *PLOS One* 9 (8):

e103645.

<https://doi.org/10.1371/journal.pone.0103645>

- Wickham, H., Chang, W., Henry, L., Pedersen, T.L., Takahashi, K., Wilke, C., Woo, K., Yutani, H. & Dunnington, D. (2020) *RStudio. ggplot2: Create Elegant Data Visualisations Using the Grammar of Graphics* (Version 3.3.0). [<https://cran.r-project.org/web/packages/ggplot2/index.html>]
- Wussow, J.R., Urbatsch, L.E. & Sullivan, G.A. (1985) *Calea* (Asteraceae) in Mexico, Central America and Jamaica. *Systematic Botany* 10 (3): 241–267.  
<https://doi.org/10.2307/2418590>
- Xaxars, G.M., Fridlender, A., Garnatje, T. & Valles, J. (2015) Molecular and cytogenetic confirmation of the hybrid origin of *Jacobaea* × *mirabilis* (Asteraceae, Senecioneae), with nomenclatural notes on this name. *Phytologia* 234 (3): 271–279.  
<https://doi.org/10.11646/phytotaxa.234.3.8>
- Yu, J., Kuroda, C. & Gong, X. (2014) Natural hybridization and introgression between *Ligularia cymbulifera* and *L. tongolensis* (Asteraceae, Senecioneae) in four different locations. *PLoS One* 9 (12): e115167.  
<https://doi.org/10.1371/journal.pone.0115167>
- Zhang, R., Gong, X. & Folk, R. (2017) Evidence for continual hybridization rather than hybrid speciation between *Ligularia duciformis* and *L. paradoxa* (Asteraceae). *PeerJ* 5: e3884.  
<https://doi.org/10.7717/peerj.3884>