

# Disentangling the taxonomy of the *Galactia*-*Camptosema*-*Collaea* complex with new generic circumscriptions in the *Galactia* clade (Leguminosae, Diocleae)

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## ABSTRACT

The *Galactia* clade is one of three major lineages of the papilionoid legume tribe Diocleae. It comprises eight genera and approximately 140 species almost entirely restricted to the Americas. Establishing stable generic boundaries within this clade has been a challenge because of its tortuous taxonomic history and the broad polyphyly of the genera of the so-called *Galactia*-*Camptosema*-*Collaea* complex. Previous molecular phylogenetic studies revealed some well-supported lineages, but did not advance towards any new taxonomic arrangements. We carried out maximum parsimony and Bayesian phylogenetic analyses of a combined dataset including our previously published multilocus molecular data (nrITS and ETS and plastid *trnK/matK* and *trnT-Y* regions) and 82 morphological characters. The resulting topologies largely concur with those previously reported based on molecular data only, where *Camptosema* and *Galactia* appear as broadly polyphyletic, with species scattered among five (*Camptosema*) and seven (*Galactia*) of the twelve lineages that are newly recognized here at genus level. We are therefore proposing the following new taxonomic rearrangements within the *Galactia* clade: descriptions of the new genera *Caetangil*, *Cerradicola*, *Mantiqueira*, and *Nanogalactia*; resurrection of *Betencourtia*; and the subsuming of *Neorudolphia* into *Rhodopis* and of *Camptosema* sect. *Macropetalum* into *Cratyliia*.

## 1 | INTRODUCTION

Diocleae Hutch. is a tribe of the Leguminosae subfamily Papilionoideae comprising 13 genera and approximately 200 mostly New World species. It has been treated as a subtribe of the tribe Phaseoleae (Bentham 1865; Lackey 1981) due to its trifoliolate leaves, mostly asymmetrical lateral leaflets, and flowers arranged in a pseudoracemose inflorescence. The tribe was resurrected by Queiroz et al. (2015) who demonstrated that it is a monophyletic group more closely related to

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Millettieae representatives than to those of Phaseoleae. That study also revealed three major lineages comprising Diocleae. The genus *Canavalia* (the Canavalia clade) appears as a sister to a large clade that includes the remaining genera in two major lineages: the Dioclea and the Galactia clades (Queiroz *et al.* 2015). A taxonomic account of the four genera of the Dioclea clade (*Dioclea* Kunth, *Macropsyчанthus* Harms, *Cleobulia* Mart. ex Benth., and *Cymbosema* Benth.) was recently presented (Queiroz & Snak 2020).

The Galactia clade includes the traditionally recognized genera *Bionia* Mart. ex Benth., *Camptosema* Hook. & Arn., *Collaea* DC., *Cratylia* Mart. ex Benth., *Galactia* P. Browne, *Lackeya* Fortunato, L.P. Queiroz & G.P. Lewis, *Neorudolphia* Britton, and *Rhodopis* Urb. Except for a few species of *Galactia*, the clade is entirely restricted to the Americas, mostly in open vegetation exposed to seasonally dry climates. It embraces wide morphological variation, although presenting rather unspecialized flowers and fruits. Generic delimitation within the Galactia clade has been problematic, largely due to the fluid boundaries in the so-called Galactia-Camptosema-Collaea complex (hereafter, the GCC complex; Sede *et al.* 2003).

There is a multifaceted, yet unresolved taxonomic history of the genera associated with the GCC complex. *Galactia* was described by Browne (1756) to include *G. rubra* P. Browne, a Caribbean species with leaves pinnately trifoliolate ("*pinnato ternatis*"), flowers arranged in elongated pseudoracemes ("*spicis elongatis*"), and androecium diadelphous ("*Filamenta decem diadelphia regularia*"). Candolle (1825) established the genus *Collaea* for woody shrubs with subsessile palmately trifoliolate leaves ("*Folia palmatim trifoliata breviter petiolata*") and flowers arranged in strobiliform fascicles with pseudomonadelphous androecium. Bentham (1837) classified *Galactia* and *Collaea* in different subtribes of the tribe Phaseoleae, overemphasizing the vexillary stamen free in *Galactia* (included in the subtribe Glycininae) or joined to the remaining staminal sheath in *Collaea* (included in subtribe Diocleinae). Bentham (1859) later transferred several species from *Galactia* to *Collaea*, and finally subsumed *Collaea* into *Galactia* (Bentham 1865), a position followed by Taubert (1894). Burkart (1971) reinstated the genus *Collaea*, but with the original (and much narrower) circumscription of Candolle (1825).

*Camptosema* has a similarly tortuous taxonomic history. Hooker & Arnott (1833) established the genus for a southern South American vine with pinnately trifoliolate leaves, large red flowers arranged in elongate pseudoracemes, and a pseudomonadelphous androecium. A few years later, Bentham (1837) validated the genus *Bionia* proposed by Martius for a group of shrubs and vines with uni- or trifoliolate leaves, and large red flowers, but with a straight corolla and stipitate ovary. Bentham (1837) also commented that he was not aware of the genus *Camptosema*, but that it could be akin to *Bionia*. Bentham (1859) later subsumed *Bionia* into *Camptosema*, and created the section *Macropetalum* to include two species of lianas. Burkart (1970) entangled the taxonomy of *Camptosema* with that of *Galactia* and *Collaea* by overemphasizing the large flowers, red petals, and a stipitate ovary to characterize *Camptosema*, and moving several species then included in *Galactia* (*sensu* Bentham 1859; Taubert 1894) to that genus.

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The first phylogenetic analyses based on morphological traits (Queiroz *et al.* 2003) indicated that *Collaea* (sensu Candolle 1825; Burkart 1971) should be monophyletic, and that both *Galactia* and *Camptosema* are broadly polyphyletic. Based on those analyses, Queiroz (2008) reinstated the genus *Bionia* in its original definition (Bentham 1837). Additional attempts to solve the Gordian knot of the GCC complex were carried out in a series of works using different evidences, such as chromosomes (Sede *et al.* 2003, 2006), AFLP markers (Sede *et al.* 2008), and a phylogenetic approach using both molecular (nrITS and plastid *trnL-F* regions) and morphological characters (Sede *et al.* 2009). All of those studies agreed with previous results indicating *Collaea* as possibly monophyletic and both *Galactia* and *Camptosema* as polyphyletic. None of those studies advanced with any new taxonomic arrangement, probably because of sparse taxonomic sampling in the genera of the GCC complex and the lack of representatives of other critical genera of the Diocleae.

A multilocus phylogenetic study of the Diocleae (Queiroz *et al.* 2015) broadly sampled different morphotypes of the genera *Galactia*, *Camptosema*, and *Collaea*, as well as all of the other genera of the Galactia clade. That study confirmed the monophyly of *Collaea* in its original circumscription (Candolle 1825; Burkart 1971) as well as the broad polyphyly of both *Galactia* and *Camptosema*. More importantly, it demonstrated some species of *Galactia* or *Camptosema* to be more closely related to other genera of the Galactia clade (such as *Cratylia* and *Rhodopis*), and indicated several well-supported clades combining putative bee pollinated species of *Galactia* with bird pollinated species of *Camptosema*. That result seemed to confirm the previous hypothesis that the unspecialized bee pollinated flowers of species of the Galactia clade were prone to rapid shifts towards a bird pollination syndrome (Queiroz *et al.* 2003; Queiroz 2008). The noted differences in floral traits associated with pollination syndromes in the Galactia clade are consequently evolutionarily labile, so that *Camptosema*-like flowers reflect convergence to bird pollination rather than the true relatedness as envisaged by Burkart (1970, 1971).

Here, we combined a newly assembled morphological dataset with our previously published densely-sampled molecular dataset (nuclear ribosomal ETS and ITS, and the plastid *trnK/matK* and *trnT-Y*) of the tribe Diocleae (Queiroz *et al.* 2015) to refine the phylogeny of the Galactia clade with the aim of proposing a new taxonomic arrangement, especially for the controversial GCC complex.

## 2 | MATERIALS AND METHODS

The taxonomy of the Galactia clade was assessed by combining a dataset of 82 morphological characters and the molecular dataset previously used for inferring phylogenetic relationships within the tribe Diocleae (Queiroz *et al.* 2015). The molecular dataset thus made use of the *trnT-Y* and *3'trnK-matK* plastid regions (including the *trnK* intron and the *matK* gene), and the nuclear ribosomal ITS/5.8S (Internal Transcribed Spacer – ITS1 and ITS2 regions, and the intervening 5.8S region), and part of the ETS (External Transcribed Spacer) region, plus 409 simple coded gaps. Detailed descriptions of DNA extraction, molecular primers, PCR and sequencing conditions,

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sequence assembling and alignments, and molecular evolution models can be found in Queiroz *et al.* (2015).

A total of 82 morphological characters extracted from Queiroz (1999) and Queiroz *et al.* (2003) were revised and included for the phylogenetic analyses reported here (Table 1). Those characters were sampled from the same voucher specimens from which molecular data were obtained (see Queiroz *et al.* 2015 and the Suppl. Table 1 for a list of sampled specimens). All morphological character state transformations were weighted equally and unordered (Fitch 1971). A total of eight vegetative characters, 46 from flowers, 16 from fruits and seeds, and one from pollen were sampled. The final data matrix is available for downloading as a supplementary file.

As Queiroz *et al.* (2015) did not find strongly supported incongruences between molecular datasets, the total combined dataset was used for the maximum parsimony (MP) and Bayesian inference (BI) analyses carried out here. Individual MP and BI analyses of the morphological dataset resulted in poorly resolved and mostly unsupported trees. The morphological data were therefore analyzed together with the molecular data in a total evidence dataset to explore their evolution and determine potential synapomorphies for the monophyletic groups that could be recognized at the genus rank.

Searches for the most parsimonious trees (MPTs) were carried out using a heuristic search with 2,000 random taxon-additions and tree bisection-reconnection (TBR) branch swapping, saving 15 trees per replicate. Trees saved in this first round were used as starting trees in a second search using the same parameters, but saving a maximum of 10,000 trees. Nonparametric bootstrap resampling was implemented in PAUP\* 4.0b10 (Swofford 2002) to estimate clade support (Felsenstein 1985) which was assessed through 2,000 bootstrap replicates, each analyzed using the heuristic search parameters mentioned above, with 15 trees retained per replicate. Nucleotide substitution models for Bayesian analyses were selected using Akaike information criterion, implemented in MrModeltest v.2.3 (Nylander *et al.* 2004) for each DNA region. GTR+G was selected for all partitions, except for the 5.8S of the ITS region, for which the simpler K80+G model was the best match. The Markov  $k$  model (Lewis 2001) was used for morphological data. The Bayesian analyses were carried out in MrBayes v.3.2.7a (Ronquist *et al.* 2012) in Cyberinfrastructure for Phylogenetic Research (Cipres Science Gateway; Miller *et al.* 2010). Two runs of four MCMC were carried out for  $10^7$  generations, with trees being sampled every  $10^4$  generations. The first 25% of the trees were discarded as burn-in, as assessed in Tracer v.1.5 (Rambaut & Drummond 2007). Convergence of runs was tested by inspecting whether the standard deviation of the split frequencies of the runs was  $<0.01$ , and by using the effective sample sizes (ESS)  $>200$ , as calculated with Tracer v.1.5 (Rambaut & Drummond 2007). We then used MrBayes v3.1.2 to summarize trees sampled from post burn-in generations in a majority rule consensus tree that included posterior probabilities as branch support estimates. Trees were visualized and partially edited in FigTree v.1.4 (Rambaut 2012).

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**Table 1.** Morphological characters and character states used for the phylogenetic analyses of the tribe Diocleae.

Character	Character states
1 Habit	[0] – Lianas [1] – Shrubs [2] – Vines [3] – Erect subshrubs or herbs [4] – Prostrate
2 Stipule attachment	[0] – Basifixed (stipule not peltate) [1] – Medifixed (stipule peltate)
3 Leaves: presence of a rachis	[0] – Present (pinnately compound leaves) [1] – Absent (palmately compound or simple leaves)
4 Leaves: lateral leaflets symmetry	[0] – Symmetrical [1] – Asymmetrical
5 Leaves: number of leaflets	[0] – More than 3 [1] – Three [2] – One leaflet or leaves simple
6 Leaves: presence of a petiole	[0] – Present (petiolate leaves) [1] – Absent or very short (sessile or shortly petiolate leaves)
7 Leaves: presence of stipels	[0] – Present (stipellate leaflets) [1] – Absent (stipellate leaflets)
8 Inflorescence: cauliflory	[0] – Absent [1] – Present
9 Inflorescence: relative length	[0] – More than 2× longer than the subtending leaf [1] – Smaller to ca. the same size of the subtending leaf
10 Inflorescence: peduncle woodiness	[0] – Woody [1] – Not woody
11 Inflorescence: flowers per node	[0] – More than five [1] – One to five
12 Inflorescence: shape of the nodes	[0] – Slender, sometimes branched [1] – Clavate or globose [2] – Capitate [3] – Vestigial
13 Inflorescence: flower arrangement at the node	[0] – Secundiflorous [1] – Not secundiflorous
14 Inflorescence: presence of a stalk supporting the node	[0] – Present (stalked or pedunculate node) [1] – Absent (sessile node)
15 Inflorescence: overall architecture	[0] – Elongate pseudoraceme [1] – Umbelliform pseudoraceme [2] – Nodose (strobiliform) fascicle
16 Inflorescence: presence of an involucre of bracts	[0] – Absent [1] – Present
17 Inflorescence: multinerved	[0] – Absent

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	Character	Character states
	bracts	[1] – Present
18	Inflorescence: wide bracteoles covering the entire flower bud	[0] – Absent [1] – Present
19	Flower bud: apex	[0] – Acuminate [1] – Obtuse
20	Flower bud: outline	[0] – Ovate to cylindrical [1] – Suborbicular
21	Flowers: resupination	[0] – Absent (the standard petal facing upwards) [1] – Present (the standard petal facing downwards)
22	Flowers: position against the inflorescence rachis	[0] – Flowers not deflexed [1] – Flowers deflexed backwards against the inflorescence rachis
23	Flowers: calyx color	[0] – Green or greenish [1] – Red to wine-red
24	Flowers: calyx lobation	[0] – A 4–5-lobed calyx [1] – A bilabiate calyx with the upper lip bigger than the lower one
25	Flowers: calyx shape	[0] – Short and campanulate [1] – Long and cylindrical
26	Flowers: upper margin humped or convex	[0] – Absent [1] – Present
27	Flowers: lobes / calyx tube ratio	[0] – More than one (lobes longer than the calyx tube) [1] – Less than one (lobes shorter than the calyx tube)
28	Flowers: shape of the vexillary calyx lobe	[0] – Lanceolate [1] – Ovate (obtuse) [2] – Widely ovate (usually truncate)
29	Flowers: degree of merging of the two vexillary lobes of the calyx	[0] – Entirely joined making an entire lobe [1] – Partially joined making an emarginate lobe [2] – Two separate lobes
30	Flowers: color of the petals in fresh flowers	[0] – Purple (mauve to violet) [1] – Red [2] – White
31	Flowers: color of the petals in dried flowers	[0] – Straw colored [1] – Yellow
32	Flowers: standard petal indumentum	[0] – Glabrous [1] – Pubescent at the outer surface
33	Flowers: shape of the standard petal	[0] – (Sub)orbicular (almost as wide as long) [1] – Obovate [2] – Narrowly elliptical
34	Flowers: apex of the standard petal	[0] – Emarginate [1] – Entire

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Character	Character states
35 Flowers: standard petal bending	[0] – Bent (reflexed, usually erect at the anthesis) [1] – Not bent (straight at the anthesis)
36 Flowers: standard petal longitudinally folded	[0] – Not folded [1] – Folded (and then somewhat tubular at the anthesis)
37 Flowers: standard petal basal auricles	[0] – Present and inflected [1] – Present or vestigial but not inflected [2] – Absent
38 Flowers: standard petal callus	[0] – Vestigial [1] – Bicallose [2] – Absent
39 Flowers: dwarf wings	[0] – Absent (elongate wing petals) [1] – Present
40 Flowers: relative wing / keel petals length	[0] – Wings shorter or almost the same length than the keel petals [1] – Wings much longer than the keel petals
41 Flowers: wing petals shape	[0] – Widely obovate [1] – Elliptical to oblong [2] – Narrowly elliptical to linear
42 Flowers: wing petals basal auricle	[0] – Sagittate [1] – Vestigial [2] – Absent
43 Flowers: sculptured areas on the wing petals	[0] – Conspicuous [1] – Vestigial or absent
44 Flowers: keel shape	[0] – Triangular to semicircular (incurved) [1] – Oblong
45 Flowers: keel petals apex	[0] – Free [1] – Joined (rostrate)
46 Flowers: shape of the keel petals rostrum	[0] – Absent [1] – Obtuse [2] – Acuminate [3] – Truncate
47 Flowers: apex of the keel twisted	[0] – Not twisted (straight) [1] – Twisted
48 Flowers: keel petals fimbriate or serrate at the upper margin	[0] – Absent (upper margin smooth) [1] – Present (upper margin fimbriate or serrate)
49 Flowers: median lobe at the upper margin of the keel petals	[0] – Absent [1] – Present
50 Flowers: androecium	[0] – Pseudomonadelphous (all stamens joined but the base of the vexillary stamen free) [1] – Diadelphous (the vexillary stamen entirely free)
51 Flowers: base of the	[0] – Widened



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	Character	Character states
	androecium widened	[1] – Not widened
52	Flowers: indumentum of the base of the androecium	[0] – Glabrous [1] – Pubescent
53	Flowers: apex of the staminal tube	[0] – Bent ca. 90° [1] – Straight
54	Flowers: comparative length of the outer and inner stamen cycles	[0] – Not or slightly differentiated [1] – Strongly differentiated
55	Flowers: anthers dimorphism	[0] – Anthers uniform (all anthers with the same shape) [1] – Anthers dimorphic
56	Flowers: anthers indumentum	[0] – Glabrous [1] – Pubescent
57	Flowers: disc margin	[0] – 10-lobed [1] – Toothed [2] – Smooth (margin truncate)
58	Flowers: disc shape	[0] – Short cylindrical [1] – Conic
59	Flowers: receptacle indumentum	[0] – Glabrous [1] – Pubescent
60	Flowers: stipe / ovary ratio	[0] – 0 a 0.2 (ovary sessile) [1] – 0.45 a 0.6 (ovary shortly stipitate) [2] – ≥ 1 (ovary stipitate)
61	Flowers: number of ovules per ovary	[0] – Exactly 1 or 2 [1] – More than 2 to 5 [2] – More than 5
62	Flowers: style bent c. 90° at the base or middle	[0] – Not [1] – Yes
63	Flowers: style broadened near the middle	[0] – Not [1] – Yes (broadened and usually flattened)
64	Flowers: style hooked near the apex:	[0] – Not (straight) [1] – Hooked
65	Fruit: dehiscence	[0] – Indehiscent [1] – Partially dehiscent (lower suture open but not releasing the seeds) [2] – Dehiscent forming two valves
66	Fruit: elastic dehiscence	[0] – Absent [1] – Present (the valves becoming twisted after seed releasing)
67	Fruit: mesocarp	[0] – Dry [1] – Fleshy
68	Fruit: endocarp	[0] – Thin and translucent



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Character	Character states
	[1] – Thick and usually adhering to the seed testa
69 Fruit: valves consistency	[0] – Woody [1] – Firmly coriaceous or chartaceous
70 Fruit: margins	[0] – Straight [1] – Undulate
71 Fruit: ornamentation parallel to the suture (upper margin)	[0] – Absent [1] – Ribs [2] – Wings
72 Fruit: cross section	[0] – Planar [1] – Slightly compressed (biconvex) [2] – Swollen (almost circular)
73 Fruit: constriction of the valves between the seeds	[0] – Not constricted [1] – Constricted between the seeds
74 Seeds: overgrown	[0] – Not overgrown [1] – Overgrown
75 Seeds: testa consistency	[0] – Leathery [1] – Bony
76 Seeds: color distribution	[0] – Uniform [1] – Marbled
77 Seeds: hilum shape	[0] – Oblong or elliptical [1] – Linear
78 Seeds; hilum length	[0] – Short (< 1/10th of the seed circumference) [1] – Encircling ca. half of the seed circumference [2] – Encircling 2/3 or more of the seed circumference
79 Seeds: lateral compression	[0] – Laterally compressed (faces flat or convex) [1] – Not compressed
80 Seeds: shape	[0] – Oblongoid [1] – Orbicular (globose) [2] – Cuboidal
81 Thickened underground system	[0] – Absent [1] – Xylopodium or napiform roots? [2] – Thickened rhizome
82 Pollen: polarity	[0] – Isopolar [1] – Heteropolar

### 3 | RESULTS AND DISCUSSION

Maximum parsimony analysis of the total evidence dataset (5,603 aligned characters of which 973 were parsimony-informative) found 3,888 most parsimonious trees with 4,080 steps, a consistency index 0.56, and a retention index 0.85 (Suppl. Fig. 1). The Bayesian 50% majority rule consensus tree presented a well-resolved phylogenetic backbone. Both analyses converged in

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resolving the same well-supported clades, although internal relationships within those clades were not necessarily identical. Additionally, the results are largely congruent with those reported before in analyses based on an exclusively molecular dataset (Queiroz *et al.* 2015). Optimization of the morphological traits onto the Bayesian tree showed that most characters traditionally used for defining genera of the Galactia clade were reconstructed as homoplasies (Suppl. Fig. 2). Despite that, sets of characters were identified as potentially diagnostic for the monophyletic groups recognized here as genera, as presented and discussed below.

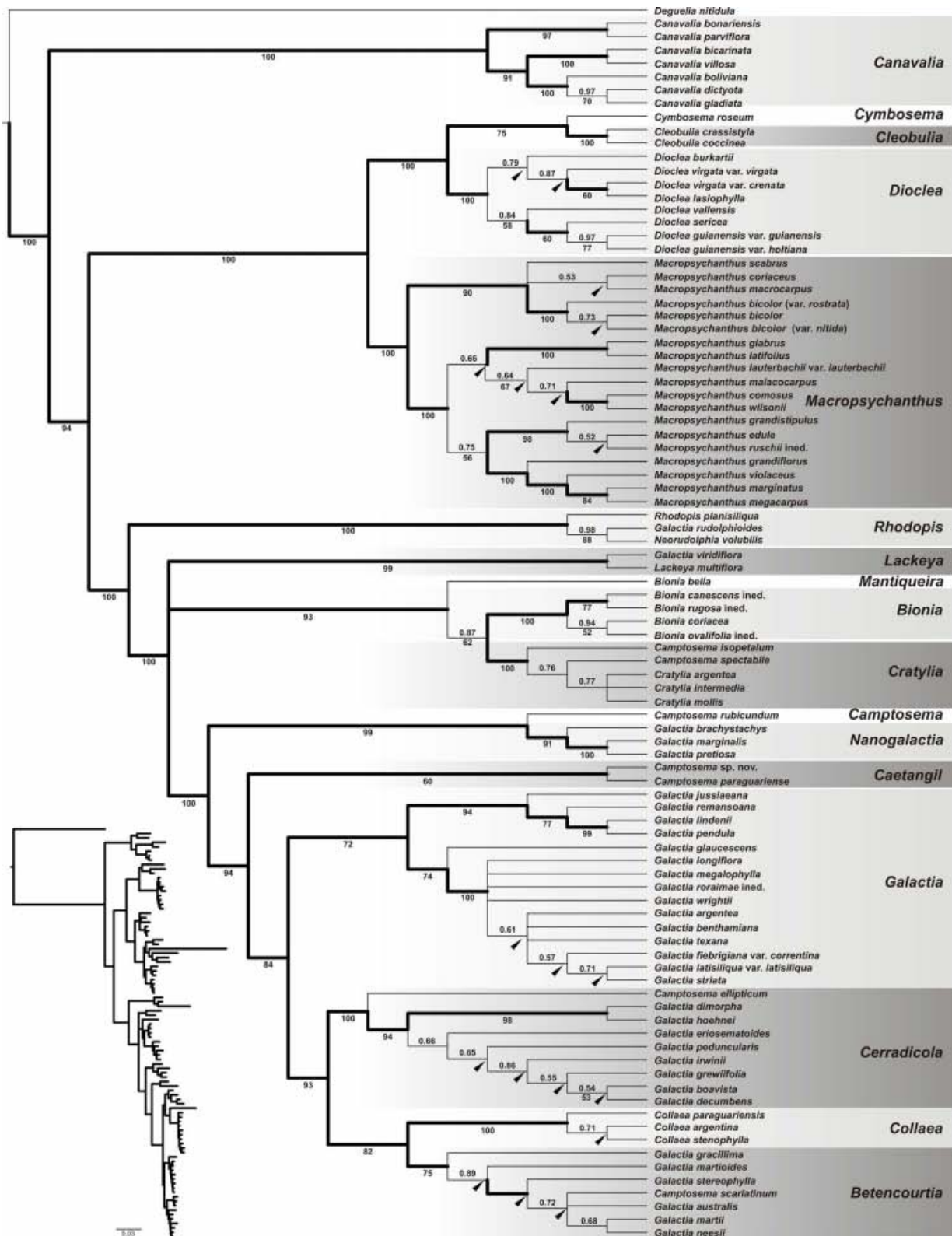
Because most genera of the Galactia clade have long been demonstrated as non-monophyletic (Fig. 1; Varela *et al.* 2004; Maxwell & Taylor 2003; Queiroz *et al.* 2003, 2015; LPWG 2017), they should be recircumscribed to preserve the principle of monophyly. Different taxonomic solutions recognizing only monophyletic genera could result from the same phylogenetic tree. However, other principles besides monophyly should also be considered, such as maximizing the support for monophyly and the phylogenetic information (Backlund & Bremer 1998), morphological diagnosability (Queiroz & Snak 2020), and preserving as much as possible historically recognized genera.

Keeping all species of the broadly polyphyletic *Galactia* in the same genus would require that all genera nested in the Galactia clade should be subsumed under *Galactia*, the earliest validly published generic name within the clade. Although having high phylogenetic support, such a solution presents several drawbacks. The morphologically coherent and long recognized genera *Rhodopis*, *Cratylia*, *Collaea*, and *Camptosema* (Lackey 1981; Lewis *et al.* 2005) would have to be abandoned. More importantly, such a broadly-circumscribed *Galactia* would lack morphological diagnosability within the tribe Diocleae because it would result in a genus as highly variable as embracing almost all characters traditionally used to diagnose the genera in the tribe. On the other hand, the alternative classification discussed below recognizes as different genera the lineages that are highly supported as monophyletic, present morphological diagnosability, and show ecological coherence by having predilection for a particular biome.

*Cratylia* was recovered as paraphyletic because the two species of *Camptosema* sect. *Macropetalum* Benth. [*C. isopetalum* (Lam.) Taub. and *C. spectabile* (Tul.) Burkart] appeared nested within it. That result agrees with previous phylogenetic studies based on both morphological (Queiroz 1999; Queiroz *et al.* 2003) and molecular data (Queiroz *et al.* 2015). The transfer of *Camptosema isopetalum* and *C. spectabile* to *Cratylia*, as proposed by Queiroz (1999), fits the diagnostic features of this genus quite well, which is characterized by having a coarse shrubby or vine habit, pseudoracemes with thick and multi-flowered nodes, standard petal pubescent on the outer surface, and ovary shortly stipitate (Queiroz 1991).

*Bionia* was not recovered as monophyletic because of the phylogenetic position of *B. bella* Mart. ex Benth. as sister to a clade that brings together the genera *Cratylia* and the remaining species of *Bionia*, as previously reported by Queiroz *et al.* (2015). *Bionia* was reinstated by Queiroz (2008) after having been treated as a synonym of *Camptosema* for 150 years. *Bionia bella* presents flowers that superficially resemble those of the remaining species of *Bionia*, probably resulting from

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**Figure 1.** Majority-rule Bayesian tree and respective phylogram (scale bar = 0.03) of the Dioclea clade resulting from the total evidence analysis (combined nuclear ETS and ITS, plastid *trnK/matK* and *trnT-Y* and 82 morphological characters). Bold lines represent clades with Bayesian posterior probabilities (PP) = 1; other PP values are reported above branches and parsimony bootstrap support values are reported below branches. Bootstrap values below 50% are represented by arrows. The gray scale boxes represent the genera as circumscribed here.

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convergence towards highly specialized hummingbird pollination, but it is an herbaceous twining vine from the understories of montane rain forests, with membranaceous leaflets and calyx tube, long stipitate ovary, and the wing and keel petals bearing claws longer than the blade (Queiroz 2008; Fernandes & Garcia 2014). Because of its isolated phylogenetic position and distinctive morphology, *Bionia bella* is being segregated as the new monospecific genus *Mantiqueira*, named after its restricted geographic position in the Mantiqueira mountain range of Eastern Brazil. With the exclusion of *B. bella*, the genus *Bionia* constitutes a morphologically and ecologically coherent genus diagnosed by a coarse, shrubby habit, coriaceous leaflets, short and stout pseudoracemes that are usually held almost horizontally, a fleshy calyx with an elongate tube much longer than the lobes, long stipitate ovary, red petals, and the standard petal spreading and folded at anthesis, lending a tubular aspect to the flower. *Bionia*, as defined here, is largely concentrated in montane rocky grasslands (campos rupestres) and savanna vegetation in eastern and central Brazil (Queiroz 2008; Queiroz *et al.* 2015).

The taxonomy of the so-called Galactia-Camptosema-Collaea complex (Sede *et al.* 2003) has been a significant challenge, with their species being moved among the genera *Camptosema*, *Collaea*, and *Galactia*, depending on the weight given to particularly 'critical' characters (Bentham 1837, 1859, 1865; Taubert 1894; Burkart 1970, 1971). *Collaea*, as circumscribed by Burkart (1971), is supported here as monophyletic, as previously reported by Sede *et al.* (2009) and Queiroz *et al.* (2003, 2015), and including South American species of shrubs with sessile or subsessile, digitately compound leaves, axillary and strobiliform inflorescences with wide and striated bracts, and standard petals pubescent and strongly bicallose. Not surprisingly, *Camptosema* and *Galactia* appeared broadly polyphyletic, as demonstrated in previous studies (Queiroz *et al.* 2003, 2015; Varela *et al.* 2004; Sede *et al.* 2009), with their species scattered among seven lineages: [1] *Camptosema isopetalum* and *C. spectabile* are nested in *Cratylia*, and should be moved to that genus (see discussion above); [2] *Camptosema scarlatinum* and the species of *Galactia* sect. *Galactioides* Benth. compose a strongly supported clade defined by inflorescences with a contracted flowering rachis, and thus presenting umbelliform appearances (the resurrected genus *Betencourtia*); [3] *Camptosema ellipticum* and the species of *Galactia* sect. *Collearia* (except *G. glaucescens*) compose a well-supported clade of small shrubs and subshrubs with pseudomonadelphous androecium and the standard petal pubescent on the outer surface (the new genus *Cerradicola*); [4] *Camptosema paraguariense* and a related new species from Bahia comprising an isolated lineage (the new genus *Caetangil*), sister to a larger clade bringing together most species of *Galactia*, *Collaea*, and *Camptosema*; [5] *Camptosema rubicundum* appearing as sister to a clade of morphologically quite distinct and tiny herbaceous species of *Galactia* (the new genus *Nanogalactia*); [6] *Galactia rudolphioides*, nested in a clade together with representatives of *Rhodopis* and *Neorudolphia*, making a clade restricted to the Greater Antilles with red, bird-pollinated flowers; and [7] the Mexican *Galactia viridiflora* as sister to the southeastern U.S.A. *Lackeya multiflora*, both comprising a clade defined by a coarse vine habit, broad leaflets, and flowers bent against the peduncle due to an inflexed pedicel.

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New taxonomic arrangements are thus necessary to solve the long-standing controversies of the generic boundaries within the *Camptosema*-*Galactia*-*Collaea* complex so as to result in highly-supported monophyletic genera that are readily diagnosed by morphological characters.

*Camptosema rubicundum* is the type species of *Camptosema* and is strongly supported as sister to a clade of *Galactia* species (here ascribed to the new genus *Nanogalactia*), a result previously described in other studies (Sede *et al.* 2009; Ceolin 2011; Queiroz *et al.* 2015). Including the species of *Nanogalactia* into *Camptosema* appears to be undesirable, as they are morphologically very distinct. *Nanogalactia* species are tiny herbaceous plants (*vs.* a woody vine habit in *C. rubicundum*), inflorescences reduced to 1 to 3 flowers in an axillary fascicle or along a tenuous peduncle (*vs.* inflorescence an elongate pseudoraceme with several multiflorous nodes), small flowers up to 15 mm long with mauve petals (*vs.* flowers 25–30 mm long with bright red petals), ovary sessile (*vs.* ovary stipitate), and fruits up to 3 cm long and 6 mm wide (*vs.* fruits 5–9 cm long and 9–15 mm wide). The genus *Nanogalactia* is thus being proposed to accommodate those distinctive species of *Galactia*. *Camptosema* is thus being reduced to a monospecific genus from southern South America.

The genus *Betencourtia* A.St.-Hil. originally included only one species (*B. rhynchosioides* A.St.-Hil.; Saint-Hilaire 1833) conspecific with *Collaea martii* [ $\equiv$  *Galactia martii* (DC.) Benth.]. Bentham (1859) established *Collaea* sect. *Galactioides* Benth. for species similar to *C. martii*. This section was later subsumed into *Galactia* (Bentham 1865) and was named as the unranked group *Galactiaria* of *Galactia* sect. *Collaea* by Taubert (1894). Burkart (1970) transferred *Collaea scarlatina* Benth. to *Camptosema*, a position rejected by our analyses, showing that all of the species related to *Collaea* sect. *Galactioides* make a well-supported clade sharing petiolate and trifoliolate leaves, but with a short rachis (or lacking it), stipelled leaflets, and a pseudoracemous inflorescence with a contracted flowering rachis (rendering an umbelliform aspect to the floral arrangement). *Betencourtia* is strongly supported as sister to the genus *Collaea*, yet the two lineages are morphologically quite distinct. As currently circumscribed (Candolle 1825; Burkart 1971; this work), *Collaea* represents a morphologically coherent genus including species with an erect shrub habit (*vs.* prostrate trailing herbs or twining vines in *Betencourtia*), sessile or shortly petiolate and palmately compound leaves (*vs.* leaves petiolate and pinnately compound), inflorescence reduced to an axillary, sessile, or shortly pedunculate and glomeruliform fascicle with wide multinerved bracts (*vs.* an umbelliform pedunculate pseudoraceme), standard petal bicallose and pubescent (*vs.* standard petal ecallose and glabrous), and a pseudomonadelphous androecium (*vs.* androecium diadelphous or pseudomonadelphous). *Collaea* is thus being kept in its current circumscription (Burkart 1971; Miotto 1980; Fortunato 1995; Ceolin & Miotto 2009), while the genus *Betencourtia* is being resurrected and expanded to include the species related to *Collaea* sect. *Galactioides*.

The new genus *Cerradicola* combines species of *Camptosema* [*C. ellipticum* (Desv.) Burk., *C. douradense* H.S. Irwin & Arroyo, and *C. praeandinum* Burk.] with species of *Galactia* sect. *Collearia* (*sensu* Burkart 1971) except for *G. glaucescens* Kunth. Except for their longer red petals and longer



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petioles, *Camptosema ellipticum* and *C. praeandinum* fit the diagnostic features of *Galactia* sect. *Collearia* as they show an erect subshrub or small shrub habit, nodose pseudoracemes, standard petal pubescent on the outer surface, and a pseudomonadelphous androecium. Additionally, this clade is ecologically coherent, as their species occur in the fire-prone savanna vegetation of the central Brazilian Cerrado extending to eastern Bolivia and northwestern Argentina.

Besides appearing intermixed with species of *Camptosema*, as stated above, species of *Galactia* also appear as related to the genera *Rhodopis*, *Neorudolphia*, and *Lackeya*. The Cuban and Jamaican *Galactia rudolphoides* (Griseb.) Benth. & Hook. f. ex C. Wright was recovered as strongly related to the Caribbean genera *Rhodopis* (two species) and *Neorudolphia* (monospecific). The presence of trifoliolate leaves and the standard petal reflexed ca. 90° probably hid previous recognition of its close affinity with *Rhodopis* and *Neorudolphia*, both with unifoliolate leaves and somewhat tubular corollas, due to the spreading and longitudinally folded standard petal. All of those taxa share a twinning and weakly woody habit, coriaceous leaves, and large flowers with bright red petals (Judd 1984; Beyra-Matos *et al.* 2005), so that combining them into the same genus seems to be the most parsimonious solution. Indeed, Lackey (1981) and Bruneau *et al.* (1995) had already considered *Neorudolphia* close to, and possibly congeneric with, *Rhodopis*.

*Galactia viridiflora* Standl. was strongly resolved as sister to *Lackeya multiflora* (Torr. & A.Gray) Fortunato, L.P.Queiroz & G.P.Lewis. Fortunato *et al.* (1996) previously discussed the putative affinity between *G. viridiflora* and *L. multiflora* but did not include *G. viridiflora* in *Lackeya* because of petal pilosity (glabrous in *L. multiflora* vs. pubescent at the apex in *G. viridiflora*) and the presence of callosities on the inner surface of the standard petal of *G. viridiflora*. However, *G. viridiflora* shares with *L. multiflora* a coarse vine habit forming dense mats, inflorescences with multi-flowered nodes, a woody vine habit, long-petiolate leaves, and wide (sub)orbicular leaflets with acuminate apices that could support its inclusion into *Lackeya*.

## 4 | TAXONOMY

### Identification key for the genera of the Galactia clade

1. Inflorescence nodes with more than three flowers .....2
1. Inflorescence nodes 2–3-flowered .....7
2. Inflorescence a glomeruliform axillary multi-flowered fascicle with wide and multinerved bracts; standard petal pubescent at the outer surface; androecium pseudomonadelphous; virgate and woody shrubs or subshrubs .....**Collaea**
2. Inflorescence an elongate pseudoraceme; bracts uninerved; standard petal glabrous or pubescent; androecium diadelphous or pseudomonadelphous; habit various .....3

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3. Ovary stipitate, the stipe at least as long as half of the ovary length .....4
3. Ovary sessile or shortly stipitate, the stipe, if present, much shorter than half of the ovary length .....6
4. Standard petal pubescent at the outer surface, at least towards the apex .....***Cratylia***
4. Standard petal glabrous .....5
5. Woody shrubs with ecological predilection to fire-prone savanna vegetation (Cerrado and campos rupestres); standard petal straight in anthesis making a somewhat tubular corolla .....***Bionia***
5. Semi-woody vines of gallery forests in Southern South America; standard petal reflexed backwards in anthesis (the corolla thus truly papilionate) .....***Camptosema***
6. Flowers with red calyx and red petals; restricted to the Greater Antilles (Cuba, Bahamas, Hispaniola, Puerto Rico and Jamaica) .....***Rhodopis***
6. Flowers with greenish calyx and mauve to purple petals; continental North America (Mexico and U.S.A.) .....***Lackeya***
7. All petals straight and red, only slightly raised near the apex making a trumpet like corolla; gynoeceium with a stipe longer than the ovary .....***Mantiqueira***
7. Standard petal bent backwards in anthesis; ovary sessile or shortly stipitate, the stipe (if present) shorter than half of the ovary length .....8
8. Standard petal pubescent at the outer surface, at least at the apex; erect shrubs or subshrubs with at least a woody base or woody underground .....***Cerradicola***
8. Standard petal glabrous; twining vines, erect or prostrate herbs or subshrubs lacking a woody base .....9
9. Anthers pubescent .....***Caetangil***
9. Anthers glabrous .....10
10. Inflorescence an umbelliform pseudoraceme, the flowering portion strongly contracted .....***Betencourtia***
10. Inflorescence an elongate pseudoraceme or reduced to an axillary fascicle .....11
11. Tiny herbs with a napiform root, sometimes with twining branches; inflorescence reduced to a 2–3-flowered axillary fascicle or to a 2–3-flowered axillary raceme with a filiform peduncle .....***Nanogalactia***



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11. Herbs or subshrubs, either erect or voluble; inflorescence mostly an elongate pseudoraceme with 2–3-flowered nodes or contracted into an axillary fascicle but then with more than three flowers .....*Galactia*

### Synopsis, new genera and new combinations in the Galactia clade

**Rhodopis** Urb., Symb. Antill. 2: 304. 1900. Type: *Rhodopis planisiliqua* (L.) Urb.

= *Neorudolphia* Britton, Sci. Surv. Porto Rico & Virgin Islands 5: 426. 1924. Type: *Neorudolphia volubilis* (Willd.) Britton, *syn. nov.*

**Description**— Twinning woody vines. **Leaves** unifoliolate or pinnately trifoliolate, leaflets stipelled, lateral leaflets (when present) symmetrical. **Inflorescence** an elongate axillary pseudoraceme, nodes 2–3-flowered; flowers pedicellate and provided with a pair of bracteoles just below the calyx. **Flowers** with calyx red, tubular or campanulate, 4-lobed, the lobes c. the same length or shorter than the tube; petals red, clawed, the claws shorter than the blade, standard petal longitudinally folded, spreading, or reflexed ca. 45°, glabrous, wing and keel petals straight, either equal or much reduced, and linear; androecium diadelphous or pseudomonadelphous, stamens 10, anthers monomorphic, glabrous; gynoecium slightly stipitate, the stipe shorter than the ovary, style hooked at apex. **Fruit** an elastically dehiscent legume, linear, flat compressed, valves thin and woody, upper margin with two tiny ribs parallel to the suture. **Seeds** ellipsoid, slightly compressed; testa smooth, coriaceous; hilum short, elliptic to oblong. Fig. 2 (A–C).

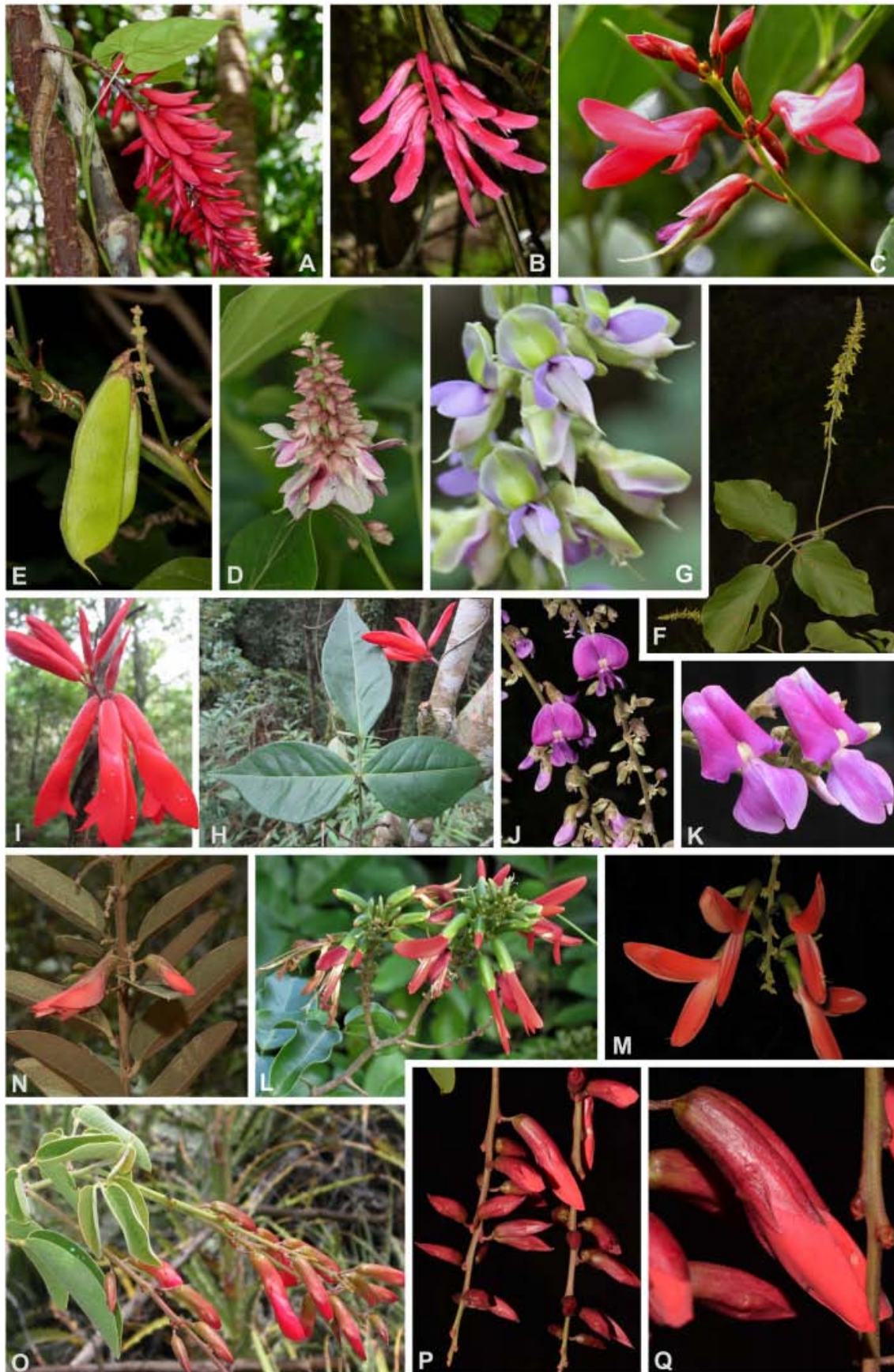
**Etymology**— From the Greek *ρόδινος* (*ródinos*) referring to the rosy color of the petals.

When proposing the genus *Rhodopis*, Urban (1900) compared the new genus with *Neorudolphia* (as *Rudolphia* Willd.) and concluded that the pseudomonadelphous androecium in *Rhodopis* (vs. diadelphous in *Neorudolphia*), the shapes of the upper calyx lobe and the anthers, and the degrees of style curvature justified treating them as different genera. That classification was followed by Britton (1924). Those genera, however, present several morphological ties that are rarely found in other groups of the Galactia clade, such as a woody vine habit, unifoliolate and stipelled leaves, flowers relatively large with reduced wing and keel petals (Judd 1984), to the point that both Lackey (1981) and Bruneau *et al.* (1995) considered them as possibly congeneric.

The position of *Galactia rudophioides* as closely related to *Rhodopis* was previously reported by Queiroz *et al.* (2015). That species was originally described in the genus *Dioclea* because of its woody vine habit, and could be distinguished from both *Rhodopis* and *Neorudolphia* by having trifoliolate leaves, shorter flowers with a mostly campanulate calyx, petals all approximately the same length, and the standard petal raised ca. 45° from the middle. However, it shares with those genera an elongate pseudoraceme with 2–3-flowered nodes, a 4-lobed red calyx, bright red petals,

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**Figure 2.** Species of the Antillean genus *Rhodopis* (A–C): A. *Rhodopis volubilis*; B. *Rhodopis planisiliqua*; C. *Rhodopis rudolphoides*. Representatives of the continental North American genus *Lackeya*: D–E. *Lackeya multiflora*; F–G. *Lackeya viridiflora*. *Mantiqueira bella* (H–I), a delicate vine from understory of montane forest (H) with a trumpet shape corolla (I). Species of *Cratylia* (J–M): J. *Cratylia argentea*; K. *Cratylia* sp. nov.; L. *Cratylia isopetala*; M. *Cratylia spectabilis*. Representatives of *Bionia* (N–Q), an entirely bird-pollinated genus: N. *Bionia pedicellata*; O. *Bionia coriacea*; P–Q. *Bionia* sp. nov. Photos: A.A. Conceição (B); D. Cardoso (J, M, P–Q); E. Freid (C); F. Areces (A); J. Gwaltney (D–E); L.G. Pedrosa (H–I); L.P. Queiroz (F, K, N–O); M. Dominguez-Laso (G); M.I. Calhau (L).

and ovary shortly stipitate (Beyra-Matos *et al.* 2005). The subsuming of *Neorudolphia* and of *G. rudolphoides* under *Rhodopis* seems to be the most parsimonious taxonomic solution for this clade.

As circumscribed here, *Rhodopis* embraces four species distributed in the Greater Antilles: Hispaniola Island [*R. planisiliqua* (L.) Urb. and *R. lowdenii* Judd], Puerto Rico [*R. volubilis*], and Cuba, Jamaica and the Bahamas [*R. rudolphoides*].

### New combinations in *Rhodopis*

***Rhodopis rudolphoides*** (Griseb.) L.P. Queiroz, *comb. nov.*

Basionym: *Dioclea rudolphoides* Griseb., *Pl. Wright.* 1: 768 [≡ *Galactia rudolphoides* (Griseb.) Benth. & Hook. f. ex C. Wright, *Anales Acad. Ci. Méd. Fís. Nat. Habana* 5: 337. 1869].

***Rhodopis volubilis*** (Willd.) L.P. Queiroz, *comb. nov.*

Basionym: *Rudolphia volubilis* Willd., *Ges. Naturf. Freunde Berlin Neue Schriften* 3: 452. 1801 [≡ *Butea volubilis* (Willd.) Pers., *Syn. Pl.* 2(2): 279. 1807 [≡ *Neorudolphia volubilis* (Willd.) Britton, *Sci. Surv. Porto Rico & Virgin Islands* 5: 426. 1924].

***Lackeya*** Fortunato, L.P. Queiroz & G.P. Lewis, *Kew Bull.* 51(2): 365–370, f. 1. 1996. Type: *Lackeya multiflora* (Torr. & A. Gray) Fortunato, L.P. Queiroz & G.P. Lewis [≡ *Dolichos multiflorus* Torr. & A. Gray, *Fl. N. Amer.* 1(2): 281. 1838; ≡ *Dioclea multiflora* (Torr. & A. Gray) C. Mohr, *Contr. U.S. Natl. Herb.* 6: 580. 1901.; ≡ *Galactia mohlenbrockii* R.H. Maxwell, *Castanea* 44(4): 242–243. 1979].

**Description**— Perennial woody climber. **Leaves** pinnately trifoliolate, leaflets large (4–12 × 4–10 cm), stipelled, lateral leaflets asymmetrical. **Inflorescence** an axillary elongate pseudoraceme, nodes swollen, 3–6-flowered, either along the peduncle or crowded toward the apex of the peduncle and becoming pyramidal; flowers shortly pedicelled and provided with a pair of bracteoles just below the calyx. **Flowers** deflexed against the peduncle (thus facing down) at the anthesis; calyx campanulate, 4-lobed, the lobes shorter or longer than the tube; petals with about the same length, whitish mauve or purple, clawed, the claws shorter than the blade, standard petal reflexed, glabrous or pubescent toward the apex, wing and keel petals straight; androecium pseudomonadelphous or diadelphous (sometimes varying in the same species), stamens 10, anthers monomorphic, glabrous;



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gynoecium sessile. **Fruit** an elastically dehiscent legume, obovate or linear-oblongate, upper margin not constricted and provided with two tiny ribs parallel to the suture; valves thin woody. **Seeds** globose, not compressed; testa bony; hilum short and elliptical to oblong. Fig. 2 (D–E).

**Etymology**— The genus was named after James Lackey, an American botanist that worked on the tribe Phaseoleae (Fortunato *et al.* 1996).

*Lackeya* was described by Fortunato *et al.* (1996) to accommodate a species (*L. multiflora*) tentatively placed before in *Dioclea* or *Galactia*. In describing the genus *Lackeya*, Fortunato *et al.* (1996) compared *L. multiflora* with the similar *Galactia viridiflora* (Rose) Standl. but did not include this species in *Lackeya* because it presents a pubescent standard petal (*vs.* glabrous in *L. multiflora*), a diadelphous androecium (*vs.* pseudomonadelphous but variable in different individuals) and fruits linear-oblongate (*vs.* mostly obovate). The supported phylogenetic position of *G. viridiflora* as sister to *L. multiflora* indicates that their similarity could more probably result from their shared most recent common ancestry. This resemblance could be expressed in a set of shared traits as the robust vine habit, the big suborbicular leaflets, the asymmetrical lateral leaflets, the shortly pedicellate flowers bent against the peduncle and thus facing down in anthesis, justifying the inclusion of *G. viridiflora* in *Lackeya* rather than segregating it as a new monospecific genus.

As here circumscribed, *Lackeya* makes a North American endemic genus from southeastern United States (*L. multiflora*) and central and western Mexico (*L. viridiflora*).

### New combination in *Lackeya*

***Lackeya viridiflora*** (Rose) L.P. Queiroz, *comb. nov.*

Basionym: *Odonia viridiflora* Rose, *Contr. U.S. Natl. Herb.* 10 (3): 103, pl. 33. 1906. [≡ *Galactia viridiflora* (Rose) Standl., *Contr. U.S. Natl. Herb.* 23(2): 502. 1922].

***Mantiqueira*** L.P. Queiroz, *gen. nov.*

**Diagnosis**— Similar to *Bionia* by presenting flowers with a tubular calyx, red petals and the standard petal spreading and longitudinally folded, but differing by the weakly herbaceous vine habit (*vs.* erect shrubs in *Bionia*), membranaceous leaflets (*vs.* leaflets strongly coriaceous), delicate inflorescence with linear 2(–3)-flowered nodes (*vs.* woody inflorescence with multiflorous nodes), a membranaceous calyx (*vs.* calyx fleshly coriaceous), and petals slightly raised at the apex rendering to the corolla a trumpet aspect (*vs.* petals straight making a tubular corolla).

**Type**— *Mantiqueira bella* (Mart. ex Benth.) L.P. Queiroz [≡ *Bionia bella* Mart. ex Benth., *Comm. Legum. Gen.*: 66. 1837].

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**Description**— Delicate semi-woody vine. **Leaves** pinnately trifoliolate, leaflets membranaceous, stipelled, lateral leaflets symmetrical. **Inflorescence** an axillary pseudoraceme, shorter than the subtending leaf, peduncle fragile and herbaceous, nodes linear, 2(–3)-flowered, flowers pedicelled and provided with a pair of bracteoles just below the calyx. **Flowers** 5–6 cm long; calyx tubular, membranaceous, reddish wine, 4-lobed, the lobes shorter than the tube; corolla trumpet shaped due to the petals slightly raised at the apex, petals dark red, about the same length, clawed, the claws almost as long as the blades, standard petal spreading (i.e., not reflexed) and longitudinally folded, wing and keel petals straight; androecium pseudomonadelphous, anthers of the ten stamens monomorphic, glabrous; gynoecium long stipitate, the stipe as long as the ovary. **Fruit** a legume, linear, elastically dehiscent, stipitate, margins not constricted lacking ribs or wings; valves thin, woody. **Seeds** flat compressed; testa coriaceous; hilum short, elliptical to oblong. Fig. 2 (H–I).

**Etymology**— The genus is named after its geographical distribution restricted to the Mantiqueira mountain range of Eastern Brazil.

*Mantiqueira* is proposed here to include the species originally described as *Bionia bella* Mart. ex Benth. (Bentham 1837), later transferred to *Camptosema* as *C. bellum* (Mart. ex Benth.) Benth. (Bentham 1859). To include this species in *Bionia* or *Camptosema*, Bentham (1837, 1859) emphasized the shared floral traits as the big flowers with red petals, a spreading (i.e., not reflexed) standard petal and a stipitate ovary. However, the floral resemblance of *Mantiqueira bella* and the species of *Bionia* had probably resulted from convergence to a highly specialized hummingbird pollination (Queiroz *et al.* 2003; Queiroz 2008) rather than reflecting an ancestrally shared homology.

The genus includes just one species that is a delicate vine of shady environments in montane forests. It is known only from the Mantiqueira mountain range in the eastern Brazilian states of Espírito Santo and Minas Gerais.

### New combination in *Mantiqueira*

***Mantiqueira bella*** (Mart. ex Benth.) L.P. Queiroz, *comb. nov.*

Basionym: *Bionia bella* Mart. ex Benth., *Comm. Legum. Gen.* 66. 1837. [≡ *Camptosema bellum* (Mart. ex Benth.) Benth., *Fl. Bras.* 15(1): 156. 1859].

***Cratylia*** Mart. ex Benth., *Comm. Legum. Gen.*: 67. 1837. Type: *Cratylia hypargyrea* Mart. ex Benth.

= *Camptosema* sect. *Macropetalum* Benth., *Fl. Bras.* 15(1): 154. 1859. Lectotype (designated here): *Camptosema grandiflorum* Benth. (= *Cratylia spectabilis* Tul.), *syn. nov.*

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**Description**— Tall shrubs or lianas. **Stipules** with swollen and secreting base. **Leaves** pinnately trifoliolate, leaflets stipelled, lateral leaflets asymmetrical. **Inflorescence** an axillary woody pseudoraceme, longer than subtending leaf, nodes swollen, multiflowered; flowers pedicelled and provided with a pair of bracteoles just below the calyx. **Flowers** with the calyx campanulate or tubular, 4-lobed, the lobes c. the same length or shorter than the tube; petals purple, red or orangish red, clawed, the claws shorter than the blade, standard petal reflexed, pubescent toward the apex, wing and keel petals straight; androecium pseudomonadelphous, stamens 10, anthers monomorphic, glabrous; gynoecium shortly stipitate. the stipe c. half of the length of the ovary. **Fruit** an elastically dehiscent legume, valves woody, margins constricted between the seeds. **Seeds** compressed, suborbicular; testa leathery; hilum short and elliptical to oblong. Fig. 2 (J–M).

**Etymology**— From the Greek *κραταιόω* (*krataiόo*) meaning strong, firm, referring to the firm woody stem (Schrire 2005).

The circumscription of *Cratylia* did not change since Bentham (1859), being defined by the woody lianescent or shrubby habit, leaves with asymmetrical lateral leaflets, inflorescences with a woody peduncle and swollen multiflowered nodes, a pubescent standard petal and pseudomonadelphous androecium (Queiroz 1991). This set of diagnostic features is not affected by the inclusion of the two species of *Camptosema* sect. *Macropetalum*: *Camptosema isopetalum* and *Camptosema spectabile* [originally described in *Cratylia* by Tulasne (1841)], their difference from the remaining species of *Cratylia* probably reflecting changing from bee to bird pollination (Queiroz 2008), as they present red and more elongate petals, the standard petal narrowly elliptic to oblong (vs. petals purple and comparatively wider, the standard petal widely ovate to suborbicular). In all other morphological traits they fit quite well the limits of the genus *Cratylia*.

*Cratylia* now embraces seven species from Brazil, southward from the Amazon basin, to eastern Bolivia and Peru, in seasonally dry forests and woodlands, rain forests and savanna vegetation.

### New combination in *Cratylia*

***Cratylia isopetala*** (Lam.) L.P. Queiroz, *comb. nov.*

Basionym: *Erythrina isopetala* Lam., *Encycl.* 2(1): 392. 1786 [= *Camptosema isopetalum* (Lam.) Taub., *Nat. Pflanzenfam.* 3(3): 369. 1894].

***Bionia*** Mart. ex Benth., *Comm. Legum. Gen.*: 66. 1837. Type: *Bionia coccinea* Mart. ex Benth.

**Description**— Spindly virgate shrubs. **Stipules** with a swollen and secreting base. **Leaves** pinnately trifoliolate and petiolate, unifoliolate and shortly petiolate or simple and sessile, in compound

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leaves leaflets stipelled, the lateral ones symmetrical. **Inflorescence** an axillary pseudoraceme, peduncle patent, almost horizontal, woody, nodes swollen, multiflorous, flowers pedicelled and provided with a pair of bracteoles just below the calyx. **Flowers** 2.5–4 cm long; calyx tubular, fleshy, reddish wine, 4-lobed, the lobes shorter than the tube; corolla tubular, almost actinomorphic, petals red, clawed, standard petal spreading (i.e., not reflexed) and longitudinally folded, wing and keel petals straight; androecium pseudomonadelphous, anthers of the ten stamens monomorphic, glabrous; gynoecium long stipitate, the stipe as long as the ovary. **Fruit** a legume, elastically dehiscent, stipitate, valves woody. **Seeds** flat compressed; testa leathery; hilum short and oblong. Fig. 2 (N–Q).

**Etymology**— Probably dedicated to Bion of Smyrna, a Greek bucolic poet that flourished about 100 BC.

With the transfer of *B. bella* to *Mantiqueira*, *Bionia* includes four species (Queiroz 2008) but at least four other undescribed species were reported (Queiroz 1999). The genus as circumscribed here makes a morphologically consistent group characterized by the habit of low shrubs with virgate and little ramified branches, coriaceous leaves, inflorescences almost horizontal and big flowers with a tubular and red corolla.

The genus *Bionia* occurs in campo rupestre vegetation in the Espinhaço mountain range (states of Bahia and Minas Gerais) extending to Cerrado in western Bahia and Goiás states.

**Camptosema** Hook. & Arn., *Bot. Misc.* 3: 200. 1833. Type: *Camptosema rubicundum* Hook. & Arn.

**Description**— Weakly woody perennial vines (usually with a woody base but the new branches herbaceous). **Stipules** with a swollen and secreting base. **Leaves** pinnately trifoliolate and petiolate, leaflets stipelled, the lateral ones symmetrical. **Inflorescence** an axillary pseudoraceme, peduncle ascending, woody, nodes swollen, multiflorous, flowers pedicelled and provided with a pair of bracteoles just below the calyx. **Flowers** 2.5–3 cm long; calyx shortly tubular, fleshy, reddish wine, 4-lobed, the lobes slightly shorter than the tube; petals red, clawed, standard petal reflexed, wing and keel petals straight; androecium pseudomonadelphous, anthers of the ten stamens monomorphic, glabrous; gynoecium shortly stipitate, the stipe c. half of the ovary length. **Fruit** a legume, elastically dehiscent, stipitate, valves thin coriaceous. **Seeds** globose; testa leathery; hilum short and oblong. Fig. 3 (A–C).

**Etymology**— From the Greek *καμπύλος* ('*campto-*', curved) and *σημαία* ('*-semeia*', the standard petal), referring to the standard petal reflexed at the anthesis.



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Figure 3. *Camptosema rubicundum*, the sole species of the genus *Camptosema* (A–C): A. The vine habit at its habitat in a creek gallery; B. Detail of a flower; C. The hummingbird *Chlorostilbon lucidus* visiting a flower. Species of the new genus *Nanogalactia* (D–G): D. *Nanogalactia brachystachys* in its habitat; E–F. *Nanogalactia heterophylla* showing the delicate herbaceous habit with a napiform root and the axillary few-flowered fascicle; G. *Nanogalactia pretiosa*, showing the axillary racemes with a tenuous peduncle. Representatives of the new genus *Caetangil*: H–J. Leaves (H) and flowers (I) of *Caetangil chacoensis*; J. Flowers and fruits of *Caetangil* sp. nov. Species of the heterogenous genus *Galactia* (K–N): K. The Colombian *G. lindenii*; L. *Galactia glaucescens*; M. *Galactia jussiaeana*; N. *Galactia remansoana*. Photos: D.D. Giraldo-Cañas (K); D. Cardoso (J, N); L.P. Queiroz (A–G, L–M); M. Ross (H–I).

*Camptosema* is here reduced to just one species, *C. rubicundum*. The remaining species are being moved to *Betencourtia*, *Bionia*, *Caetangil*, *Cerradicola*, *Cratylia*, and *Mantiqueira*. It can be diagnosed by the combination of a weakly woody vine habit, petiolate and pinnately trifoliolate leaves, typical papilionate flowers with red petals and the standard petal reflexed, and ovary shortly stipitate. The genus is distributed in southern South America, in Uruguay, northern Argentina and the Brazilian state of Rio Grande do Sul, in thickets and gallery forests along the streams.

***Nanogalactia*** L.P. Queiroz, *gen. nov.*

**Diagnosis**— Similar to *Galactia* by presenting flowers small with typical papilionate corolla and a diadelphous androecium, but differing by the reduced herbaceous habit, leaflets with a marginal vein (vs. marginal vein absent), inflorescence reduced to 2–3 flowers in a sessile axillary fascicle or along a tenuous peduncle (vs. inflorescence an elongate pseudoraceme or an axillary fascicle but with several flowering nodes).

**Type**— *Nanogalactia heterophylla* (Gillies ex Hook. & Arn.) L.P. Queiroz [= *Galactia marginalis* Benth.]

**Description**— Erect or twinning herb, usually under 40 cm tall, the stems usually under 1 mm diam. **Leaves** either sessile and simple, or unifoliolate, palmately or pinnately trifoliolate, leaflets stipelled, lateral leaflets (when present) symmetrical. **Inflorescence** mostly an axillary, few-flowered axillary fascicle, sometimes a slender pseudoraceme with 1–2 nodes, each node vestigial, 1–3-flowered, flowers pedicellate and provided with a pair of bracteoles just below the calyx. **Flowers** 1–2 cm long; calyx campanulate, membranaceous, 4-lobed, the lobes equal to or longer than the tube; corolla typically papilionate, petals purple, clawed, the claws shorter than the blades, standard petal reflexed, wing and keel petals straight; androecium diadelphous, anthers of the ten stamens monomorphic, glabrous; gynoecium shortly stipitate. **Fruit** a legume, elastically dehiscent, erect, valves thin, woody. **Seeds** globose; testa bony; hilum short and oblong. Fig. 3 (D–G).

**Etymology**— From the Greek *νάνος* ('nanos-', dwarf) and *Galactia*, referring to the reduced habit of the plants and their similarity to *Galactia*.

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The genus *Nanogalactia* is being proposed here to accommodate a group of species formerly included in *Galactia* that make a highly supported clade sister to *Camptosema rubicundum*. The three species recovered in *Nanogalactia* are morphologically heterogeneous, two are erect herbaceous plants with napiform thick roots and sessile or shortly petiolate leaves [*N. heterophylla* and *N. pretiosa*] and another is a twinning herbaceous plant with petiolate and pinnately trifoliolate leaves [*N. brachystachys*] (Vail 1895; Burkart 1949, 1971; Nesom 2015), but they share a tiny herbaceous habit, the branches under 1 mm diam., inflorescence with few (1–3) flowers, mostly packed and fasciculate in a leaf axil or on a very delicate peduncle (< 0.5 mm diam.), flowers under 2 cm long, and fruits erect. This set of characters make this entire clade quite distinct from its sister group, *Camptosema rubicundum*, which resulted in it being the sole species of *Camptosema*. We did not include these species in *Camptosema* because that would result in a quite heterogeneous genus losing diagnosability (see the diagnostic features of *Camptosema* above).

*Nanogalactia* is barely distinguishable from *Galactia*, and it is possible that some other unsampled species of *Galactia* with reduced axillary inflorescences and erect fruits should be included in *Nanogalactia*, as may be the case of *G. sessiliflora* Torr. & A.Gray and *G. erecta* (Walt.) Vail.

The genus is widely distributed in tropical and subtropical America, from Mexico to northern Argentina.

### New combinations in *Nanogalactia*

***Nanogalactia brachystachys*** (Benth.) L.P. Queiroz, *comb. nov.*

Basionym: *Galactia brachystachys* Benth., *Comm. Legum. Gen.*: 63. 1837. [≡ *Odonia brachystachys* (Benth.) Rose, *Contr. U.S. Natl. Herb.* 10(3): 102. 1906].

***Nanogalactia heterophylla*** (Gillies ex Hook. & Arn.) L.P. Queiroz, *comb. nov.*

Basionym: *Cologania heterophylla* Gillies ex Hook. & Arn., *Bot. Misc.* 3: 181–182. 1833 [≡ *Galactia heterophylla* (Gillies ex Hook. & Arn.) Vail, *Bull. Torrey Bot. Club* 22: 502. 1895 [*nom. illeg.*].  
= *Galactia marginalis* Benth., *Comm. Legum. Gen.*: 62. 1837, *syn. nov.*

Vail (1895) made the combination *Galactia heterophylla* from *Cologania heterophylla* Gillies ex Hook. & Arn. but overlooked that this name was already occupied by *Galactia heterophylla* A.Gray. Burkart (1971) and Nesom (2015) thus considered *Galactia marginalis* Benth. as the correct name for this taxon. We agree that these species are synonymous, but *N. heterophylla* should be the correct name for this taxon as *Cologania heterophylla* has priority over *Galactia marginalis*.

***Nanogalactia pretiosa*** (Burkart) L.P. Queiroz, *comb. nov.*

Basionym: *Galactia pretiosa* Burkart, *Darwiniana* 9: 93, f. 10. 1949.



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***Nanogalactia pretiosa* var. *trifoliolata*** (Hassl.) L.P. Queiroz, *comb. nov.*

Basionym: *Galactia marginalis* var. *trifoliolata* Hassl., *Repert. Spec. Nov. Regni Veg.* 16: 227. 1919. [≡ *Galactia pretiosa* var. *trifoliolata* (Hassl.) Burkart, *Darwiniana* 16(3–4): 753. 1971].

***Caetangil*** L.P. Queiroz, *gen. nov.*

**Diagnosis**— Similar to *Galactia* by presenting small flowers with typical papilionate corollas in an elongate, weakly nodose pseudoraceme, but differing by the reddish petals (*vs.* petals mostly mauve or purple), bearded anthers (*vs.* anthers glabrous), and a stipitate ovary (*vs.* ovary sessile).

**Type**— *Caetangil paraguariensis* (Chodat & Hassl.) L.P. Queiroz [≡ *Galactia paraguariensis* Chodat & Hassl.].

**Description**— Prostrate or twinning subshrubs. **Leaves** pinnately trifoliolate, petiolate, leaflets stipelled, lateral leaflets symmetrical. **Inflorescence** an axillary elongate pseudoraceme, with a long and slender peduncle, and remote 2–3-flowered nodes, flowers shortly pedicellate and provided with a pair of bracteoles just below the calyx. **Flower** buds ovoid and shortly acuminate; flowers 1–1.7 cm long; calyx campanulate, membranaceous, 4-lobed, the lobes slightly longer than the tube; corolla typically papilionate, petals red or reddish purple, clawed, the claws shorter than the blades, standard petal reflexed and glabrous, wing and keel petals straight; androecium pseudomonadelphous, anthers of the ten stamens monomorphic and pubescent; gynoecium stipitate. **Fruit** a legume, elastically dehiscent, valves thin, woody. **Seeds** globose, slightly compressed; testa bony; hilum short and oblong. Fig. 3 (H–J).

**Etymology**— The genus is named after the Brazilian singers Caetano Veloso and Gilberto Gil for their huge cultural contributions, including their support of environment causes.

This genus includes the species once known as *Camptosema paraguariense* (with two varieties being raised to species) plus two undescribed species. *Camptosema paraguariense* was moved between *Galactia* and *Camptosema* and, in fact, it combines the habit and inflorescence more similar to that found in *Galactia* species, but with the stipitate ovary and the pseudomonadelphous androecium then considered as diagnostic features of *Camptosema* (Hassler 1919; Burkart 1970). Besides presenting an isolated phylogenetic position, this genus has bearded anthers, which represent a unique synapomorphy of *Caetangil*.

Both *Caetangil paraguariensis* and the two undescribed species are found in seasonally dry vegetation, including the southern South American Chaco, the northeastern Brazilian Caatinga, and open fields in southern Guiana and northern Brazil.

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Two described species are accepted here.

### New names and new combinations in *Caetangil*

*Caetangil paraguariensis* (Chodat & Hassl.) L.P. Queiroz, *comb. nov.*

Basionym: *Galactia paraguariensis* Chodat & Hassl., *Bull. Herb. Boissier, sér. 2*, 4(9): 900. 1904. [≡ *Camptosema paraguariense* (Chodat & Hassl.) Hassl., *Repert. Spec. Nov. Regni Veg.* 16: 228. 1919].

*Caetangil chacoensis* L.P. Queiroz, *nom. et stat. nov.*

Basionym: *Camptosema paraguariense* var. *parviflorum* Hassl., *Repert. Spec. Nov. Regni Veg.* 16: 228. 1919.

*Cerradicola* L.P. Queiroz, *gen. nov.*

≡ *Collaea* sect. *Collearia* Benth., *Fl. Bras.* 15(1): 147. 1859. *Galactia* sect. *Collaea* subsect. or ser. [unranked] *Collearia* (Benth.) Taub., *Nat. Pflanzenfam.* 3(3): 369. 1894. *Galactia* sect. *Collearia* (Benth.) Burkart, *Darwiniana* 16 (3-4): 668. 1971.

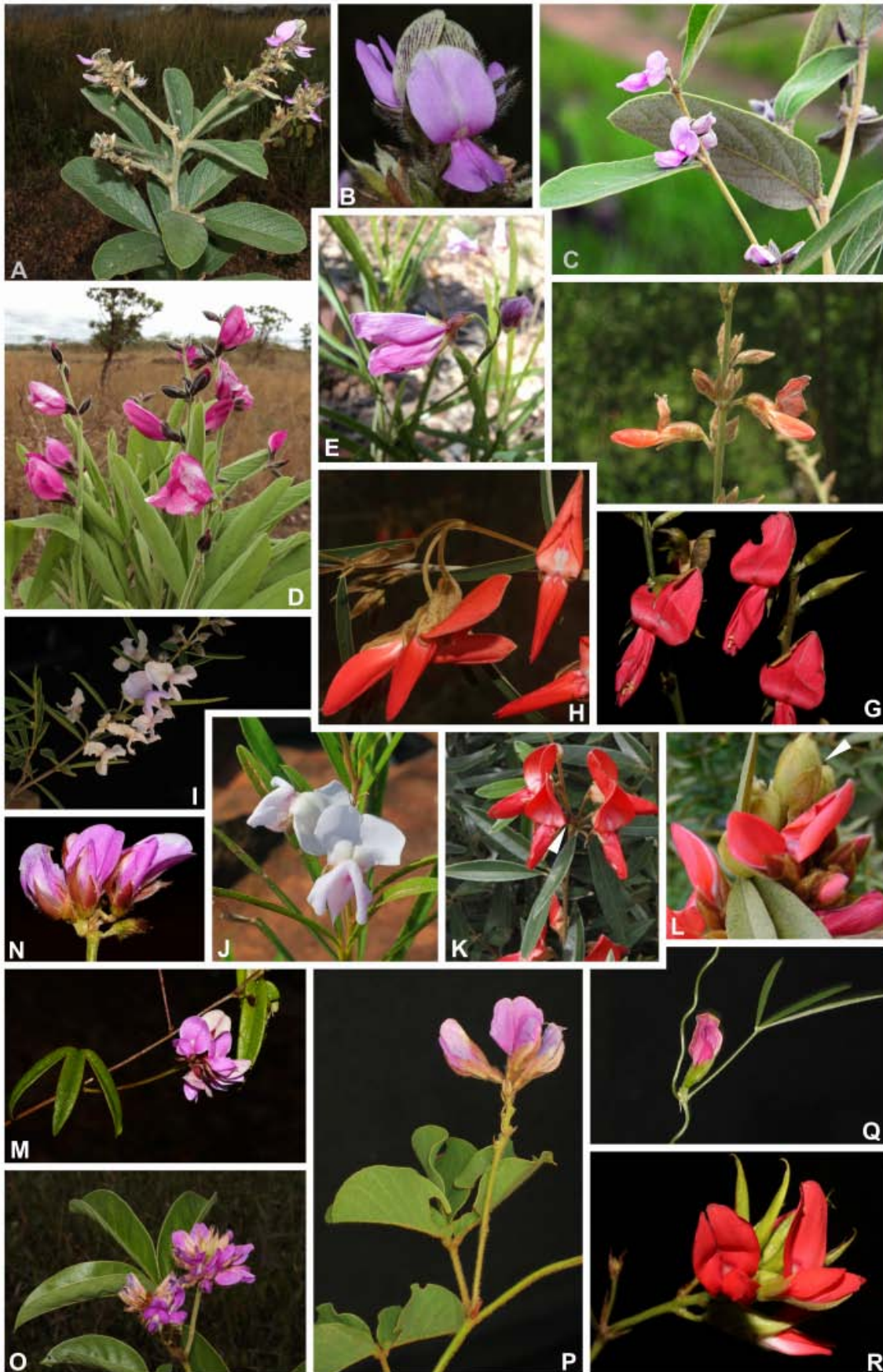
**Diagnosis**— Similar to *Galactia* by presenting small flowers, arranged in a typical papilionate corolla, and a sessile ovary, but differing by a subshrubby habit with hard and woody branches (sometimes underground), standard petal pubescent on the outer surface (vs. standard petal glabrous), and a pseudomonadelphous (rarely diadelphous) androecium (vs. androecium diadelphous).

**Type**— *Cerradicola peduncularis* (Benth.) L.P. Queiroz [≡ *Collaea peduncularis* Benth.].

**Description**— Mostly perennial erect subshrubs, sometimes prostrate but not twinning, frequently with hard underground rhizomes or xylopodia. **Leaves** pinnately trifoliolate or unifoliolate, sessile or shortly petiolate (rarely with an elongate petiole), rachis short, leaflets stipelled, lateral leaflets symmetrical. **Inflorescence** an axillary elongate pseudoraceme with an elongate, hard, and erect peduncle, nodes 1–3-flowered, flowers shortly pedicellate and provided with a pair of bracteoles just below the calyx. **Flower** buds lanceolate in profile, acuminate; flowers 1.5–3.5 cm long; calyx campanulate (rarely tubulose), coriaceous, 4-lobed, the lobes longer than the tube; corolla typically papilionate, petals mauve, purple, or red, clawed, the claws shorter than the blades, standard petal reflexed, pubescent on the outer surface towards the apex, wing and keel petals straight; androecium pseudomonadelphous or diadelphous, anthers of the ten stamens monomorphic and glabrous; gynoecium sessile. **Fruit** a legume, elastically dehiscent, valves thin, coriaceous. **Seeds** globose; testa bony; hilum short and oblong. Fig. 4 (A–G).

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**Figure 4.** Representatives of the new genus *Cerradicola* (A–G), mostly pyrophytic subshrubs from Savanna vegetation: A–B. *Cerradicola eriosematoides*; C. *Cerradicola grewiifolia*; D. *Cerradicola peduncularis*; E. *Cerradicola longifolia*; F. *Cerradicola praeandina*; G. *Cerradicola elliptica*. Species of the genus *Collaea* (H–L), self-standing virgate shrubs with sessile palmately trifoliolate leaves and inflorescence in an axillary fascicle (arrow) protected by wide bracts (arrow): H. *Collaea cipoensis*; I–J. *Collaea stenophylla*; K–L. *Collaea speciosa*. Species of the resurrected genus *Betencourtia* (M–R), with petiolate leaves but with a contracted rachis rendering an almost palmately compound leaf, and the umbelliform pseudoracemous inflorescence: M–N. *Betencourtia martii*; O. *Betencourtia stereophylla*; P. *Betencourtia australis*; Q. *Betencourtia gracillima*; R. *Betencourtia scarlatina*. Photos: C. Snak (D–E, J); D. Cardoso (A–B, G–H, O, R); E.L.H. Gehl (K); L.P. Queiroz (C, F, I, L, M–N, P, Q).

**Etymology—** From Cerrado and the Latin suffix *-incola* (inhabitant), making reference to the fact that almost all species occur in the Cerrado phytogeographic domain.

*Cerradicola* corresponds to *Galactia* sect. *Collearia* (Benth.) Burkart (with the exclusion of *Galactia glaucescens* Kunth., which was supported as a member of the genus *Galactia*, and the species related to *Camptosema ellipticum* (Desv.) Burkart. It constitutes a morphologically cohesive group of pyrophytic subshrubs from savanna vegetation with mostly coriaceous leaves with both a short petiole and rachis, typical papilionate flowers, with the standard petal pubescent on the outer surface, a mostly pseudomonadelphous androecium, and sessile ovary. *Camptosema ellipticum* and the related *C. douradense* H.S.Irwin & Arroyo and *C. praeandinum* Burkart, differ from *Galactia* sect. *Collearia* (sensu Burkart 1971) by having larger flowers with red petals (Burkart 1970), probably reflecting a shift from a bee pollinated to a bird pollinated syndrome (Queiroz 2008).

Species of *Cerradicola* are typical elements of the herbaceous-subshrubby layer of the fire-prone Cerrado phytogeographic domain of the central Brazilian plateau, extending to the eastern Andean slopes of eastern Bolivia and northwestern Argentina. Some species also occur in similar environments in the campos rupestres vegetation of the Espinhaço mountain range (in the Brazilian states of Bahia and Minas Gerais).

The genus includes 16 species.

### New combinations in *Cerradicola*

***Cerradicola aurea*** L.P.Queiroz, *nom. nov.*

Basionym: *Camptosema douradense* H.S. Irwin & Arroyo, *Brittonia* 26(1): 27–29, f. 1. 1974.

This new name is necessary because there is an older species whose basionym has the same specific epithet (see *Cerradicola douradense*, below).

***Cerradicola boavista*** (Vell.) L.P. Queiroz, *comb. nov.*

Basionym: *Cytisus boavista* Vell., *Fl. Flumin.*: (descr.) 309, 1825, *Icones* 7, p. 115. 1827 [≡ *Galactia boavista* (Vell.) Burkart, *Darwiniana* 16(3–4): 783. 1971].



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***Cerradicola bullata*** (Benth.) L.P. Queiroz, *comb. nov.*

Basionym: *Collaea bullata* Benth., *Fl. Bras.* 15(1): 149–150. 1859 [≡ *Galactia bullata* (Benth.) Taub., *Nat. Pflanzenfam.* 3(3): 368. 1894].

***Cerradicola bullata*** var. ***magnifolia*** (Burkart) L.P. Queiroz, *comb. nov.*

Basionym: *Galactia bullata* var. *magnifolia* Burkart, *Darwiniana* 16(3–4): 767–769. 1971.

***Cerradicola diversifolia*** (Benth.) L.P. Queiroz, *comb. nov.*

Basionym: *Collaea diversifolia* Benth., *Fl. Bras.* 15(1): 147–148. 1859. [≡ *Galactia diversifolia* (Benth.) Hoehne, *Revista Mus. Paul. Univ. São Paulo* 10: 695. 1918, *nom. inval.*; ≡ *Galactia dimorpha* Burkart, *Darwiniana* 16(3–4): 766. 1971].

The combination *Galactia dimorpha* Burkart (Burkart 1971) was proposed to replace the invalid name *G. diversifolia* (Benth.) Hoehne, a later homonym of *G. diversifolia* Bojer. As the combination *Cerradicola diversifolia* is not occupied, the older epithet is being reinstated as the valid name for this species.

***Cerradicola douradensis*** (Taub.) L.P. Queiroz, *comb. nov.*

Basionym: *Galactia douradensis* Taub., *Bot. Jahrb. Syst.* 21: 438. 1896.

***Cerradicola decumbens*** (Benth.) L.P. Queiroz, *comb. nov.*

Basionym: *Collaea decumbens* Benth., *Linnaea* 22: 515. 1849 [≡ *Galactia decumbens* (Benth.) Hoehne, *Revista Mus. Paul. Univ. São Paulo* 10: 695. 1918; ≡ *Galactia decumbens* (Benth.) Hassl., *Repert. Spec. Nov. Regni Veg.* 16: 227. 1919; ≡ *Galactia decumbens* (Benth.) Malme, *Ark. Bot.* 23A(13): 89. 1931].

***Cerradicola elliptica*** (Desv.) L.P. Queiroz, *comb. nov.*

Basionym: *Rudolphia elliptica* Desv., *Ann. Sci. Nat. (Paris)* 9: 422. 1826.

***Cerradicola eriosematoides*** (Harms) L.P. Queiroz, *comb. nov.*

Basionym: *Galactia eriosematoides* Harms, *Bot. Jahrb. Syst.* 33, Beibl.: 27. 1903.

***Cerradicola grewiifolia*** (Benth.) L.P. Queiroz, *comb. nov.*

Basionym: *Collaea grewiifolia* Benth., *Comm. Legum. Gen.* 64. 1837 [≡ *Galactia grewiifolia* (Benth.) Taub., *Nat. Pflanzenfam.*: 3(3): 368. 1894].

***Cerradicola heringeri*** (Burkart) L.P. Queiroz, *comb. nov.*

Basionym: *Galactia heringeri* Burkart, *Darwiniana* 16(3–4): 772–775. 1971.

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***Cerradicola irwinii*** (R.S. Cowan) L.P. Queiroz, *comb. nov.*

Basionym: *Galactia irwinii* R.S. Cowan, *Bol. Soc. Venez. Ci. Nat.* 22(100): 284–285, f. 1d. 1961.

***Cerradicola lamprophylla*** (Harms) L.P. Queiroz, *comb. nov.*

Basionym: *Galactia lamprophylla* Harms, *Bot. Jahrb. Syst.* 33, Beibl. 72: 28. 1903.

***Cerradicola longifolia*** (Benth.) L.P. Queiroz, *comb. nov.*

Basionym: *Collaea longifolia* Benth., *Fl. Bras.* 15 (1): 151. 1859 [≡ *Galactia longifolia* (Benth.) Hoehne, *Comm. Lin. Telegr., Bot.* 74(12): 26. 1922, *nom. inval.*; ≡ *Galactia longifolia* (Benth.) Malme, *Ark. Bot.* 23A(13): 89. 1931, *nom. inval.*; ≡ *Galactia hoehnei* Burkart, *Darwiniana* 16(3–4): 763. 1971].

Burkart (1971) proposed the name *Galactia hoehnei* to replace *G. longifolia* (Benth.) Hoehne because it is a later homonym of *G. longifolia* (Jacq.) Benth. However, the combination *Cerradicola longifolia* is not occupied, and *Collaea longifolia* (Benth.) 1837 has priority over *Galactia hoehnei* (Burkart 1971).

***Cerradicola nana*** (Burkart) L.P. Queiroz, *comb. nov.*

Basionym: *Galactia nana* Burkart, *Darwiniana* 16(3–4): 775–777. 1971.

***Cerradicola peduncularis*** (Benth.) L.P. Queiroz, *comb. nov.*

Basionym: *Collaea peduncularis* Benth., *Comm. Legum. Gen.* 64. 1837. [≡ *Galactia peduncularis* (Benth.) Taub., *Bot. Jahrb. Syst.* 21: 439. 1896].

***Cerradicola rotundifolia*** (Benth.) L.P. Queiroz, *comb. nov.*

Basionym: *Collaea rotundifolia* Benth., *Fl. Bras.* 15 (1): 149. 1859. [≡ *Galactia rotundifolia* (Benth.) Malme, *Ark. Bot.* 23A(13): 89. 1931, *nom. inval. non Galactia rotundifolia* Micheli, *J. Bot. (Morot)* 6: 188, pl. 8. 1892].

***Betencourtia*** A. St.-Hil., *Voy. Distr. Diam.* 1: 376. 1833. Type: *Betencourtia rhynchosioides* A. St.-Hil. [= *Betencourtia martii* (DC.) L.P. Queiroz]

= *Collaea* sect. *Galactioides* Benth., *Fl. Bras.* 15(1): 151. 1859. *Galactia* sect. *Collaea* subsect. or ser. [unranked] *Galactaria* Taub., *Nat. Pflanzenfam.* 3(3): 369. 1894. Lectotype (designated here): *Collaea crassifolia* Benth. [≡ *Betencourtia crassifolia* (Benth.) L.P. Queiroz], *syn. nov.*

**Description**— Herbs or subshrubs, either prostrate or twining vines, sometimes with tuberous roots. **Leaves** palmately trifoliolate or pinnately trifoliolate, but with a short leaf rachis, petiolate, leaflets stipelled, lateral leaflets symmetrical. **Inflorescence** an axillary and umbelliform pseudoraceme, pedunculate, the flowering rachis contracted so that the flowering nodes are congested at the inflorescence apex, rarely reduced to an axillary fascicle, flowers pedicellate and provided with a pair

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of bracteoles just below the calyx. **Flower** buds lanceolate in profile, acuminate; flowers 1.5–3.5 cm long; calyx campanulate, coriaceous, 4-lobed, the lobes longer than the tube; corolla typically papilionate, petals mauve, purple or red, clawed, the claws shorter than the blades, standard petal reflexed, glabrous, wing and keel petals straight; androecium pseudomonadelphous or diadelphous, anthers of the ten stamens monomorphic and glabrous; gynoecium sessile or shortly stipitate. **Fruit** a legume, elastically dehiscent, valves thin, coriaceous. **Seeds** globose; testa bony; hilum short and oblong. Fig. 4 (M–R).

**Etymology**— The genus was named by Saint-Hilaire (1833) after José de Sá Betencourt [José de Sá de Bittencourt e Acióli] for his monograph on the cotton culture in Brazil. He was also responsible for discovering kaolin mines in Villa Nova do Príncipe (currently municipality of Caetité, Bahia State) and was involved with the Minas Conspiracy (*Inconfidência Mineira*), a Brazilian independence movement (Carrato 1968).

*Betencourtia* was described by Saint-Hilaire (1833) to include just one species, *B. rhynchosoides*, which is considered a synonym of *B. martii* (Burkart 1971). The genus circumscription is here broadened to include species formerly classified in *Collaea* sect. *Galactioides* Benth. (Bentham 1859), which corresponds to the informal group named as *Galactia* sect. *Collaea* § *Galactiaria* (Taubert 1894). The species of that group were later split into the genera *Galactia* and *Camptosema* by Burkart (1970, 1971). The results of phylogenetic analyses (Fig. 1; Queiroz *et al.* 2015) better support the older concepts presented by Bentham (1859) and Taubert (1894) than that of Burkart (1970, 1971).

The genus *Betencourtia* differs from both *Galactia* and *Camptosema* by the distinct architecture of its inflorescence, with the flowering portion of the peduncle contracted, leaving the flowering nodes congested towards the apex and the pedicellate flowers arranged in a umbelliform fashion. It also differs from *Camptosema* by the petiolate leaves with contracted or absent leaf rachis producing (sub)palmately compound leaves (*vs.* leaves clearly pinnately trifoliolate) and from *Galactia* by the mostly pseudomonadelphous androecium (*vs.* androecium mostly diadelphous).

The genus comprises eight species mostly from tropical (Cerrado and campos rupestres) and subtropical (Pampas) open fields, with one species (*B. scarlatina*) from montane and gallery forests in (south)eastern and central South America.

### New combinations in *Betencourtia*

***Betencourtia australis*** (Malme) L.P. Queiroz, *comb. nov.*

Basionym: *Galactia neesii* var. *australis* Malme, *Ark. Bot.* 13A(13): 35. 1931 [≡ *Galactia australis* (Malme) Ceolin & Miotto, *Pl. Syst. Evol.* 298(3): 650. 2012].

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***Betencourtia crassifolia*** (Benth.) L.P. Queiroz, *comb. nov.*

Basionym: *Collaea crassifolia* Benth., *Comm. Legum. Gen.* 65. 1837 [≡ *Galactia crassifolia* (Benth.) Taub., *Nat. Pflanzenfam.* 3(3): 368. 1894].

***Betencourtia gracillima*** (Benth.) L.P. Queiroz, *comb. nov.*

Basionym: *Galactia gracillima* Benth., *Fl. Bras.* 15(1): 142. 1859.

***Betencourtia martii*** (DC.) L.P. Queiroz, *comb. nov.*

Basionym: *Galactia martii* DC., *Prodr.* 2: 238. 1825 [≡ *Collaea martii* (DC.) Benth., *Comm. Legum. Gen.*: 65. 1837].

= *Betencourtia rhynchosoides* A. St.-Hil., *Voy. Distr. Diam.* 1: 376. 1833.

***Betencourtia martioides*** (Burkart) L.P. Queiroz, *comb. nov.*

Basionym: *Galactia martioides* Burkart, *Darwiniana* 16(3-4): 742. 1971.

***Betencourtia neesii*** (DC.) L.P. Queiroz, *comb. nov.*

Basionym: *Galactia neesii* DC., *Prodr.* 2: 238. 1825 [≡ *Collaea neesii* (DC.) Benth., *Comm. Legum. Gen.*: 65. 1837].

***Betencourtia scarlatina*** (Mart. ex Benth.) L.P. Queiroz, *comb. nov.*

Basionym: *Collaea scarlatina* Mart. ex Benth., *Comm. Legum. Gen.* 65. 1837 [≡ *Galactia scarlatina* (Mart. ex Benth.) Taub., *Nat. Pflanzenfam.* 3(3): 368. 1894 ≡ *Camptosema scarlatinum* (Mart. ex Benth.) Burkart, *Darwiniana* 16(1-2): 199. 1970].

***Betencourtia stereophylla*** (Harms) L.P. Queiroz, *comb. nov.*

Basionym: *Galactia stereophylla* Harms, *Repert. Spec. Nov. Regni Veg.* 19: 17. 1923.

***Collaea*** DC., *Ann. Sci. Nat. (Paris)* 4: 96. 1825. Type: *Collaea speciosa* (Loisel.) DC. [≡ *Cytisus speciosus* Loisel.].

**Description**— Erect and virgate subshrubs or shrubs, few ramified. **Leaves** palmately trifoliolate, sessile or shortly petiolate, leaflets undifferentiated, estipellate, lateral leaflets symmetrical. **Inflorescence** mostly an axillary, sessile or subsessile, globose strobiliform fascicle, with strongly packed wide bracts and bracteoles, sometimes the inflorescence becomes a terminal pseudoraceme due to the falling or underdevelopment of its leaves. **Flowers** typically papilionate, 1–3.7 cm long; calyx broadly campanulate, 4-lobed, the lobes shorter than the tube; petals red, purple or white, clawed, the claws shorter than the blade, standard petal reflexed, pubescent on the outer surface, 2-callose toward the base, wing and keel petals straight; androecium pseudomonadelphous, stamens 10, anthers monomorphic, glabrous; gynoecium sessile. **Fruit** an elastically dehiscent legume, laterally compressed, valves thin and woody. **Seeds** globose, slightly compressed; hilum short and elliptic to oblong. Fig. 4 (H–L).

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**Etymology**— The genus was named after the Italian naturalist Luigi A. Colla (Schrire 2005).

*Collaea* is here accepted in its original definition (Candolle 1825). Bentham (1865) adopted a much wider circumscription, including species that are included here in all of the genera of the Galactia clade except *Bionia*, *Camptosema*, and *Mantiqueira*. Taubert (1894) subsumed *Collaea* into *Galactia*, a position that was followed by most authors until Burkart (1971) reinstated the genus *Collaea* to its original circumscription. As delimited by Burkart (1971), *Collaea* composes a morphologically coherent genus that has been supported as monophyletic in different phylogenetic studies (Queiroz *et al.* 2003, 2015; Sede *et al.* 2009; LPWG 2017). As defined here, *Collaea* can be diagnosed by an erect woody habit, sessile or shortly petiolate palmately trifoliolate leaves, inflorescences in packed (sub)sessile axillary fascicles with broad bracts and bracteoles, and standard 2-callose towards the base. This set of characters promptly differentiates *Collaea* from its sister genus *Betencourtia*. Those two genera have been supported as closely related in several phylogenetic studies (Sede *et al.* 2009; Queiroz *et al.* 2015), and they share leaves with a leaf rachis short or absent. However, *Betencourtia* includes twining vines or prostrate herbs or subshrubs, inflorescence in umbelliform pseudoracemes, and an ecallose standard petal.

*Collaea* includes 6–7 species (Ceolin & Miotto 2009) mostly from southern South America (Uruguay, Paraguay, and northern Argentina) extending northward to the Brazilian states of Minas Gerais and Espírito Santo, and westward to Bolivia. Species of *Collaea* are found mostly in subtropical and tropical open field vegetations, usually in montane environments.

**Galactia** P. Browne, *Civ. Nat. Hist. Jamaica*: 298, pl. 32, f. 2. 1756. Type: *Galactia pendula* Pers.

= *Odonia* Bertol., *Lucubr. Re Herb.* 35–36, pl. 1. 1822. Type: *Odonia tomentosa* Bertol. [= *Galactia striata* (Jacq.) Urb.].

= *Sweetia* DC., *Prodr.* 2: 381. 1825. Lectotype (here designated): *Sweetia longifolia* (Jacq.) DC. [≡ *Galega longifolia* Jacq.; *Galactia longifolia* (Jacq.) Benth.].

= *Heterocarphaea* Scheele, *Linnaea* 21(4): 467–468. 1848. Type: *Heterocarphaea texana* Scheele [= *Galactia canescens* Benth.].

= *Leucodyction* Dalzell, *Hooker's J. Bot. Kew Gard. Misc.* 2: 264. 1850. Type: *Leucodyction malvensis* Dalzell & A.Gibson [= *Galactia striata* (Jacq.) Urb.].

**Description**— Twining vines, erect or prostrate herbs or subshrubs, rarely shrubs. **Leaves** pinnately 3, rarely 5–7-foliolate, palmately trifoliolate or unifoliolate, petiolate, stipellate, lateral leaflets mostly symmetrical. **Inflorescence** mostly an elongate pseudoraceme, sometimes reduced to axillary fascicles, flowers pedicellate and provided with two bracteoles just below the calyx. **Flowers** typically papilionate, 1–2.5 cm long; calyx campanulate, 4-lobed, the lobes equal to or longer than the tube; petals mauve, purple or red, clawed, the claws shorter than the blade, standard petal reflexed, glabrous, ecallose, wing and keel petals straight; androecium diadelphous, rarely

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pseudomonadelphous, stamens 10, anthers monomorphic, glabrous; gynoecium sessile. **Fruit** an elastically dehiscent legume, slightly laterally compressed, valves coriaceous. **Seeds** ellipsoid, slightly compressed; hilum short and elliptic to oblong. Fig. 3 (K–N).

**Etymology**— from the Greek γάλα (*gala*, milk) referring to the milky sap of the type species (Browne 1756).

*Galactia*, in its broadest circumscription, embraces species included in seven other genera as defined here: *Betencourtia*, *Caetangil*, *Cerradicola*, *Collaea*, *Lackeya*, *Nanogalactia*, and *Rhodopis*. Even after having removed the species of those seven genera, *Galactia* still embraces a broad morphological diversity, although constituting a more homogeneous genus.

As circumscribed here, *Galactia* includes mostly species with herbaceous habits, either prostrate, erect or twining, leaves with one, three, or rarely five or seven leaflets, palmately or pinnately compound, inflorescences mostly elongate pseudoracemes, but also reduced axillary fascicles, flowering nodes with two or three flowers, flowers small, rarely more than 1.5 cm long, petals glabrous, androecium mostly diadelphous, with the vexillary stamen free, and ovary sessile.

Some North American and Caribbean species with tiny herbaceous habits and inflorescences reduced to an axillary fascicle present morphological ties with *Nanogalactia*. As those species have not yet been sampled in any phylogenetic study, it is not possible to determine if their similarities are due to convergence or reflect a common ancestry; they are therefore provisionally maintained in *Galactia*.

The phylogenetic and taxonomic position of *G. glaucescens* should also be better investigated. It is a small shrub from South American savannas with short petiolate and coriaceous leaves and a slightly pubescent standard petal. Because of that set of characters, it was included in *Galactia* sect. *Collearia* (sensu Burkart 1971), a group treated here as the genus *Cerradicola*. Previous phylogenetic studies indicated instability in the phylogenetic position of *G. glaucescens* depending on the molecular marker employed (Queiroz *et al.* 2015). We are therefore taking a more conservative approach here and maintaining this species in *Galactia*, pending new phylogenetic analyses.

As circumscribed here, *Galactia* includes approximately 84 species distributed in North America (31 species), the West Indies (45), Central America (9), South America (16), Australia (3), Asia (2), and Africa (1) (adapted from Nesom 2015).

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### 6 | SUPPLEMENTARY MATERIAL

Supplementary material can be found at the URL:

<https://dx.doi.org/10.6084/m9.figshare.13017188>, including: a) Molecular and morphological data matrix; b) Supplementary Figure 1. Maximum parsimony 50% majority rule tree derived from the 2,000 bootstrap resampling analysis of 82 morphological characters. A list of the morphological characters is presented at Table 1. Numbers at nodes are bootstrap support values. c) Supplementary Figure 2—Optimization of 82 morphological characters on the 50% majority rule consensus tree obtained in the Bayesian analysis of the total evidence dataset including 5,603 characters: 82 morphological and 5,521 from the molecular regions nrETS, nrITS, plastid *trnK/matK*, and plastid *trnT-Y*. The list of optimized morphological characters is provided in Table 1. Ambiguous optimization among acctran or deltran algorithms are shown in gray. Genera are showed in color. d) Supplementary Table 1. Voucher information and GenBank accession codes for the DNA sequences used in this study. Morphological characters were sampled from the same specimens. Taxa are sorted according to the taxonomic system presented here for the Galactia clade.

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