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A new infrageneric classification of the pantropical genus *Chamaecrista* (Fabaceae: Caesalpinioideae) based on a comprehensive molecular phylogenetic analysis and morphology

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Chamaecrista with > 330 species, six sections, three subsections and 39 series has had a long and complex taxonomic history. The genus is monophyletic, but most of its traditional infrageneric categories are not. To test the monophyly of sections, subsections and series of *Chamaecrista*, we used two molecular phylogenetic approaches. The first (*Broad*) based on two DNA regions (ITS and *trnL-F*) includes a comprehensive sampling of *Chamaecrista* spp. and infrageneric taxa. The second (*Multilocus*) is based on four molecular regions (ITS, ETS, *trnL-F* and *trnE-T*) for a smaller but representative sampling. We performed ancestral character reconstructions to identify morphological characters that could serve as synapomorphies for major clades. Both molecular approaches support *Chamaecrista* and sections *Apoucouita*, *Grimaldia* and *Xerocalyx* as monophyletic, but sections *Chamaecrista*, *Caliciopsis* and *Absus* and most of the series are not monophyletic. The four main clades recovered are all characterized by a combination of morphological characters: a clade of tree species with cauliflorous inflorescences (including species of section *Apoucouita*); a mostly Brazilian campo rupestre clade (including all species of subsections *Adenophyllum*, *Baseophyllum* and *Otophyllum*); a clade of mostly herbaceous/shrubby species with solitary flowers or fascicles (including sections *Chamaecrista*, *Caliciopsis* and *Xerocalyx* and extra-American species) and a clade (with three main subclades) of species with viscous indumentum (including section *Grimaldia* and section *Absus* subsection *Absus*). We propose a new infrageneric classification for *Chamaecrista* supported by molecular phylogenetic analyses and morphology, recognizing the four main clades as sections *Apoucouita*, *Baseophyllum*, *Chamaecrista* and *Absus*, the last with three subsections (*Absus*, *Viscosa* and *Zygophyllum*), but we do not recognize any previously circumscribed series. Our taxonomic treatment includes descriptions of and a key to the newly defined infrageneric taxa and an updated species list for the genus under the new classification.

ADDITIONAL KEYWORDS: *Cassia* – large-scale phylogeny – Leguminosae – molecular systematics – morphology.

INTRODUCTION

Chamaecrista (L.) Moench with > 330 species is one of the largest genera of caesalpinioid Fabaceae (Lewis *et al.*, 2005; LPWG, 2017). The genus has a pantropical distribution, 85% of the species occurs in the Americas and 15% occurs in the Africa, Madagascar, Middle East, Southern Asia and Oceania, but it is far more diverse in the Brazil where 272 species occur (Flora do Brazil, 2020). *Chamaecrista* includes small annual herbs, perennial shrubs and subshrubs with several growth aspects and habits; rarely, they are trees. Species

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have paripinnate leaves, bi-bracteolate pedicels, asymmetrical enantiostylic flowers pollinated by bees, actinomorphic androecium, anthers pubescent along the sutures, elastically dehiscent fruits and a diversity of trichome types and extrafloral nectaries (Irwin & Barneby, 1982). The genus is ecologically important because it is one of the genera of Caesalpinioideae able to fix atmospheric nitrogen through bacteria-inhabited root nodules (Irwin & Barneby, 1982; Lewis *et al.*, 2005).

Chamaecrista with *Cassia* L. and *Senna* Mill. make up subtribe Cassiinae of tribe Cassieae (Irwin & Barneby, 1982). The genus has a long taxonomic history with inclusion in, or separation from, *Cassia* over > 200 years. *Chamaecrista* was established by Moench (1794) based on a few *Cassia* spp., but much later considered by Bentham (1870) and Irwin & Barneby (1978) as a subgenus of *Cassia* (= *Cassia* subgenus *Lasiorhegma* Benth.). One hundred and twelve years after Bentham (1870), *Chamaecrista* was re-established as an independent genus and revised for the Americas by Irwin & Barneby (1982), who assigned to it 275 species, distributed in six sections, four subsections and 39 series, on the basis of a set of morphological characters including leaflet number per leaf, consistency and orientation of the leaflets, leaflet venation pattern, presence/absence and location of extrafloral nectaries and glandular trichomes, types and location of the inflorescences and floral characters. The classification of Irwin & Barneby (1982) is the current standard work for the genus, especially in the Americas.

With the advancement of phylogenetic studies in the late 20th century, classifications started to be based more on the recognition of monophyletic groups, and this required changes in circumscription at various taxonomic ranks (LPWG, 2017). A number of pioneering studies with *Chamaecrista* and its infrageneric taxa were developed to ascertain their monophyly and the relationship of *Chamaecrista* with its assumed closely related *Cassia* and *Senna*. Conceição *et al.* (2009) conducted the first phylogenetic study focused on *Chamaecrista*. It used the molecular markers *trnL-F* (plastid DNA) and ITS (nuclear ribosomal DNA) and sampled 47 species, representing six sections, two subsections and 11 series of *Chamaecrista*. Their study (Conceição *et al.*, 2009) demonstrated the monophyly of *Chamaecrista* and sections *Apoucouita* (H.S.Irwin & Barneby) H.S.Irwin & Barneby and *Xerocalyx* (Benth.) H.S.Irwin & Barneby, but highlighted the para- or polyphyletic status of other sections and most of the series in the genus.

Torres *et al.* (2011) performed a phylogenetic analysis of *Chamaecrista* section *Xerocalyx* based on ITS and plastid *trnE-T* markers. Their study supported the monophyly of section *Xerocalyx* and suggested that it would better be considered a subcategory of section *Chamaecrista*. More recently, Rando *et al.* (2016), Souza *et al.* (2019a) and Mendes, Souza & Silva (2020) recovered the phylogenetic history of series *Coriaceae* (Benth.) H.S.Irwin & Barneby, *Rigidulae* (Benth.) H.S.Irwin & Barneby and *Paniculatae* (Benth.) H.S.Irwin & Barneby, respectively, and found that the series are all polyphyletic and proposed their recircumscription based on monophyletic groups. These three studies demonstrated new species-level relationships and indicated that the classification of *Chamaecrista* proposed by Irwin & Barneby (1982) at section and series level did not reflect our current phylogenetic knowledge of the genus.

No new infrageneric classification at section level has been proposed for *Chamaecrista* since Irwin & Barneby (1982). This is largely because the previous phylogenetic studies: (1) sampled < 25% of the species of the genus; (2) subsections *Adenophyllum* (H.S.Irwin & Barneby) H.S.Irwin & Barneby and *Otophyllum* (H.S.Irwin & Barneby) H.S.Irwin & Barneby and 16 series [including *Bracteolatae* (Collad.) H.S.Irwin & Barneby, *Ericifoliae* (H.S.Irwin & Barneby) H.S.Irwin & Barneby and *Strictifoliae* (H.S.Irwin & Barneby) H.S.Irwin & Barneby] were not sampled; (3) the most species-rich sections, sections *Chamaecrista* and *Absus* (Collad.) H.S.Irwin & Barneby were represented by < 33% of their species and (4) other species-rich series were poorly sampled [e.g. *Microphyllae* (Benth.) H.S.Irwin & Barneby and *Ochnaceae* (H.S.Irwin & Barneby) H.S.Irwin & Barneby]. Therefore, more densely sampled phylogenetic studies are needed to fill taxonomic gaps not previously sampled with the aim to clarify intrageneric relationships and more accurately circumscribe infrageneric taxa.

In view of these factors, this study aims to reconstruct the phylogenetic history of *Chamaecrista* with a comprehensive species sampling to: (1) test the monophyly of its infrageneric taxa (sections, subsections and series) and understand the relationships between them; (2) perform ancestral character reconstructions to identify morphological characters that could serve as synapomorphies for the main clades and (3) propose a new infrageneric classification for *Chamaecrista* supported by phylogenetic and morphological evidence.

MATERIAL AND METHODS

Taxon sampling

Two sampling strategies were developed to achieve the proposed aims. In the *Broad* approach, the dataset comprises the largest sampling ever carried out for *Chamaecrista* and aims to retest the monophyly of

the genus and its sections based on broad taxonomic sampling of its species and infrageneric taxa above species level. Our sampling covers > 67% of all *Chamaecrista* spp., all sections and subsections and 34 out of 39 of the traditionally recognized series (*sensu* Irwin & Barneby, 1982), covering the pantropical distribution of the genus, sampling 95% American species and 5% extra-American species. In this broad approach, we used the two most commonly used markers in previously published phylogenetic analyses of *Chamaecrista*, namely ITS (nrDNA) and *trnL-F* (plastid DNA) (Conceição *et al.*, 2009; Rando *et al.*, 2016; Souza *et al.*, 2019a; Mendes *et al.*, 2020). We sampled 232 species (286 accessions), 217 species belong to *Chamaecrista* (270 accessions) and the other 15 species (16 accessions) belong to selected outgroup taxa including *Cassia* (three species), *Senna* (seven species), *Melanoxylon* Schott in K.Sprengel (one species), *Recordoxylon* Ducke (one species), *Vouacapoua* Aubl. (two species) and *Pterogyne* Tul. (one species). *Pterogyne* was used to root the trees. It was not possible to sample all markers for all species, the missing data between the matrices in this approach was *c*. 4%.

In the *Multilocus* approach, the dataset was designed to recover better internal taxon resolution in *Chamaecrista* and to seek support for major clades in the genus, especially for the species-rich sections *Chamaecrista* and *Absus*. The overall aim was to be able to propose a new infrageneric classification for the genus based on well-supported clades. We used four molecular markers (ITS, ETS, *trnL-F* and *trnE-T*) and a smaller sample of 150 species (193 accessions), of which 144 species (187 accessions) are of *Chamaecrista* and representative of all taxonomic infrageneric taxa (sections, subsections and series). We used six species as the outgroup. The missing data between the markers matrices in this approach was *c*. 10%. The complete list of accessions, sequences generated in this study and those obtained from GenBank from previous studies of the genus (e.g. Conceição *et al.*, 2009; Torres *et al.*, 2011; Rando *et al.*, 2016; Souza *et al.*, 2019a; Mendes *et al.*, 2020), and vouchers are presented in Table 1.

DNA extraction, amplification and sequencing

Total genomic DNA was extracted from fresh fragments of leaves stored in silica or from herbarium material, using the Doyle & Doyle (1987) extraction protocol with 2% CTAB (cetyltrimethylammonium bromide). ITS (including the ITS1 and ITS2 spacer regions and the 5.8S ribosomal subunit) was amplified and sequenced using primers ITS1 and ITS4 (White *et al.*, 1990) or for some samples the primer pair 17SE and 26SE (Sun *et al.*, 1994). The primers 18S-IGS and 26-IGS (Baldwin & Markos 1998) were used to amplify and sequence the marker ETS. The *trnL-F* locus was amplified and sequenced in two steps and assembled later using the pairs of primers (c and d, e and f; Taberlet *et al.*, 1991). For *trnE-T*, the primers *trnE-T-Forward* and *trnE-T-Reverse* (Kato *et al.*, 2000) were used for amplification and sequencing.

All PCR amplifications were performed in a reaction with a final volume of 25 µL, containing 2 µL of 1× buffer, 1.5 µL of $MgCl_2$ (1.5 mM), 1 µL of dNTPs (1 mM), 2 µL of each primer (5 µM), 1 µL of BSA, 0.2 µL of Taq DNA polymerase and H_2O ultrapure (q.s.p. 25 µL). For the amplification of ITS and ETS, we added 1 µL of DMSO (dimethyl sulphoxide) and 1 µL of betaine. The sequences of the primers used and the thermocycling cycles for each marker are listed in Tables 2 and 3, respectively. The products of all amplifications were purified and sequenced through a commercial external service (Macrogen, South Korea).

Alignment and phylogenetic analysis

The sequences were visualized and base calling accuracy confirmed using the software Chromas Lite v.2.1.1 and edited in the BioEdit v.7.2.5 (Hall, 1999). The individual matrices were edited in the software MEGA 6 (Tamura *et al.*, 2013) and aligned using the software MAFFT 7 available online (Katoh, Rozewicki & Yamada, 2017) and corrected manually. The indels of the molecular markers were encoded by the simple coding method (Simmons & Ochoterena, 2000) using the software FastGap v.1.2 (Borchsenius, 2009) and analysed individually to verify their level of information, then incorporated into the matrices as informative characters.

Potential incongruences between nuclear and plastid datasets were evaluated using the incongruence length difference (ILD) test (Farris *et al.*, 1994, 1995) implemented in PAUP* v.4.0 (Swofford, 2003) as the partition-homogeneity test, with 1,000 replicates, a heuristic search, with simple addition of taxa, tree bisection-reconnection and the 'multrees' option in effect and saving up to ten trees per replicate. The indels were not considered in this analysis.

For the two sampling approaches, analyses of maximum likelihood (ML) and Bayesian inference (BI) were performed for the individual and combined datasets (ITS+ETS, ITS+ *trnL-F*+, *trnL-F*+*trnE-T* and four markers combined) considering and not considering the indels to investigate possible topology conflicts. The ML analysis was performed in the RAxML-HPC2 v.8.1.11 (Stamatakis, 2006) under the substitution model GTR+I+G and bootstrap (BT) support was estimated using 1,000 pseudo-replicates. The BI analysis was performed in MrBayes v.3.2 (Ronquist *et al.*, 2012). The models of evolution were selected for each marker in JModelTest v.2.1.5

Table 1. List of taxa and GenBank accessions used in the phylogenetic analysis. Vouchers (first collector, collection number and acronym of the herbarium where the specimen is housed) followed by locality (country and first political division, when given on the field label) and GenBank accession numbers. Asterisks indicate sequences generated in this study. Underlined taxa were used in the reconstruction of ancestral character analysis. Infrageneric taxa of *Chamaecrista* follow Irwin & Barneby (1982) with updates by Rando *et al.* (2016), Souza *et al.* (2019a) and Mendes *et al.* (2020). Sections are numbered 1 to 6. Numbers in square brackets indicate the number of species sampled in this study/total of species in the taxon

Taxon	Voucher	Locality	ITS	ETS	*trnL-F*	*trnE-T*
Outgroup						
Cassia fistula	*W.M. Bezerra 5* (EAC)	Brazil, Ceará	GU175310	—	EU361781	GU175321
Cassia grandis	*L.P. Queiroz 2878* (HUEFS)	Brazil, Bahia	FJ009820	—	FJ009875	—
Cassia javanica	*L.P. Queiroz 11039* (HUEFS)	Brazil, Bahia	FJ009821	—	FJ009876	—
Melanoxylon brauna	*M. Nuscheler 10* (CEPEC)	Brazil, Bahia	—	—	AY899700	—
Pterogyne nitens	*P.S. Herendeen 13/XII/97/1* (US)	Tanzania	KX372782	—	AF365074	—
Recordoxylon speciosum	*H.C. Lima 3333* (INPA)	Brazil, Amazonas	—	—	AY899699	—
Senna alata	*A. Bruneau 1076* (MT)	Cameroon	KX372780	MW681928*	AF365091	GU175334
Senna cana	*A.O. Souza 423* (UFG)	Brazil, Goiás	MH835400	—	MH835400	—
Senna corifolia var. *caesia*	*A.O. Souza 289* (UFG)	Brazil, Goiás	MH835401	—	MH835401	—
Senna corifolia var. *corifolia*	*A.O. Souza 1037* (UFG)	Brazil, Goiás	MH835402	—	MH835402	—
Senna gardneri	*L.P. Queiroz 7860* (HUEFS)	Brazil, Bahia	FJ009822	—	FJ009877	—
Senna occidentalis	*A. Bruneau 1257* (MT)	—	MH050236	MW681929*	AF365030	GU175337
Senna pendula	*A.O. Souza 190* (UFG)	Brazil, Goiás	MH835403	MW681930*	MH835403	—
Senna rugosa	*A.O. Souza 201* (UFG)	Brazil, Goiás	MH835404	—	MH835404	—
Vouacapoua americana	*D. Cardoso 3444*	Brazil, Amazonas	KR134125	KP999911	AY899701	—
Vouacapoua macropetala	*Breteler 13793* (WAG)	Guyana	—	—	AF365110	—
Chamaecrista (L.) Moench [217/363]						
1. *Chamaecrista* section *Chamaecrista* [39/58]						
Chamaecrista* section *Chamaecrista* series *Chamaecrista [6/18]						
Chamaecrista fasciculata	USDA DLEG920271	United States	EF590760	—	—	—
Chamaecrista glandulosa var. brasiliensis	*A.O. Souza 859* (UFG)	Brazil, Goiás	MW683419*	MW681882*	MW681984*	MW682103*
Chamaecrista lineata	*J.G. Rando 958* (SPF)	Bahamas	—	KP967085	KP966912	KP966967
Chamaecrista nictitans subsp. *brachypoda*	*L.P. Queiroz 10335* (HUEFS)	Brazil, Goiás	FJ009855	KP999907	FJ009909	—
Chamaecrista nictitans subsp. *disadena*	*A.S. Conceição 790* (HUEFS)	Brazil, Minas Gerais	FJ009852	—	FJ009906	KU720163
Chamaecrista nictitans subsp. *nictitans* var. *jaliscensis*	*Klitgaard 654* (K)	Costa Rica	KU720159	—	AF365093	KU720161

Table 1. Continued

Taxon	Voucher	Locality	ITS	ETS	*trnL-F*	*trnE-T*
Chamaecrista nictitans subsp. patellaria var. ramosa	*L.P. Queiroz 10406* (HUEFS)	Brazil, Mato Grosso	FJ009853	MW681897*	FJ009907	MW682121*
Chamaecrista pascuorum	*L.P. Queiroz 9169* (HUEFS)	Brazil, Bahia	FJ009851	KP999909	FJ009905	KP966979
Chamaecrista repens	*A.M. Giulietti 2325* (HUEFS)	Brazil, Minas Gerais	KP967098	KP967036	KP966925	KP966982
Chamaecrista* section *Chamaecrista* series *Bauhinianae [2/2]						
Chamaecrista basifolia	*A.O. Souza 1018* (UFG)	Brazil, Goiás	MW683379*	MW681840*	MW681942*	MW682057*
Chamaecrista rotundifolia var. grandiflora	*C.B.N. Costa 128* (HUEFS)	Brazil, Bahia	FJ009857	MW681910*	FJ009911	GU175331
Chamaecrista* section *Chamaecrista* series *Coriaceae [18/19]						
Chamaecrista anceps	*M.M.T. Cota 410* (DIAM)	Brazil, Minas Gerais	—	—	KP966898	KP966953
Chamaecrista aristata	*J.G. Rando 976* (SPF)	Brazil, Minas Gerais	KP967072	KP967070	KP966899	KP966954
Chamaecrista burchellii	*J.G. Rando 1092* (SPF)	Brazil, Goiás	KP967073	KP967068	KP966900	KP966956
Chamaecrista cardiostegia	*J.G. Rando 1125* (SPF)	Brazil, Minas Gerais	KP967074	KP967067	KP966901	KP966957
Chamaecrista choriophylla	*J.G. Rando 1034* (HUEFS)	Brazil, Minas Gerais	KP967076	KP967063	KP966904	KP966959
Chamaecrista cinerascens	*J.G. Rando 661* (SPF)	Brazil, Minas Gerais	KP967077	KP967062	KP966905	KP966960
Chamaecrista distichoclada	*J.G. Rando 1230* (SPF)	Brazil, Minas Gerais	KP967078	KP967060	KP966906	KP966961
Chamaecrista lagotois	*J.G. Rando 1029* (HUEFS)	Brazil, Minas Gerais	KP967079	KP967058	KP966907	KP966963
Chamaecrista latifolia	*J.G. Rando 1024* (HUEFS)	Brazil, Minas Gerais	KP967081	KP967056	KP966909	KP966964
Chamaecrista mucronata	*J.G. Rando 879* (SPF)	Brazil, Minas Gerais	KP967086	KP967050	KP966913	KP966968
Chamaecrista olesiphylla	*J.G. Rando 632* (SPF)	Brazil, Minas Gerais	KP967088	KP967046	KP966915	KP966971
Chamaecrista papillata	*J.G. Rando 1011* (HUEFS)	Brazil, Minas Gerais	KP967093	KP967043	KP966920	KP966976
Chamaecrista potentilla	*J.G. Rando 1139* (SPF)	Brazil, Minas Gerais	KP967096	KP967038	KP966923	KP966980
Chamaecrista rossicorum	*J.G. Rando 1045* (HUEFS)	Brazil, Minas Gerais	KP967101	KP967029	KP966931	KP966988
Chamaecrista rotundata var. *grandistipula*	*J.G. Rando 1240* (SPF)	Brazil, Minas Gerais	KP967106	KP967025	KP966937	KP966994
Chamaecrista rotundata var. *interstes*	*J.G. Rando 1145* (SPF)	Brazil, Minas Gerais	KP967107	KP967024	KP966938	KP966995
Chamaecrista rotundata var. *rotundata*	*J.G. Rando 1144* (SPF)	Brazil, Minas Gerais	KP967103	KP967022	KP966933	KP966990
Chamaecrista simplifacta	*J.G. Rando 802* (SPF)	Brazil, Minas Gerais	KP967109	KP967019	KP966942	KP966999
Chamaecrista tragacanthoides var. *rasa*	*J.G. Rando 969* (SPF)	Brazil, Minas Gerais	KP967113	KP967015	KP966946	KP967003
Chamaecrista tragacanthoides var. *tragacanthoides*	*J.R. Pirani 6334* (SPF)	Brazil, Minas Gerais	KP967114	KP967013	KP966948	KP967004
Chamaecrista ulmea	*M.F. Santos 650* (SPF)	Brazil, Minas Gerais	KP967115	KP967012	KP966949	KP967005

Table 1. Continued

Taxon	Voucher	Locality	ITS	ETS	*trnL-F*	*trnE-T*
Excluded from series *Coriaceae* [3/3]						
Chamaecrista caribaea	*J.G. Rando 963* (SPF)	Bahamas, Ragged Island	KP967075	KP967066	KP966902	KP966958
Chamaecrista roraimae 1	*J.G. Rando 1154* (SPF)	Brazil, Roraima	KP967099	KP967033	KP966927	KP966983
Chamaecrista roraimae 2	*R.M. Harley 55036* (HUEFS)	Brazil, Bahia	—	KP967034	KP966928	KP966984
Chamaecrista venulosa	*J.G. Rando 1015* (HUEFS)	Brazil, Minas Gerais	KP967116	KP967011	KP966950	KP967006
Chamaecrista* section *Chamaecrista* series *Flexuosae [5/6]						
Chamaecrista flexuosa var. flexuosa	*A.M. Giulietti 2344* (HUEFS)	Brazil, Minas Gerais	FJ009858	KP967059	FJ009912	GU175327
Chamaecrista gonoclada	*G.G. Hatschbach 58737* (NY)	Brazil, Mato Grosso do Sul	MW683420*	MW681883*	MW681985*	MW682104*
Chamaecrista oligandra	*M.J. Silva 8131* (UFG)	Brazil, Goiás	MK228886	MW681899*	MK224843	MW682123*
Chamaecrista parvistipula	*A.O. Souza 183* (UFG)	Brazil, Goiás	MK228887	MW681904*	MK224844	MW682128*
Chamaecrista swainsonii	*L.P. Queiroz 12314* (HUEFS)	Brazil, Bahia	KP967111	KP967016	KP966944	KP967001
Chamaecrista* section *Chamaecrista* series *Prostratae [5/9]						
Chamaecrista kunthiana 1	*A.O. Souza 2268* (UFG)	Brazil, Goiás	—	MW681888*	MW681995*	MW682110*
Chamaecrista kunthiana 2	*A.O. Souza 238* (UFG)	Brazil, Goiás	—	MW681889*	MW681996*	MW682111*
Chamaecrista pilosa	*L.P. Queiroz 10221* (HUEFS)	Brazil, Bahia	FJ009856	KP999910	FJ009910	—
Chamaecrista supplex 1	*L.P. Queiroz 10217* (HUEFS)	Brazil, Bahia	FJ009869	—	FJ009923	—
Chamaecrista supplex 2	*A.O. Souza 2099* (UFG)	Brazil, Goiás	MW683468*	MW681916*	MW682035*	MW682143*
Chamaecrista tenuisepala	*A.O. Souza 2221* (UB)	Brazil, Bahia	MW683469*	MW681917*	MW682036*	MW682144*
Chamaecrista trichopoda	*M. Aparecida 636* (EAC)	Brazil, Bahia	GU175318	MW681919*	MW682038*	GU175333
2. *Chamaecrista* section *Absus* [158/206]						
Chamaecrista* section *Absus* subsection *Absus [148/196]						
Chamaecrista* section *Absus* subsection *Absus* series *Absoideae [26/26]						
Chamaecrista acosmifolia var. *acosmifolia*	*A.O. Souza 2089* (UB)	Brazil, Bahia	MK056255	MW681829*	MK390616	MW682046*
Chamaecrista acosmifolia var. *euryloba*	*H.S. Irwin 28000* (K)	Brazil, Minas Gerais	MW683370*	MW681830*	MW681932*	MW682047*

Table 1. Continued

Taxon	Voucher	Locality	ITS	ETS	*trnL-F*	*trnE-T*
Chamaecrista acosmifolia var. *oropedii*	*J.E.Q. Faria 3953* (UB)	Brazil, Goiás	MW683371*	MW681831*	MW681931*	MW682048*
Chamaecrista amiciella	*A.O. Souza 2226* (UB)	Brazil, Bahia	MW683373*	MW681834*	MW681935*	MW682050*
Chamaecrista andersonii	*A.O. Souza 2240* (UB)	Brazil, Goiás	MW683374*	—	MW681936*	MW682051*
Chamaecrista arboae	*A.O. Souza 2197* (UB)	Brazil, Bahia	MW683376*	MW681836*	MW681938*	MW682053*
Chamaecrista barbata	*A.O. Souza 2072* (UB)	Brazil, Bahia	MK056256	MW681839*	MK390617	MW682056*
Chamaecrista belemii var. belemii	*A.O. Souza 2231* (UB)	Brazil, Bahia	MW683380*	—	MW681943*	MW682058*
Chamaecrista belemii var. *paludicola*	*L.P. Queiroz 3841* (NY)	Brazil, Bahia	MW683381*	—	MW681944*	MW682059*
Chamaecrista brevicalyx var. brevicalyx	*A.O. Souza 1245* (UFG)	Brazil, Bahia	MH835360	MW681847*	MH828383	MW682066*
Chamaecrista brevicalyx var. *elliptica*	*A.O. Souza 2078* (UB)	Brazil, Bahia	MW683386*	MW681848*	MW681949*	MW682067*
Chamaecrista campestris	*A.O. Souza 1596* (UFG)	Brazil, Mato Grosso	MH835361	—	MH828384	MW682071*
Chamaecrista carobinha	*A.O. Souza 2190* (UB)	Brazil, Bahia	MK056257	MW681852*	MK390618	MW682072*
Chamaecrista chapadae	*A.O. Souza 1541* (UB)	Brazil, Bahia	MW683394*	MW681854*	MW681958*	MW682074*
Chamaecrista egleri	*W.R. Anderson 11071* (NY)	Brazil, Pará	MW683409*	—	MW681974*	MW682094*
Chamaecrista fagonioides var. *fagonioides*	*S. Zamudio 11764* (XAL)	Mexico, Michoacán	MW683414*	MW681876*	MW681979*	MW682097*
Chamaecrista fagonioides var. macrocalyx	*A.O. Souza 910* (UFG)	Brazil, Goiás	MH835373	MW681877*	MH828396	MW682098*
Chamaecrista hispidula	*A.O. Souza 1570* (UFG)	Brazil, Sergipe	MH835379	MW681884*	MH828402	MW682105*
Chamaecrista jacobinea	*M.J.G. Andrade 610* (HUEFS)	Brazil, Bahia	FJ009827	—	FJ009882	—
Chamaecrista juruenensis	*A.O. Souza 2045* (UB)	Brazil, Bahia	MW683428*	MW681887*	MW681993*	MW682108*
Chamaecrista longicuspis	*A.O. Souza 1832* (UB)	Brazil, Goiás	MW683435*	—	MW682002*	MW682113*
Chamaecrista longistyla	*D. Sasaki 1605* (UFG)	Brazil, Mato Grosso	MK056259	MW681891*	MK390620	MW682114*
Chamaecrista multiseta	*A.O. Souza 1300* (UFG)	Brazil, Goiás	MH835384	—	MH828407	MW682118*
Chamaecrista paraunana	*A.O. Souza 2115* (UB)	Brazil, Bahia	MK056261	MW681903*	MK390622	MW682127*
Chamaecrista punctulata	*S. Zamudio 11764* (XAL)	Mexico, Michoacán	MW683455*	MW681908*	MW682022*	MW682132*
Chamaecrista aff. *roncadorensis*	*L.P. Queiroz 10279* (HUEFS)	Brazil, Goiás	FJ009831	—	—	—
Chamaecrista roncadorensis	*A.O. Souza 2223* (UB)	Brazil, Goiás	MW683456*	MW681909*	MW682023*	MW682133*
Chamaecrista rugosula	*A.O. Souza 1225* (UB)	Brazil, Bahia	MW683457*	—	MW682024*	MW682134*
Chamaecrista salvatoris	*W. Santana 12181* (BHCB)	Brazil, Bahia	MW683458*	—	MW682025*	MW682136*
Chamaecrista souzana	*A.O Souza 2105* (UB)	Brazil, Minas Gerais	MW683463*	MW681913*	MW682030*	MW682140*
Chamaecrista viscosa var. *major*	*A.O. Souza 2092* (UB)	Brazil, Bahia	MW683474*	MW681922*	MW682042*	MW682148*
Chamaecrista viscosa var. *paraguayensis*	*A.O. Souza 1641* (UFG)	Brazil, Mato Grosso	MH835399	MW681923*	MH828422	MW682149*
Chamaecrista viscosa var. *viscosa*	*E. Martinez 5753* (XAL)	Mexico, Guerrero	MW683475*	MW681924*	MW682043*	MW682150*
Chamaecrista zygophylloides var. *colligans*	*A.O. Souza & al. 2050*	Brazil, Bahia	MK056262	MW681925*	MK390623	MW682151*

Table 1. Continued

Taxon	Voucher	Locality	ITS	ETS	*trnL-F*	*trnE-T*
Chamaecrista zygophylloides var. *deamii*	*A.O. Souza 2237* (UB)	Brazil, Bahia	MW683476*	MW681926*	MW682044*	MW682152*
Chamaecrista zygophylloides var. *zygophylloides*	*A.O. Souza 2236* (UB)	Brazil, Bahia	MW683477*	MW681927*	MW682045*	MW682153*
Chamaecrista* section *Absus* subsection *Absus* series *Adenophyllae [3/5]						
Chamaecrista adenophylla	*A.O. Souza 2122* (UB)	Brazil, Minas Gerais	MW683372*	MW681832*	MW681933*	—
Chamaecrista axilliflora	*N. Roque 4359* (US)	Brazil, Bahia	MW683378*	—	MW681941*	—
Chamaecrista chrysosepala	*A.O. Souza 582* (UFG)	Brazil, Goiás	MW683395*	MW681855*	MW681959*	MW682075*
Chamaecrista* section *Absus* subsection *Absus* series *Bracteolatae [2/3]						
Chamaecrista bracteolata	*A.O. Souza 2124* (UB)	Brazil, Minas Gerais	MW683385*	MW681846*	MW681948*	MW682065*
Chamaecrista phyllostachya	*A.O. Souza 2110* (UB)	Brazil, Minas Gerais	MW683450*	—	MW682017*	—
Chamaecrista* section *Absus* subsection *Absus* series *Catharticae [1/3]						
Chamaecrista cathartica	*A.S. Conceição 789* (HUEFS)	Brazil, Minas Gerais	FJ009841	—	FJ009895	—
Chamaecrista* section *Absus* subsection *Absus* series *Confertae [4/4]						
Chamaecrista anamariae	*A.S. Conceição 787* (HUEFS)	Brazil, Bahia	FJ009826	—	FJ009881	—
Chamaecrista caespitosa	*A.O. Souza 2126* (UB)	Brazil, Minas Gerais	MW683388*	MW681850*	MW681951*	MW682069*
Chamaecrista conferta var. conferta	*A.O. Souza 2121* (UB)	Brazil, Minas Gerais	MW683396*	MW681860*	MW681960*	MW682080*
Chamaecrista conferta var. *gurgueiana*	*A.O. Souza 2173* (UB)	Brazil, Piauí	MW683397*	MW681861*	MW681961*	MW682081*
Chamaecrista conferta var. *machrisiana*	*A.O. Souza 1815* (UFG)	Brazil, Goiás	MW683398*	MW681862*	MW681962*	MW682082*
Chamaecrista conferta var. *simulans*	A.O. Souza 1062 (UFG)	Brazil, Goiás	MW683399*	MW681863*	MW681963*	MW682083*
Chamaecrista conferta var. *virgata*	A.O. Souza 168 (UFG)	Brazil, Goiás	MW683400*	MW681864*	MW681964*	MW682084*
Chamaecrista crommyotricha	A.O. Souza 1183 (UFG)	Brazil, Distrito Federal	MW683402*	MW681867*	MW681966*	MW682087*
Chamaecrista* section *Absus* subsection *Absus* series *Ericifoliae [1/1]						
Chamaecrista ericifolia	*M.F. Simon 1814* (CEN)	Brazil, Minas Gerais	MW683412*	—	MW681977*	—

Table 1. Continued

Taxon	Voucher	Locality	ITS	ETS	*trnL-F*	*trnE-T*
Chamaecrista* section *Absus* subsection *Absus* series *Geminatae [2/2]						
Chamaecrista didyma	*J. H. Kirkbride Jr. 2906* (NY)	Brazil, Pará	MW683405*	MW681871*	MW681970*	MW682091*
Chamaecrista geminata	*G.P. Silva 1648* (CEN)	Brazil, Goiás	MW683418*	MW681881*	MW681983*	MW682102*
Chamaecrista* section *Absus* subsection *Absus* series *Glutinosae [6/14]						
Chamaecrista dentata	*R.G. Chacon 569* (UEC)	Brazil, Minas Gerais	MW683403*	—	MW681968*	—
Chamaecrista echinocarpa	*E.T. Neto 4079* (BHCB)	Brazil, Minas Gerais	MW683408*	—	MW681973*	—
Chamaecrista gumminans	*G.P. Silva 2879* (CEN)	Brazil, Minas Gerais	MW683421*	—	MW681986*	—
Chamaecrista myrophenges	*M.B. Vasconcellos 21730* (UEC)	Brazil, Minas Gerais	MW683438*	—	MW682005*	—
Chamaecrista stillifera	*A.O. Souza 2103* (UB)	Brazil, Minas Gerais	MW683465*	MW681914*	MW682032*	MW682141*
Chamaecrista verruculosa	*A.O. Souza 2165* (UB)	Brazil, Piauí	MW683473*	MW681921*	MW682041*	MW682147*
Chamaecrista* section *Absus* subsection *Absus* series *Gracilimae [1/1]						
Chamaecrista benthamii	*A.O. Souza 1056* (UFG)	Brazil, Goiás	MW683382*	—	MW681945*	—
Chamaecrista* section *Absus* subsection *Absus* series *Hedysaroides [2/2]						
Chamaecrista fulgida	*A.O. Souza 1283* (UFG)	Brazil, Goiás	MW683417*	—	MW681982*	—
Chamaecrista hedysaroides	*A.O. Souza 2127* (UB)	Brazil, Minas Gerais	MW683423*	—	MW681988*	—
Chamaecrista* section *Absus* subsection *Absus* series *Incurvatae [3/5]						
Chamaecrista incurvata	*E.P. Heringer 7536* (NY)	Brazil, Minas Gerais	MW683426*	—	MW681991*	—
Chamaecrista lavradioides	*A.O. Souza 590* (UFG)	Brazil, Goiás	MW683432*	—	MW681999*	—
Chamaecrista planifolia	*E.M. Teixeira s/n* (BHCB)	Brazil, Minas Gerais	MW683451*	—	MW682018*	—
Chamaecrista* section *Absus* subsection *Absus* series *Lomatopodae [1/1]						
Chamaecrista lomatopoda	*H.S. Irwin 25557* (NY)	Brazil, Minas Gerais	MW683434*	—	MW682001*	—
Chamaecrista* section *Absus* subsection *Absus* series *Lucidae [2/5]						
Chamaecrista caiapo	*R.C. Sodré 2374* (UFG)	Brazil, Goiás	MW683389*	MW681851*	MW681952*	MW682070*

Table 1. Continued

Taxon	Voucher	Locality	ITS	ETS	*trnL-F*	*trnE-T*
Chamaecrista lamprosperma	*M.M. Cota 671* (NY)	Brazil, Minas Gerais	MW683430*	—	MW681997*	—
Chamaecrista* section *Absus* subsection *Absus* series *Microphyllae [17/20]						
Chamaecrista barnebyana	*M.J. Silva 6059* (UFG)	Brazil, Goiás	MH835363	—	MH828386	—
Chamaecrista belladonna	*M.J. Silva 5993* (UFG)	Brazil, Goiás	MH835356	—	MH828379	—
Chamaecrista cristalinae	*A.O. Souza 1459* (UFG)	Brazil, Goiás	MW683401*	MW681866*	MW681965*	MW682086*
Chamaecrista dalbergiifolia	*L.P. Queiroz 10318* (HUEFS),	Brazil, Goiás	FJ009837	—	FJ009891	—
Chamaecrista dumalis	*A.O. Souza 1650* (UFG)	Brazil, Rondônia	MW683407*	MW681873*	MW681972*	MW682093*
Chamaecrista elachistophylla	*A.O. Souza 1382* (UFG)	Brazil, Distrito Federal	MW683410*	—	MW681975*	—
Chamaecrista foederalis	*R.G. Matos 173* (UFG)	Brazil, Distrito Federal	MW683415*	MW681880*	MW681980*	MW682101*
Chamaecrista frondosa	*A.O. Souza 1849* (UFG)	Brazil, Goiás	MW683416*	—	MW681981*	—
Chamaecrista harmsiana	*R.G. Matos 430* (UFG)	Brazil, Goiás	MW683422*	—	MW681987*	—
Chamaecrista huntii var. *correntina*	*R.G. Matos 75* (UFG)	Brazil, Bahia	MW683424*	—	MW681989*	—
Chamaecrista imbricans	*R.G. Matos 63* (UFG)	Brazil, Goiás	MW683425*	MW681885*	MW681990*	MW682106*
Chamaecrista isidorea	*M.J. Silva 6059* (UFG)	Brazil, Goiás	MW683427*	—	MW681992*	—
Chamaecrista neesiana var. *goyazensis*	*R.G. Matos 117* (UFG)	Brazil, Goiás	MW683439*	—	MW682006*	—
Chamaecrista neesiana var. *laxiracemosa* 1	*M.J. Silva 5183* (UFG)	Brazil, Goiás	MH835386	MW681896*	MH828409	MW682120*
Chamaecrista neesiana var. *laxiracemosa* 2	*A.O. Souza 1393* (UFG)	Brazil, Minas Gerais	MW683440*	—	MW682007*	—
Chamaecrista neesiana var. *neesiana*	*R.G. Matos 124* (UFG)	Brazil, Minas Gerais	MW683441*	—	MW682008*	—
Chamaecrista neesiana var. *subnitida*	*R.G. Matos 65* (UFG)	Brazil, Bahia	MW683442*	—	MW682009*	—
Chamaecrista pohliana	*R.G. Matos 208* (UFG)	Brazil, Distrito Federal	MW683452*	—	MW682019*	—
Chamaecrista polymorpha	*R.G. Matos 1* (UFG)	Brazil, Goiás	MW683453*	MW681907*	MW682020*	MW682131*
Chamaecrista psoraleopsis	*R.G. Matos 9* (UFG)	Brazil, Goiás	MW683454*	—	MW682021*	—
Chamaecrista subdecrescens	*R.G. Matos 135* (UFG)	Brazil, Minas Gerais	MW683467*	—	MW682034*	—
Chamaecrista* section *Absus* subsection *Absus* series *Nigricantes [5/12]						
Chamaecrista machaeriifolia	*A.O. Souza 1177* (UFG)	Brazil, Distrito Federal	MW683436*	—	MW682003*	—
Chamaecrista philippi	*A.M. Giulietti 2245* (HUEFS)	Brazil, Bahia	FJ009838	—	FJ009892	—
Chamaecrista speciosa	*A.S. Conceição 546* (HUESF)	Brazil, Bahia	FJ009839	—	FJ009893	—
Chamaecrista tephrosiifolia	*A.O. Souza 2104* (UB)	Brazil, Minas Gerais	MW683470*	—	MW682037*	—
Chamaecrista urophyllidia	*R.M. Harley 54656* (HUEFS)	Brazil, Bahia	FJ009840	—	FJ009894	—

Table 1. Continued

Taxon	Voucher	Locality	ITS	ETS	*trnL-F*	*trnE-T*
Chamaecrista* section *Absus* subsection *Absus* series *Ochnaceae [4/8]						
Chamaecrista bifoliola	*A.O. Souza 928* (UFG)	Brazil, Goiás	MW683383*	—	MW681946*	—
Chamaecrista cotinifolia var. *cotinifolia*	*T.P. Mendes 261* (UFG)	Brazil, Minas Gerais	MK839193	—	MK836327	—
Chamaecrista cotinifolia var. *glaberrima*	*T.P. Mendes 338* (UFG)	Brazil, Goiás	MK839194	—	MK836328	—
Chamaecrista cotinifolia var. *leptodictya*	*T.P. Mendes 270* (UFG)	Brazil, Minas Gerais	MK839195	—	MK836329	—
Chamaecrista lavradiiflora	*A.O. Souza 927* (UFG)	Brazil, Goiás	MW683431*	MW681890*	MW681998*	MW682112*
Chamaecrista ochnacea var. *purpurascens*	*P.O. Rosa 1322* (HUFU)	Brazil, Minas Gerais	MW683444*	—	MW682011*	—
Chamaecrista ochnacea var. *speluncae*	*J.N. Nakajima 751* (HUFU)	Brazil, Minas Gerais	MW683445*	—	MW682012*	—
Chamaecrista* section *Absus* subsection *Absus* series *Oligospermae [1/1]						
Chamaecrista oligosperma	*A.O. Souza 1212* (UFG)	Brazil, Goiás	MW683447*	—	MW682014*	—
Chamaecrista aff. *oligosperma*	*L.P. Queiroz 10265* (HUEFS)	Brazil, Bahia	FJ009830	—	FJ009884	—
Chamaecrista* section *Absus* subsection *Absus* series *Paniculatae [13/13]						
Chamaecrista celiae	*T.P. Mendes 284* (UFG)	Brazil, Minas Gerais	MK839190	—	MK836324	—
Chamaecrista cercidifolia	*T.P. Mendes 279* (UFG)	Brazil, Minas Gerais	MK839201	MW681853*	MK836335	MW682073*
Chamaecrista claussenii	*A.O. Souza 979* (UFG)	Brazil, Goiás	MH835367	MW681859*	MH828390	MW682079*
Chamaecrista crenulata	*T.P. Mendes 42* (UFG)	Brazil, Goiás	MK839196	—	MK836330	—
Chamaecrista cyclophylla	*T.P. Mendes 90* (UFG)	Brazil, Goiás	MK839191	MW681868*	MK836325	MW682088*
Chamaecrista megacycla	*T.P. Mendes 333* (UFG)	Brazil, Goiás	MK839192	MW681892*	MK836326	MW682115*
Chamaecrista orbiculata	*T.P. Mendes 193* (UFG)	Brazil, Goiás	MK839198	MW681901*	MK836332	MW682125*
Chamaecrista pachyclada	*A.O. Souza 557* (UFG)	Brazil, Goiás	MH835389	—	MH828412	—
Chamaecrista rigidifolia	*T.P. Mendes 155* (UFG)	Brazil, Mato Grosso	MK839202	—	MK836336	—
Chamaecrista tocantinensis	*T.P. Mendes 312* (UFG)	Brazil, Tocantins	MK839204	MW681918*	MK836338	MW682145*
Chamaecrista trichorthyrsus	*T.P. Mendes 169* (UFG)	Brazil, Goiás	MK839199	—	MK836333	—
Chamaecrista ustulata	*T.P. Mendes 290* (UFG)	Brazil, Minas Gerais	MK839200	—	MK836334	—
Chamaecrista veadeirana	*T.P. Mendes 215* (UFG)	Brazil, Goiás	MK839203	—	MK836337	—
Excluded from series *Paniculatae* [1/1]						
Chamaecrista lundii	*T.P. Mendes 168* (UFG)	Brazil, Goiás	MK839197	—	MK836331	—

Table 1. Continued

Taxon	Voucher	Locality	ITS	ETS	*trnL-F*	*trnE-T*
Chamaecrista* section *Absus* subsection *Absus* series *Pinifoliae [1/1]						
Chamaecrista paniculata	*A.O. Souza 654* (UFG)	Brazil, Goiás	MW683448*	MW681902*	MW682015*	MW682126*
Chamaecrista* section *Absus* subsection *Absus* series *Rigidulae [32/32]						
Chamaecrista altoana	*M.J. Silva 6465* (UFG)	Brazil, Goiás	MH806439	—	MH828377	—
Chamaecrista azulana	*A.O. Souza 1116* (UFG)	Brazil, Mato Grosso	MH835355	MW681838*	MH828378	MW682055*
Chamaecrista benthamiana	*A.O. Souza 1576* (UFG)	Brazil, Goiás	MH835357	MW681841*	MH828380	MW682060*
Chamaecrista botryoides	*A.O. Souza 2230* (UFG)	Brazil, Bahia	MW683384*	MW681843*	MW681947*	MW682062*
Chamaecrista brachyrachis	*A.O. Souza 1179* (UFG)	Brazil, Distrito Federal	MH835359	—	MH828382	—
Chamaecrista chaetostegia	*H.S. Irwin 29729* (NY)	Brazil, Distrito Federal	MW683393*	—	MW681957*	—
Chamaecrista cipoana	*A.O. Souza 1414* (UFG)	Brazil, Minas Gerais	MH835366	MW681858*	MH828389	MW682078*
Chamaecrista dawsonii	*M.J. Silva 4474* (UFG)	Brazil, Goiás	MH835369	—	MH828392	—
Chamaecrista decumbens	*A.O. Souza 802* (UFG)	Brazil, Goiás	MH835370	—	MH828393	—
Chamaecrista densifolia	*A.O. Souza 1159* (UFG)	Brazil, Goiás	MH835371	—	MH828394	—
Chamaecrista elata	*M.J. Silva 6187* (UFG)	Brazil, Goiás	MH835372	MW681874*	MH828395	MW682095*
Chamaecrista feliciana	*A.O. Souza 1500* (UFG)	Brazil, Goiás	MH835374	MW681878*	MH828397	MW682099*
Chamaecrista filicifolia	*A.O. Souza 781* (UFG)	Brazil, Goiás	MH835375	MW681879*	MH828398	MW682100*
Chamaecrista floribunda	*A.O. Souza 1288* (UFG)	Brazil, Goiás	MH835376	—	MH828399	—
Chamaecrista glaucofilix	*A.O. Souza 1550* (UFG)	Brazil, Bahia	MH835377	—	MH828400	—
Chamaecrista gymnothyrsa	*R.C. Sodré 1330* (UFG)	Brazil, Goiás	MH835378	—	MH828401	—
Chamaecrista irwiniana	*A.O. Souza 605* (UFG)	Brazil, Goiás	MH835380	MW681886*	MH828403	MW682107*
Chamaecrista macedoi	*M.J. Silva 6073* (UFG)	Brazil, Goiás	MH835381	—	MH828404	—
Chamaecrista mollicaulis	*M.J. Silva 5693* (UFG)	Brazil, Distrito Federal	MH835382	MW681893*	MH828405	MW682116*
Chamaecrista multipennis	*A.O. Souza 1411* (UFG)	Brazil, Minas Gerais	MH835383	MW681894*	MH828406	MW682117*
Chamaecrista nanodes	*A.O. Souza 1763* (UFG)	Brazil, Goiás	MH835385	MW681895*	MH828408	MW682119*
Chamaecrista nummulariifolia	*A.O. Souza 790* (UFG)	Brazil, Goiás	MH835387	—	MH828410	—
Chamaecrista obolaria	*A.O. Souza 864* (UFG)	Brazil, Goiás	MH835388	MW681898*	MH828411	MW682122*
Chamaecrista oppositifolia	*A.O. Souza 1246* (UFG)	Brazil, Bahia	MK056260	MW681900*	MK390621	MW682124*
Chamaecrista pauciflora	*A.O. Souza 2153* (UB)	Brazil, Tocantins	MW683449*	MW681905*	MW682016*	MW682129*
Chamaecrista planaltoana	*A.O. Souza 1355* (UFG)	Brazil, Distrito Federal	MH835390	—	MH828413	—
Chamaecrista polita	*A.O. Souza 352* (UFG)	Brazil, Goiás	MH835391	MW681906*	MH828414	MW682130*
Chamaecrista rupestrium	*A.O. Souza 1234* (UFG)	Brazil, Bahia	MH835392	MW681911*	MH828415	MW682135*
Chamaecrista sincorana	*R.G. Matos 73* (UFG)	Brazil, Bahia	MH835395	MW681912*	MH828418	MW682139*
Chamaecrista sparsifolia	*A.O. Souza 1050* (UFG)	Brazil, Goiás	MH835396	—	MH828419	—
Chamaecrista strictula	*A.O. Souza 1324* (UFG)	Brazil, Goiás	MH835397	MW681915*	MH828420	MW682142*

Table 1. Continued

Taxon	Voucher	Locality	ITS	ETS	*trnL-F*	*trnE-T*
Chamaecrista tenuicaulis	*A.O. Souza 1256* (UFG)	Brazil, Goiás	MH835398	—	MH828421	—
Excluded from series *Rigidulae* [2/2]						
Chamaecrista brachyblepharis	*M.J. Silva 4472* (UFG)	Brazil, Goiás	MH835358	MW681844*	MH828381	MW682063*
Chamaecrista ciliolata var. *ciliolata*	*J.G. Rando 1115* (HUEFS)	Brazil, Minas Gerais	MH835364	MW681856*	MH828387	MW682076*
Chamaecrista ciliolata var. *pulchella*	*A.O. Souza 1423* (UFG)	Brazil, Minas Gerais	MH835365	MW681857*	MH828388	MW682077*
Chamaecrista* section *Absus* subsection *Absus* series *Secundae [1/1]						
Chamaecrista secunda	*A.O. Souza 1449* (UFG)	Brazil, Minas Gerais	MW683459*	—	MW682026*	—
Chamaecrista* section *Absus* subsection *Absus* series *Setosae [7/9]						
Chamaecrista auris-zerdae	*J.A. Oliveira 120* (UFG)	Brazil, Minas Gerais	MW683377*	—	MW681940*	—
Chamaecrista campicola	*A.O. Souza 893* (UFG),	Brazil, Distrito Federal	MH835362	—	MH828385	—
Chamaecrista coradinii	*L.L.C. Antunes 1579* (UFG)	Brazil, Tocantins	MH835368	—	MH828391	—
Chamaecrista obtecta	*J.A. Oliveira 60* (UFG)	Brazil, Goiás	MW683443*	—	MW682010*	—
Chamaecrista ochrosperma	*M.N. Rissi 659* (CEN)	Brazil, Goiás	MW683446*	—	MW682013*	—
Chamaecrista scabra	*A.O. Souza 1456* (UFG)	Brazil, Goiás	MH835393	—	MH828416	MW682137*
Chamaecrista setosa var. dentosa	*A.O. Souza 405* (UFG)	Brazil, Goiás	MH835394	—	MH828417	MW682138*
Chamaecrista setosa var. *paucivenia*	*J.A. Oliveira 110* (UFG)	Brazil, Minas Gerais	MW683460*	—	MW682027*	—
Chamaecrista setosa var. *setosa*	*J.A. Oliveira 166* (UFG)	Brazil, Mato Grosso	MW683461*	—	MW682028*	—
Chamaecrista setosa var. *subsetosa*	*J.A. Oliveira 50* (UFG)	Brazil, Goiás	MW683462*	—	MW682029*	—
Chamaecrista* section *Absus* subsection *Absus* series *Spinulosae [1/1]						
Chamaecrista spinulosa	*A.O. Souza 2258* (UFG)	Brazil, Goiás	MW683464*	—	MW682031*	—
Chamaecrista* section *Absus* subsection *Absus* series *Strictifoliae [1/1]						
Chamaecrista strictifolia	*E.T. Neto 4080* (BHCB)	Brazil, Minas Gerais	MW683466*	—	MW682033*	—
Chamaecrista* section *Absus* subsection *Absus* series *Trachycarpae [2/3]						
Chamaecrista cavalcantina	*A.O. Souza 862* (UFG)	Brazil, Goiás	MW683390*	—	MW681954*	—
Chamaecrista venatoria	*A.O. Souza 1258* (UFG)	Brazil, Goiás	MW683472*	—	MW682040*	—

Table 1. Continued

Taxon	Voucher	Locality	ITS	ETS	*trnL-F*	*trnE-T*
Chamaecrista* section *Absus* subsection *Absus* series *Unijugae [1/4]						
Chamaecrista monticola	*A.O. Souza 2128* (UB)	Brazil, Minas Gerais	MW683437*	—	MW682004*	—
Chamaecrista* section *Absus* subsection *Absus* series *Ursinae [5/11]						
Chamaecrista exsudans	*A.O. Souza 2107* (UB)	Brazil, Minas Gerais	MW683413*	—	MW681978*	—
Chamaecrista fuscescens	*A.O. Souza 2117* (UB)	Brazil, Minas Gerais	MW683391*	—	MW681955*	—
Chamaecrista leucopilis	*A.O. Souza 1822* (UFG)	Brazil, Goiás	MW683433*	—	MW682000*	—
Chamaecrista ursina	*A.O. Souza 2131* (UB)	Brazil, Minas Gerais	MW683471*	—	MW682039*	—
Chamaecrista xanthadena	*G.G. Hatschbach 41481* (NY)	Brazil, Minas Gerais	MW683392*	—	MW681956*	—
Chamaecrista* section *Absus* subsection *Adenophyllum [1/1]						
Chamaecrista bucherae	*Marie-Victorium 21759* (MT)	Cuba	MW683387*	MW681849*	MW681950*	MW682068*
Chamaecrista* section *Absus* subsection *Baseophyllum [8/8]						
Chamaecrista blanchetii	*M.J.G. Andrade 607* (HUEFS)	Brazil, Bahia	FJ009846	MW681842*	FJ009890	MW682061*
Chamaecrista brachystachya	*A.S. Conceição 713* (HUEFS)	Brazil, Minas Gerais	FJ009847	MW681845*	FJ009901	MW682064*
Chamaecrista confertiformis	*C.B.N. Costa 132* (HUEFS)	Brazil, Bahia	FJ009848	MW681865*	FJ009902	MW682085*
Chamaecrista coriacea	*A.S. Conceição 869* (HUEFS)	Brazil, Minas Gerais	FJ009843	—	FJ009897	—
Chamaecrista cytisoides	*A.S. Conceição 870* (HUEFS)	Brazil, Minas Gerais	FJ009844	—	FJ009898	—
Chamaecrista decora	*A.S. Conceição 810* (HUEFS)	Brazil, Minas Gerais	FJ009849	—	FJ009903	—
Chamaecrista depauperata	*A.S. Conceição 863* (HUEFS)	Brazil, Bahia	FJ009850	—	FJ009904	—
Chamaecrista unijuga	*A.S. Conceição 694* (HUEFS)	Brazil, Bahia	FJ009845	MW681920*	FJ009899	MW682146*
Chamaecrista* section *Absus* subsection *Otophyllum [1/1]						
Chamaecrista debilis	*A.O. Souza 1869* (UB)	Brazil, Minas Gerais	—	MW681869*	MW681967*	MW682089*
3. *Chamaecrista* section *Apoucouita* [7/22]						
Chamaecrista* section *Apoucouita* series *Apoucouita [5/20]						
Chamaecrista amorimii	*A.S. Conceição 795* (HUEFS)	Brazil, Bahia	FJ009823	KP967071	FJ009878	KP966952
Chamaecrista apoucouita	*L.A.G. Souza 66/09* (INPA)	Brazil, Amazonas	MW683375*	MW681835*	MW681937*	MW682052*

Table 1. Continued

Taxon	Voucher	Locality	ITS	ETS	*trnL-F*	*trnE-T*
Chamaecrista eitenorum 1	*D. Cardoso 3484*	Brazil, Rio Grande do Norte	KR134121	KP999905	—	—
Chamaecrista eitenorum 2	*D. Cardoso 3483*	Brazil, Rio Grande do Norte	KR134120	KP999904	—	—
Chamaecrista ensiformis	*C.A. Sousa IFN-4802171.5* (UB)	Brazil, Maranhão	MW683411*	MW681875*	MW681976*	MW682096*
Chamaecrista onusta	*A.S. Conceição 800* (HUEFS)	Brazil, Bahia	FJ009824	—	FJ009879	—
4. *Chamaecrista* section *Caliciopsis* [2/2]						
Chamaecrista calycioides 1	*L.P. Queiroz 11* (HUEFS)	Brazil, Rio Grande do Norte	FJ009863	—	FJ009917	—
Chamaecrista calycioides 2	*EAC 26229*	Brazil, Ceará	GU175311	—	MW681953*	GU175322
Chamaecrista duckeana	*A. Fernandes s/n* (NY)	Brazil, Ceará	MW683406*	MW681872*	MW681971*	MW682092*
5. *Chamaecrista* section *Grimaldia* [1/1]						
Chamaecrista absus var. absus 1	*A.S. Conceição 1056* (HUEFS)	Brazil, Rio Grande do Norte	FJ009832	—	FJ009886	—
Chamaecrista absus var. *absus* 2	*V. Sundaresan s/n*	India	KT279729	—	—	—
Chamaecrista absus var. *absus* 3	—	—	KC817015	—	—	—
6. *Chamaecrista* section *Xerocalyx* [4/4]						
Chamaecrista cultrifolia	*N.F.O. Mota 2161* (HUEFS)	Brazil, Mato Grosso	KR134033	KP999796	—	—
Chamaecrista desvauxii var. *brevipes*	*A.R. Barbosa 794* (HUEFS)	Brazil, Bahia	KR134094	KP999848	—	—
Chamaecrista desvauxii var. *desvauxii*	*L.P. Queiroz 10453* (HUEFS)	Brazil, Bahia	FJ009864	—	FJ009918	—
Chamaecrista desvauxii var. glauca	*A.O. Souza 2147* (UB)	Brazil, Tocantins	MW683404*	MW681870*	MW681969*	MW682090*
Chamaecrista desvauxii var. *graminea*	*A.R. Barbosa 782* (HUEFS)	Brazil, Bahia	KR134102	KP999854	—	—
Chamaecrista desvauxii var. *langsdorffii*	*A.S. Conceição 674* (HUEFS)	Brazil, Bahia	FJ009866	KP999886	FJ009920	—
Chamaecrista desvauxii var. *latifolia*	*A.R. Barbosa 1068* (HUEFS)	Brazil, Minas Gerais	KR134092	KP999846	—	—

Table 1. Continued

Taxon	Voucher	Locality	ITS	ETS	*trnL-F*	*trnE-T*
Chamaecrista desvauxii var. *latistipula*	*A.S. Conceição 912* (HUEFS)	Brazil, Espírito Santo	FJ009867	KP967061	FJ009921	KP967008
Chamaecrista desvauxii var. *mollissima*	*A.K.A. Santos 356* (HUEFS)	Brazil, Bahia	FJ009865	—	FJ009919	GU175325
Chamaecrista desvauxii var. *piptostegia*	*A.R. Barbosa 867* (HUEFS)	Brazil, Minas Gerais	KR134101	KP999853	—	—
Chamaecrista desvauxii var. *pirebebuiensis*	*A.R. Barbosa 957* (HUEFS)	Brazil, Goiás	KR134110	KP999860	—	—
Chamaecrista diphylla	*L.P. Queiroz 10269* (HUEFS)	Brazil, Bahia	FJ009868	KP999896	FJ009922	GU175326
Chamaecrista ramosa var. *curvifolia*	*A.R. Barbosa 1075* (HUEFS)	Brazil, Maranhão	KR134046	KR133795	—	—
Chamaecrista ramosa var. erythrocalyx	*A.R. Barbosa 882* (HUEFS)	Brazil, Minas Gerais	KR134113	KP999863	—	—
Chamaecrista ramosa var. *lucida*	*EAC 28606*	Brazil, Goiás	GU175316	—	—	GU175330
Chamaecrista ramosa var. *mollissima*	*EAC 24258*	Brazil, Piauí	GU175317	—	—	GU175329
Chamaecrista ramosa var. *parvifoliola*	*A.R. Barbosa 812* (HUEFS)	Brazil, Minas Gerais	KR134099	KP999851	—	—
Chamaecrista ramosa var. *ramosa*	*A.R. Barbosa 815* (HUEFS)	Brazil, Minas Gerais	KR134105	KP999855	—	—
Extra-American species without classification [6/62]						
Chamaecrista grantii	*Hohbein B10-K1267*	Kenya, Rift Valley	KR734123	—	KR738334	—
Chamaecrista kirkii	*Carvalho 2403* (NY)	Equatorial Guinea	MW683429*	—	MW681994*	MW682109*
Chamaecrista kleinii	*RRCBI-MUS132A* (MUS)	India	KJ605907	—	—	—
Chamaecrista mimosoides	*LUH:5201*	Nigeria	KX057847	—	KX268162	—
Chamaecrista nigricans	*LUH:5131*	Nigeria	KX057848	—	KX268163	—
Chamaecrista pumila	*LSC125*	India	MH768080	—	KU551117	—

(Darriba *et al.*, 2012) using the Akaike information criterion test; each fittest model is available in Table 4. The BI analysis consisted of two simultaneous independent runs of four Markov chain Monte Carlo with 10^7 generations, sampling trees and parameters each thousand generations. After excluding 25% as burn-in the remaining samples were used to calculate the tree of maximum clade credibility using TreeAnnotator in the BEAST package v.1.8.0 (Drummond *et al.*, 2012), with clade support indicated as posterior probabilities (PP). All analyses were performed on the platform CIPRES Science Gateway

Table 2. Sequences and references of primers used in this study

Region	Primer	Primer sequence (5′–3′)	Reference
ITS	17SE	ACGAATTCATGGTCCGGTGAAGTGTTCG	Sun *et al.*, 1994
	26SE	TAGAATTCCCCGGTTCGCTCGCCGTTAC	
	ITS1	GCTACGTTCTTCATCGAT	White *et al.*, 1990
	ITS4	TCCTCCGCTTATTGATATGC	
ETS	18IGS	GCCTGCTGCCTTCCTTGGATGTGG	Baldwin & Markos, 1998
	26IGS	GGGAACGTGAGCTGGGTTTAGACCGTC	
trnL-F	d	GGGGATAGAGGGACTTGAAC	Taberlet *et al.*, 1991
	c	CGAAATCGGTAGACGCTACG	
	f	ATTTGAACTGGTGACACGAG	
	e	GGTTCAAGTCCCTCTATCCC	
trnE-T	*trnE-T* forward	ATCGGATTTGAACCGATGAC	Kato *et al.*, 2000
	trnE-T reverse	CCCAGGGGAAGTCGAATC	

Table 3. PCR cycles used for each region studied

Steps	ITS	ETS	*trnL-F*	*trnE-T*
Initial denaturation	94 °C for 4 min	94 °C for 4 min	94 °C for 2 min	94 °C for 3 min
Denaturation	94 °C for 1 min	94 °C for 1 min	94 °C for 1 min	94 °C for 1 min
Annealing	61.5 °C for 1 min	55 °C for 1 min	61.5 °C for 45 s	61 °C for 45 s
Extension	72 °C for 1 min	72 °C for 2 min	72 °C for 1.2 min	72 °C for 1.3 min
Final extension	72 °C for 4 min	72 °C for 4 min	72 °C for 4 min	72 °C for 9 min
Number of cycles	33	35	32	35

Table 4. Statistical information of each matrix and sample set analysed

	ITS		ETS	*trnL-F*		*trnE-T*	Four markers combined	
	Broad	*Multilocus*	*Multilocus*	*Broad*	*Multilocus*	*Multilocus*	*Broad*	*Multilocus*
Number of accessions	275	185	150	267	174	153	286	193
Alignment length (bp)	1296	1258	742	1112	1186	937	2519	4123
Variable sites	1041	981	562	341	328	223	1493	2123
Potentially informative sites	823	749	453	187	195	138	1074	1535
Average number of indels (bp)	140	132	134	105	94	71	—	—
Evolution model	TIM1+G	TIM1+G	TIM3+G	GTR+G	GTR+G	TVM+G	Partitioned	Partitioned

3.3 (Miller, Pfeiffer & Schwartz, 2010, https://www.phylo.org/), and the resulting trees were viewed and edited in the program FigTree v.1.4.3 (Rambaut, 2016).

Ancestral character reconstruction

To ascertain potential morphological synapomorphies, another majority-rule consensus tree from the BI analysis of the combined molecular data set with 80 selected taxa was elaborated and used to trace the evolution of 20 morphological characters previously used in the diagnoses and differentiation of infrageneric taxa of *Chamaecrista* by Irwin & Barneby (1982). The characters were evaluated in Mesquite v.3.51 (Maddison & Maddison, 2018) using the 'trace character history' option in the 'stochastic character mapping' method using the 'current probability models' (Maddison & Maddison, 2006). All morphological characters were considered unordered and unweighted. The 80 selected taxa were chosen to represent all the morphological diversity of the main clades, and the lack of some species is not predicted to alter the results since the missing species have similar characteristics analysed to the selected taxa from respective clades (Irwin & Barneby, 1982). Characters were coded from information in the relevant literature (Irwin & Barneby, 1977, 1978, 1982) or by direct examination of specimens from the herbaria ALCB, BHCB, CEN, CEPEC, CGMS, EAC, ESA, F, G, HRB, HTO, HUEFS, HUTO, IAN, IBGE, INPA, K, M, MBM, MO, NY, P, R, RBSP, SPF, UB, UEC, UFG, UFMT, US, VIES and W (acronyms according to Thiers, 2020). Morphological terminologies follow Radford *et al.* (1974) and Irwin & Barneby (1978, 1982). The list of selected characters and coding is presented in Supporting Information, Appendix S1, and the data matrix with the character states for each species is presented in Supporting Information, Appendix S2.

Taxonomic treatment

Taxonomic decisions were based on the phylogenetic relationships obtained and morphological evidence. The proposed combinations and new taxonomic categories follow the standards and recommendations of the *International Code of Nomenclature for Algae, Fungi and Plants* (Turland *et al.*, 2018). Descriptions of the infrageneric taxa (sections and subsections) recognized in *Chamaecrista* consider the distinguishing morphological characters of the species which comprise the supraspecific taxa. To confirm the accepted species names in *Chamaecrista*, we consulted in the literature around the world (e.g. Irwin & Barneby, 1977, 1978, 1982; Lock, 1988; Randell, 1988; Souza, Lewis & Silva, 2019b; Cota, Rando & Mello-Silva, 2020; Souza & Silva, 2020) to create a list of updated binomials of *Chamaecrista*. The types of vegetation cited follow Ribeiro & Walter (2008) and IBGE (2012) for Brazilian vegetation.

RESULTS

Data matrices and phylogenetic analyses

We produced 434 new sequences (108 ITS, 102 ETS, 115 *trnL-F* and 109 *trnE-T*) for 167 accessions corresponding to 140 species (137 *Chamaecrista* spp. and three *Senna* spp.). We sampled all six sections, all four subsections and 34 out of the 39 series of *Chamaecrista*, making it the largest molecular sampling of the genus so far and covering the pantropical distribution of the genus with 204 out of the 280 American species and six out of the 62 extra-American species. We were unable to sample the monospecific series *Andromedeae* (H.S.Irwin & Barneby) H.S.Irwin & Barneby, *Atroglandulosae* (H.S.Irwin & Barneby) H.S.Irwin & Barneby, *Hassleranae* (H.S.Irwin & Barneby) H.S.Irwin & Barneby and *Incanae* (H.S.Irwin & Barneby) H.S.Irwin & Barneby from *Chamaecrista* section *Absus* subsection *Absus* and series *Greggianae* H.S.Irwin & Barneby from *Chamaecrista* section *Chamaecrista* due to the difficulty of extracting and sequencing DNA from herbarium specimens.

The ILD test showed negative incongruity ($\rho = 0.9$) between the four markers used. Therefore, as the trees were congruent the markers could be combined. Complete information on the composition of each matrix in each sampling approach is given in Table 4.

Results from the BI and ML analyses, either individually or combined in the *Broad* and *Multilocus* approaches strongly supported *Chamaecrista* as a monophyletic genus (PP = 1.0 and BT = 100%) (Figs 1–6, Supporting Information, Appendices S3–S10). All the analyses recovered the same main clades in *Chamaecrista*, and therefore we chose to present and discuss the BI trees from the combined analyses considering the indels in both the *Broad* and *Multilocus* approaches (ITS + *trnL-F* + indels from the *Broad* approach and four markers + indels from the *Multilocus* approach) because they provided more resolution at infrageneric level. The bootstrap values obtained from the ML analyses were plotted on the BI trees. The trees resulting from the ML analyses are presented for comparison (Supporting Information, Appendices S3–S10). The nuclear markers (ETS and ITS) had the largest number of indels and potentially informative sites (Table 4) and recovered the four main clades in *Chamaecrista* (Supporting Information, Appendix S3), whereas the plastid markers (*trnL-F* and *trnE-T*) recovered the same clades, although with

lower internal resolution (Supporting Information, Appendices S2, S6). Individual trees from the *trnE-T* and ETS analyses were the only ones to recover subclades D1, D2 and D3 of clade D (Supporting Information, Appendices S5, S6). The trees resulted from only the coded indels of the nuclear and plastid markers showed a good level of resolution, especially in the *Multilocus* analysis (Supporting Information, Appendices S7–S10).

Broad analysis

The *Broad* analysis strategy comprised the larger number of taxa and provided an overview at section level in *Chamaecrista* and support for the relationships among the sampled genera, but relationships within and between series and species are poorly supported (Fig. 1). For this reason, we used the results of the *Broad* analysis to discuss only the sectional level.

In analyses of individual and combined data sets (ITS + *trnL-F* + indels) *Vouacapoua americana* Aubl. emerged as sister to *Chamaecrista* with maximum support (1.0 PP and 100% BT) (Fig. 1), and *Chamaecrista*+*V. americana*) emerged in a polytomy with *Cassia*, *Melanoxylon* and *Recordoxylon*, the last two as sister genera, and *Vouacapoua macropetala* Sandwith (Fig. 1).

In *Chamaecrista*, sections *Apoucouita*, *Grimaldia* and *Xerocalyx* were recovered as monophyletic, whereas section *Caliciopsis* H.S.Irwin & Barneby is paraphyletic and sections *Chamaecrista* and *Absus* are polyphyletic (Fig. 1). Section *Apoucouita* in all analyses had maximum support (1.0 PP and 100% BT) and is always placed as the earliest-diverging lineage (Fig. 1, clade A), whereas taxa of sections *Chamaecrista* and *Caliciopsis* emerged mixed in a clade (Fig. 1 clade C, 1.0 PP, 100% BT) with the monophyletic section *Xerocalyx* and Extra-American species. *Chamaecrista* section *Absus* appears in two distinct and well-supported clades; the first (Fig. 1 clade B, 1.0 PP, 100% BT) includes all taxa of subsections *Adenophyllum*, *Baseophyllum* (Collad.) H.S.Irwin & Barneby and *Otophyllum* and emerged as the sister of clade C; and the second (Fig. 1 clade D, 1.0 PP, 100% BT) includes all species of subsection *Absus* and the monophyletic section *Grimaldia* (Schrank) H.S.Irwin & Barneby. Clade D had the longest branch and maximum support in all analyses, although it is the clade with the lowest internal resolution in the *Broad* approach analyses (Fig. 1).

Multilocus analysis

The *Multilocus* analysis included fewer taxa than the *Broad* analysis but achieved better internal resolution in *Chamaecrista* (Fig. 2). As for the *Broad* approach analysis, the *Multilocus* analysis recovered four main well-supported clades, A, B, C and D (Fig. 2) with the individual and combined datasets, although more resolution was observed in clades C and D. Based on this, the *Multilocus* results are used to discuss the taxonomic relationships at section, subsection and series levels, and they are used later as the basis for a proposed new infrageneric classification of *Chamaecrista*.

Chamaecrista section *Apoucouita* emerged as monophyletic (1.0 PP and 100% BT) (Figs 2, 3, clade A), although series *Apoucouita* and *Pteridophyllae* (H.S.Irwin & Barneby) H.S.Irwin & Barneby in this section appeared in a polytomy of three subclades, one of which (Fig. 3, subclade A2) corresponds to the monophyletic series *Pteridophyllae* (0.99 PP, 100% BT) and the others (Fig. 3, subclades A1 and A3) include taxa of series *Apoucouita*.

Chamaecrista section *Xerocalyx* is supported as monophyletic, with an increase in its internal resolution (Figs 2 and 4 subclade C6) and is nested in a clade that includes taxa from sections *Chamaecrista* and *Caliciopsis* (Fig. 2 clade C). Section *Chamaecrista* maintains the same phylogenetic structure as revealed by the *Broad* approach analysis, although with better resolution (Fig. 2). Of the six series belonging to *Chamaecrista* section *Chamaecrista*, only series *Bauhinianae* (Collad.) H.S.Irwin & Barneby (*sensu* Irwin & Barneby, 1982) and *Coriaceae* (*sensu* Rando *et al.*, 2019) are recovered as monophyletic; the others are para- or polyphyletic (Fig. 4).

Chamaecrista section *Absus* is polyphyletic and divided into two main isolated clades (Fig. 2, clades B and D) as also revealed in the *Broad* strategy analysis. Clade B includes species from subsections *Baseophyllum*, *Adenophyllum* and *Otophyllum* and recovered *C. bucherae* (Moldenke) H.S.Irwin & Barneby (subsection *Adenophyllum*) as sister to *C. debilis* (Vogel) H.S.Irwin & Barneby (subsection *Otophyllum*), the two together in a clade sister to the monophyletic subsection *Baseophyllum* (1.0 PP and 98% BT; Fig 3). Clade D groups species of subsection *Absus* and section *Grimaldia* with better resolution than the *Broad* analysis, and recovers three well-supported subclades (subclade D1: 0.96 PP and 89% BT; subclade D2: 0.98 PP and 85% BT; subclade D3: 0.99 PP and 90% BT; Figs 2, 5). Subclade D1 comprises some species belonging to series *Absoideae* (Benth.) H.S.Irwin & Barneby, *Confertae* (H.S.Irwin & Barneby) H.S.Irwin & Barneby and *Oligospermae* (H.S.Irwin & Barneby) H.S.Irwin & Barneby of *C.* section *Absus* subsection *Absus* with *C. absus* (L.) H.S.Irwin & Barneby from *Chamaecrista* section *Grimaldia* (*sensu* Irwin & Barneby, 1982). Subclade D2 comprises only species from series *Absoideae*, and subclade D3 groups species from the remaining 33 series of *Chamaecrista* section *Absus* subsection *Absus*, although this subclade has poor

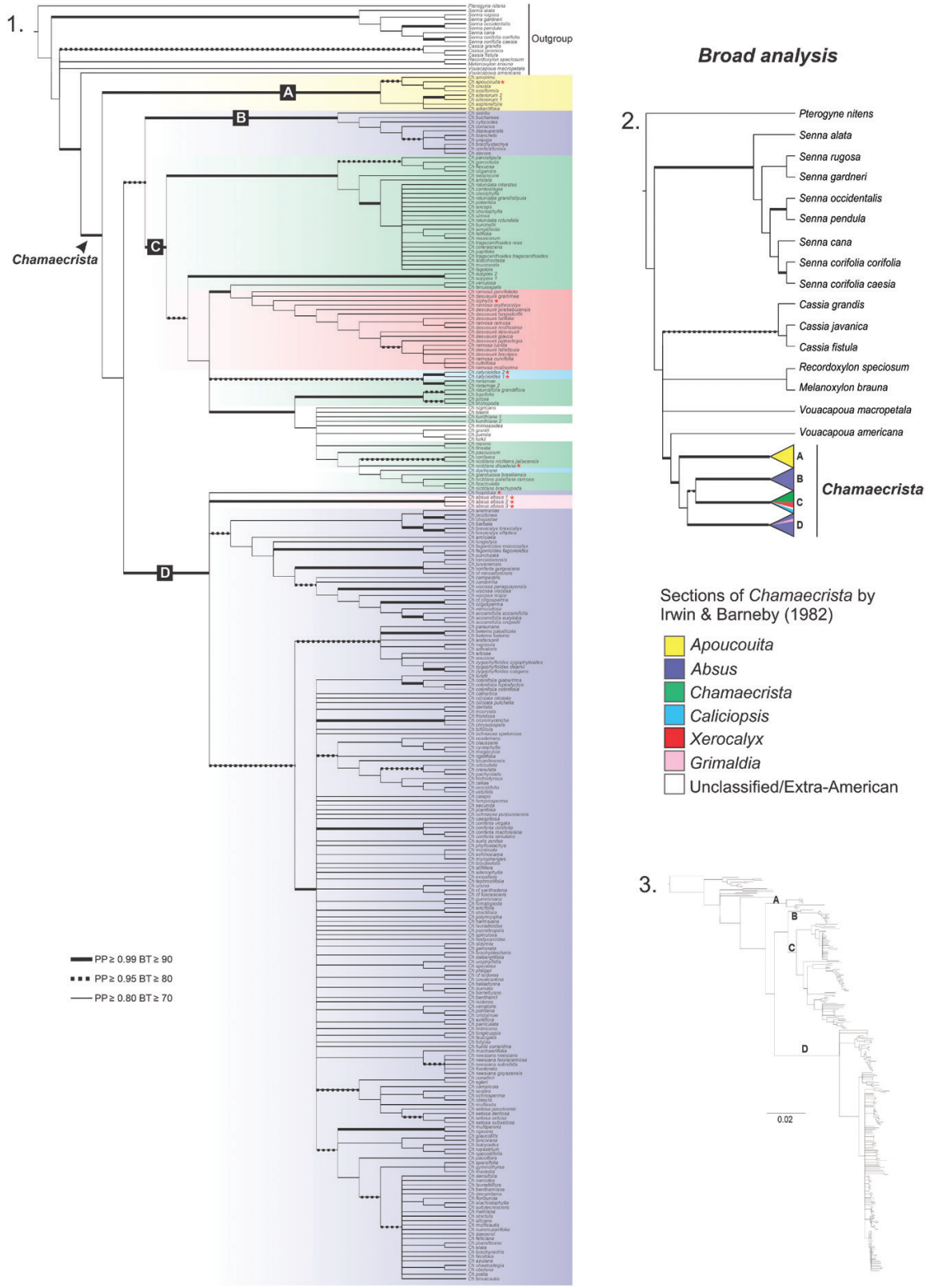

Figure 1. Majority consensus tree of the Bayesian analysis resulting from *Broad* sampling (ITS + *trnL-F* + indels). 1, Cladogram with the sections recognized in the classification of Irwin & Barneby (1982). 2, Representative scheme showing

internal resolution (Fig. 5). The analysis demonstrated that most of the traditionally recognized series sampled of subsection *Absus* are polyphyletic (e.g. *Absoideae*, *Microphyllae* and *Ochnaceae*), and require further analysis before species can be accurately assigned to named subclades (Fig. 5).

Ancestral character reconstruction

Our analysis of the evolution of morphological characters demonstrated that ten of the 20 studied characters are homoplastic. Nevertheless, the isomorphic androecium (character 14), pubescence of the anther suture (character 15), fruits elastically dehiscent (character 18) and pedicels bi-bracteolate (character 20) emerged as potential synapormorphies for *Chamaecrista*. The character states: cauliflorous inflorescence (character 10) and nectaries on the inflorescence axis (character 7) emerged as potential synapomorphies for clade A. Alternate-distichous leaves (character 8), leaflets with palmate venation (character 9) and flowers solitary or grouped in fascicles (character 10) are synapomorphic characters for clade C, and the presence of glandular trichomes (character 5) and loss of nectaries (character 6) are synapomorphies for clade D. Appendices S11–S20 in the Supporting Information present the reconstructions of the individual characters studied.

A new infrageneric classification of *Chamaecrista*

A new classification of *Chamaecrista* is proposed supported by a molecular phylogenetic analysis and the results of a morphological character evolution study. The genus is divided into four sections: (1) section *Apoucouita* maintains the same composition as that established by Irwin & Barneby (1982), although we do not recognize any series within it; (2) section *Baseophyllum* raises the rank of subsection *Baseophyllum* of Irwin & Barneby and now includes in synonymy subsections *Adenophyllum* and *Otophyllum*; (3) section *Chamaecrista* now includes the former sections *Caliciopsis* and *Xerocalyx* and (4) section *Absus* now includes the former section *Grimaldia*. Section *Absus* is divided into three subsections: (1) subsection *Absus*; (2) subsection *Viscosa* and (3) subsection *Zygophyllum*.

A taxonomic treatment is presented based on the new infrageneric classification. A bibliographic survey resulted in a list of 363 *Chamaecrista* spp. in the world, of which 64 are exclusively extra-American and have never been formally placed in any infrageneric category. These extra-American species are allocated here to section *Chamaecrista* based on our molecular phylogenetic analysis and morphological evidence. A complete list of all currently accepted binomials is available in Supporting Information, Appendix S21.

DISCUSSION

Our results confirm the monophyly of *Chamaecrista* based on a comprehensive sampling of its species (210 species) and infrageneric categories (six sections, four subsections and 34 series). All previous phylogenetic studies that included *Chamaecrista* also supported its monophyly, although all included fewer species (≤ 85 species, e.g. Conceição *et al.*, 2009; Torres *et al.*, 2011; Rando *et al.*, 2016; Souza *et al.*, 2019a; Mendes *et al.*, 2020). Our work made use of several strategies such as coding indels, which presented a good level of resolution, demonstrating their information potential, although they are largely ignored in phylogenetic analyses and removed from the alignment of sequences being considered as missing data (Sanyal *et al.*, 2015). In addition, the strategy of multiple nuclear and plastid markers has been widely used in phylogenetic studies at lower levels to provide an increase in resolution in order to reach consistent classifications (Trovó *et al.*, 2013; Ribeiro *et al.*, 2014; Inglis & Cavalcanti, 2018; Cândido *et al.*, 2020). The use of all these strategies has allowed us to have a good understanding of general relationships in *Chamaecrista* as discussed next.

Relationships within *Chamaecrista*

The results from all our analyses revealed the non-monophyly of the traditionally recognized major taxonomic ranks of *Chamaecrista*, suggesting that the current infrageneric classification of Irwin & Barneby (1982) should be redefined. The same conclusion was reached by Conceição *et al.* (2009), Torres *et al.* (2011), Rando *et al.* (2016), Souza *et al.* (2019a) and Mendes *et al.* (2020), whose studies revealed the incongruence between the traditional hierarchical classification and the phylogenetic relationships in *Chamaecrista*.

the outgroup and the four main clades recovered in *Chamaecrista*. 3, Phylogram of the tree shown in 1, with branch lengths proportional to the number of substitutions. Clades marked with letters are discussed in the text. Red asterisks indicate type species for each section. Taxa with three names are varieties and those with four names are subspecies and varieties. Support of the branches is represented by the thickness of the line, PP = posterior probability and BT = bootstrap value.

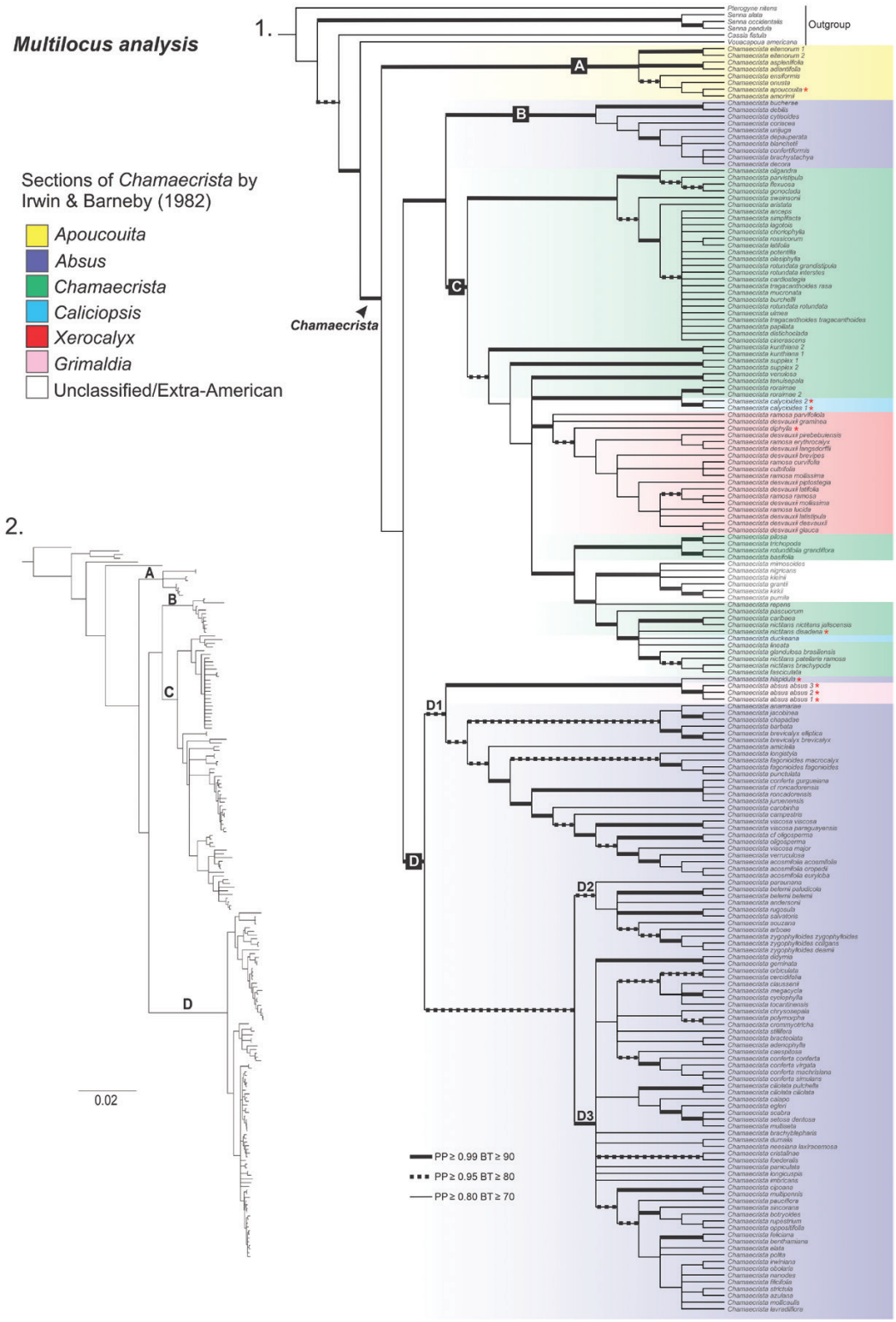

Figure 2. Majority consensus tree of the Bayesian analysis resulting from a *Multilocus* sampling (ITS + ETS + *trnL-F* + *trnE-T* + Indels). 1, Cladogram with the sections of *Chamaecrista* recognized by Irwin & Barneby (1982). 2, Phylogram of the tree shown in 1 with branch lengths proportional to the number of substitutions. Clades marked with letters are discussed in the text. Red asterisks indicate type species for each section. Taxa with three names are varieties and those with four names are subspecies and varieties. Support for the branches is represented by the thickness of the line, PP = posterior probability and BT = bootstrap value.

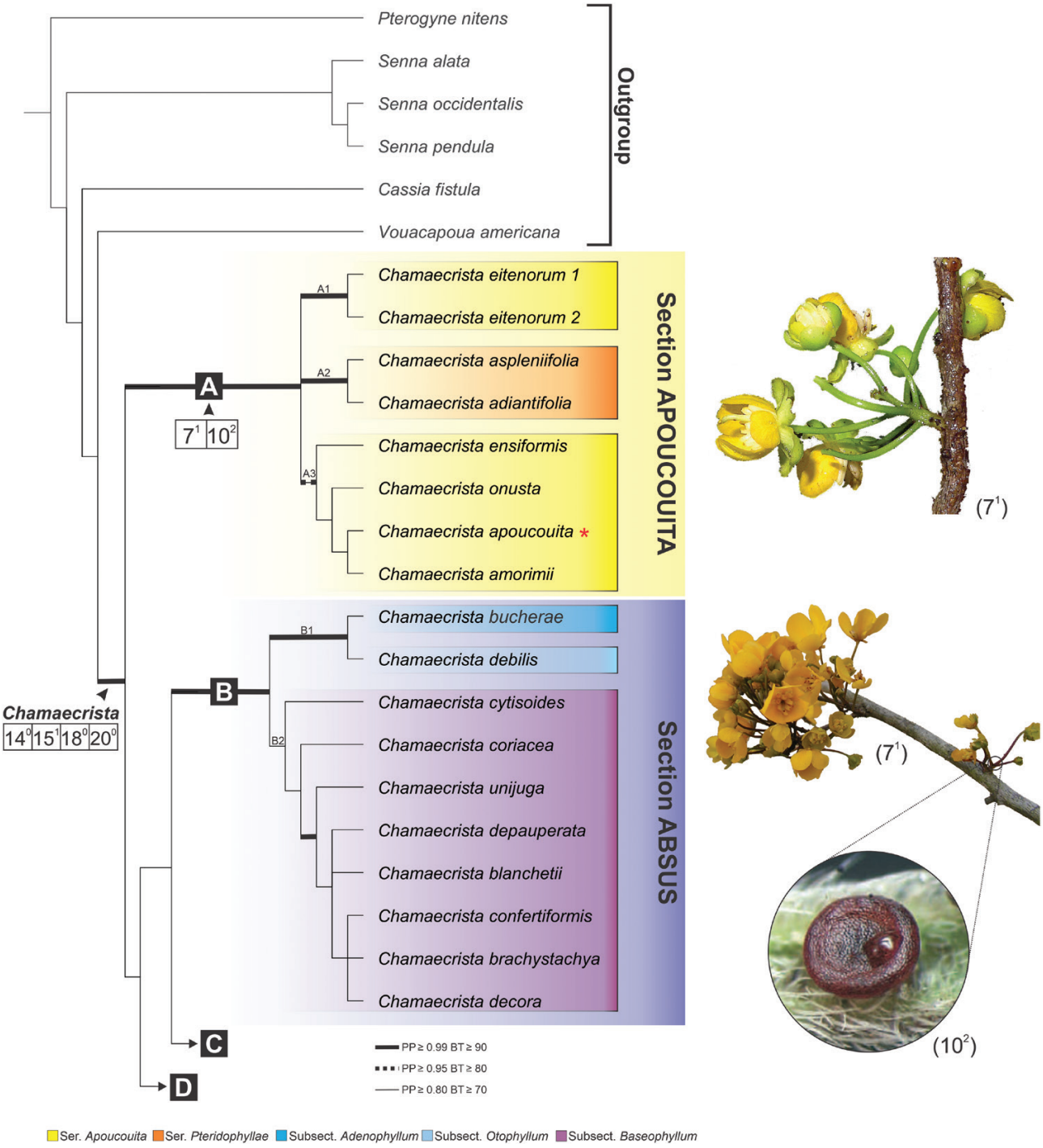

Figure 3. Part of the tree resulting from the Bayesian analysis of a *Multilocus* sampling showing clades A and B and outgroup. Clades and species marked in colours correspond to the taxa recognized in the classification of Irwin & Barneby (1982). Clades marked with letters are discussed in the text. Red asterisks indicate type species for a section. Numbers in the squares indicate the synapomorphies with the annotation character^{state} and some of these are illustrated on the right. Support of the branches is represented by the thickness of the line, PP = posterior probability and BT = bootstrap value.

Despite the contributions of previous studies, no major changes to the classification of *Chamaecrista* were made, mainly because < 33% of the diversity of the genus was sampled in these studies. Compared to the studies of Conceição *et al.* (2009), Rando *et al.* (2016) and Souza *et al.* (2019a) who sampled 45, 55

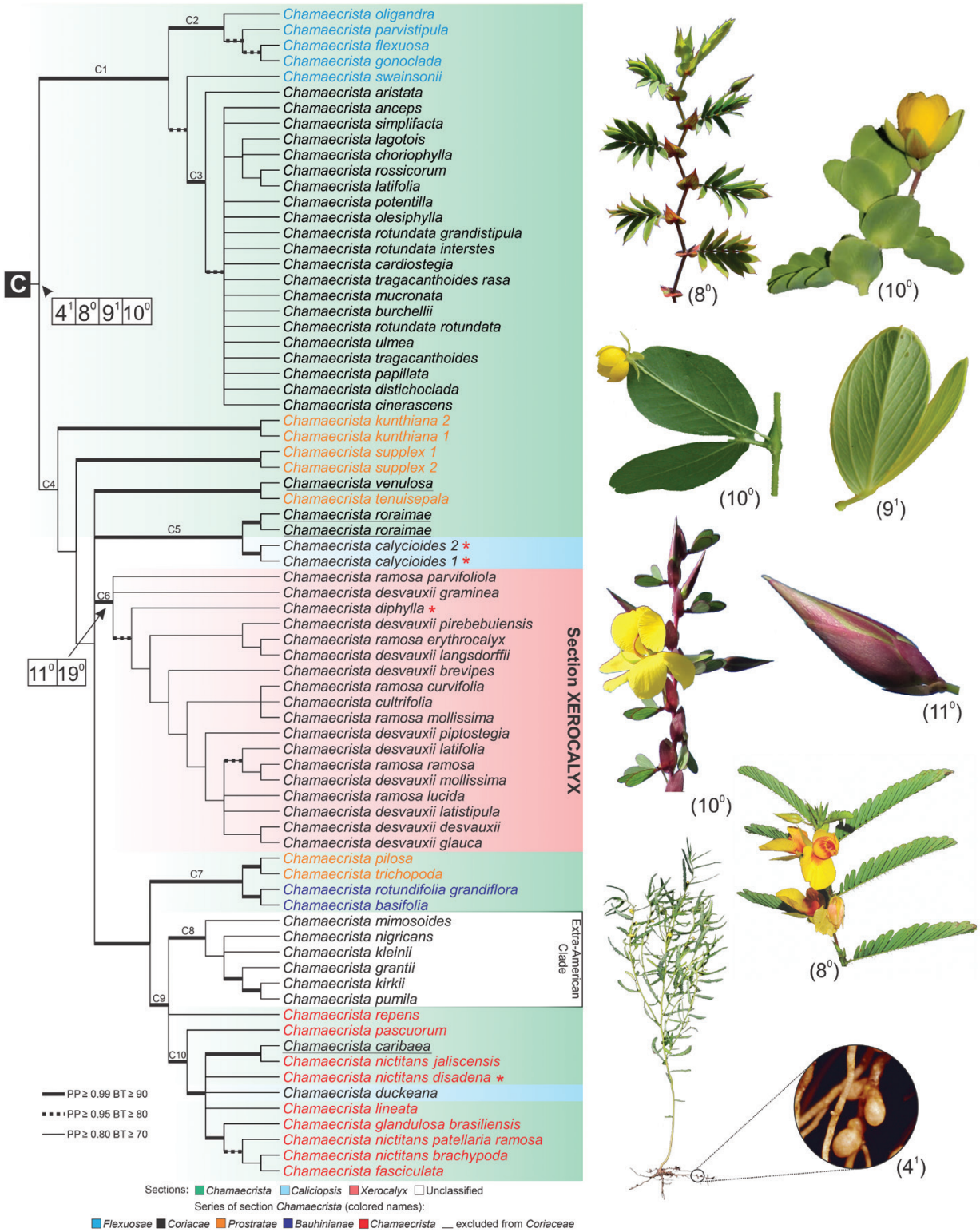

Figure 4. Part of the tree resulting from the Bayesian analysis of a *Multilocus* sampling showing clade C. Clades and species marked in colours correspond to the taxa recognized in the classification of Irwin & Barneby (1982). Clades marked with letters are discussed in the text. Red asterisks indicate type species for a section. Taxa with three names are varieties

and 85 *Chamaecrista* spp., respectively, our study comprises 210 species, which together covers 90% of the categories recognized by Irwin & Barneby (1982) and the pantropical distribution. Our overview of the infrageneric relations in *Chamaecrista* recovered four main clades (A, B, C and D), which we discuss next.

Clade A: the tree group with cauliflorous inflorescences

Clade A comprises exclusively species from *Chamaecrista* section *Apoucouita*, which is a phylogenetically and morphologically well-supported group (Figs 1–3). In our analyses section *Apoucouita* was represented by seven out of its 22 species and emerged as monophyletic and sister to all other species of the genus; a similar relationship was observed by Conceição *et al.* (2009) and Souza *et al.* (2019a) in which the section was represented by only two species. The species of *Chamaecrista* section *Apoucouita* are easily recognized and distinguished by a unique combination of characters that include the arboreal or shrubby habit, leaves with extrafloral nectaries on the petiole, rachis and/or inflorescence, cauliflorous racemes, anthers pubescent across almost their whole surface, and legumes pendulous and relatively large (7–15 cm long). Furthermore, morpho-anatomical evidence suggests that section *Apoucouita* is the only group of *Chamaecrista* with hypostomatic leaflets (Coutinho *et al.*, 2016). Unlike most species of the genus, species of section *Apoucouita* occur in rain forests (the Atlantic Forest of north-eastern and south-eastern Brazil and in Amazonia region of Brazil and surrounding countries).

Irwin & Barneby (1982) divided the section into two series: series *Pteridophyllae* and series *Apoucouita*. Series *Pteridophyllae* comprised two species with multifoliolate leaves (ten to 20 leaflet pairs per leaf) and series *Apoucouita* contained 19 species with paucifoliolate leaves (with up to five leaflet pairs per leaf). In our analysis, the series *Pteridophyllae* is monophyletic, whereas series *Apoucouita* (represented by five species) is paraphyletic, with the species clustered in two distinct lineages (Fig. 3).

Clade B: the Baseophyllum group

Clade B includes all species of the subsections *Adenophyllum* (one species), *Otophyllum* (one species) and *Baseophyllum* (eight species) from section *Absus sensu* Irwin & Barneby (1982) (Fig. 2, 3). The clade is sister to a clade that groups species of sections *Chamaecrista*, *Caliciopsis* and *Xerocalyx* (Fig. 2, 4; Clade C). In our *Multilocus* analysis, we recovered two subclades (B1 and B2), one with species of subsections *Adenophyllum* and *Otophyllum* (B1, Fig. 3) sister to another subclade that comprises the monophyletic subsection *Baseophyllum* (B2, Fig. 3).

Conceição *et al.* (2009) observed a similar position for subsection *Baseophyllum*, demonstrated its monophyly and its relationship with sections *Chamaecrista*, *Caliciopsis* and *Xerocalyx*, and subsection *Absus* and section *Grimaldia* were also shown to be closely related. Our results strongly suggest two distinct origins of the subsections of section *Absus* pointing to its non-monophyly. In addition to corroborating these relationships, our study reveals, for the first time, the relationship of subsection *Baseophyllum* with subsections *Adenophyllum* and *Otophyllum*.

The close relationship of subsections *Baseophyllum*, *Otophyllum* and *Adenophyllum* with members of sections *Chamaecrista*, *Caliciopsis* and *Xerocalyx* is witnessed by the common presence of nectaries on the leaves of all these taxa, whereas the absence of nectaries and presence of glandular trichomes are typical of the related subsection *Absus* and section *Grimaldia*.

Species of clade B occur mainly in campo rupestre ('rocky fields') vegetation in north-eastern and south-eastern Brazil, with the exception of the peculiar, little-known and infrequently collected *C. bucherae* which is endemic to Cuba. In addition to the leaf nectaries, the species of clade B share glabrous branches, inflorescences, flowers and fruits; leaves with one to three pairs of leathery leaflets (except for *C. debilis* with eight to 15 pairs of membranous leaflets), flowers with an internal petal partially enveloping the stamens, and a pod with a thickened margin, a combination of characteristics not found in any other group of the genus. Furthermore, in the *Baseophyllum* group the leaves are epistomatic, whereas in section *Apoucouita* they are hypostomatic, and in most other species, apart from these groups, the leaves are commonly amphistomatic (Coutinho, Francino & Meira, 2013; Coutinho *et al.*, 2016).

Clade C: herbaceous/shrubby group with solitary flowers or fascicles

Clade C includes 45 species of sections *Chamaecrista* (39 species), *Caliciopsis* (two species) and *Xerocalyx* (four species) (Fig. 4), corresponding to 67, 100

and those with four names are subspecies and varieties. Numbers in the squares indicate the synapomorphies with the annotation character^{state} and some of these are illustrated on the right. Support of the branches is represented by the thickness of the line, PP = posterior probability and BT = bootstrap value.

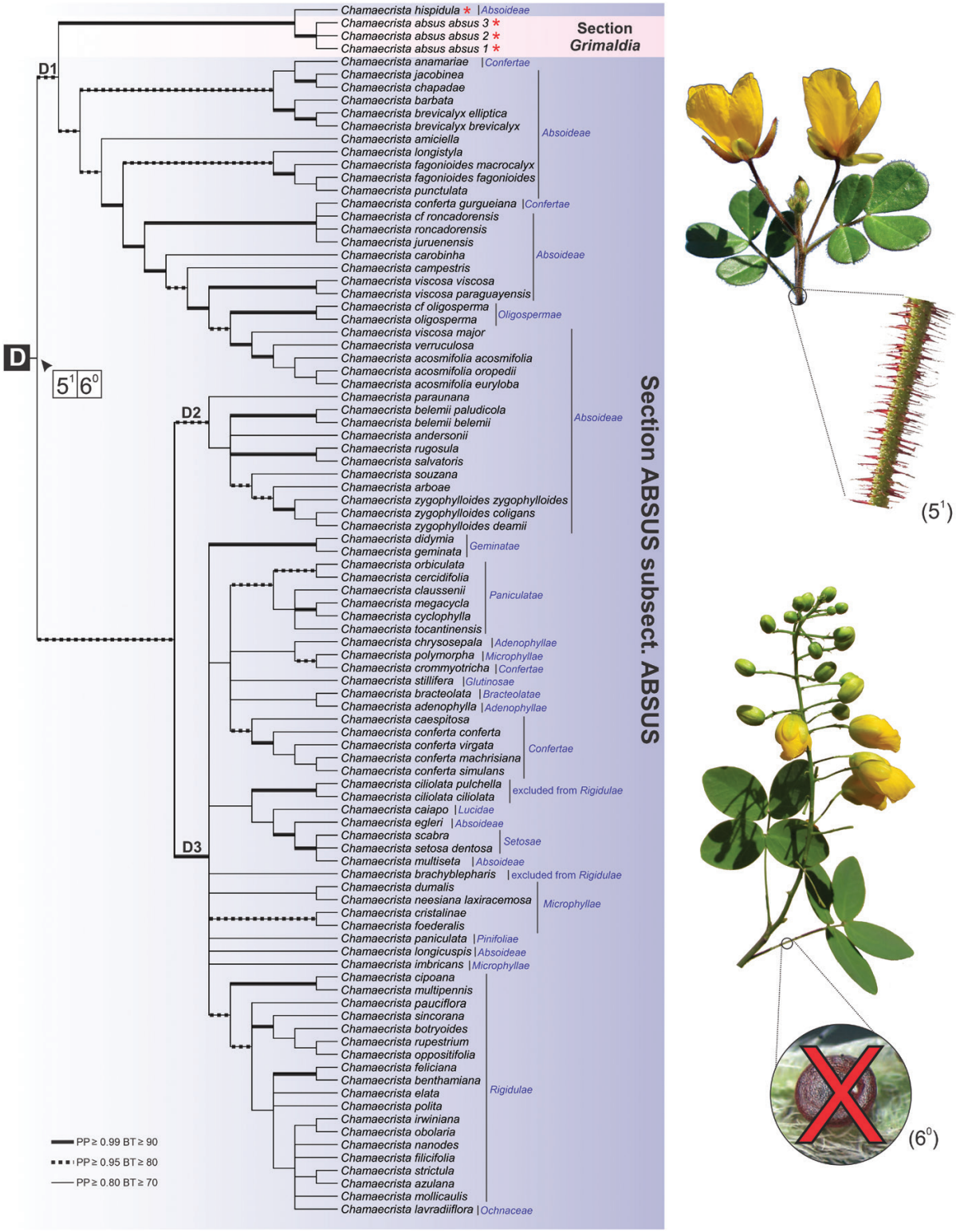

Figure 5. Part of the tree resulting from the Bayesian analysis of a *Multilocus* sampling showing clade D. Names in blue text on the right of the species correspond to the series of *Chamaecrista* section *Absus* subsection *Absus*, *sensu* Irwin & Barneby (1982) together with updates by Souza *et al*. (2019) and Mendes *et al*. (2020). Clades marked with letters are discussed in the text.

and 100% of their diversity, respectively (Table 1). Conceição *et al.* (2009) and Torres *et al.* (2011) found clades with a similar sectional composition based on a total sampling of 15 and 18 species, respectively. Our study agrees with previous results in highlighting the non-monophyly of these sections and suggesting that they should be included in a single section.

Section *Caliciopsis sensu* Irwin & Barneby (1982) comprises two species [*C. calycioides* (Collad.) Greene and *C. duckeana* (P.Bezerra & Afr. Fern.) H.S.Irwin & Barneby], and our results reveal this section to be paraphyletic. In our analyses, *C. calycioides* emerged as related to *C. roraimae* (Benth.) Gleason from section *Chamaecrista* (Fig. 4, clade C5), whereas *C. duckeana* is in a separate clade with other species of section *Chamaecrista* (Fig. 4, clade C10). In previous studies (Conceição *et al.*, 2009; Torres *et al.*, 2011), only *C. calycioides* was sampled from section *Caliciopsis* and it was found to be related to members of section *Chamaecrista*. According to Irwin & Barneby (1982), the members of section *Caliciopsis* have vegetative and floral morphologies similar to members of section *Chamaecrista*, but the section was considered to be distinct due to the peculiar calyx with prominent parallel venation that resembles more the members of section *Xerocalyx*.

Chamaecrista section *Xerocalyx* comprising four species and 24 infraspecific taxa (*sensu* Irwin & Barneby 1982; Barbosa *et al.*, 2016) is always resolved as a well-supported monophyletic group in all phylogenetic analyses of *Chamaecrista* (Conceição *et al.*, 2009; Torres *et al.*, 2011; Barbosa *et al.*, 2016). However, the specific and intraspecific internal relationships in section *Xerocalyx* remain unclear (Fig. 4). For example, *C. desvauxii* (Collad.) Killip and *C. ramosa* (Vogel) H.S.Irwin & Barneby are not monophyletic (Fig. 4, clade C6), and both are considered by some authors to be unresolved complexes (Torres *et al.*, 2011; Barbosa *et al.*, 2016). Members of section *Xerocalyx* superficially resemble the paucifoliolate species of section *Chamaecrista* [e.g. *C. rotundifolia* (Pers.) Greene], but are distinguished by their resupinate flowers, multi-striate calyces with prominent parallel veins, two sepals shorter than others and claviform seeds (Irwin & Barneby, 1982).

Section *Chamaecrista* was divided into six series by Irwin & Barneby (1982): *Bauhinianae*, *Chamaecrista*, *Coriaceae*, *Greggianae*, *Flexuosae* H.S.Irwin & Barneby and *Prostratae* (Benth.) H.S.Irwin & Barneby, differentiated mainly by characters of their branches, leaves and flower morphology. Based on our results, the section is polyphyletic and only the series *Bauhinianae* (*sensu* Irwin & Barneby 1982) and the recently re-circumscribed *Coriaceae* (*sensu* Rando *et al.*, 2019) are monophyletic, whereas the others are para- or polyphyletic (Fig. 4). Even so, some morphologically supported clades can be observed, e.g. subclade C1 (Fig. 4), which includes sub-shrubby and shrubby species with a woody underground system and typically rigid, chartaceous or coriaceous leaflets. This subclade includes members of the series *Flexuosae* and *Coriaceae*, the former is paraphyletic because one of its species [*C. swainsonii* (Benth.) H.S.Irwin & Barneby] is sister to series *Coriaceae*, whereas the remaining species form a well-supported clade (Fig. 4, subclade C2) characterized mainly by flexuous branches. *Chamaecrista swainsonii* was variously placed in previous studies, sometimes related to members of series *Coriaceae* (Conceição *et al.*, 2009) and sometimes to members of series *Flexuosae* (Rando *et al.*, 2016; Silva, Souza & Alonso, 2019). In those studies, *Flexuosae* was represented by a maximum of four species, whereas we have sampled five out of the six species considered to belong to the series.

Series *Coriaceae* was recently redefined (Rando *et al.*, 2016, 2019) as a monophyletic group by the exclusion of *C. caribaea* (Northr.) Britton, *C. roraimae* and *C. venulosa* (Benth.) H.S.Irwin & Barneby, which had been included in the series by Irwin & Barneby (1982). These three species emerged more related to series *Prostratae* and section *Caliciopsis* in the phylogenetic analysis of Rando *et al.* (2016) and in our study (Fig. 4). Our subclade C3 (Fig. 4) recovered the same species composition for 'Coriaceae' as presented by Rando *et al.* (2016); however, the subclades 'Bifoliolate' and 'Multifoliolate' proposed by Rando *et al.* (2016) in *Coriaceae* were not recovered in our analysis (Fig. 4).

Subclade C4 includes three series of section *Chamaecrista* (series *Prostratae*, *Bauhinianae* and *Chamaecrista sensu* Irwin & Barneby); two species excluded from series *Coriaceae* (*sensu* Rando *et al.*, 2016) and 18 taxa of section *Xerocalyx* and one of *Caliciopsis* (Fig. 4). Series *Prostratae* is polyphyletic with *C. kunthiana* (Schltdl. & Cham.) H.S.Irwin & Barneby and *C. supplex* (Benth.) Britton & Killip in an early-diverging position in the subclade, whereas *C. tenuisepala* (Benth.) H.S.Irwin & Barneby is sister to *C. venulosa* (series *Coriaceae*), and *C. pilosa* (L.) Greene and *C. trichopoda* (Benth.) Britton & Killip are more closely related to species of series *Bauhinianae* (Fig. 4, subclade C7). Series *Bauhinianae* is monophyletic with two species [*C. basifolia* (Vogel) H.S.Irwin & Barneby

Red asterisks indicate type species for a section. Taxa with three names are varieties and those with four names are subspecies and varieties. Numbers in the squares indicate the synapomorphies with the annotation character^{state} and are illustrated on the right. Support of the branches is represented by the thickness of the line, PP = posterior probability and BT = bootstrap value.

and *C. rotundifolia*] and is differentiated from other species of clade C by the bifoliolate leaves which lack nectaries.

Subclade C9 grouped species of the polyphyletic *Chamaecrista* series *Chamaecrista*, one species of section *Caliciopsis*, one species excluded from series *Coriaceae* (*sensu* Rando *et al.*, 2016) and a monophyletic group of six extra-American species without systematic position (Fig. 4, subclade C8). Taxa of subclade C9 have a wide distribution range and share inflorescences in fascicles in a supra-axillary position, whereas other species of clade C have axillary fascicles. All extra-American *Chamaecrista* spp. (including those not sampled and excluding *C. absus* from section *Grimaldia*) are similar to members of *Chamaecrista* section *Chamaecrista*. Irwin & Barneby (1982), however, did not treat them in their classification, nor in local floras of Africa, Asia and Oceania; these species have never been formally placed in any supraspecific categories, but it is clear from our phylogenetic and morphological results that they should be placed in a redefined section *Chamaecrista*.

Despite all this diversity, clade C groups most species known to have root nodulating capacity, leafy stipules, alternate-distichous leaves and flowers solitary or in axillary or supra-axillary fascicles. Most of the species are American, with fewer species in Africa, Asia and Oceania. The woody species occur in savannas, campo rupestre or desert habitats, but most other species occur in disturbed habitats where an herbaceous habit and rapid life cycle from germination to seed dispersal are more common. Based on this, the option of considering *Chamaecrista* a single section that includes sections *Xerocalyx* and *Caliciopsis* agrees with our phylogenetic and morphological results and corroborates the conclusions of Conceição *et al.* (2009) and Torres *et al.* (2011) in previous studies based on lower sampling.

Clade D: the viscous indumentum group

Clade D (Fig. 5) includes the monospecific section *Grimaldia* and the diverse subsection *Absus sensu* Irwin & Barneby (1982). These two taxa have always considered to be phylogenetically and morphologically related (Irwin & Barneby, 1982; Conceição *et al.*, 2009; Torres *et al.*, 2011; Souza *et al.*, 2019a) and share glandular trichomes on vegetative and/or reproductive structures, racemose inflorescences and the absence of leaf nectaries; this combination of traits easily separates them from all other sections.

Section *Grimaldia* contains a single pantropically distributed species (*C. absus*) with two varieties that can be differentiated by a unique set of characters including alternate-distichous leaves, glandular trichomes throughout the plant, a leafy appendix on the leaf rachis, racemose inflorescences, flowers without a petal enveloping the stamens and orange or red petals an the androecium with three to seven fertile stamens. Some of these characters commonly occur in members of section *Chamaecrista* and others are typical of subsection *Absus* and, due to this, Irwin & Barneby (1982) suggested that *C. absus* could represent an intermediary species between sections *Absus* and *Chamaecrista*, which is why they preferred to consider it as a separate monospecific section. However, our results indicate that *C. absus* is more related to subsection *Absus* and as sister to *C. hispidula* (Vahl) H.S.Irwin & Barneby of series *Absoideae* (Fig. 5).

Section *Absus*, as previously mentioned, is not monophyletic because subsections *Adenophyllum*, *Baseophyllum* and *Otophyllum* appear in a distinct clade (clade B, Fig. 4), whereas subsection *Absus* is positioned in clade D, related to section *Grimaldia*. The subsection *Absus* comprises *c.* 180 species and has been divided into 31 series (Irwin & Barneby 1982), of which 141 species and 27 series were sampled in this study. In our analysis, most series were recovered as para- or polyphyletic, including the species-rich series *Absoideae*, *Microphyllae* and *Ochnaceae* (Fig. 5), but we highlight that series recently redefined as *Rigidulae* and *Paniculatae* (Souza *et al.*, 2019a, and Mendes *et al.*, 2020, respectively) were recovered as monophyletic based on their new circumscriptions. Nevertheless, the resolution in clade D is generally low and it is not possible to constructively comment on relationships among all the series of subsection *Absus*. This group is mainly from the Brazilian cerrado and campo rupestre vegetation and appears to have had a recent and rapid diversification in these vegetation types, as hypothesized in studies of time divergence for series *Rigidulae* and *Paniculatae* (Souza *et al.*, 2019a, and Mendes *et al.*, 2020, respectively). This is a common pattern in other genera of Fabaceae diverse in these two vegetation types (Simon *et al.*, 2009; Souza *et al.*, 2013; Queiroz *et al.*, 2015; Alcantara, Ree & Mello-Silva, 2018; Inglis & Cavalcanti, 2018; Vaconcelos *et al.*, 2020).

Despite the low resolution at species level, our *Multilocus* analysis results recovered three well-supported subclades in clade D (subclade D1: 0.96 PP and 89% BT; subclade D2: 0.98 PP and 85% BT; subclade D3: 0.99 PP and 90% BT, Fig. 5). Subclade D1 includes *C. absus* (section *Grimaldia*) and members of series *Absoideae*, *Confertae* and *Oligospermae* (subsection *Absus*). These taxa share leaves predominantly with two pairs of papyraceous leaflets, non-striate branches and bark sometimes exfoliating, and they are distributed mainly in the Americas with six species endemic to Brazil.

Subclade D2 (Fig. 5) consists of 11 taxa from series *Absoideae* (*sensu* Irwin & Barneby 1982) all

endemic to Brazil and growing in cerrado, campo rupestre, caatinga or restinga vegetation in north-eastern Brazil. The species of this subclade have leaves consistently tetra-foliolate with papyraceous or chartaceous leaflets and their branches are commonly striate.

Subclade D3 (Fig. 5) includes taxa of 26 series of subsection *Absus* and encompasses the greatest diversity in the genus with species differing in habit, foliage (leaves with one to 70 pairs of leaflets) and organization of their inflorescences and flowers. Nevertheless, the taxa of subclade D3 share the characters of an androecium with ten fertile, isomorphic stamens and oblong fruits covered by glandular trichomes. In contrast to the tetra-foliolate species in subclades D1 and D2 the leaflets of tetra-foliolate species in subclade D3 are conspicuously dorsoventrally differentiated in colour and/or texture, coriaceous or papyraceous, oblanceolate to obovate and glabrous or not; when papyraceous, the leaflet apex is acuminate or cuspidate. Species of this subclade are closely associated with the Brazilian cerrado and campo rupestre, where *c*. 130 species are endemic.

Character evolution in *Chamaecrista*

Inflorescence type, leaflet venation pattern, leaflet number per leaf, trichome type, presence, location and type of extrafloral nectaries and androecium arrangement have long been used in the classification of *Chamaecrista* (Irwin & Barneby, 1982). Our study shows that most of these characters are homoplastic, having evolved independently several times (Supporting Information, Appendices S11–S20). However, some characters, including isomorphic androecium (character 14), pubescence of the anther suture (character 15), elastic fruit dehiscence (character 18) and bi-bracteolate pedicels (character 20), emerged as potential synapomorphies of *Chamaecrista* (Supporting Information, Appendices S17–S20) and were the main characters used to reinstate the genus and differentiate it from *Cassia* and *Senna* (Irwin & Barneby, 1982).

Cauliflorous inflorescence (character 10) and nectaries on the inflorescence axis (character 7) emerged as synapomorphies for clade A (Supporting Information, Appendices S14, S15). The species of section *Apoucouita* are trees mostly from forest margins, and the cauliflorous inflorescences could be an adaptation to partition pollinators, since cauliflorous inflorescences can allow trees to be pollinated by animals that cannot climb or bees that cannot fly high (Diniz, Domingos-Melo & Machado, 2019). Nectaries on the inflorescence axes may have evolved together with cauliflory, since their mutualistic interactions with ants provides a secondary defence against herbivory (Del-Claro, Rico-Gray & Torezan-Silingardi, 2016). Moreover, although pendulous fruits (character 17) are a plesiomorphic condition in *Chamaecrista* it is a character exclusive to section *Apoucouita* (Supporting Information, Appendix S19) shared with rain forest species of *Cassia* and some *Senna* spp.

Clade B does not have any morphological synapomorphies, although its species share a shrubby habit (character 1), racemose inflorescences (character 10) and a decamerous androecium concealed by a strongly heteromorphic corolla, with an ovate or falcate, convolute petal interposed between the stamens (character 13). Irwin & Barneby (1982) classified subsections *Baseophyllum*, *Adenophyllum* and *Otophyllum* as part of section *Absus* based on these characters. However, our analyses do not support this taxonomy, instead suggesting an independent evolution and convergence of floral morphology between clades B and D. Flowers of clade B species are more 'closed' with the internal petal more open, whereas those of clade D, in general, are more 'open' with the internal petal strongly interposed between the stamens. These slight floral differences in clade D may be related to a more effective pollination system in this group (Costa *et al.*, 2012) which led to a greater diversification than observed in clade B.

Alternate-distichous leaves (character 8), leaflets with a palmate venation (character 9) and flowers solitary or grouped in fascicles (character 10) are synapomorphies of clade C, which includes taxa of sections *Chamaecrista*, *Xerocalyx* and *Caliciopsis*. In section *Xerocalyx*, leaflet venation evolved further into a parallel pattern (character 9) (Supporting Information, Appendix S15). Species of this clade also commonly have short life cycles and abundant seed-production, as observed in many species of section *Chamaecrista* [e.g. *C. fasciculata* (Michx.) Greene and *C. nictitans* (L.) Moench], allowing them to survive the winter in temperate regions as seeds. This might explain their colonization of various disturbed environments in North America and throughout the Tropics (Irwin & Barneby, 1982; Naisbitt, James & Sprent, 1992).

Clade D, including sections *Grimaldia* and *Absus* (subsection *Absus*), shares two synapomorphies, the presence of glandular trichomes (character 5) and loss of extrafloral nectaries (character 6) (Supporting Information, Appendix S13), supporting the combining of these taxa into one section. The emergence of glandular trichomes has probably played an important role in the rapid diversification of this group in open areas of the Brazilian cerrado, where > 100 of the species are endemic (Irwin & Barneby, 1982). According to Wagner (1991), glandular trichomes, when present on vegetative structures, provide protection to the plant by secreting compounds that prevent herbivory

by insects. This important evolutionary step seems to have been accompanied by several changes in DNA, as observed in the long length of the branches of clade D in all analyses (Figs 1, 2, Supporting Information, Appendices S3–S10). In our alignments, we also observed that the sequences of species in clade D are quite different, especially in their nuclear regions (ITS and ETS), which on average are 200–300 bp larger than other species analysed in our study. These DNA changes may represent molecular synapormophies of clade D.

Proposed new infrageneric classification of *Chamaecrista*

Our molecular and morphological results and those of previous studies (e.g. Conceição *et al.*, 2009; Torres *et al.*, 2011; Rando *et al.*, 2016; Souza *et al.*, 2019a; Mendes *et al.*, 2020) lead us to conclude that *Chamaecrista* should have its infrageneric classification modified based on the monophyletic groups revealed in our molecular analyses. The four main clades (A–D) recovered in all of our analyses are proposed here as the newly circumscribed sections of *Chamaecrista*, namely *Chamaecrista* section *Apoucouita* (Clade A: a tree group with cauliflorous inflorescences), *Chamaecrista* section *Baseophyllum* (Clade B: Baseophyllum group), *Chamaecrista* section *Chamaecrista* (Clade C: herbaceous/shrubby group with solitary flowers or fascicles) and *Chamaecrista* section *Absus* (Clade D: a viscous indumentum group). In addition, we recognize the subclades of clade D (D1–D3) as subsections of section *Absus*. (D1: *Chamaecrista* section *Absus* subsection *Absus*; D2: *Chamaecrista* section *Absus* subsection *Zygophyllum* and D3: *Chamaecrista* section *Absus* subsection *Viscosa*) (Fig. 6). The proposed new classification is presented in Figure 6 and the adjustments to previous classifications (essentially that of Irwin & Barneby 1982, with some more recent minor adjustments) are explained next.

Our concept of section *Apoucouita* is the same as that proposed by Irwin & Barneby (1982). However, at least for now, we decided not to retain series *Apoucouita* and *Pteridophyllae* proposed by Irwin & Barneby (1982) due to the low sampling of these taxa and their unclear relationship.

Section *Baseophyllum* is up-ranked from subsection *Baseophyllum* and subsections *Adenophyllum* and *Otophyllum* are placed in synonymy. No internal division is proposed for this group that only comprises ten species.

Section *Chamaecrista* now includes sections *Xerocalyx* and *Caliciopsis*, and all extra-American *Chamaecrista* spp. (except *C. absus*), and we no longer recognize any series within the section. Although *Xerocalyx* is a genetically and morphologically well-defined subgroup of section *Chamaecrista*, to recognize it as a distinct section would necessitate the creation of at least six other sections, each of which would lack diagnostic characters and thus be difficult to recognize. Based on the same reasoning, we do not recognize any taxa at the rank of series in our redefined section *Chamaecrista*. The monospecific series *Greggianae*, the only series of section *Chamaecrista* not sampled in our study, is included in the section because morphologically it shares some key characters of section *Chamaecrista*, such as alternate-distichous leaves: leaflets with a palmate venation and flowers solitary or grouped in fascicles.

Chamaecrista section *Absus* in our proposed classification includes as a synonym *Chamaecrista* section *Grimaldia* (*sensu* Irwin & Barneby, 1982), since *Absus* has nomenclatural priority because it was first described at section level by Colladon (1816) in *Cassia* (= *Cassia* section *Absus*). In our comprehensive sampling of the series of section *Absus*, most emerged as non-monophyletic and appear, in many cases, in a large polytomy. Based on these findings we decided not to recognize any of the series of subsection *Absus* proposed by Irwin & Barneby (1982). Nevertheless, we did recover three phylogenetically and morphologically well-supported subclades (D1–D3), and we propose these as three subsections: (1) *Chamaecrista* section *Absus* subsection *Absus*, including the type species of the section (*C. hispidula*), and with series *Absoideae* and *Oligospermae* (*sensu* Irwin & Barneby, 1982) included in synonymy; (2) *Chamaecrista* section *Absus* subsection *Zygophyllum*, a new subsection proposed here [its name is based on the selected type species of the taxon (*C. zygophylloides* (Taub.) H.S.Irwin & Barneby], comprising eight species from the former series *Absoideae* (*sensu* Irwin & Barneby, 1982) and (3) *Chamaecrista* section *Absus* subsection *Viscosa* is created to place the remaining taxa from the 29 series of *Chamaecrista* section *Absus* subsection *Absus* (*sensu* Irwin & Barneby, 1982). All series previously recognized are considered, at least preliminarily, as synonyms of these subsections due to a lack of resolution at species level. The four monospecific series of subsection *Absus* not sampled in our study (*Andromedeae*, *Atroglandulosae*, *Hassleranae* and *Incanae*) are also being temporarily allocated to section *Absus* subsection *Viscosa* because they share similar morphologies with this subsection.

TAXONOMIC TREATMENT

Given the changes proposed here to the higher level infrageneric classification of *Chamaecrista*, we now provide a key to the four sections recognized

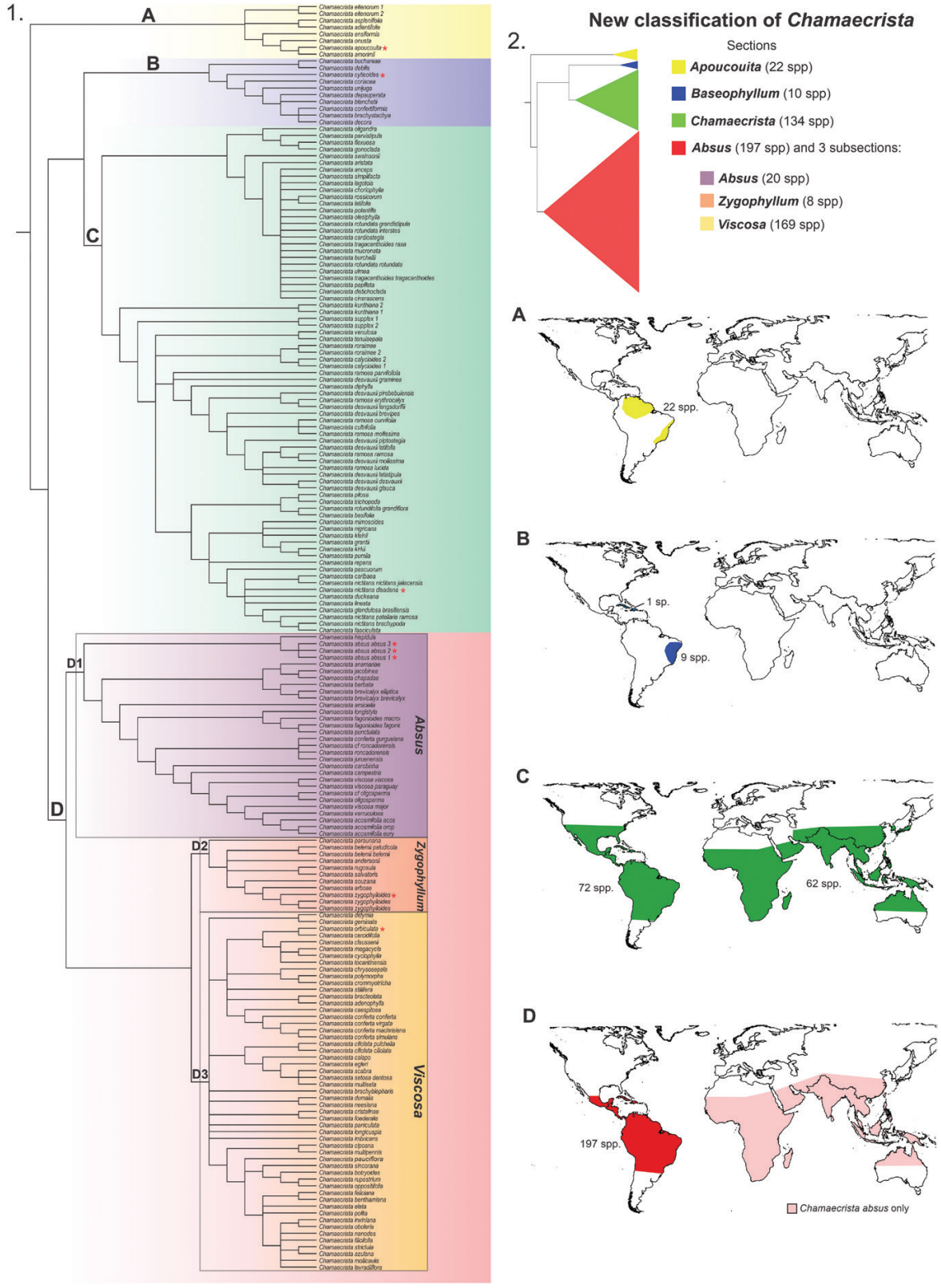

Figure 6. New infrageneric classification for *Chamaecrista*. 1, Cladogram showing the taxa recognized in the new classification. 2, Compressed version of 1 giving number of species in each section with geographical distribution of clades A, B, C and D. Red asterisks indicate type species of a section.

in our treatment (*Apoucouita*, *Baseophyllum*, *Chamaecrista* and *Absus*) and descriptions in which we highlight the diagnostic characters in bold type. We provide comments on their species composition, their geographical distribution and photographs to show their morphological diversity (Figs 7–12). In addition, an up-to-date list of all accepted binomials in the genus, and the sections to which each species belongs is provided in Supporting Information, Appendix S21.

1. ***Chamaecrista*** section ***Apoucouita*** (Benth.) H.S.Irwin & Barneby, Brittonia 31(1): 155. 1979. ≡ *Cassia* section *Apoucouita* Benth. *In* Martius, Fl. Bras. 15(2): 129. 1870. – Type species: *Chamaecrista apoucouita* (Aubl.) H.S.Irwin & Barneby.

= *Chamaecrista* series *Pteridophyllae* (H.S.Irwin & Barneby) H.S.Irwin & Barneby, Mem. New York Bot. Gard. 35: 641. 1982. ≡ *Cassia* series *Pteridophyllae* H.S.Irwin & Barneby, Brittonia 29(3): 279. 1977. ***Syn. nov***. Type species: *Chamaecrista adiantifolia* (Benth.) H.S.Irwin & Barneby.

Trees or perennial **shrubs**, 2–15 m tall, glabrous or pubescent without glandular trichomes. Stipules usually caducous or inconspicuous. **Extrafloral nectaries** patelliform or discoid on the leaf petiole, leaf rachis and/or **on the inflorescence rachis or pedicels**. Leaves petiolate, alternate, spirally arranged or rarely distichous, (one–) two–35 pairs of leaflets per leaf, venation brochidodromous. Racemes cauliflorous or, less frequently, axillary. Buds globose with rounded or obtuse apex. Flowers with sepals similar in size and shape, with venation reticulate and inconspicuous, glabrous or with an external indumentum; petals yellowish, the three adaxial petals similar in size and length, and one of the two abaxial petals slightly asymmetrical, but not falcate nor interposed between the stamens; androecium with ten fertile isomorphic stamens, **anthers pubescent throughout their surface** or, less frequently, only on the sutures; ovary glabrescent or glabrous, style slightly curved at the apex. **Legumes 8–20 cm long**, **pendulous** with coriaceous valves. **Seeds 7–10 mm long**.

Chamaecrista section *Apoucouita* is a South American taxon with 22 species distributed mainly in the phytogeographic domains of Mata Atlântica and Amazonia in Brazil and neighbouring countries (Fig. 6), usually growing along humid forest margins. The morphological diversity of the section is illustrated in Figure 7.

2. ***Chamaecrista*** section ***Baseophyllum*** (Collad.) A.O.Souza, G.P.Lewis & M.J.Silva, ***comb. nov.*** ≡ *Cassia* section *Baseophyllum* Collad., Hist. Nat. Méd. Casses. 115. 1816. ≡ *Cassia* subsection *Baseophyllum* (Collad.) H.S.Irwin & Barneby, Mem. New York Bot. Gard. 30: 9. 1978. ≡ *Chamaecrista* subsection *Baseophyllum* (Collad.) H.S.Irwin & Barneby, Mem. New York Bot. Gard. 35: 646. 1982. Type species: *Chamaecrista cytisoides* (DC.) H.S.Irwin & Barneby.

KEY TO THE SECTIONS OF *CHAMAECRISTA*

1. Plants predominantly viscous due to the presence of glandular trichomes, glutinous dots or other secretory structures on the vegetative and/or reproductive organs; extrafloral nectaries absent, androecium decamerous (tri- to heptamerous only in *C. absus*) ..... 4. *Chamaecrista* section ***Absus***
1'. Plants non-viscous; glabrous or with an indumentum composed of non-glandular trichomes; extrafloral nectaries present on the petiole, leaf rachis and/or axis of the inflorescence, if nectaries are lacking (only two species) then the androecium is pentamerous 2
2. Trees or shrubs; racemes cauliflorous, commonly with nectaries on the inflorescence axis; anthers commonly pubescent throughout their surface; fruits pendulous and relatively large (8–20 cm long) ..... 1. *Chamaecrista* section ***Apoucouita***
2'. Shrubs, subshrubs or perennial herbs; racemes terminal or axillary, or in fascicles, or flowers solitary; nectaries on the inflorescece absent; anthers pubescent only in the sutures; fruits not pendulous and smaller (1.5–6 cm long) 3
3. Leaves alternate and spirally arranged; stipules caducous or inconspicuous or lanceolate when persistent; inflorescences racemose; flowers with one strongly heteromorphic petal interposed between the stamens ..... 2. *Chamaecrista* section ***Baseophyllum***
3'. Leaves alternate-distichous; stipules persistent, conspicuous and commonly foliaceous; inflorescences axillary or supra-axillary fascicles or flowers solitary, corolla with an asymmetrical abaxial petal, not interposed among the stamens ..... 3. *Chamaecrista* section ***Chamaecrista***

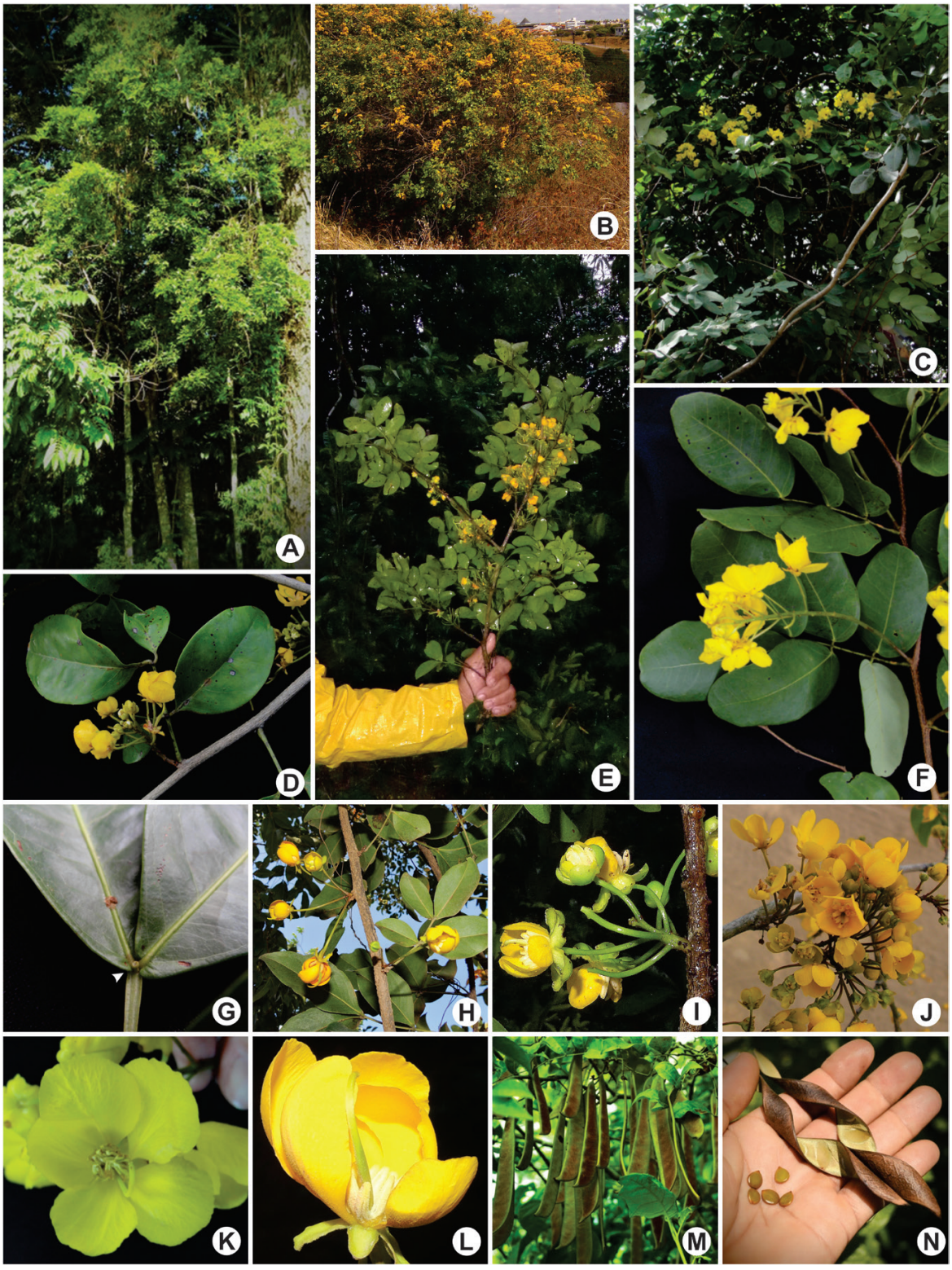

Figure 7. Morphological diversity of section *Apoucouita*. Tree habit: A, B, *Chamaecrista ensiformis*. Fertile branches: C–E, *C. ensiformis* and F, *C. xinguensis*. Extrafloral nectary between leaflets. G, *C. apoucouita*. Cauliflorous inflorescences: H–J, *C. ensiformis*. Flowers: K, *C. xinguensis* and L, *C. ensiformis*. Fruits: M, N, *C. ensiformis*. Photographs provided by Rubens Teixeira de Queiroz.

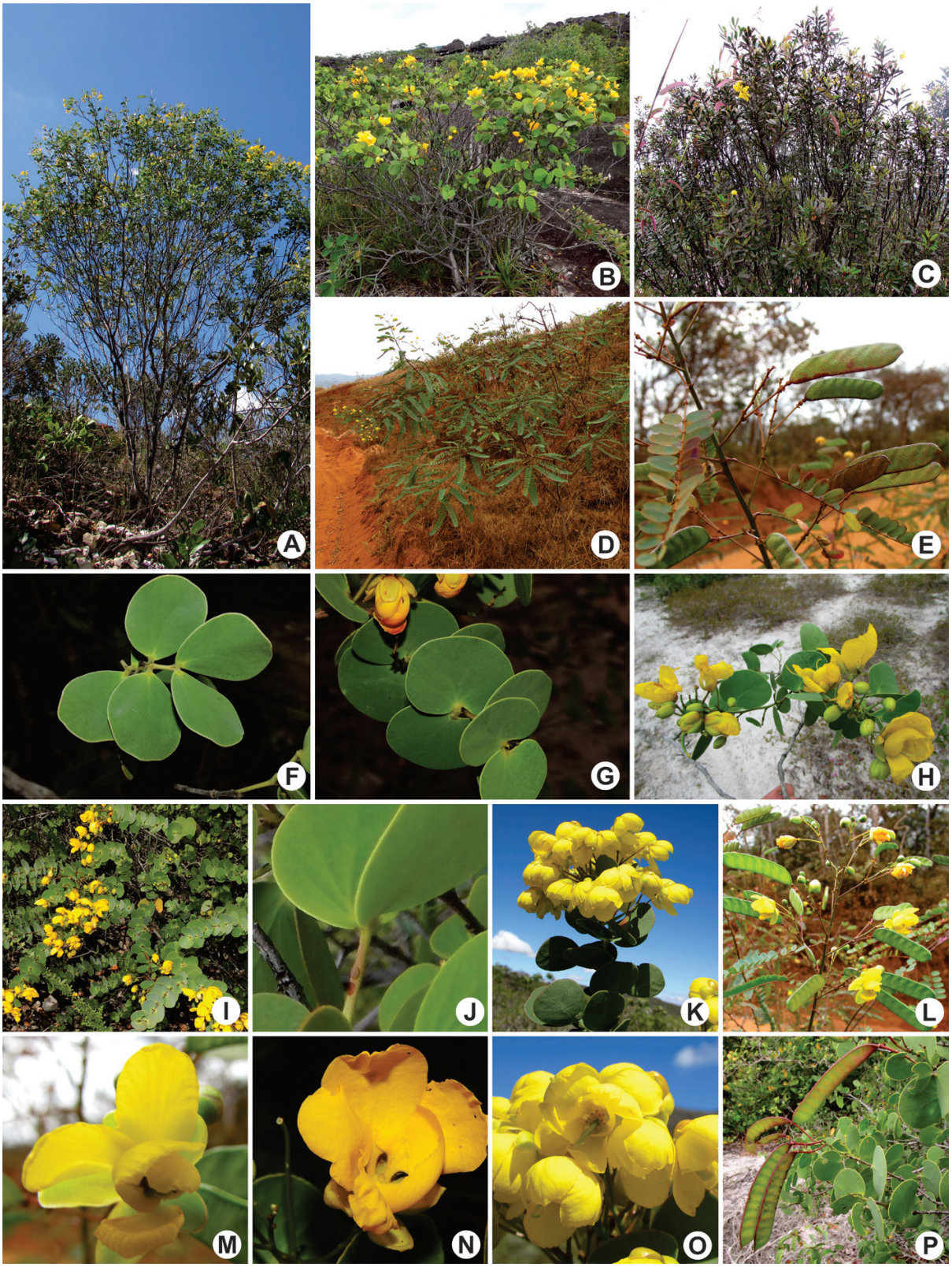

Figure 8. Morphological diversity of section *Baseophyllum*. Shrub habit: A, *Chamaecrista brachystachya*. B, *C. decora*. C, *C. confertiformis*. D, E, *C. debilis*. Leaves: F, *C. brachystachya* and G, *C. blanchetii*. Fertile branches: H, *C. unijuga*, I,

KEY TO THE SUBSECTIONS OF SECTION *ABSUS*

1. Leaves with one to 70 pairs of leaflets of varying shape, consistency and apex; when in exactly two pairs they are coriaceous and differentiated dorsoventrally in colour and texture, or they are oblanceolate or with an acuminate, acute or cuspidate apex; flowers with yellow petals ..... 4.2. subsection ***Viscosa***
1'. Leaves with exactly two pairs of membranaceous, papyraceous or chartaceous, elliptical, obovate or ovate leaflets, their apices rounded, emarginate or obtuse; flowers with yellow, orange or red petals (seven to 18 pairs of leaflets only in *C. oligosperma*, which has orange or red petals).....2
2. Branches commonly striate with whitish streaks and without exfoliating bark; petiole 1.0–1.5 times longer than the leaf rachis; flowers with yellow petals ..... 4.3. subsection ***Zygophyllum***
2'. Branches lack streaks and sometimes have exfoliating bark; petioles two to four times longer than the leaf rachis (except in *C. oligosperma*); flowers with yellow, orange or red petals ..... 4.1. subsection ***Absus***

= *Chamaecrista* subsection *Adenophyllum* (H.S.Irwin & Barneby) H.S.Irwin & Barneby, Mem. New York Bot. Gard. 35: 647. 1982. ≡ *Cassia* subsection *Adenophyllum* H.S.Irwin & Barneby, Mem. New York Bot. Gard. 30: 16. 1978. Type species: *Chamaecrista bucherae* (Moldenke) H.S.Irwin & Barneby. ***Syn. nov.***

= *Chamaecrista* subsection *Otophyllum* (H.S.Irwin & Barneby) H.S.Irwin & Barneby, Mem. New York Bot. Gard. 35: 647. 1982. ≡ *Cassia* subsection *Otophyllum* H.S.Irwin & Barneby, Mem. New York Bot. Gard. 30: 17. 1978. Type species: *Chamaecrista debilis* (Vogel) H.S.Irwin & Barneby. ***Syn. nov.***

Perennial shrubs and treelets, 1–5 m tall, erect, without a xylopodium, or less frequently a decumbent subshrub with a xylopodium, and 10–20 cm tall, **glabrous**. Stipules lanceolate or inconspicuous, persistent or caducous. Extrafloral nectaries discoid, positioned on the petiole or the leaf rachis between the leaflets, or in inter-foliolar regions of the rachis and on the peduncles. Leaves petiolate or sessile, alternate, spirally arranged, with one to 20(–25) pairs of leaflets, these chartaceous or coriaceous (membranaceous only in *C. debilis*), leaflet venation palmate or brochidodromous. **Racemes terminal**. Buds globose or ovoid with a rounded or obtuse apex. Flowers with the sepals equal in shape and size, with venation reticulate and inconspicuous, glabrous; petals yellowish, the three adaxial petals similar in size and one of the two abaxial petals **strongly heteromorphic and interposed between the stamens**; androecium with ten fertile isomorphic stamens, anthers pubescent along their sutures; ovary glabrous or with an indumentum, style curved at the apex. Legume 2–7 cm long, ascendant, valves coriaceous. Seeds 4–7 mm long.

Chamaecrista section *Baseophyllum* is an American taxon comprising ten species, nine of which are narrowly endemic to the states of Bahia and Minas Gerais, occurring in campo rupestre vegetation of the Espinhaço range in eastern Brazil, and one species is endemic to Cuba (*C. bucherae*) (Fig. 6). The section, as circumscribed here, includes *Chamaecrista* section *Absus* subsection *Adenophyllum* and section *Absus* subsection *Otophyllum sensu* Irwin & Barneby (1982) as synonyms. We recognize no infrasectional taxa above the rank of species. The morphological diversity of the section is illustrated in Figure 8.

3. ***Chamaecrista*** (L.) Moench section ***Chamaecrista***, Methodus, 272. 1794. **emend**. A.O. Souza, G.P. Lewis & M.J. Silva. Type species: *Chamaecrista nictitans* (L.) Moench.

= *Chamaecrista* section *Caliciopsis* H.S.Irwin & Barneby, Mem. New York Bot. Gard. 30: 9. 1978. Type species: *Chamaecrista calycioides* (Collad.) Greene. ***Syn. nov.***

= *Chamaecrista* section *Xerocalyx* (Benth.) H.S.Irwin & Barneby, Mem. New York Bot. Gard. 35: 862. 1982. ≡ *Cassia* section *Chamaecrista* subsection *Xerocalyx* Benth. *In* Martius, Fl. Bras. 15(2): 155. 1870. Type species: *Chamaecrista diphylla* (L.) Greene. ***Syn. nov.***

= *Chamaecrista* series *Bauhinianae* (Collad.) H.S.Irwin & Barneby, Mem. New York Bot. Gard. 35: 727. 1982. ≡ *Cassia* series *Bauhinianae* Collad. Hist. Nat. Méd. Casses. 119. 1816. Type species: *Chamaecrista rotundifolia* (Pers.) Greene. ***Syn. nov.***

= *Chamaecrista* series *Coriaceae* (Benth.) H.S.Irwin & Barneby, Mem. New York Bot. Gard. 35: 667. 1982. ≡ *Cassia* series *Coriaceae* Benth. Trans. Linn. Soc. London 27: 537. 1871. Type species: *Chamaecrista*

C. blanchetii. Petiolar extrafloral nectary: J, *C. decora*. Corymbiform raceme: K, *C. brachystachya*. Racemes: L, *C. debilis*. Flowers: M, *C. debilis*, N, *C. blanchetii* and O, *C. brachystachya*. Fruits: P, *C. unijuga*. Photographs provided by Rubens Teixeira de Queiroz and A. O. Souza.

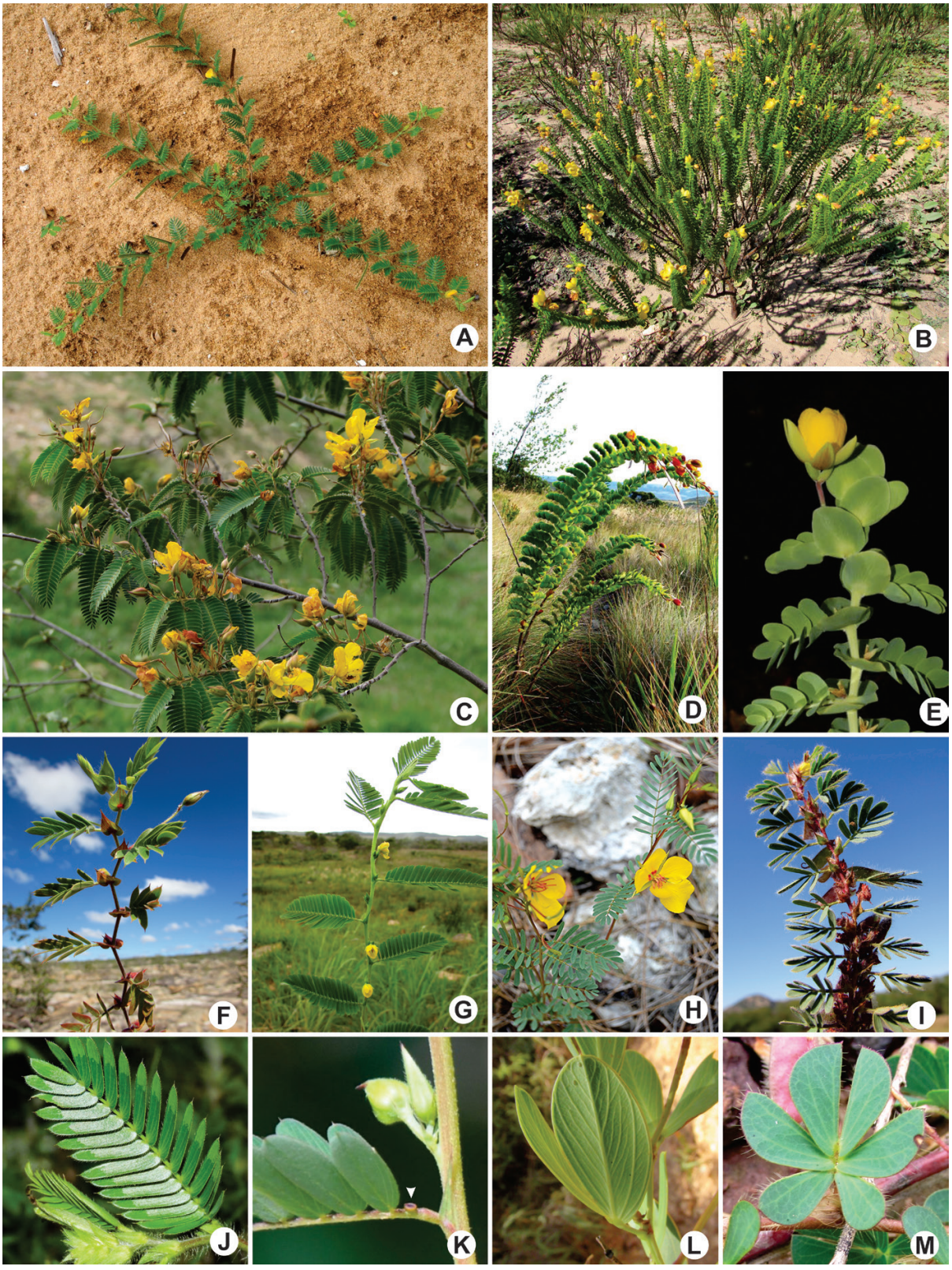

Figure 9. Morphological diversity of section *Chamaecrista*. Prostrate herb: A, *Chamaecrista serpens*. Shrub habit: B, *C. ramosa*, C, *C. roraimae* and D, *C. rotundata*. Branches and stipules: E, *C. rotundata*, F, *C. swainsonii* and G, *C. nictitans*.

choriophylla (Vogel) H.S.Irwin & Barneby. ***Syn. nov.***

= *Chamaecrista* series *Flexuosae* H.S.Irwin & Barneby, Mem. New York Bot. Gard. 35: 695. 1982. Type species: *Chamaecrista flexuosa* (L.) Greene. ***Syn. nov.***

= *Chamaecrista* series *Greggianae* H.S.Irwin & Barneby, Mem. New York Bot. Gard. 35: 735. 1982. Type species: *Chamaecrista greggii* (A. Gray) Pollard. ***Syn. nov.***

= *Chamaecrista* series *Prostratae* (Benth.) H.S.Irwin & Barneby, Mem. New York Bot. Gard. 35: 667. 1982. ≡ *Cassia* series *Prostratae* Benth., Fl. Bras. 15(2): 162. 1870. Type species: *Chamaecrista serpens* (L.) Greene. ***Syn. nov.***

Monocarpic herbs with a short life cycle or perennial subshrubs or shrubs with or without a xylopodium, 0.1–1.5 m tall, glabrous or with an indumentum of non-glandular trichomes. Stipules foliaceous, ovate or deltoid, persistent. Extrafloral nectaries, patelliform or discoid, on petioles, and less commonly on the distal interfoliolar segments, rarely absent. **Leaves** petiolate, **alternate, distichous**, leaflets in one to 65 pairs per leaf, venation palmate or parallel, rarely brochidodromus. **Flowers solitary or in axillary or supra-axillary fascicles**. Buds ovoid, with an acute or acuminate apex, less frequently obtuse. Flowers with sepals equal in shape and size or with two sepals reduced, venation reticulate and inconspicuous or parallel and prominent, glabrous or with an indumentum; petals yellowish, the three adaxial petals similar in size and of the two abaxial petals one asymmetrical and curved **but not covering the stamens**; androecium with three to ten fertile stamens, these isomorphic or slightly differing in size, anthers pubescent along the sutures; ovary glabrous or hairy, style curved at the apex. Legume 3–6 cm long, ascending, valves chartaceous. Seeds 2–5 mm long.

Chamaecrista section *Chamaecrista*, as defined here, comprises 134 species and includes *Chamaecrista* sections *Xerocalyx* and *Caliciopsis* (*sensu* Irwin & Barneby 1982) and 64 extra-American species, previously unclassified to infrageneric category. The section thus has a pantropical distribution but with its main centre of diversity in the Americas (*c.* 72 species) and the other species distributed in Africa, Asia and Oceania (Fig. 6). The species inhabit diverse environments and are often found at the edges of natural vegetation or in anthropogenically altered habitats. The morphological diversity of the section is illustrated in Figures 9 and 10.

4. ***Chamaecrista*** section ***Absus*** (Collad.) H.S.Irwin & Barneby, Mem. New York Bot. Gard., 35: 644. 1982. **emend**. A.O.Souza, G.P.Lewis & M.J.Silva ≡ *Cassia* section *Absus* Collad., Hist. Nat. Méd. Casses, 116. 1816. Type species: *Chamaecrista hispidula* (Vahl) Irwin & Barneby.

= *Chamaecrista* section *Grimaldia* (Schrank) H.S.Irwin & Barneby, Mem. New York Bot. Gard., 35: 664. 1982. ≡ *Cassia* section *Grimaldia* (Schrank) H.S.Irwin & Barneby, Mem. New York Bot. Gard., 30: 277. 1978. ≡ *Grimaldia* Schrank, Bot. Zeitung (Regensburg), 4: 184. 1805. Type species: *Chamaecrista absus* (L.) H.S.Irwin & Barneby.

Perennial shrubs or subshrubs, commonly with a xylopodium, or rarely trees or herbs, 0.1–10.0 m tall, with an indumentum of glandular and non-glandular trichomes, glutinous dots or other secretory structures, at least on the inflorescence, branches and/or leaflets, rarely glabrous. Stipules linear or lanceolate, rarely foliaceous, persistent or caducous. Extrafloral nectaries absent. Leaves petiolate, alternate and spirally arranged, distichous only in *C. absus*, with (one–) two to 45 pairs of leaflets, venation brochidodromus. Inflorescences racemose, mostly terminal, or axillary. Flowers with sepals equal in shape and size with venation reticulate and inconspicuous, with an indumentum or (rarely) glabrous; petals yellowish, rarely orange or reddish, the three adaxial petals similar in size or the adaxial-lateral petal shorter, of the two abaxial petals one strongly heteromorphic and interposed between the stamens; androecium with ten fertile isomorphic stamens (three to seven only in *C. absus*), anthers pubescent along the sutures; ovary hairy or (rarely) glabrous, style curved at the apex (straight only in *C. absus*). Legumes 1–6 cm long, ascending, valves chartaceous or coriaceous. Seeds 3–5 mm long.

Chamaecrista section *Absus* here includes *Chamaecrista* section *Grimaldia* (*sensu* Irwin & Barneby 1982) in synonymy. In our classification, the section comprises 197 species, 196 of which are exclusively American and *C. absus* is pantropical. Brazil is the main centre of diversity with 165 endemic species, mainly in cerrado and caatinga (Fig. 6). The morphological diversity of the section is illustrated in Figures 11 and 12. We recognize three subsections within section *Absus*, identified in the following key:

Leaves: H, *C. capensis*, I, *C. supplex* and J, *C. fasciculata*. Petiolar extrafloral nectary: K, *C. nictitans*. Leaflets: L, *C. choriophylla* and M, *C. kunthiana*. Photographs provided by Rubens Teixeira de Queiroz and A. O. Souza.

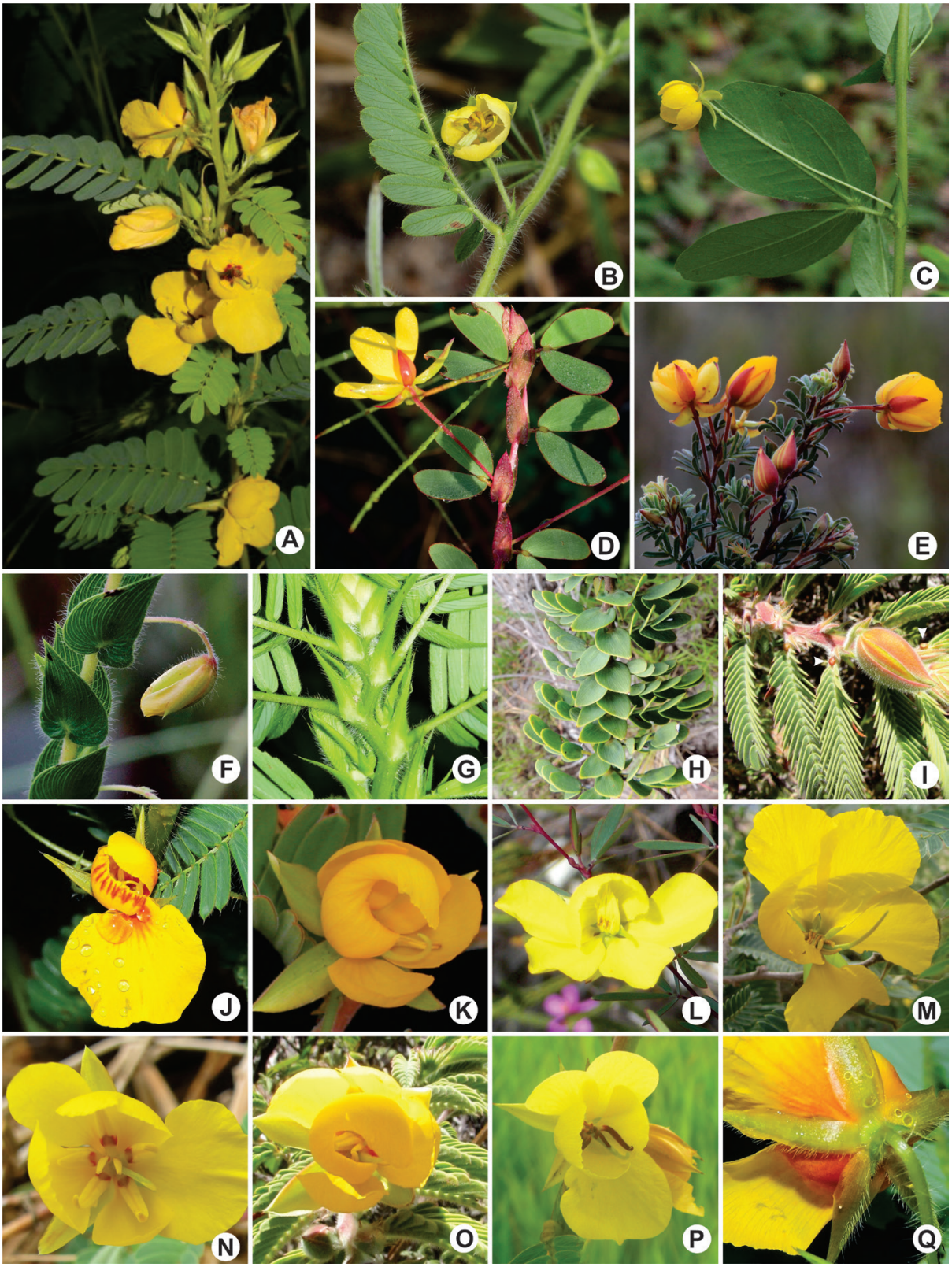

Figure 10. Morphological diversity of section *Chamaecrista*. Fascicles: A, *C. fasciculata*. Solitary flowers: B, *C. pilosa*, C, *C. rotundifolia*, D, *C. diphylla*, E, *C. tragacanthoides* and F, *C. basifolia*. Stipules: G, *C. glandulosa* and H, *C. potentilla*. Buds:

4.1. *Chamaecrista* section *Absus* subsection *Absus*

= *Chamaecrista* series *Absoideae* (Benth.) H.S.Irwin & Barneby, Mem. New York Bot. Gard. 35: 660. 1982. ≡ *Cassia* series *Absoideae* Benth., Fl. Bras. 15(2): 131. 1870. Type species: *Chamaecrista hispidula* (Vahl) H.S.Irwin & Barneby. ***Syn. nov.***

= *Chamaecrista* series *Oligospermae* (H.S.Irwin & Barneby) H.S.Irwin & Barneby, Mem. New York Bot. Gard. 35: 648. 1982. ≡ *Cassia* series *Oligospermae* H.S.Irwin & Barneby, Mem. New York Bot. Gard. 30: 38. 1978. Type species: *Chamaecrista oligosperma* (Benth.) H.S.Irwin & Barneby. ***Syn. nov.***

Shrubs or subshrubs with a xylopodium (this lacking only in *C. absus*, which is a herb). Leaves alternate and spirally arranged (distichous only in *C. absus*); **leaflets in two pairs per leaf** with distal pairs slightly larger than the proximal pair (seven to 18 pairs only in *C. oligosperma*). Racemes terminal or axillary. Flowers with hairy sepals; **petals yellowish, orange or reddish**; androecium with ten stamens [(two–) three to seven in *C. absus*]; ovary hairy, style curved at the apex (straight in *C. absus*). Root nodules known only in *C. absus*.

Chamaecrista section *Absus* subsection *Absus* comprises 20 species (27 taxa) and now includes the former *Chamaecrista* section *Absus* series *Absoideae* and *Oligospermae* (*sensu* Irwin & Barneby 1982). This subsection is a predominantly American group with 17 species endemic in Brazil; *C. absus* is pantropical. The species grow from lowland to montane areas in open, dry vegetation, including in cerrado and caatinga in Brazil, and in forest margins, coastal vegetation and disturbed environments.

4.2. ***Chamaecrista*** section ***Absus*** subsection ***Viscosa*** (Benth.) A.O. Souza, G.P. Lewis & M.J. Silva, ***comb & stat nov***. ≡ *Chamaecrista* series *Paniculatae* (Benth.) H.S.Irwin & Barneby, Mem. New York Bot. Gard. 35: 655. 1982. ≡ *Cassia* series *Paniculatae* Benth. Fl. Bras. 15(2): 140. 1870. Type species: *Chamaecrista orbiculata* (Benth.) H.S.Irwin & Barneby.

= *Chamaecrista* series *Andromedeae* (H.S.Irwin & Barneby) H.S.Irwin & Barneby, Mem. New York Bot. Gard. 35: 651. 1982. ≡ *Cassia* series *Andromedeae* H.S.Irwin & Barneby, Mem. New York Bot. Gard. 30: 83. 1978. Type species: *Chamaecrista andromeda* (Benth.) H.S.Irwin & Barneby. ***Syn. nov.***

= *Chamaecrista* series *Atroglandulosae* (H.S.Irwin & Barneby) H.S.Irwin & Barneby, Mem. New York Bot. Gard. 35: 648. 1982. ≡ *Cassia* series *Atroglandulosae* H.S.Irwin & Barneby, Mem. New York Bot. Gard. 30: 39. 1978. Type species: *Chamaecrista atroglandulosa* (Harms) H.S.Irwin & Barneby. ***Syn. nov.***

= *Chamaecrista* series *Bracteolatae* (H.S.Irwin & Barneby) H.S.Irwin & Barneby, Mem. New York Bot. Gard. 35: 650. 1982. ≡ *Cassia* series *Bracteolatae* H.S.Irwin & Barneby, Mem. New York Bot. Gard. 30: 51. 1978. Type species: *Chamaecrista bracteolata* (Vogel) H.S.Irwin & Barneby. ***Syn. nov.***

= *Chamaecrista* series *Catharticae* (H.S.Irwin & Barneby) H.S.Irwin & Barneby, Mem. New York Bot. Gard. 35: 647. 1982. ≡ *Cassia* series *Catharticae* H.S.Irwin & Barneby, Mem. New York Bot. Gard. 30: 27. 1978. Type species: *Chamaecrista cathatica* (Mart.) H.S.Irwin & Barneby. ***Syn. nov.***

= *Chamaecrista* series *Confertae* (H.S.Irwin & Barneby) H.S.Irwin & Barneby, Mem. New York Bot. Gard. 35: 658. 1982. ≡ *Cassia* series *Confertae* H.S.Irwin & Barneby, Mem. New York Bot. Gard. 30: 193. 1978. Type species: *Chamaecrista conferta* (Benth.) H.S.Irwin & Barneby. ***Syn. nov.***

= *Chamaecrista* series *Ericifoliae* (H.S.Irwin & Barneby) H.S.Irwin & Barneby, Mem. New York Bot. Gard. 35: 660. 1982. ≡ *Cassia* series *Ericifoliae* H.S.Irwin & Barneby, Mem. New York Bot. Gard. 30: 229. 1978. Type species: *Chamaecrista ericifolia* (Benth.) H.S.Irwin & Barneby. ***Syn. nov.***

= *Chamaecrista* series *Glutinosae* (H.S.Irwin & Barneby) H.S.Irwin & Barneby, Mem. New York Bot. Gard. 35: 658. 1982. ≡ *Cassia* series *Glutinosae* H.S.Irwin & Barneby, Mem. New York Bot. Gard. 30: 201. 1978. Type species: *Chamaecrista dentata* (Vogel) H.S.Irwin & Barneby. ***Syn. nov.***

= *Chamaecrista* series *Gracillimae* (H.S.Irwin & Barneby) H.S.Irwin & Barneby, Mem. New York Bot. Gard. 35: 660. 1982. ≡ *Cassia* series *Gracillimae* H.S.Irwin & Barneby, Mem. New York Bot. Gard. 30: 229. 1978. Type species: *Chamaecrista benthamii* (Ghesq.) H.S.Irwin & Barneby. ***Syn. nov.***

= *Chamaecrista* series *Hassleranae* (H.S.Irwin & Barneby) H.S.Irwin & Barneby, Mem. New York Bot. Gard. 35: 656. 1982. ≡ *Cassia* series *Hassleranae* H.S.Irwin & Barneby, Mem. New York Bot. Gard. 30: 172. 1978. Type species: *Chamaecrista hassleri* (H.S.Irwin & Barneby) H.S.Irwin & Barneby. ***Syn. nov.***

= *Chamaecrista* series *Hedysaroides* (H.S.Irwin & Barneby) H.S.Irwin & Barneby, Mem. New York Bot. Gard. 35: 656. 1982. ≡ *Cassia* series *Hedysaroides* H.S.Irwin & Barneby, Mem. New York Bot. Gard. 30: 174. 1978. Type species: *Chamaecrista hedysaroides* (Vogel) H.S.Irwin & Barneby. ***Syn. nov.***

= *Chamaecrista* series *Incanae* (H.S.Irwin & Barneby) H.S.Irwin & Barneby, Mem. New York Bot. Gard.

I, *C. olesiphylla*. Flowers: J, *C. duckeana*, K, *C. papillata*, L, *C. ramosa*, M, *C. roraimae*, N, *C. pascuorum*, O, *C. olesiphylla* and P, *C. nictitans*. Sepals: Q, *C. fasciculata*. Photographs provided by Rubens Teixeira de Queiroz and A. O. Souza.

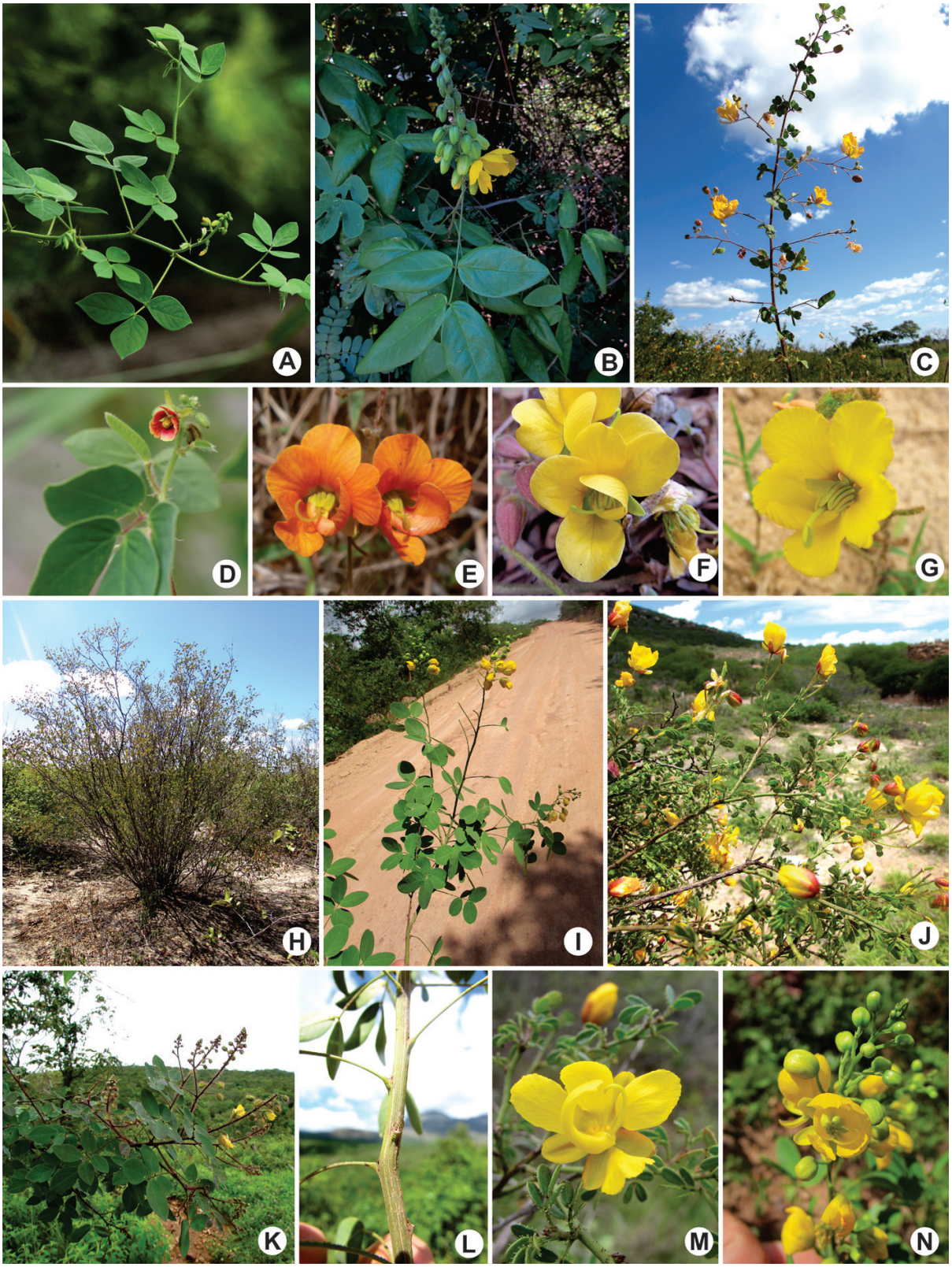

Figure 11. Morphological diversity of section *Absus* subsection *Absus* (A–G) and subsection *Zygophyllum* (H–N). Fertile branches: A, *C. absus*, B, *C. barbata*, C, *C. viscosa*. Flowers: D, *C. absus*, E, *C. fagonioides*, F, *C. carobinha* and G, *C. hispidula*.

35: 648. 1982. ≡ *Cassia* series *Incanae* H.S.Irwin & Barneby, Mem. New York Bot. Gard. 30: 40. 1978. Type species: *Chamaecrista incana* (Vogel) H.S.Irwin & Barneby. ***Syn. nov.***

= *Chamaecrista* series *Incurvatae* (H.S.Irwin & Barneby) H.S.Irwin & Barneby, Brittonia 31(4): 467. 1979. ≡ *Cassia* series *Incurvatae* H.S.Irwin & Barneby, Mem. New York Bot. Gard. 30: 214. 1978. Type species: *Chamaecrista incurvata* (Benth.) H.S.Irwin & Barneby. ***Syn. nov.***

= *Chamaecrista* series *Lomatopodae* (H.S.Irwin & Barneby) H.S.Irwin & Barneby, Mem. New York Bot. Gard. 35: 651. 1982. ≡ *Cassia* series *Lomatopodae* H.S.Irwin & Barneby, Mem. New York Bot. Gard. 30: 85. 1978. Type species: *Chamaecrista lomatopoda* (Benth.) H.S.Irwin & Barneby. ***Syn. nov.***

= *Chamaecrista* series *Lucidae* (H.S.Irwin & Barneby) H.S.Irwin & Barneby, Mem. New York Bot. Gard. 35: 656. 1982. ≡ *Cassia* series *Lucidae* Beth., Fl. Bras. 15(2): 146. 1870. Type species: *Chamaecrista lamprosperma* (Benth.) H.S.Irwin & Barneby. ***Syn. nov.***

= *Chamaecrista* series *Microphyllae* (H.S.Irwin & Barneby) H.S.Irwin & Barneby, Mem. New York Bot. Gard. 35: 651. 1982. ≡ *Cassia* series *Microphyllae* Benth., Fl. Bras. 15(2): 146. 1870. Type species: *Chamaecrista pohliana* (Benth.) H.S.Irwin & Barneby. ***Syn. nov.***

= *Chamaecrista* series *Ochnaceae* (H.S.Irwin & Barneby) H.S.Irwin & Barneby, Mem. New York Bot. Gard. 35: 656. 1982. ≡ *Cassia* series *Ochnaceae* H.S.Irwin & Barneby, Mem. New York Bot. Gard. 30: 176. 1978. Type species: *Chamaecrista ochnacea* (Vogel) H.S.Irwin & Barneby. ***Syn. nov.***

= *Chamaecrista* series *Pinifoliae* (H.S.Irwin & Barneby) H.S.Irwin & Barneby, Mem. New York Bot. Gard. 35: 650. 1982. ≡ *Cassia* series *Pinifoliae* H.S.Irwin & Barneby, Mem. New York Bot. Gard. 30: 66. 1978. Type species: *Chamaecrista paniculata* (Benth.) H.S.Irwin & Barneby. ***Syn. nov.***

= *Chamaecrista* series *Rigidulae* (Benth.) H.S.Irwin & Barneby, Mem. New York Bot. Gard. 35: 654. 1982. ≡ *Cassia* series *Rigidulae* Benth., Fl. Bras. 15(2): 142. 1870. Type species: *Chamaecrista decumbens* (Benth.) H.S.Irwin & Barneby. ***Syn. nov.***

= *Chamaecrista* series *Secundae* (H.S.Irwin & Barneby) H.S.Irwin & Barneby, Mem. New York Bot. Gard. 35: 651. 1982. ≡ *Cassia* series *Secundae* H.S.Irwin & Barneby, Mem. New York Bot. Gard. 30: 86. 1978. Type species: *Chamaecrista secunda* (Benth.) H.S.Irwin & Barneby. ***Syn. nov.***

= *Chamaecrista* series *Setosae* (H.S.Irwin & Barneby) H.S.Irwin & Barneby, Mem. New York Bot. Gard. 35: 650. 1982. ≡ *Cassia* series *Setosae* H.S.Irwin & Barneby, Mem. New York Bot. Gard. 30: 86. 1978. Type species: *Chamaecrista setosa* (Vogel) H.S.Irwin & Barneby. ***Syn. nov.***

= *Chamaecrista* series *Spinulosae* (H.S.Irwin & Barneby) H.S.Irwin & Barneby, Mem. New York Bot. Gard. 35: 659. 1982. ≡ *Cassia* series *Spinulosae* H.S.Irwin & Barneby, Mem. New York Bot. Gard. 30: 221. 1978. Type species: *Chamaecrista setosa* (H.S.Irwin & Barneby) H.S.Irwin & Barneby. ***Syn. nov.***

= *Chamaecrista* series *Strictifoliae* (H.S.Irwin & Barneby) H.S.Irwin & Barneby, Mem. New York Bot. Gard. 35: 659. 1982. ≡ *Cassia* series *Strictifoliae* H.S.Irwin & Barneby, Mem. New York Bot. Gard. 30: 227. 1978. Type species: *Chamaecrista strictifolia* (Benth.) H.S.Irwin & Barneby. ***Syn. nov.***

= *Chamaecrista* series *Trachycarpae* (H.S.Irwin & Barneby) H.S.Irwin & Barneby, Mem. New York Bot. Gard. 35: 648. 1982. ≡ *Cassia* series *Trachycarpae* H.S.Irwin & Barneby, Mem. New York Bot. Gard. 30: 33. 1978. Type species: *Chamaecrista trachycarpa* (Vogel) H.S.Irwin & Barneby. ***Syn. nov.***

= *Chamaecrista* series *Unijugae* (Benth.) H.S.Irwin & Barneby, Mem. New York Bot. Gard. 35: 659. 1982. ≡ *Cassia* series *Unijugae* Benth., Fl. Bras. 15(2): 134. 1870. Type species: *Chamaecrista monticola* (Benth.) H.S.Irwin & Barneby. ***Syn. nov.***

= *Chamaecrista* series *Ursinae* (H.S.Irwin & Barneby) H.S.Irwin & Barneby, Mem. New York Bot. Gard. 35: 650. 1982. ≡ *Cassia* series *Ursinae* H.S.Irwin & Barneby, Mem. New York Bot. Gard. 30: 54. 1978. Type species: *Chamaecrista ursina* (Benth.) H.S.Irwin & Barneby. ***Syn. nov.***

Shrubs or subshrubs with a xylopodium or this lacking, rarely trees. Leaves with one to 70 pairs of leaflets, with different shapes, consistency and apices, but when with exactly two pairs of leaflets they are coriaceous and differentiated dorsoventrally in colour and texture, or they are oblanceolate, or with an acuminate, acute or cuspidate apex. Racemes terminal or axillary. Flowers with hairy sepals; petals yellowish; androecium with ten fertile stamens; ovary hairy, style curved at the apex.

Chamaecrista section *Absus* subsection *Viscosa* contains 169 species and includes the taxa of the 29 series of *Chamaecrista* section *Absus* subsection *Absus* (*sensu* Irwin & Barneby, 1982). The subsection is South American with its main centre of diversity

Shrubby habit: H, *C. belemii*. Fertile branches: I, *C. zygophylloides*, J, *C. arboae* and K, *C. andersonii*. Striate branch: L, *C. zygophylloides*. Flowers: M, *C. arboae* and N, *C. zygophylloides*.

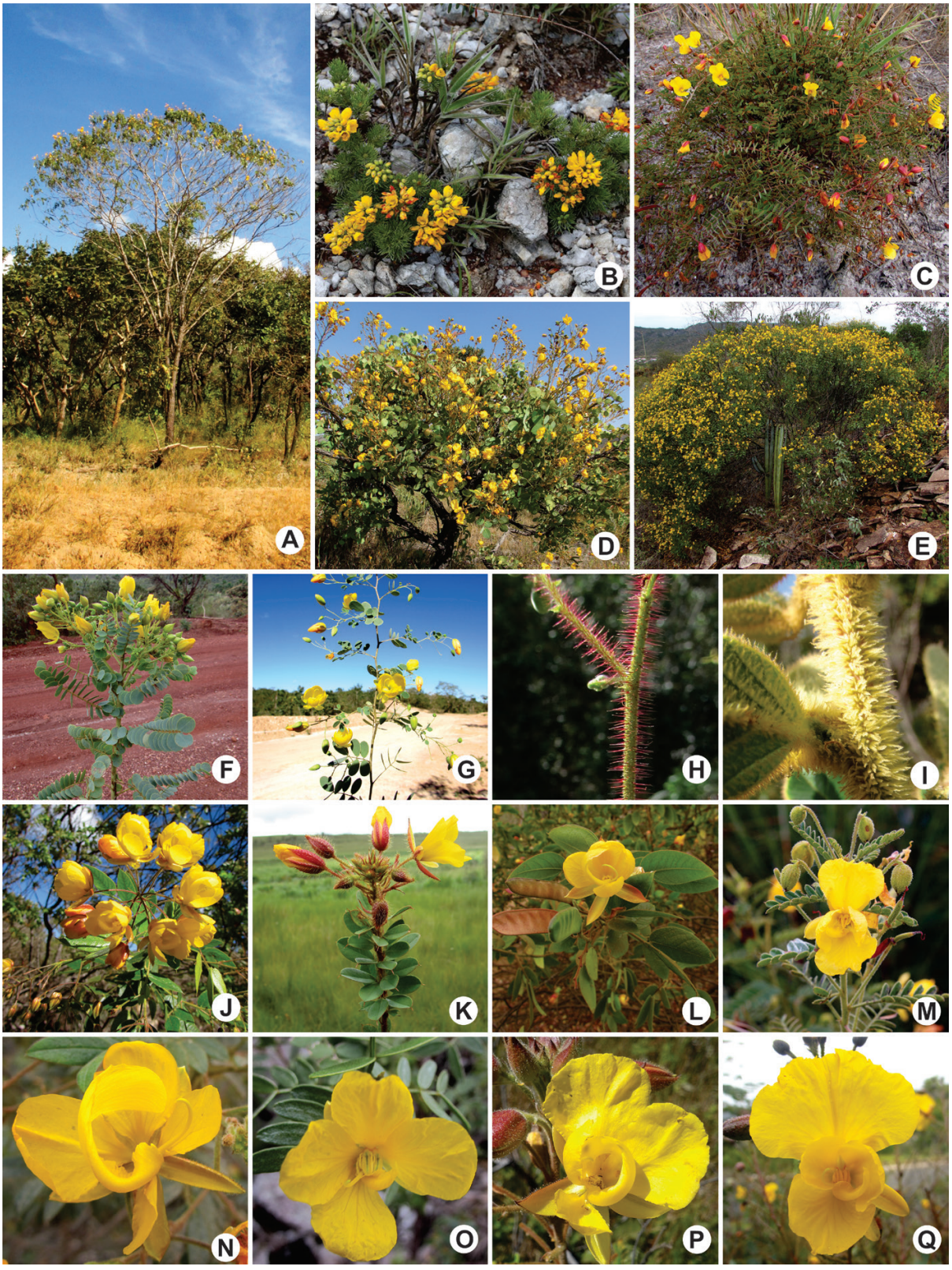

Figure 12. Morphological diversity of section *Absus* subsection *Viscosa*. Tree habit: A, *C. fulgida*. Sub-shrubby habit: B, *C. ericifolia* and C, *C. strictula*. Shrubby habit: D, *C. orbiculata* and E, *C. stillifera*. Fertile branches: F, *C. obolaria* and

in Brazil with *c*. 160 species, many endemic to the cerrado.

4.3. ***Chamaecrista*** section ***Absus*** subsection ***Zygophyllum*** A.O.Souza, G.P.Lewis & M.J.Silva ***subsection nov.*** Type species: *Chamaecrista zygophylloides* (Taub.) H.S.Irwin & Barneby.

Shrubs or subshrubs with xylopodium or this lacking. **Branches with whitish streaks and without exfoliating bark**. Leaves alternate and spiral, **two pairs of leaflets**; **petiole 1.0–1.5 times longer than the rachis**. Raceme terminal. Flowers with sepals indumented externally, or glabrous; petals yellow; androecium with ten stamens; ovary indumented or glabrous, style curved at the apex.

Chamaecrista section *Absus* subsection *Zygophyllum* has eight species and includes some taxa from former *Chamaecrista* section *Absus* subsection *Absus* series *Absoideae* (*sensu* Irwin & Barneby, 1982). This subsection is American with five species endemic to Brazil and occurring in caatinga in north-eastern Brazil and one (*C. zygophylloides*) occurring from north-eastern Brazil to Mexico.

CONCLUSIONS AND FUTURE DIRECTIONS

This work, based on a multiple markers associated with indels strategy, presents the most comprehensively sampled phylogenetic reconstruction of *Chamaecrista* so far and sheds greater light on the status of its infrageneric categories (sections, subsections and series). Newly discovered evolutionary relationships in the genus have led us to propose a modified infrageneric classification. In our analysis, most of the previously recognized infrageneric taxa are found not to be monophyletic. In our new classification, the genus comprises four sections, *Apoucouita*, *Baseophyllum*, *Chamaecrista* and *Absus* (the last with three subsections: *Absus*, *Viscosa* and *Zygophyllum*), all phylogenetically and morphologically well-supported. No series in *Chamaecrista* proposed by Irwin & Barneby (1982) are retained because of their low phylogenetic support and/or non-monophyletic status. Nevertheless, we highlight that the recently redefined series *Coriaceae*, *Rigidulae* and *Paniculatae* were supported in our analyses, although we have temporarily placed the first in section *Chamaecrista* and the other two in subsection *Viscosa*, pending further study. Notwithstanding the findings of our study, we consider the published revisions of Irwin & Barneby (1977, 1978, 1982) still to be the most useful publications for the identification of *Chamaecrista* spp. in the Americas.

The lack of some extra-American species of section *Chamaecrista* should not alter the results found here. However, the inclusion of more extra-American species could provide better estimations of the number of lineages outside the Americas from section *Chamaecrista*. Additionally, new studies with new markers will be needed to clarify some of the deeper relationships in subsection *Viscosa* and to resolve the relationships between species further leading to the understanding of the evolution of the genus in low levels; also, population-level studies would promote an understanding of the relationships of some of the species with disjunct distributions.

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SUPPORTING INFORMATION

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Appendix S1. List of morphological characters and their encoded states used for the reconstruction of the ancestral states.
Appendix S2. Morphological matrix with character states of each taxon (? = missing).
Appendix S3. Maximum likelihood tree from analysis of ITS in the *Broad* approach. Colours represent the sections recognized in the new classification proposed in this study. Branch support is in bootstrap values.
Appendix S4. Maximum likelihood tree from analysis of *trnL-F* in the *Broad* approach. Colours represent the sections recognized in the new classification proposed in this study. Branch support is in bootstrap values.
Appendix S5. Maximum likelihood tree from analysis of ETS in the *Multilocus* approach. Colours represent the sections recognized in the new classification proposed in this study. Branch support is in bootstrap values.
Appendix S6. Maximum likelihood tree from analysis of *trnE-T* in the *Multilocus* approach. Colours represent the sections recognized in the new classification proposed in this study. Branch support is in bootstrap values.
Appendix S7. Maximum likelihood tree from analysis of the indels of ITS in the *Multilocus* approach. Colours represent the sections recognized in the new classification proposed in this study. Branch support is in bootstrap values.
Appendix S8. Maximum likelihood tree from analysis of the indels of *trnL-F* in the *Multilocus* approach. Colours represent the sections recognized in the new classification proposed in this study. Branch support is in bootstrap values.
Appendix S9. Maximum likelihood tree from analysis of the indels of ETS in the *Multilocus* approach. Colours represent the sections recognized in the new classification proposed in this study. Branch support is in bootstrap values.
Appendix S10. Maximum likelihood tree from analysis of the indels of *trnE-T* in the *Multilocus* approach. Colours represent the sections recognized in the new classification proposed in this study. Branch support is in bootstrap values.
Appendix S11. Ancestral character reconstruction for selected morphological characters (1) and (2).
Appendix S12. Ancestral character reconstruction for selected morphological characters (3) and (4).
Appendix S13. Ancestral character reconstruction for selected morphological characters (5) and (6).
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Appendix S20. Ancestral character reconstruction for selected morphological characters (19) and (20).
Appendix S21. Updated list of accepted binomials and infrageneric categories (sections and subsections) of *Chamaecrista* proposed in the new classification presented in this study and their area of occurrence. The number in square brackets indicates the updated number of species for each infrageneric taxon. Asterisks indicate extra-American species that were placed in the section *Chamaecrista* for the first time.