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2 **PROGRAMA DE PÓS-GRADUAÇÃO EM BOTÂNICA**

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8 **Phylogeny and historical biogeography of the Neotropical genus**
9 ***Besleria* (Gesneriaceae)**

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Gabriel Emiliano Ferreira da Silva

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Manaus, Amazonas

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Junho, 2018

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GABRIEL EMILIANO FERREIRA DA SILVA

**Phylogeny and historical biogeography of the Neotropical genus *Besleria*
(Gesneriaceae)**

Orientador: Dr. Michael John Gilbert Hopkins

Tese apresentada ao Instituto Nacional de Pesquisas da Amazônia como parte dos requisitos para obtenção do título de Doutor em Ciências Biológicas (Botânica).

Manaus, Amazonas

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Sinopse:

Buscou-se inferir as relações filogenéticas dos gêneros *Besleria* baseado em filogenias moleculares datadas, testar a monofilia das seções e subseções de Morton (1939) e reconstruir a história biogeográfica do gênero. Realizou-se também o estudo taxonômico do clado endêmico do Brasil.

Palavras-chave: Gesneriaceae; *Besleria*; Neotropicos; Filogenia molecular; Datação molecular; Andes; Taxonomia.

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122 trabalho, mas foi um exemplo de pessoa, de perseverança, de ética, me mostrando que,
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DIVISÃO DOS CURSOS DE PÓS-GRADUAÇÃO

AULA DE QUALIFICAÇÃO

PARECER



MINISTÉRIO DA CIÊNCIA, TECNOLOGIA, INOVAÇÕES E COMUNICAÇÕES



ATA DA DEFESA PÚBLICA DA TESE DE DOUTORADO DE DISCENTE DO PROGRAMA DE PÓS-GRADUAÇÃO EM BOTÂNICA DO INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA

Aos trinta e um dias do mês de julho de 2018, às 9:30h, na sala de seminários da biblioteca do INPA-Campus I, reuniu-se a Comissão Examinadora da Defesa Presencial, composta pelos seguintes membros: Dra. Camila Cherem Ribas, do Instituto Nacional de Pesquisas da Amazônia, Programa de Coleções e Acervos Científicos, Dr. Mário Henrique Terra Araújo, da Faculdade Estácio de Sá do Amazonas, Dr. Bruno Sampaio Amorim, Universidade do Estado do Amazonas, Programa de Pós-Graduação em Biotecnologia e Recursos Naturais da Amazônia (UEA), Dr. Leandro Lacerda Giacomini, da Universidade Federal do Oeste do Pará, Instituto de Ciências e Tecnologia das Águas, Dr. Mario Eric Cohn Haft, do Instituto Nacional de Pesquisas da Amazônia – INPA, tendo como suplentes: Dra. Nállarett Marina Dávila Cardozo, da Universidade Estadual de Campinas e Dr. Jansen Alfredo Sampaio Zuanon do Instituto Nacional de Pesquisas da Amazônia, Coordenação de Biodiversidade, sob a presidência do primeiro titular, a fim de proceder a arguição pública da TESE DOUTORADO do discente: **Gabriel Emiliano Ferreira da Silva**, intitulada: **“Phylogeny and historical biogeography of the Neotropical genus *Besleria* (Gesneriaceae)”** sob a orientação: Dr. Michael John Gilbert Hopkins. Após a exposição, dentro do tempo regulamentar, o discente foi arguido oralmente pelos membros da Comissão Examinadora, tendo recebido o conceito final:

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Manaus (AM), 31 de julho de 2018.

OBS: A banca recomenda a aprovação, mas reforça que as recomendações, em especial do primeiro capítulo e do formato geral da tese são essenciais para a melhoria do trabalho e devem ser considerados para a versão final.

Nada mais havendo, foi lavrado a presente ata, que, após lida e aprovada, foi assinada pelos membros da Comissão Examinadora



DIVISÃO DOS CURSOS DE PÓS-GRADUAÇÃO



AULA DE QUALIFICAÇÃO

PARECER

Aluno: GABRIEL EMILIANO FERREIRA DA SILVA
Curso: BOTÂNICA
Nível: Doutorado
Orientador: Michael John Gilbert Hopkins (INPA)

Título:

"FILOGENIA E ESTUDOS TAXONOMICOS DE BESLERIA L. (BESLERIEAE, GESNERIACEAE)"

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- CHARLES EUGENE ZARTMAN
- DORIANE RODRIGUES
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SUPLENTES:

- OTILENE SANTOS MATTOS
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Manaus (AM), 22 de Setembro de 2014.

OBS: FAZOU CONTEXTUALIZAÇÃO NAS PERGUNTAS/OBJETIVOS NA INTRODUÇÃO

143 **Resumo**

144 *Besleria* L. é um gênero neotropical de ervas perenes, arbustos ou arvoretas que crescem no
145 sub-bosque das florestas tropicais. Com mais de 165 espécies, *Besleria* é o segundo maior
146 gênero Gesneriaceae do Novo Mundo. A taxonomia e a evolução de *Besleria* têm sido pouco
147 exploradas utilizando abordagens filogenéticas moleculares. Assim, estimamos a filogenia de
148 *Besleria* incluindo cerca de 50% das espécies reconhecidas, usando regiões nucleares e
149 plastidiais (ITS, *matK*, *rps16* e *trnL-trnF*) e dois pontos de calibração secundários para
150 estimar os tempos de divergência do gênero. Utilizamos essa filogenia para revisar a
151 classificação e a história biogeográfica de *Besleria*. Nossas análises filogenéticas suportam o
152 monofiletismo de *Besleria* e sua relação irmã com *Cremosperma*. Cinco grandes clados foram
153 reconhecidos dentro do gênero, que não correspondem às seções e subseções atualmente
154 conhecidas. Os clados são melhor caracterizados por seu padrão de distribuição do que por
155 sinapomorfias morfológicas. A reconstrução biogeográfica indica que *Besleria* originou-se no
156 norte dos Andes durante o Mioceno Médio (ca. 15 Ma). Eventos geológicos e climáticos
157 relacionados à elevação dos Andes e à formação do istmo do Panamá explicam os padrões
158 atuais de distribuição e ajudam a esclarecer a história biogeográfica do grupo.

159 **Abstract**

160 *Besleria* L. is a Neotropical genus of perennial herbs, shrubs or small tree growing in the
161 understory of rainforests. With over 165 species *Besleria* is the second largest genus of the
162 New World Gesneriaceae. Taxonomy and evolution of *Besleria* has been little explored in
163 molecular phylogenetic studies. Here, we estimated the phylogeny of *Besleria* including about
164 50% of the recognized species using nuclear and plastidial regions (ITS, *matK*, *rps16* and
165 *trnL-trnF*) and two secondary calibrations points to estimate divergence times. We used this
166 phylogeny to revise the classification and biogeographic history of the genus. Our
167 phylogenetic analyses support the monophyly of *Besleria* and its sister relationship with
168 *Cremosperma*. Five major clades were resolved within the genus that do not correspond with
169 the sections and subsections currently recognized for the genus. Clades are better
170 characterized by their distribution pattern rather than morphological synapomorphies.
171 Biogeographic reconstruction indicates that *Besleria* originated in northern Andes during the
172 Middle Miocene (ca. 15 Mya). Geological and climatic events related to the Andes uplift and
173 Panama Isthmus formation explain the current distribution patterns and help to clarify the
174 biogeographic history of the group.

175 Sumário

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204INTRODUÇÃO GERAL

205

206 *Besleria* L. é um gênero Neotropical de ervas perenes, arbustos ou arvoretas que
207crescem no sub-bosque de florestas tropicais desde o nível do mar até próximo de 3000 m de
208altitude. Com mais de 165 espécies reconhecidas, *Besleria* é um dos maiores e menos
209conhecidos gêneros de Gesneriaceae do Novo Mundo. É o gênero-tipo da tribo Beslerieae
210Bartl., que deu origem a uma elevada diversidade morfológica, de hábitos, formas de flores e
211tipos de frutos, durante os últimos ca. 22-15 Ma (Roalson and Clark 2006, Clark et al. 2010,
212Roalson and Roberts 2016).

213 As espécies de *Besleria* ocorrem na maioria das florestas neotropicais, com centros de
214diversidade nos Andes tropical (mais de 100 espécies) e América Central (20 espécies). As
215espécies remanescentes são endêmicas da Floresta Atlântica brasileira (11 spp.), do Escudo
216das Guianas (8 spp.), ou das Ilhas do Caribe (7 spp.) (Skog and Boggan 2007, Ferreira et al.
2172016). Embora a maioria das espécies sejam endêmicas e com distribuição restrita, algumas
218são amplamente distribuídas, como *B. flavo-virens* e *B. laxiflora*, que ocorrem da América
219Central até a Floresta Atlântica brasileira, ou *B. solanoides*, que ocorre da Nicarágua à Bolívia
220(Kvist et al. 2005, Skog and Boggan 2007, BFG et al. 2015, Clavijo et al. 2015). Espécies de
221*Besleria* são geralmente reconhecidas por um caule bem desenvolvido e pouco ramificado,
222vários pares de folhas grandes, inflorescências com brácteas axilares e frutos globosos
223carneiros (Weber 2004, Berger et al. 2015). A maioria dos caracteres diagnósticos para
224identificação de espécies são: presença ou ausência de pedúnculo na inflorescência, as
225dimensões dos lóbulos do cálice, as cores das flores (vermelho-laranja, amarelo ou branco) e
226forma da corola, que varia de tubular a hipocirtóide (ou seja, com tubo de corola fortemente
227inflado e uma boca contraída).

228 A morfologia dos frutos tem sido largamente ignorada em *Besleria*, embora apresente
229uma interessante diversidade de cor e deiscência, podendo ser uma baga indeiscente ou uma
230“baga que se rompe”, ou seja, que se abre irregularmente na maturidade, e exibe o tecido
231placentário vermelho embutido com sementes vermelhas (Wiehler 1975, Berger et al. 2015).
232Muitas espécies de *Besleria* são polinizadas por beija-flores (Serrano-Serrano et al. 2017), e seus
233frutos, visivelmente coloridos ou com ruptura, são provavelmente dispersos por animais como
234pássaros e/ou pequenos mamíferos (Berger et al., 2015). Sabe-se que uma espécie de *Besleria*

235 é mirmecofílica, ou seja, hospeda formigas em domáceas em ambos os lados da nervura
236 central das folhas (Windsor and Jolivet 1996).

237 A circunscrição de espécies e classificação infragenérica dentro de *Besleria*
238 permanecem pouco definidas devido à falta de uma revisão morfológica e filogenética global
239 para o grupo. A primeira e ainda mais abrangente revisão disponível da *Besleria* foi proposta
240 por (Morton 1939) e baseada essencialmente no estudo das coleções de herbários. Este
241 tratamento reconhece 141 espécies classificadas em 4 seções e 18 subseções, agrupamentos
242 estes baseados em caracteres visíveis em espécimes de herbário, como morfologia de flor e
243 estrutura de inflorescência. Portanto, *Besleria* precisa de uma revisão mais atual, que inclua
244 todas as espécies publicadas recentemente, para melhorar a circunscrição das espécies
245 atualmente reconhecidas e a classificação do crescente número de espécies recém descritas no
246 gênero (González et al. 2001, Feuillet 2008, Salinas 2008, Ferreira et al. 2016, 2017).

247 Os estudos filogenéticos moleculares da tribo Beslerieae confirmaram o
248 monofiletismo dos gêneros atualmente reconhecidos no grupo e a relação irmã entre *Besleria*
249 e *Cremosperma* Benth. (Clark et al., 2010; Roalson e Clark, 2006; Roalson e Roberts, 2016).
250 No entanto, as relações filogenéticas dentro de *Besleria* foram pouco exploradas até o
251 presente. Por exemplo, as espécies de *Besleria* da Mata Atlântica brasileira nunca foram
252 incluídas em um estudo filogenético, deixando desconhecidas suas afinidades sistemáticas e
253 biogeográficas. Até hoje, a filogenia mais completa de *Besleria* está baseada apenas na análise
254 de sequências ITS de uma amostragem taxonômica limitada, focada principalmente em
255 espécies equatorianas (27 acessos; Roalson e Clark, 2006). Embora preliminarmente, as
256 hipóteses filogenéticas disponíveis sugeriram o parafiletismo das seções infragenéricas de
257 Morton, mas uma filogenia mais com maior número de espécies e melhor resolvida é
258 necessária para delinear grupos monofiléticos e revisar seus caracteres diagnósticos. Além da
259 promessa de esclarecer as relações dentro do gênero, uma filogenia bem resolvida também
260 pode contribuir para a compreensão da história biogeográfica do grupo.

261 A distribuição ampla de *Besleria* e sua forte afinidade ecológica pelo sub-bosque das
262 florestas tropicais, faz deste gênero um bom modelo para investigar o momento e as causas da
263 diversificação de plantas nestes ecossistemas (Antonelli et al. 2018). De acordo com a análise
264 de datação na família Gesneriaceae (Perret et al. 2013, Roalson and Roberts 2016), *Besleria*
265 começou a se diversificar ca. 15 Ma, no início de um intenso período de elevação do norte dos
266 Andes (Hoorn et al. 2010). A alta riqueza de espécies de *Besleria*, encontrada nos Andes da

267Colômbia ao Equador, concorda com a hipótese de um importante papel da orogenia andina
 268na diversificação desse grupo de plantas. No entanto, não se sabe se esta área é o local de
 269origem do gênero, e como e quando outras regiões – como a América Central, a Mata
 270Atlântica brasileira e as Antilhas – foram colonizadas.

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- 319

320 OBJETIVOS

321

- 322 • Avaliar a classificação infragenérica e a história evolutiva das principais
- 323 características morfológicas do grupo.
- 324 • Circunscrever a distribuição geográfica das principais linhagens.
- 325 • Inferir os processos biogeográficos que podem ter contribuído para a distribuição atual
- 326 de espécies de *Besleria*.
- 327 • Realizar o tratamento taxonômico do clado endêmico da Mata Atlântica brasileira.

328

23

329

Capítulo 1

330

331Ferreira, G.E; Chautems, A.; Clavijo, L.; Clark, J.L.;
332Hopkins, M.J.G.; Perret, M. Phylogeny and historical
333biogeography of the Neotropical genus *Besleria*
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336 **Phylogeny and historical biogeography of the Neotropical**
337 **genus *Besleria* (Gesneriaceae)**

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362Abstract

363*Besleria* L. is a Neotropical genus of perennial herbs, shrubs or small tree growing in the
364understory of rainforests. With over 165 species *Besleria* is the second largest genus of the
365New World Gesneriaceae. Despite the ecological importance and ubiquity of this genus in the
366rainforest ecosystem, taxonomy and evolution of *Besleria* has been little explored using
367molecular phylogenetic studies. Here, we estimated the phylogeny of *Besleria* including about
36850% of the recognized species using nuclear and chloroplastic regions (ITS, *matK*, *rps16* and
369*trnL-trnF*) and two secondary calibrations points to estimate divergence times. We used this
370phylogeny to revise the classification and biogeographic history of the genus. Our
371phylogenetic analyses support the monophyly of *Besleria* and its sister relationship with
372*Cremosperma*. Five major clades were identified within the genus that do not correspond with
373the sections and subsections currently recognized in the genus. Clades are better characterized
374by their distribution pattern rather than by morphological synapomorphies. The best-fit model
375compared in BioGeoBEARS was DEC +J. Biogeographic reconstruction indicates that
376*Besleria* originated in northern Andes during the Middle Miocene (ca. 15 Mya). Geological
377and climatic events related to the Andes uplift and Panama Isthmus formation explain the
378current distribution patterns and help to clarify the biogeographic history of the group.

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381**Keywords** Gesneriaceae, Beslerieae, Neotropics, Molecular phylogeny, Molecular dating,
382Andes, taxonomy.

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385 **1.1 1. Introduction**

386 *Besleria* L. is a Neotropical genus of perennial herbs, shrubs or small tree growing in the
 387 understory of rainforests between near sea level up to 3000 m in elevation. With over 165
 388 recognized species, *Besleria* is one of the largest and less known genus of the New World
 389 Gesneriaceae. It is the type genus of the tribe Beslerieae that gave rise to an outstanding
 390 morphological diversity in habits, flowers shapes and fruit types during the last ca. 22-15 Mya
 391 (Clark et al., 2010; Roalson and Clark, 2006; Roalson and Roberts, 2016). *Besleria* species
 392 occur in most Neotropical rainforests with centers of diversity in the tropical Andes, (>100
 393 species) and Central America (20 species). Remaining species are endemic to the Brazilian
 394 Atlantic forest (11 spp.), Guiana Shield (8 spp.) and West Indies (7 spp.) ((Skog and Boggan,
 395 2007). Although most species are local endemics, some are widely distributed, like *B. flavo-*
 396 *virens* and *B. laxiflora*, that occur from Central America to the Brazilian Atlantic Rainforest,
 397 or *B. solanoides* that ranges from Nicaragua to Bolivia (Araújo et al., 2015; Clavijo et al.,
 398 2015; Kvist et al., 2005; Skog and Boggan, 2007). Species of *Besleria* are usually recognized
 399 by a well-developed and sparsely branched stem, several pairs of large leaves, axillary
 400 bractless inflorescences and fleshy globose fruits (Weber, 2004; Wiehler, 1975). Most of the
 401 diagnostic characters for species identification rely on the presence or absence of a peduncle
 402 in the inflorescence, dimensions of calyx lobes, flower colors (red-orange, yellow or white),
 403 and corolla shape ranging from tubular to hypocyrtoid (*i.e.* with a strongly inflated corolla
 404 tube and a constricted mouth - Wiehler, 1975). Fruit morphology has been largely overlooked
 405 in *Besleria* although it presents an interesting diversity in color and dehiscence being either an
 406 indehiscent berry or a “rupturing berry” that split open irregularly at maturity displaying a red
 407 placental tissue embedded with red seeds (Berger et al., 2015; Wiehler, 1975). Several
 408 *Besleria* species are pollinated by hummingbirds (Serrano-Serrano et al. 2017), whereas the
 409 conspicuously colored fruit or rupturing display fruit is likely attractive to dispersing animals
 410 like birds and/or small mammals (Berger et al. 2015). One species of *Besleria* is known to be
 411 myrmecophilous, hosting ants in domatia on both sides of the mid-vein of the leaves
 412 (Windsor and Jolivet, 1996).

413 Species boundaries and infrageneric classification within *Besleria* remain poorly
 414 defined because of the lack of a global morphological and phylogenetic revision for the group.
 415 The first and still most comprehensive available revision of *Besleria* was proposed by
 416 (Morton, 1939) based essentially on the study of herbarium collections. This treatment and
 417 posterior additional studies (Morton, 1968, 1953, 1944, 1942) recognized 141 species classify

418 into 4 sections and 18 subsections based on characteristics visible on herbarium specimens
419 such as flower morphology (calix shape, nectary glands) and inflorescence structure. Since
420 Morton's seminal contributions, *Besleria* has been subject to few studies besides the
421 segregation of *Gasteranthus* Benth. from *Besleria* (Wiehler 1975) and regional floristic
422 treatments for Brazil (Lopes et al., 2008), Panama (Skog, 1978) and the Guianas (Skog and
423 Feuillet, 2008). Therefore, *Besleria* needs a modern revision to improve the circumscription
424 of currently recognized species and the classification of the growing number of newly
425 described species in the genus (CORTÉS-CEBALLOS et al., 2017; Ferreira et al., 2017,
426 2016b; Feuillet, 2008; González et al., 2001; Salinas, 2008).

427 Latest molecular phylogenetic studies in the tribe Beslerieae have confirmed the
428 monophyly of the currently recognized genera in the group and the sister relationship between
429 *Besleria* and *Cremosperma* Benth. (Clark et al., 2010; Roalson and Clark, 2006; Roalson and
430 Roberts, 2016). However, phylogenetic relationships within *Besleria* have been little
431 explored. For example, *Besleria* species from the Brazilian Atlantic Rainforest have never
432 been included in a phylogenetic study, leaving unknown their systematic and biogeographic
433 affinities. To date, the most complete phylogeny of *Besleria* has relied solely on the analysis
434 of ITS sequences and a limited taxonomic sampling mainly focused on Ecuadorian species
435 (27 accessions; Roalson and Clark 2006). Although preliminary, the available phylogenetic
436 hypotheses suggested the Morton's infrageneric sections are paraphyly but a more
437 comprehensive and resolved phylogeny is necessary to delineate monophyletic groups and
438 revise their diagnostic characters.

439 Beyond the promise of clarifying relationships within the genus, a well-resolved
440 phylogeny could also contribute to understand the biogeographic history of the group. The
441 widespread distribution of *Besleria* and its strong ecological affinity for the understory of the
442 tropical rain forest makes this genus a good model to investigate the timing and the causes of
443 plant diversification in this biome (Antonelli et al., 2018). According to dating analysis in the
444 family Gesneriaceae (Perret et al., 2013; Roalson and Roberts, 2016), *Besleria* started to
445 diversify ca. 15 Mya, at the beginning of an intense period of the northern Andes uplift
446 (Hoorn et al., 2010). The high species richness of *Besleria* found in the Andes of Colombia
447 and Ecuador agree with the hypothesis of a role of Andean orogeny in the diversification of
448 this plant group. However, it is unknown if this area is the place of origin of the genus
449 and how and when the other regions like Central America, the Brazilian Atlantic Forest and
450 the West Indies have been colonized.

451 In this study, we estimated a time-calibrated phylogeny of *Besleria* based on one
 452 nuclear and three plastidial loci. Our taxon sampling was designed to include representative
 453 species from all major Neotropical regions. We then used this phylogenetic framework to 1)
 454 evaluate the infrageneric classification and evolutionary history of key morphological features
 455 of the group 2) circumscribe the geographic distribution of major lineages, and 3) infer the
 456 biogeographic processes that may have contributed to the present-day distribution of *Besleria*
 457 species. The current study, which encompass the broadest species-level sampling assembled
 458 to date, will facilitate future revisions of this taxonomically challenging group and shed light
 459 on the timing and biogeographic context of understory plant diversification across the
 460 Neotropical rainforests.

461 1.2 2. Materials and methods

462 2.1. Taxon sampling

463 Plant material was collected during fieldworks in Brazil, Panama and Colombia
 464 between 2014 and 2017. Additional samples from other localities in the Andes, Central
 465 America and West Indies were provided by JLC. We sampled a total of 155 accessions
 466 representing 117 species among which 80 belong to the genus *Besleria* (ca 50% of all
 467 species). Sampling in *Besleria* was designed to include representative species of all
 468 subsections defined by Morton (1939) and all biogeographic areas occupied by the genus
 469 (Skog and Boggan, 2007; Weber et al., 2013). Two to three accessions per species were
 470 sampled in 36 species to test their monophyly. To evaluate the phylogenetic relationships of
 471 *Besleria* with other Neotropical Gesneriaceae, we sampled representatives of all genera of the
 472 tribe Beslerieae, excepted *Tylopsacas*, and representatives of all other taxonomical units
 473 recognized within the subfamilies Gesnerioideae and Sanangoideae (Weber et al. 2013):
 474 Gesneriinae (*Gesneria humilis* L.), Gloxiniinae (*Gloxinia perennis* (L.) Druce and *Monopyle*
 475 *maxonii* C.V.Morton), Columneinae (*Columnea sanguinea* (Pers.) Hanst. and *Episcia*
 476 *fimbriata* Fritsch), Sphaerorrhizinae (*Sphaerorrhiza sarmentiana* (Gardner ex Hook.) Roalson
 477 & Boggan), Ligeriinae (*Sinningia brasiliensis* (Regel & E.Schmidt) Wiehler and *Sinningia*
 478 *schiffneri* Fritsch), and Sanango (1). *Peltanthera floribunda* was chosen as an outgroup based
 479 on previous phylogenetic results showing its sister relationship with the Gesneriaceae (Perret
 480 et al., 2013; Roalson and Roberts, 2016; APG IV, 2016). All taxa and voucher information
 481 are listed in Table 1.

482 2.2. DNA sequencing and alignment

483DNA was isolated from silica-gel dried leaf tissue using the NucleoSpin Plant II (Macherey-
484Nagel, Düren, Germany) following the manufacturer's protocol. Sequences of ITS, *matK*,
485*rps16* and *trnL-trnF* of *Besleria* species were newly acquired for this study. Sequences of
486other taxa were obtained from published data (Serrano-Serrano et al., 2017). Both polymerase
487chain reaction (PCR) amplifications and sequencing reactions followed the procedures
488described in (Perret et al., 2013). The primers used to amplify the *matK*, *rps16*, *trnL-trnF*
489intron-spacer are given in (Perret et al., 2013, 2003). ITS was amplified and sequenced with
490primers ITS 5P and ITS 8P (Moller and Cronk, 1997). The program Sequencher 4.7 (Gene
491Code Corp., Ann Arbor, MI, USA) was used to edit and assemble complementary strands.
492Newly acquired sequences have been deposited in GenBank (Appendix A). All sequences
493were first aligned using MAFFT (Kato and Toh, 2010) and then imported to Mesquite 3.03
494(Maddison and Maddison, 2017) for verification and manual adjustment.

4952.3. Phylogenetic Analysis and Divergence Times

496 Phylogenetic relationships between species were reconstructed by maximum
497likelihood (ML) using the software RAxML (Stamatakis, 2014). Analyses were performed on
498the CIPRES portal (www.phylo.org; (Miller et al., 2010)). Each DNA region was treated as a
499separate data partition, allowing parameters of each region to be unlinked. The best fitting
500substitution model for each DNA region was selected with jModelTest2 (Darriba et al., 2012)
501using to the Akaike information criterion (AIC). The test selected HKY for *trnL-trnF* and
502GTR + Γ for ITS, *matK* and *rps16*. We performed 100 runs with the preferred models for the
503data partitions described above. The robustness of the tree was calculated with non-parametric
504standard bootstrap resampling and 1,000 pseudo-replicates (Felsenstein, 1985). To examine
505potential incongruences between datasets we inspected whether the topology resulting from
506the combined analyses of all the regions conflicted with the topologies obtained through
507separate analyses of the plastidic and nuclear sequences. Only conflicting nodes with 60% BS
508or higher were considered.

509 Divergence time analyses were conducted in BEAST 1.8.4 (Drummond et al., 2012;
510Heled and Drummond, 2012), applying the same partitions and substitution models as
511described above. Substitution and clock models were set as unlinked, whereas tree models
512were linked among partitions. We performed two runs of 100 million generations each,
513sampling every 20000th generation, assuming an uncorrelated lognormal clock and, a Yule
514speciation model (Udny Yule, 1925). Convergence of individual runs was assessed by

515inspection of the highest posterior density (HPD) of the MCMC parameters in Tracer v1.6
516(Drummond and Rambaut, 2007). We checked that effective sample sizes for all relevant
517parameters were above the recommended minimum of 200 (Drummond and Rambaut, 2007).
518After removing 10% as burn-in, tree files from the independent chains were combined using
519TreeAnnotator v1.8.3 (Drummond et al., 2012; Drummond and Rambaut, 2007). Because of
520the lack of known fossils in Gesneriaceae, we used secondary calibration points derived from
521the time-calibrated phylogenetic tree of Gesneriaceae obtained by Roalson and Roberts
522(2016). We chose to use the divergence between *Peltanthera* and the rest of Gesneriaceae,
523estimated at 81.9 Ma to constraint the age of the root, and the split of Gesnerioideae from the
524remaining Gesneriaceae, estimated at 69.66 Ma. For each calibration point, we used a normal
525distribution priors with a high degree of flexibility (SD 5.0).

5262.4. Historical Biogeography

527 The geographical distribution of each species of Beslerieae was categorized into eight
528eco-geographical regions, defined to reflect floristic and vegetation patterns as well as the
529geological history of those rainforest areas (Antonelli et al., 2009; Cabrera and Willink, 1973;
530Hoorn et al., 2010; Morrone, 2014; Perret et al., 2013; Ribas et al., 2012). These regions are:
531(C) Central America; (N) Northern Andes, from Venezuela to Ecuador, limited by the
532Western Andean Portal ((Antonelli et al., 2009); (S) Tropical southern Andes, including
533Bolivia and Peru; (A) Amazonia lowlands; (B) Brazilian Atlantic rainforest; (G) Guiana
534shield and northeast Venezuela; and (W) West Indies. Taxa ranging outside the American
535continents were assigned to either (O) Old world. The occurrence of the species was obtained
536through the data available at the Global Biodiversity Information Facility (GBIF
537doi.org/10.15468/dl.raohzu, <http://www.gbif.org>) and World Checklist of Gesneriaceae (Skog
538and Boggan, 2007).

539 Comparison of biogeographic models and ancestral area reconstruction (AAR) were
540performed using the R package BioGeoBEARS (Matzke, 2014; Van Dam and Matzke, 2016).
541BioGeoBEARS implements the three most commonly used methods in historical
542biogeography and allows their comparisons (Dupin et al., 2016). These are DEC (dispersal–
543extinction–cladogenesis; (Ree and Smith, 2008), DIVA (dispersal–vicariance analysis;
544(Ronquist, 1997) and BayArea (Bayesian Inference of Historical Biogeography for Discrete
545Areas;(Landis et al., 2013). Each model was implemented with and without the parameter “j”
546accounting for the probability of founder-event speciation. The resulting six models were

547tested using the Akaike information criterion (AIC). The best fit model with the lowest AIC
548score was used to infer the relative probabilities of ancestral ranges at each node of the time-
549calibrated phylogeny derived from the BEAST analysis described here above.

5502.5. *Morphological traits*

551 Herbarium specimens were examined or obtained from loans in the following herbaria
552B, F, G, G-DC, M, P, R, S, W, ALCB, BAH, BHCB, CAY, CEN, CEPEC, CESJ, COL, ESA,
553FCAB, FLOR, GZU, HAS, HERBAM, HPL, HRCB, HUEFS, HUFU, IAC, INPA, IPA,
554LABEV, LE, MBM, MBML, MG, MO, NY, RB, RBW, RON, SINBIOTA, SP, SPSF, UB,
555UEC, UPCB, US and VIES, acronyms according to (Thiers, n.d.). Wherever possible, floral
556and fruit features were examined in the field on living material, on parts kept in alcohol
557(pickled collection), or using the extensive collection of pictures documented and made
558available by JLC (also mostly online in the Gesneriaceae Image Library, John Clark Lab
559<http://gesneriads.ua.edu/image-library/>).

560 1.3 3. Results

5613.1. *Phylogenetic Analyses*

562 The combined matrix of all DNA regions comprised a total of 4,433 characters with
5631494 variable sites. Of these, 3,631 sites (1,582 variable) derived from plastidial sequences
564(*trnL-trnF*, *matK* and *rps16*) and 802 sites (473 variable) from ITS. The comparison of
565phylogenetic analyses derived from separate analyses of nuclear and chloroplastic datasets did
566not indicate supported topological incongruences (BS>60%, PP>0.95) and only results
567derived from the combined dataset are shown. The ML and BEAST analyses resulted in
568congruent topologies (Figure 2 and 3). In both analyses, the tribe Beslerieae is monophyletic
569and sister to *Titanotrichum*, although this relationship is poorly supported. *Besleria* (PP 1, BS
570100%) is monophyletic and sister to *Cremosperma* (PP 1, BS 95%), which together form a
571basal grade in Beslerieae with *Reldia*, *Gasteranthus* and *Anethanthus+Shuarua* (Fig. 2).
572Within *Besleria*, our analyses resolved six major clades that are characterized by specific
573geographical distributions (Fig. 4 and 5). The Clade A is sister to all other *Besleria* (1 PP,
574100% BS), and comprises endemic species with a restricted distribution in the Guianas
575highlands or on specific Caribbean islands, but it also includes the most widely distributed
576species in *Besleria* like *B. flavo-virens* and *B. laxiflora* that both range from eastern Brazil to
577Mexico and *B. pauciflora* distributed from Nicaragua to Bolivia (Fig. 5a). Clade B (PP 1,
57888% BS) is only composed of two samples of *B. sprucei* distributed on the foothills along the

579 eastern side of the Andes and in the Amazon lowlands (Fig. 5b). Clade C (PP 1 BS 93%)
 580 mainly comprises Andean species excepted one, *B. aggregata*, which expands its range into
 581 the Amazon basin. Clades D (PP 1 and BS 93%) and E (PP 1, BS 72%) are sister but present a
 582 distinct distribution: Clade D is an endemic lineage from the Atlantic forest in southeastern
 583 Brazil whereas Clade E is centered in the Southern Andes between Bolivia and Peru (Fig. 5c).
 584 Finally, clade F (PP1) includes species distributed either in the northern Andes or in Central
 585 America, or across both regions (Fig. 5c).

586 3.2. Divergence Times

587 The divergence time estimates suggest that Beslerieae split from the other
 588 Gesneriaceae during the Paleocene (60 Ma, 59.95-74.87 Mya; mean, 95% HPD) and that
 589 current diversity in *Besleria* originated in the Early Miocene (19 Mya, 15.13–25.17 Ma) (Fig.
 590 3). All major crown groups recognized within *Besleria* emerged between 11 and 8 Mya and
 591 diversified intensively during the Late Miocene.

592 3.3. Biogeographic Analyses

593 The best-fit model was DEC+*j* (lnL = -204.2; Table 2) followed with a difference of -
 594 205.1 log-likelihood units by the DIVALIKE model. Biogeographic reconstruction using this
 595 model indicates that *Besleria* most probably originated in the northern Andes around the
 596 Middle Miocene. Subsequent colonization of the other Neotropical regions occupied by
 597 *Besleria* followed different clade-specific trajectories. The most recent common ancestor
 598 (MRCA) of Clade A and C were likely distributed in Northern Andes (combined with
 599 Amazon lowlands for Clade C). Diversification of Clade C occurred mainly within northern
 600 Andes, whereas Clade A species reached the Guiana shield and the West Indies ca. 7 Mya.
 601 Range expansion of few species (e.g., *B. laxiflora* and *B. falvo-virens*) into the lowland
 602 rainforests of Eastern Brazil (Bahia State), and Central America account for the widespread
 603 distribution of Clade A along the eastern portion of the Neotropics up to Mexico. Remaining
 604 *Besleria* species belong to sister lineages showing a north-south disjunction: one distributed in
 605 Central Andes and southeastern Brazil (Clade D/E), the other distributed in the northern
 606 Andes and Central America (Clade F). The dispersal event to Central Andes directly followed
 607 by a founder event to southeastern Brazil ca. 10 Mya, gave rise to the endemic radiations in
 608 Central Andes (Clade E) and in the Brazilian Atlantic forest (Clade D). Range expansion into
 609 Central America was reconstructed at the root of Clade F ca. 8-10 Ma. Followed by a
 610 vicariance, this event gave rise to a Central American endemic lineage (*B. notabilis*, *B.*

611*hirsuta*, *B. rara*, and *B. formicaria*) while the remaining Clade F in northern Andes continued
612to diversify and expanded later into Central America.

6133.4. Morphological traits

614 No clear-cut synapomorphies support the retrieved clades (Appendix, Fig. S1-5).
615Diagnostic characters used to circumscribe the species, like pedunculate or epedeunculate
616inflorescences, corolla shape or color and fruit dehiscence type are highly convergent and not
617restricted to any particular clade, although the information is missing for some taxa.
618According to our reconstruction (Fig. 3) rupturing berries evolved seven times independently
619from indehiscent berries, which is the ancestral condition in *Besleria*.

620 1.4 4. Discussion

621 Our results provide the most resolved phylogeny of the genus *Besleria* to date. Most of
622the six major clades identified within *Besleria* have not been recognized in previous
623phylogenetic and taxonomic studies. These lineages are more easily characterized by their
624geographic distribution than by morphological synapomorphies. Our divergence time analyses
625suggest that *Besleria* started diversifying in the Early Miocene probably in the northern
626Andes. The biogeographic history of *Besleria* and its expansion in South and Central America
627was largely influenced by the main geological and paleogeographic events that occurred in the
628Neotropics during the Miocene.

6294.1. Phylogenetic relationships and systematic implication

630 Our results corroborate the monophyly of *Besleria* and its sister relationship with
631*Cremosperma* (Clark et al., 2010; Roalson and Clark, 2006) Major relationships recovered
632within the tribe Beslerieae are congruent with the phylogenetic analysis by Clark et al. (2010)
633supporting the segregation of *Gasteranthus* from *Besleria* as proposed by Wiehler (1975) and
634the division of Beslerieae in two subtribes: the Besleriinae composed of *Besleria*,
635*Cremosperma*, *Reldia* and *Gasteranthus* and the Anetanthinae, represented by *Anetanthus* and
636*Shuaria* (Weber et al., 2013). Although with a low support, *Titanotrichum* was found sister to
637Beslerieae, in contrast with previous results that placed Napeantheae at this position (Perret et
638al., 2013; Roalson and Roberts, 2016).

639 Our phylogenetic results identified six major clades within *Besleria* (Clades A to F;
640Fig. 1). The current phylogenetic tree is far more resolved than previous results derived from
641the analysis of 28 accessions of *Besleria* and ITS only (Roalson and Clark 2006) or from a

642family-scale analysis of Gesneriaceae using the available sequences in Genbank at that time
643(Roalson and Roberts 2016). According to our analysis, none of the sections and subsections
644of *Besleria*, proposed by (Morton, 1939) and revised by (Wiehler, 1975), are monophyletic.
645For example, the subsection Sessiles defined by a short calyx lobes and inflorescences
646without peduncles and the subsection Pedunculatae characterized on the contrary by a well-
647developed peduncle are both segregated across four different clades (Fig. 1). This indicates
648that infrageneric classification of *Besleria* need a complete revision and that morphological
649characters used in previous classification are homoplastic. Similar rate of convergence in the
650evolution of morphological traits have been identified among the different lineages of
651Gesneriaceae stressing the difficulty in defining taxa and resolving evolutionary relationships
652among such groups using morphological data alone (Clark et al., 2015, 2012, 2011; Ferreira et
653al., 2016a; Serrano-Serrano et al., 2015).

6544.2. *Historical biogeography*

655 Our ancestral area estimation suggest that *Besleria* probably originated in the northern
656Andes around 19 Ma during the onset of the northern Andean uplift (Garzzone et al., 2008).
657The fact that *Besleria* diversity peaked at middle-elevation (500-2000 m) suggest that
658diversification of this genus was likely promoted by Andean uplifts that increased the
659availability of suitable habitats and their connectivity with the surrounding areas (Antonelli et
660al., 2009; Luebert and Weigend, 2014). Around 10 Mya, *Besleria* dispersed southward into
661Central America and southeastern Brazil and northward into Central America. Radiation
662within these areas gave rise to three main lineages with little overlap in their distribution
663(Clades D, E, and E; Fig. 4). First unambiguous colonization of Central Andes was
664reconstructed at the root of the Clade D/E. This dispersal event coincides with the closure of
665the Western Andean Portal [WAP] that served as a corridor for marine incursions into the
666Amazon basin until the Middle Miocene (13-11 Mya). This region, also named Amotape-
667Huancabamba Zone, is located between southern Ecuador and northern Peru and has
668frequently been referred to a barrier for the dispersal of Andean plant groups (Antonelli et al.,
6692009; Mutke et al., 2014; Struwe et al., 2009; Weigend et al., 2010). Similar timing for the
670colonization of Central Andes from the North has been recorded in other plant groups such as
671Rubiaceae and Chlorantaceae suggesting that the WAP acted as an effective dispersal barrier
672for mid-elevation plants in the Andes (Antonelli et al., 2009; Antonelli and Sanmartin, 2011;
673Luebert and Weigend, 2014). The mainly insitu, diversification of Clade E within Central
674Andes and the limited subsequent recolonization of northern Andes indicate that the

675Amotape- Huancabamba zone acted as a dispersal barrier for *Besleria* even after the the
676closure of the WAP due to Andean uplift. Colonization of *Besleria* in southeastern Brazil
677probably involved a single founder event from Central Andes 9-8 Mya, although the
678hypothesis of vicariance between these areas cannot be excluded. Our results indicate that
679dispersal of *Besleria* into the Atlantic forest occurred before the assemblage of the Cerrado
680biome 10-5 Mya (Simon et al., 2011) when Neotropical rainforests were probably more
681interconnected than today (Morley, 2000; Sobral-Souza et al., 2015). The strict biogeographic
682disjunction between the Andean and the Brazilian clades and their endemic radiations within
683these areas agree with previous studies suggesting that the formation of a SW-NE diagonal of
684dry vegetation across South America have strongly limited the biotic exchanges between the
685Atlantic forest and the other surrounding biomes (Costa, 2003; Ferreira et al., 2016a; Fouquet
686et al., 2012; Werneck et al., 2012).

687 Range extension of *Besleria* into Central America occurred a first time 7-10 Mya in
688concordance with the formation of the Panama Isthmus during the Middle Miocene and a
689period of intense biotic exchanges between South and North America (Bacon et al., 2015;
690Jaramillo et al., 2017a). Early vicariance in Clade F gave rise to a subclade endemic to
691Panama and Costa-Rica (*B. notabilis*, *B. hirsuta*, *B. rara*, and *B. formicaria*) whereas
692remaining *Besleria* diversity in Central America is explained by recent range expansions of
693species distributed in both Andes and Central America. All *Besleria* species occurring in the
694Guiana shield, the West Indies and northeastern of Brazil belong to the same Clade A (Fig. 4).
695Your results suggest that dispersals from the northern Andes to the Guiana Shield and West
696Indies probably started 6-8 Mya, after the drying of the Pebas system (Hoorn et al., 2010) and
697marine incursions (Jaramillo et al., 2017b) that likely limited the biotic interchanges between
698the western and eastern portions of the Neotropics (Antonelli et al. 2009). Finally, the
699widespread distribution of *B. laxiflora* and *B. flavo-virens* in the lowland rainforests of
700Central America, NE South America and eastern Brazil (Fig. 4) is probably the result of
701recent range expansions (5-7 Mya). Although the origin of this disjunct distribution may
702involve long distance dispersal, a more likely hypothesis is that range expansions of these
703species have followed the global expansion of Neotropical rainforests that led to the
704connection of the Amazon and Atlantic forest during the LGM (Sobral-Souza et al. 2015).

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720 **1.5 References**

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Table 1. Sequences of *Besleria* and outgroups used for phylogenetic analyses. Species names and their authors, herbarium vouchers, origin of the sample, and GenBank accession numbers. Herbarium acronyms follow Thiers (continuous update).

Species	Voucher	Origin	ITS	trnLF	rps16	matK
<i>Anetanthus gracilis</i> Hiern	M. Peixoto & A. Chautems 28 (G)	Brazil	KU991234.1	AJ439827	JX195806	JX195949
<i>Besleria affinis</i> C.V.Morton	J.L. Clark 5629 (UNA)	Ecuador	To submit	To submit	To submit	To submit
<i>Besleria affinis</i> C.V.Morton	J.L. Clark 9308 (UNA)	Ecuador	To submit	To submit	To submit	To submit
<i>Besleria aggregata</i> (Mart.) Hanst.	J.L. Clark 11497 (UNA)	Peru	To submit	N.A.	N.A.	To submit
<i>Besleria aggregata</i> (Mart.) Hanst.	J.L. Clark 11503 (UNA)	Peru	To submit	N.A.	To submit	To submit
<i>Besleria angustiflora</i> Fritsch	J.L. Clark 4575 (UNA)	Ecuador	To submit	To submit	To submit	To submit
<i>Besleria aurea</i> I.G.Costa & G.E.Ferreira	M. Perret et al. 65 (G)	Brazil	KY858260.1	To submit	To submit	To submit
<i>Besleria barbata</i> (Poepp.) Hanst.	J.L. Clark 5705 (UNA)	Ecuador	To submit	To submit	To submit	To submit
<i>Besleria barbata</i> (Poepp.) Hanst.	J.L. Clark 5880 (UNA)	Ecuador	To submit	To submit	To submit	To submit
<i>Besleria barbata</i> (Poepp.) Hanst.	J.L. Clark 6431 (UNA)	Ecuador	To submit	To submit	To submit	To submit
<i>Besleria barbata</i> (Poepp.) Hanst.	J.L. Clark 7854 (UNA)	Ecuador	To submit	To submit	To submit	To submit

Species	Voucher	Origin	ITS	trnLF	rps16	matK
<i>Besleria barclayi</i> L.E.Skog	J.L. Clark 4971 (UNA)	Ecuador	To submit	To submit	To submit	To submit
<i>Besleria beltranii</i> I.Salinas	J.L. Clark 8198 (UNA)	Peru	To submit	To submit	To submit	To submit
<i>Besleria brevicalyx</i> G.E.Ferreira & Chautems	G.E. Ferreira 292 (INPA)	Brazil	To submit	To submit	To submit	To submit
<i>Besleria capitata</i> Poepp.	L. Cairampoma & D. Martel 105	Peru	KY858258. 1	KY858576. 1	KY858507. 1	KY858650. 1
<i>Besleria comosa</i> C.V.Morton	J.L. Clark 6008 (UNA)	Ecuador	To submit	To submit	To submit	To submit
<i>Besleria comosa</i> C.V.Morton	J.L. Clark 9882 (UNA)	Ecuador	To submit	To submit	To submit	To submit
<i>Besleria connata</i> C.V.Morton	J.L. Clark 6890 (UNA)	Venezuela	To submit	To submit	To submit	To submit
<i>Besleria diabolica</i> G.E.Ferreira & Chautems	G.E. Ferreira 271 (INPA)	Brazil	To submit	To submit	To submit	To submit
<i>Besleria diabolica</i> G.E.Ferreira & Chautems	G.E. Ferreira 271 (INPA)	Brazil	To submit	To submit	To submit	To submit
<i>Besleria discreta</i> G.E.Ferreira	G.E. Ferreira 291 (INPA)	Brazil	To submit	To submit	To submit	To submit
<i>Besleria divaricata</i> Poepp.	J.L. Clark 11470	Peru	To submit	N.A.	To submit	To submit

Species	Voucher	Origin	ITS	trnLF	rps16	matK
<i>Besleria divaricata</i> Poepp.	L.Cairampoma & D.Martel 114	Peru	KY858256. 1	KY858575. 1	KY858505. 1	KY858648. 1
<i>Besleria emendata</i> C.V.Morton	J.L. Clark 8177 (UNA)	Peru	To submit	To submit	To submit	To submit
<i>Besleria fallax</i> C.E.González <i>et al.</i>	J.L. Clark 13028 (UNA)	Colombia	To submit	To submit	To submit	To submit
<i>Besleria filipes</i> Urb.	J.L. Clark 6559 (UNA)	Dominica	To submit	N.A.	To submit	To submit
<i>Besleria flavovirens</i> Nees & Mart.	G.E. Ferreira 313 (INPA)	Brasil	To submit	To submit	To submit	To submit
<i>Besleria flavovirens</i> Nees & Mart.	G.E. Ferreira 314 (INPA)	Brasil	To submit	To submit	To submit	To submit
<i>Besleria fluminensis</i> Brade	G.E. Ferreira 276 (INPA)	Brasil	To submit	To submit	To submit	To submit
<i>Besleria fluminensis</i> Brade	G.E. Ferreira 276 (UNA)	Brasil	To submit	To submit	To submit	To submit
<i>Besleria formicaria</i> Nowicke	M. Perret 105 (G)	Panama	To submit	To submit	To submit	To submit
<i>Besleria formicaria</i> Nowicke	M. Perret 106 (G)	Panama	To submit	To submit	To submit	To submit
<i>Besleria formicaria</i> Nowicke	M. Perret 120 (G)	Panama	To submit	To submit	To submit	To submit
<i>Besleria formosa</i> C.V.Morton	G.E. Ferreira 333 (INPA)	Colombia	To submit	To submit	To submit	To submit
<i>Besleria formosa</i> C.V.Morton	J.L. Clark 12930 (UNA)	Colombia	To submit	To submit	To submit	To submit

Species	Voucher	Origin	ITS	trnLF	rps16	matK
<i>Besleria formosa</i> C.V.Morton	J.L. Clark 8145 (UNA)	Ecuador	To submit	To submit	To submit	To submit
<i>Besleria gracilentia</i> C.V.Morton	J.L. Clark 8202 (UNA)	Peru	To submit	To submit	To submit	To submit
<i>Besleria grandifolia</i> Schott	G.E. Ferreira 279 (INPA)	Brasil	To submit	To submit	To submit	To submit
<i>Besleria grandifolia</i> Schott	G.E. Ferreira 279 (INPA)	Brasil	To submit	To submit	To submit	To submit
<i>Besleria hirsuta</i> (Oerst.) Hanst.	M. Perret 108 (G)	Panama	To submit	To submit	To submit	To submit
<i>Besleria hirsutissima</i> C.V.Morton	J.L. Clark 6901 (UNA)	Venezuela	To submit	To submit	To submit	To submit
<i>Besleria hutchisonii</i> C.V.Morton	J.L. Clark 8181 (UNA)	Peru	To submit	To submit	To submit	To submit
<i>Besleria iara</i> G.E.Ferreira & M.Hopikns	J.L. Clark 5049 (UNA)	Ecuador	To submit	To submit	To submit	To submit
<i>Besleria immitis</i> C.V.Morton	J.L. Clark 11796 (UNA)	Peru	To submit	N.A.	To submit	To submit
<i>Besleria impressa</i> C.V.Morton	J. Betancur 12678 (CUVC)	Colombia	N.A.	To submit	To submit	To submit
<i>Besleria</i> indet.	G.E. Ferreira 340 (INPA)	Colombia	To submit	To submit	To submit	To submit
<i>Besleria</i> indet.	G.E. Ferreira 344 (INPA)	Colombia	To submit	To submit	To submit	To submit
<i>Besleria</i> indet.	J. Betancur 13095 (CUVC)	Colombia	To submit	To submit	To submit	To submit

Species	Voucher	Origin	ITS	trnLF	rps16	matK
<i>Besleria</i> indet.	J. Betancur 13489 (CUVC)	Colombia	To submit	N.A.	To submit	To submit
<i>Besleria</i> indet.	J. Betancur 13734 (CUVC)	Colombia	To submit	To submit	To submit	To submit
<i>Besleria</i> indet.	J. Betancur 14356 (CUVC)	Colombia	To submit	To submit	To submit	To submit
<i>Besleria</i> indet.	J. Betancur 18011 (CUVC)	Colombia	To submit	N.A.	To submit	To submit
<i>Besleria</i> indet.	J.L. Clark 11765 (UNA)	Peru	To submit	To submit	To submit	To submit
<i>Besleria</i> indet.	J.L. Clark 11774 (UNA)	Peru	To submit	To submit	N.A.	To submit
<i>Besleria</i> indet.	J.L. Clark 11782 (UNA)	Peru	To submit	To submit	To submit	To submit
<i>Besleria</i> indet.	G.E. Ferreira 337 (INPA)	Colombia	To submit	To submit	To submit	To submit
<i>Besleria</i> indet.	G.E. Ferreira 338 (INPA)	Colombia	To submit	To submit	To submit	To submit
<i>Besleria</i> indet.	G.E. Ferreira 343 (INPA)	Colombia	To submit	To submit	To submit	To submit
<i>Besleria laxiflora</i> Benth.	G.E. Ferreira 303 (INPA)	Brasil	To submit	To submit	To submit	To submit
<i>Besleria laxiflora</i> Benth.	G.E. Ferreira 312 (INPA)	Brasil	To submit	To submit	To submit	To submit
<i>Besleria longimucronata</i> Hoehne	G.E. Ferreira 273 (INPA)	Brasil	To submit	To submit	To submit	To submit
<i>Besleria longimucronata</i> Hoehne	G.E. Ferreira 274 (INPA)	Brasil	To submit	To submit	To submit	To submit

Species	Voucher	Origin	ITS	trnLF	rps16	matK
<i>Besleria longipedunculata</i> Britton	J.L. Clark 6782 (UNA)	Bolivia	To submit	N.A.	To submit	To submit
<i>Besleria lutea</i> L.	J.L. Clark 10510 (UNA)	Cuba	To submit	To submit	To submit	N.A.
<i>Besleria lutea</i> L.	J.L. Clark 6552 (UNA)	Dominica	To submit	To submit	To submit	To submit
<i>Besleria macahensis</i> Brade	M. Perret 70 (G)	Brasil	KY858257. 1	N.A.	KY858506. 1	KY858649. 1
<i>Besleria melancholica</i> (Vell.) C.V.Morton	G.E. Ferreira 281 (INPA)	Brasil	To submit	To submit	To submit	To submit
<i>Besleria melancholica</i> (Vell.) C.V.Morton	G.E. Ferreira 281 (INPA)	Brasil	To submit	To submit	To submit	To submit
<i>Besleria melancholica</i> (Vell.) C.V.Morton	G.E. Ferreira 285 (INPA)	Brasil	To submit	To submit	To submit	To submit
<i>Besleria melancholica</i> (Vell.) C.V.Morton	R.C. Forzza 2419 (G)	Brasil	GQ344505. 1	GQ383542	GQ383580. 1	JX195952
<i>Besleria membranacea</i> C.V.Morton	J.L. Clark 6448 (UNA)	Ecuador	To submit	To submit	To submit	To submit
<i>Besleria mirifica</i> C.V.Morton	G.E. Ferreira 336 (INPA)	Colombia	To submit	To submit	To submit	To submit

Species	Voucher	Origin	ITS	trnLF	rps16	matK
<i>Besleria mirifica</i> C.V.Morton	G.E. Ferreira 346 (INPA)	Colombia	To submit	To submit	To submit	To submit
<i>Besleria modica</i> C.V.Morton	J.L. Clark 6056 (UNA)	Ecuador	To submit	To submit	To submit	To submit
<i>Besleria montana</i> Britton	Beck 25455 (G)		To submit	N.A.	N.A.	To submit
<i>Besleria montana</i> Britton	J.L. Clark 6678 (UNA)	Bolivia	To submit	To submit	To submit	To submit
<i>Besleria mortoniana</i> Steyerm.	J.L. Clark 6900 (UNA)	Venezuela	To submit	To submit	To submit	To submit
<i>Besleria nitens</i> Fritsch	G.E. Ferreira 347 (INPA)	Colombia	To submit	To submit	To submit	To submit
<i>Besleria notabilis</i> C.V.Morton	J.L. Clark 8548 (INPA)	Panama	To submit	To submit	To submit	To submit
<i>Besleria notabilis</i> C.V.Morton	M. Perret 109 (G)	Panama	To submit	To submit	To submit	To submit
<i>Besleria notabilis</i> C.V.Morton	Perret M. & A. Chautems 22 (G)	Panama	KY858259.1	JX195725.1	JX195809.1	JX195953
<i>Besleria ovalifolia</i> Britton	J.L. Clark 6707 (UNA)	Bolivia	To submit	To submit	To submit	To submit
<i>Besleria ovalifolia</i> Britton	J.L. Clark 6852 (UNA)	Bolivia	To submit	To submit	To submit	To submit
<i>Besleria patrisii</i> DC.	K.M. Redden 1881	Guyana	To submit	N.A.	To submit	N.A.
<i>Besleria pauciflora</i> Rusby	G.E. Ferreira 348 (INPA)	Colombia	To submit	To submit	To submit	To submit

Species	Voucher	Origin	ITS	trnLF	rps16	matK
<i>Besleria pauciflora</i> Rusby	J.L. Clark 12577 (UNA)	Panama	To submit	To submit	N.A.	To submit
<i>Besleria pauciflora</i> Rusby	J.L. Clark 9280 (UNA)	Ecuador	To submit	To submit	N.A.	N.A.
<i>Besleria pendula</i> Hanst.	J.L. Clark 6866 (UNA)	Venezuela	To submit	To submit	N.A.	N.A.
<i>Besleria pendula</i> Hanst.	J.L. Clark 6887 (UNA)	Venezuela	To submit	To submit	To submit	To submit
<i>Besleria petiolaris</i> (Griseb.) Urb.	J.L. Clark 6580 (UNA)	Dominica	To submit	To submit	To submit	To submit
<i>Besleria quadrangulata</i> L.E.Skog	J.L. Clark 11894 (UNA)	Peru	N.A.	To submit	N.A.	To submit
<i>Besleria quadrangulata</i> L.E.Skog	J.L. Clark 8376 (UNA)	Ecuador	To submit	To submit	To submit	To submit
<i>Besleria rara</i> L.E.Skog	M. Perret 135 (G)	Panama	To submit	To submit	To submit	To submit
<i>Besleria reticulata</i> Fritsch	G.E. Ferreira 349 (INPA)	Colombia	To submit	To submit	To submit	To submit
<i>Besleria reticulata</i> Fritsch	J.L. Clark 5848 (UNA)	Ecuador	To submit	To submit	To submit	To submit
<i>Besleria reticulata</i> Fritsch	J.L. Clark 6862 (UNA)	Venezuela	To submit	To submit	To submit	To submit
<i>Besleria robusta</i> Donn.Sm.	J.L. Clark 12645 (UNA)	Panama	To submit	To submit	To submit	To submit

Species	Voucher	Origin	ITS	trnLF	rps16	matK
<i>Besleria robusta</i> Donn.Sm.	M. Perret 134 (G)	Panama	To submit	To submit	To submit	To submit
<i>Besleria rotundifolia</i> Rusby	J.L. Clark 6786 (UNA)	Bolivia	To submit	To submit	To submit	To submit
<i>Besleria saxicola</i> C.V.Morton	K.M. Redden 2233	Guyana	To submit	To submit	N.A.	N.A.
<i>Besleria selloana</i> Klotzsch & Hanst.	A.O. Araújo (HUFABC)	Brazil	To submit	To submit	To submit	To submit
<i>Besleria selloana</i> Klotzsch & Hanst.	G.E. Ferreira 268 (INPA)	Brazil	To submit	To submit	To submit	To submit
<i>Besleria selloana</i> Klotzsch & Hanst.	G.E. Ferreira 268 (INPA)	Brazil	To submit	To submit	To submit	To submit
<i>Besleria solanoides</i> Kunth	G.E. Ferreira 342 (INPA)	Colombia	To submit	To submit	To submit	To submit
<i>Besleria solanoides</i> Kunth	J.L. Clark 6113 (UNA)	Ecuador	To submit	To submit	To submit	To submit
<i>Besleria solanoides</i> Kunth	J.L. Clark 7239 (UNA)	Ecuador	To submit	N.A.	To submit	To submit
<i>Besleria solanoides</i> Kunth	J.L. Clark 7354 (UNA)	Ecuador	To submit	To submit	To submit	To submit
<i>Besleria</i> indet.	M. Perret 122 (G)	Panama	To submit	To submit	To submit	To submit
<i>Besleria sprucei</i> Britton ex Rusby	J. Betancur 13725 (CUVC)		To submit	To submit	To submit	To submit
<i>Besleria sprucei</i> Britton ex Rusby	J. Betancur 13801 (CUVC)		To submit	To submit	To submit	To submit
<i>Besleria stricta</i> L.E.Skog	J.L. Clark 6790 (UNA)	Bolivia	To submit	To submit	To submit	To submit
<i>Besleria stricta</i> L.E.Skog	J.L. Clark 9216 (UNA)	Ecuador	To submit	To submit	To submit	To submit

Species	Voucher	Origin	ITS	trnLF	rps16	matK
<i>Besleria tambensis</i> C.V.Morton	G.E. Ferreira 353 (INPA)	Colombia	N.A.	To submit	To submit	To submit
<i>Besleria tambensis</i> C.V.Morton	J.L. Clark 13297 (UNA)	Colombia	To submit	To submit	To submit	To submit
<i>Besleria tambensis</i> C.V.Morton	J.L. Clark 7116 (UNA)	Ecuador	To submit	To submit	To submit	To submit
<i>Besleria trichiata</i> C.V.Morton	L.Cairampoma & D. Martel 102	Peru	To submit	To submit	To submit	To submit
<i>Besleria trichiata</i> C.V.Morton	L.Cairampoma & D. Martel 96	Peru	KY858261. 1	KY858577. 1	KY858508. 1	KY858651. 1
<i>Besleria vargasii</i> C.V.Morton	J.L. Clark 11388 (UNA)	Peru	To submit	To submit	To submit	To submit
<i>Besleria vargasii</i> C.V.Morton	J.L. Clark 11420 (UNA)	Peru	To submit	To submit	To submit	To submit
<i>Besleria vargasii</i> C.V.Morton	J.L. Clark 11703 (UNA)	Peru	To submit	To submit	N.A.	To submit
<i>Besleria variabilis</i> C.V.Morton	L.Cairampoma & D. Martel 107	Peru	KY858254. 1	To submit	KY858503. 1	KY858646. 1
<i>Besleria variabilis</i> C.V.Morton	L.Cairampoma & D. Martel 191	Peru	To submit	To submit	To submit	To submit
<i>Besleria ventricosa</i> C.V.Morton	G.E. Ferreira 332 (INPA)	Colombia	To submit	To submit	To submit	To submit
<i>Besleria vestita</i> Fritsch	G.E. Ferreira 334 (INPA)	Colombia	To submit	N.A.	To submit	To submit
<i>Columnea sanguinea</i> (Pers.) Hanst.	G.E. Ferreira 306 (INPA)	Brasil	To submit	To submit	To submit	To submit

Species	Voucher	Origin	ITS	trnLF	rps16	matK
<i>Creмосperma</i> indet.	M. Perret 141 (G)	Panama	To submit	To submit	To submit	To submit
<i>Creмосperma hirsutissimum</i> Benth.	M. Perret 205 (G)	Panama	To submit	To submit	To submit	N.A.
<i>Creмосperma maculatum</i> L.E.Skog	M. Perret 23 (G)	Panama	To submit	To submit	N.A.	To submit
<i>Creмосperma veraguanum</i> Wiehler	M. Perret 113 (G)	Panama	To submit	N.A.	To submit	To submit
<i>Creмосperma veraguanum</i> Wiehler	M. Perret 129 (G)	Panama	To submit	To submit	To submit	To submit
<i>Creмосperma veraguanum</i> Wiehler	M. Perret 140 (G)	Panama	To submit	To submit	To submit	To submit
<i>Episcia fimbriata</i> Fritsch	G.E. Ferreira 264 (INPA)	Brazil	To submit	To submit	To submit	To submit
<i>Gasteranthus</i> indet.	M. Perret 153 (G)	Panama	To submit	To submit	To submit	To submit
<i>Gasteranthus delphinioides</i> (Seem.) Wiehler	M. Perret 101 (G)	Panama	To submit	To submit	To submit	To submit
<i>Gasteranthus lateralis</i> (C.V.Morton) Wiehler	M. Perret 170 (G)	Panama	To submit	To submit	To submit	To submit
<i>Gasteranthus wendlandianus</i> (Hanst.) Wiehler	L.Cairampoma & D. Martel 92	Peru	To submit	To submit	N.A.	To submit
<i>Gesneria humilis</i> L.	A. Chautems & M. Perret 97-020 (G)		KY858342. 1	AJ439821	GQ383588. 1	JX195998

Species	Voucher	Origin	ITS	trnLF	rps16	matK
<i>Gloxinia perennis</i> (L.) Druce	A.O. Araujo & al. 536 (ESA)	Brazil	GQ344516. 1	GQ383551	GQ383591. 1	JX196001
<i>Mitraria coccinea</i> Cav.	A. Charpin 25967 (G)		GQ344530. 1	GQ383562. 1	GQ383604. 1	JX196014
<i>Monopyle maxonii</i> C.V.Morton	M. Perret 128 (G)	Panama	to submit	to submit	to submit	to submit
<i>Napeanthus apodemus</i> Donn.Sm.	M. Perret 197 (G)	Panama	to submit	to submit	to submit	to submit
<i>Napeanthus apodemus</i> Donn.Sm.	M. Perret 95 (G)		to submit	to submit	to submit	to submit
<i>Napeanthus primulifolius</i> (Raddi) Sandwith	A.O. Araujo 470 (ESA)	Brazil	KY858358. 1	JX195789.1	JX195872.1	JX196040
<i>Napeanthus reitzii</i> (L.B. Sm.) Burt ex Leeuwenb.	A.C. Cervi & al. AC479 (UPCB)	Brazil	KY858359. 1	GQ383563	GQ383605	JX196041
<i>Peltanthera floribunda</i> Benth.	Hammel 19855 (MO)		KY858417. 1	AJ430916	AJ431041	AJ429330
<i>Reldia longipedunculata</i> J.L.Clark	J.L. Clark 8835 (UNA)	Ecuador	GQ119609. 1	GQ166809. 1	N.A.	N.A.
<i>Reldia minutiflora</i> (L.E.Skog) L.P.Kvist	J. L. Clark 8017 (US)		GQ119610	GQ166810	N.A.	N.A.

Species	Voucher	Origin	ITS	trnLF	rps16	matK
& L.E.Skog						
<i>Reldia minutiflora</i> (L.E.Skog) L.P.Kvist & L.E.Skog	M. Perret 179 (G)	Panama	to submit	to submit	to submit	to submit
<i>Sanango racemosum</i> (Ruiz & Pav.) Barringer	D.A. Neill 9458 (US)		KU991241. 1	JX195799	JX195885	JX196060
<i>Shuaria ecuadorica</i> D.A.Neill & J.L.Clark	D.A. Neill 13180 (MO)	Ecuador	GQ119594	GQ166813	N.A.	N.A.
<i>Shuaria ecuadorica</i> D.A.Neill & J.L.Clark	D.A. Neill 15912 (MO)	Ecuador	GQ119593	GQ166812	N.A.	N.A.
<i>Sinningia brasiliensis</i> (Regel & E.Schmidt) Wiehler	A. Chautems & M. Perret 97-002 (G)		GQ344548. 1	AJ439756.1	GQ383619. 1	JX196072
<i>Sinningia schiffneri</i> Fritsch	A. Chautems & M. Perret 97-010 (G)		KY858481. 1	AJ439745.1	GQ383621. 1	JX196111
<i>Sphaerorrhiza sarmentiana</i> (Gardner ex Hook.) Roalson & Boggan	A.O. Araujo & al. 539 (ESA)		GQ344555	GQ383577. 1	GQ383626. 1	JX196125
<i>Titanotrichum oldhamii</i> (Hemsl.) Soler	A. Chautems & M. Perret 01-021 (G)		KY858494. 1	GQ383579	GQ383628	JX196127

927**Table 2.** Biogeographic models and comparative statistics. Abbreviations: Par= Number of
 928free parameters; LnL= log-likelihood; AICc=Akaike Information Criterion, corrected;
 929AICc_wt=Akaike weights; DEC = Dispersal Extinction Cladogenesis model; DIVALIKE=
 930BioGeoBEARS implementation of DIVA model; BAYAREALIKE= BioGeoBEARS
 931implementation of BayArea model; J= founder-event speciation. The best model is
 932highlighted.

Model	Par	LnL	d	e	j	AICc	AICc_wt
DEC	2	-205.7	0.021	1.0e-12	0	415.5	0.20
DEC+J	3	-204.2	0.020	1.0e-12	0.0079	414.7	0.31
DIVALIKE	2	-205.1	0.024	1.0e-12	0	414.3	0.38
DIVALIKE+J	3	-205.3	0.024	1.0e-12	1.0e-05	416.9	0.10
BAYAREALIKE	2	-232.9	0.018	0.055	0	469.9	3.1e-13
BAYAREALIKE+J	3	-219.6	0.018	1.0e-07	0.020	445.5	6.4e-08

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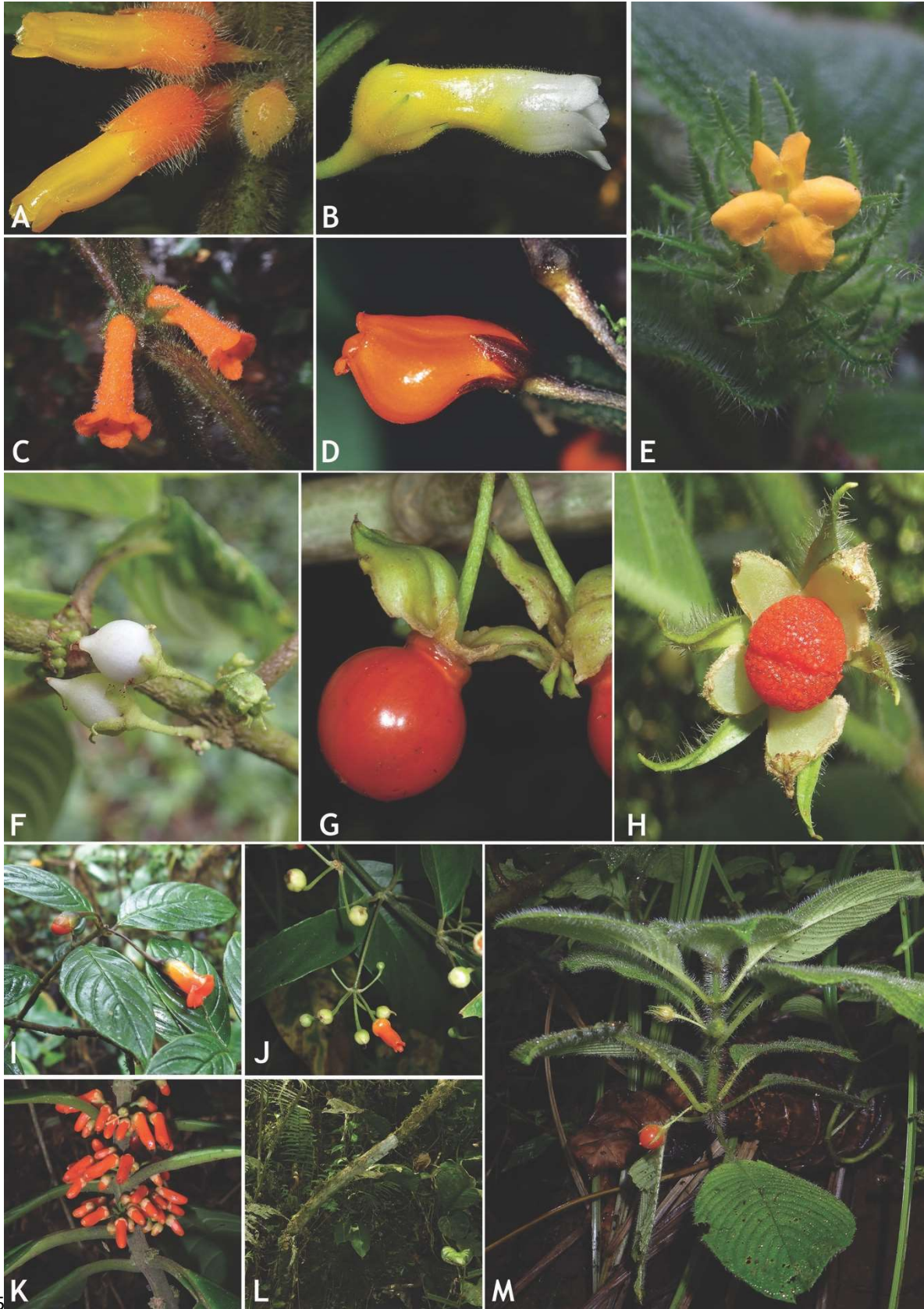
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938Figure captions:

939**Figure 1.** Hight diversity of characters in *Besleria* (Beslerieae, Gesneriaceae). (A) an
940understory shrub *B. mirifica*; flowers of (B) *B. iara*, (C) *B. brevicalyx*, (D) *B. vestita*, (E) *B.*
941*aggregate*; berry of (F) *B. lutea*, a “rupturing berry” of (G) *B. pauciflora* and (H) *B. laxiflora*;
942(I) solitary inflorescence in *B. Formosa*, (J) pedunculate inflorescence in *B. reticulata*; (K)
943axillary inflorescence in *B. longimucronata*; (L) woody trunk of *B. nitens* and (M) small herb
944*B. ventricosa*. Photos: Gabriel E. Ferreira (A–E, G–M), and John L. Clark (G).



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956posterior densities of divergence times. Green names and branches show the reconstruction of 957rupturing berries. Dashed line shows the end of Miocene. Photos: John L. Clark.



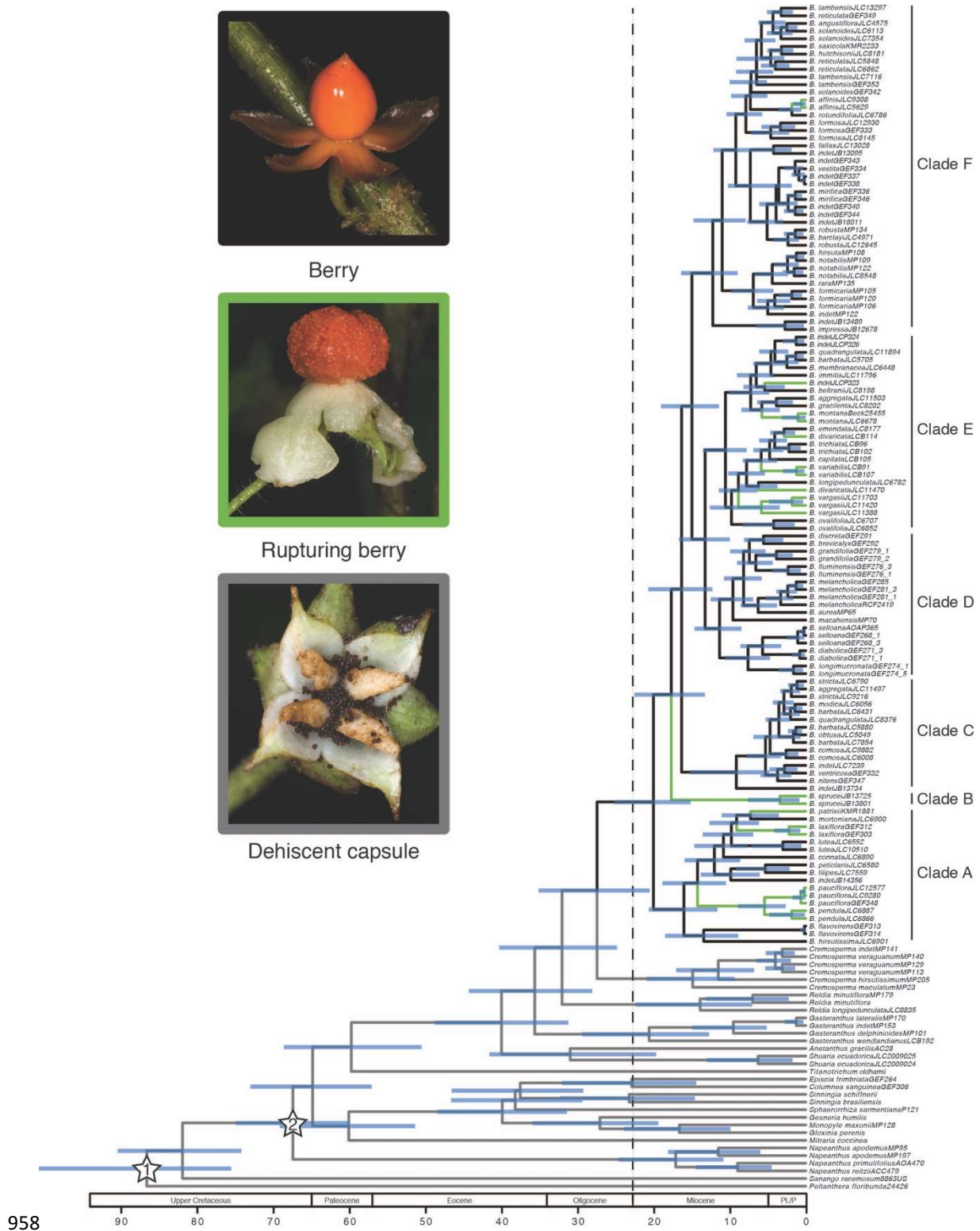
Berry



Rupturing berry



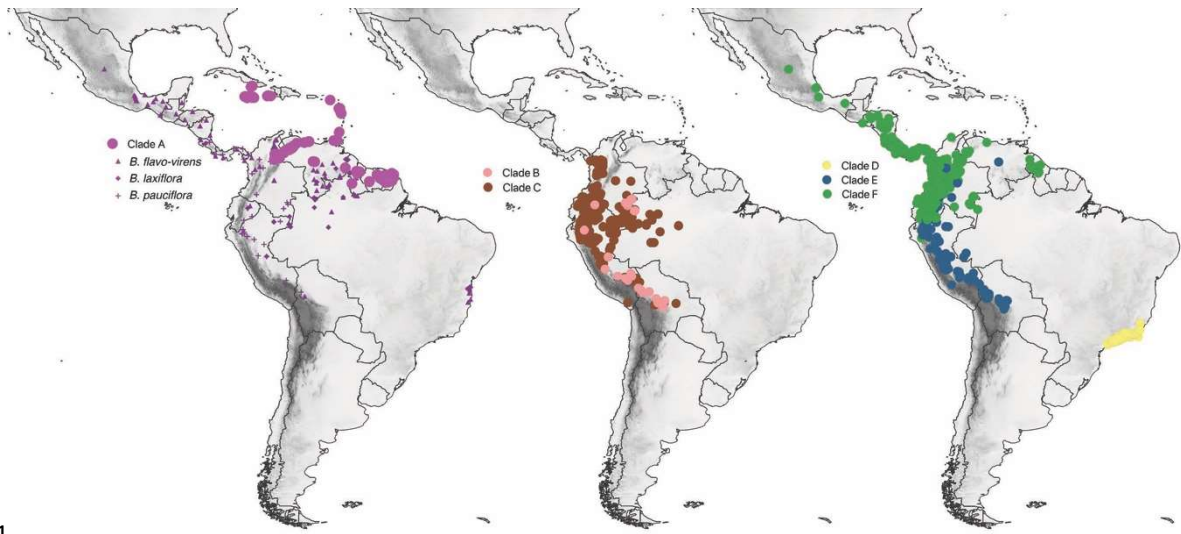
Dehiscent capsule



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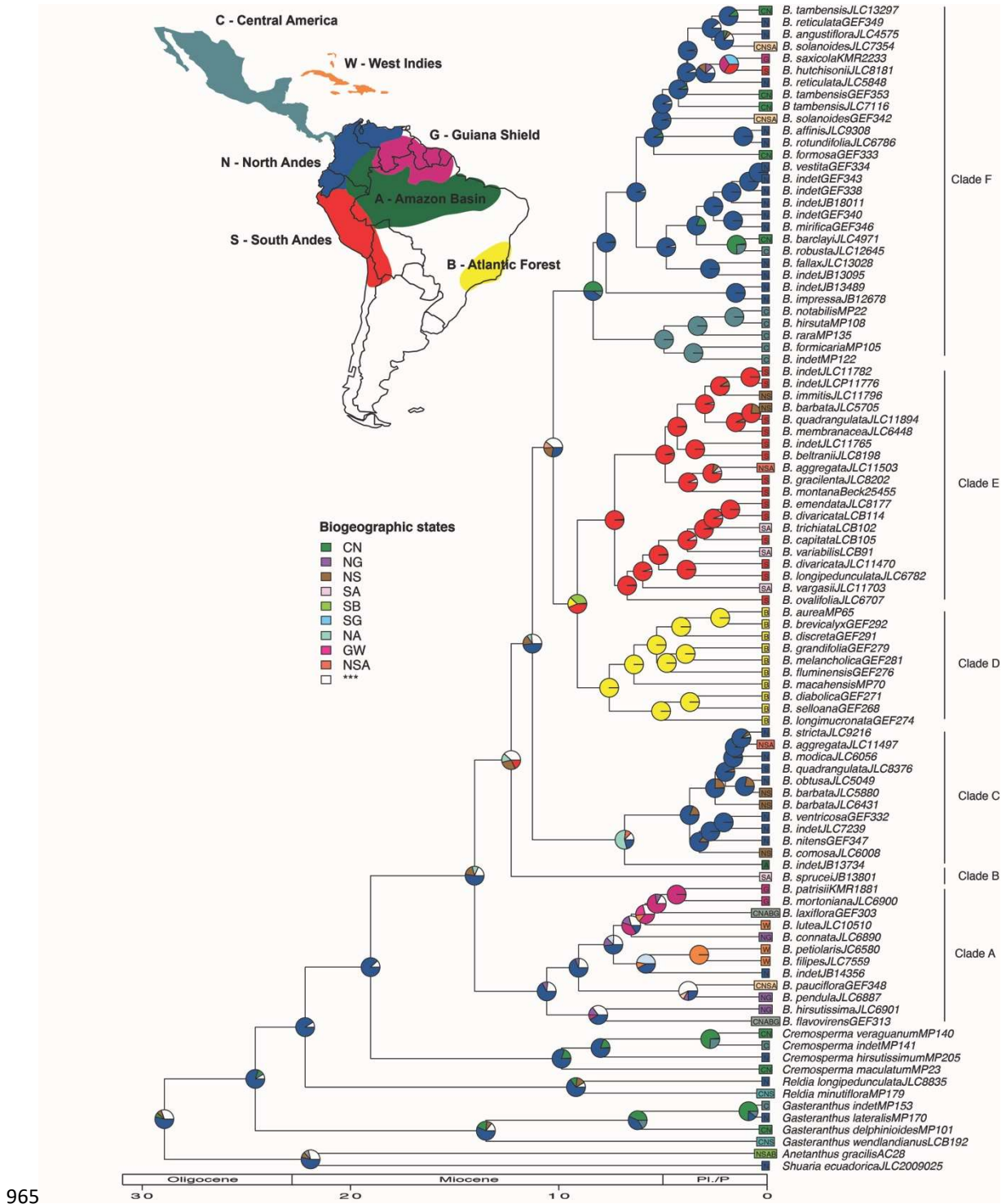
960 **Figure 4.** Distribution of the six *Besleria* clades.



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963 **Figure 5.** Ancestral range reconstruction for *Besleria* using the DEC+J model in
964 BioGeoBEARS.



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969 Highlights

- 970 • Most contemplative phylogeny in *Besleria*
- 971 • Morton sections and subsections are not monophyletic
- 972 • Origin of the genus in North Andes
- 973 • Strong geographical phylogenetic signal in the clades
- 974 • Morphological characters evolve independently on the tree
- 975

976 **1.6 Appendix**

977**Table S1. Range of each terminal taxon coded as presence–absence and dispersal**
 978**distance multiplayers matrix from BioGeoBEARS analyses.**

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Species/Range	O	C	N	S	A	B	G	W
<i>Anetanthus graciles</i> P92	0	0	1	1	1	1	0	0
<i>B. indet</i> GEF338	0	0	1	0	0	0	0	0
<i>B. indet</i> GEF340	0	0	1	0	0	0	0	0
<i>B. indet</i> GEF343	0	0	1	0	0	0	0	0
<i>B. indet</i> JB13095	0	0	1	0	0	0	0	0
<i>B. indet</i> JB13489	0	0	1	0	0	0	0	0
<i>B. indet</i> JB13734	0	0	0	0	1	0	0	0
<i>B. indet</i> JB14356	0	0	1	0	0	0	0	0
<i>B. indet</i> JB18011	0	0	1	0	0	0	0	0
<i>B. indet</i> JLCP323	0	0	0	1	0	0	0	0
<i>B. indet</i> JLCP324	0	0	0	1	0	0	0	0
<i>B. indet</i> JLCP326	0	0	0	1	0	0	0	0
<i>B. divaricata</i> JLC11470	0	0	0	1	0	0	0	0
<i>B. obtusa</i> JLC5049	0	0	1	0	0	0	0	0
<i>B. indet</i> JLC7239	0	0	1	0	0	0	0	0
<i>B. aggregata</i> JLC11497	0	0	1	1	1	0	0	0
<i>B. aggregata</i> JLC11503	0	0	1	1	1	0	0	0
<i>B. angustiflora</i> JLC4575	0	0	1	0	0	0	0	0
<i>B. aurea</i> MP65	0	0	0	0	0	1	0	0

<i>B. barbata</i> JLC5705	0	0	1	1	0	0	0	0
<i>B. barbata</i> JLC5880	0	0	1	1	0	0	0	0
<i>B. barbata</i> JLC6431	0	0	1	1	0	0	0	0
<i>B. barclayi</i> JLC4971	0	1	1	0	0	0	0	0
<i>B. beltranii</i> JLC8198	0	0	0	1	0	0	0	0
<i>B. brevicalyx</i> GEF292	0	0	0	0	0	1	0	0
<i>B. capitata</i> LCB105	0	0	0	1	0	0	0	0
<i>B. affinis</i> JLC9308	0	0	1	0	0	0	0	0
<i>B. immitis</i> JLC11796	0	0	1	1	0	0	0	0
<i>B. comosa</i> JLC6008	0	0	1	1	0	0	0	0
<i>B. connata</i> JLC6890	0	0	1	0	0	0	1	0
<i>B. diabolica</i> GEF271	0	0	0	0	0	1	0	0
<i>B. divaricata</i> LCB114	0	0	0	1	0	0	0	0
<i>B. emendata</i> JLC8177	0	0	0	1	0	0	0	0
<i>B. fallax</i> JLC13028	0	0	1	0	0	0	0	0
<i>B. filipes</i> JLC7559	0	0	0	0	0	0	0	1
<i>B. flavovirens</i> GEF313	0	1	1	0	1	1	1	0
<i>B. fluminensis</i> GEF276	0	0	0	0	0	1	0	0
<i>B. formicaria</i> MP105	0	1	0	0	0	0	0	0
<i>B. formosa</i> GEF333	0	1	1	0	0	0	0	0
<i>B. gracilenta</i> JLC8202	0	0	0	1	0	0	0	0
<i>B. grandifolia</i> GEF279	0	0	0	0	0	1	0	0
<i>B. hirsuta</i> MP108	0	1	0	0	0	0	0	0
<i>B. hirsutissima</i> JLC6901	0	0	1	0	0	0	1	0

<i>B. hutchisonii</i> JLC8181	0	0	0	1	0	0	0	0
<i>B. impressa</i> JB12678	0	0	1	0	0	0	0	0
<i>B. laxiflora</i> GEF303	0	1	1	0	1	1	1	0
<i>B. longimucronata</i> GEF274	0	0	0	0	0	1	0	0
<i>B. longipedunculata</i> JLC6782	0	0	0	1	0	0	0	0
<i>B. lutea</i> JLC10510	0	0	0	0	0	0	0	1
<i>B. macahensis</i> MP70	0	0	0	0	0	1	0	0
<i>B. melancholica</i> GEF281	0	0	0	0	0	1	0	0
<i>B. membranacea</i> JLC6448	0	0	0	1	0	0	0	0
<i>B. mirifica</i> GEF346	0	0	1	0	0	0	0	0
<i>B. modica</i> JLC6056	0	0	1	0	0	0	0	0
<i>B. montana</i> Beck25455	0	0	0	1	0	0	0	0
<i>B. mortoniana</i> JLC6900	0	0	0	0	0	0	1	0
<i>B. nitens</i> GEF347	0	0	1	0	0	0	0	0
<i>B. notabilis</i> MP22	0	1	0	0	0	0	0	0
<i>B. ovalifolia</i> JLC6707	0	0	0	1	0	0	0	0
<i>B. patrisii</i> KMR1881	0	0	0	0	0	0	1	0
<i>B. pauciflora</i> GEF348	0	1	1	1	1	0	0	0
<i>B. pendula</i> JLC6887	0	0	1	0	0	0	1	0
<i>B. petiolaris</i> JLC6580	0	0	0	0	0	0	0	1
<i>B. quadrangulata</i> JLC8376	0	0	0	1	0	0	0	0
<i>B. quadrangulata</i> JLC11894	0	0	0	1	0	0	0	0
<i>B. rara</i> MP135	0	1	0	0	0	0	0	0
<i>B. reticulata</i> GEF349	0	0	1	0	0	0	0	0

<i>B. reticulata</i> JLC5848	0	0	1	0	0	0	0	0
<i>B. robusta</i> JLC12645	0	1	0	0	0	0	0	0
<i>B. rotundifolia</i> JLC6786	0	0	1	0	0	0	0	0
<i>B. saxicola</i> KMR2233	0	0	0	0	0	0	1	0
<i>B. selloana</i> GEF268	0	0	0	0	0	1	0	0
<i>B. solanoides</i> GEF342	0	1	1	1	1	0	0	0
<i>B. solanoides</i> JLC7354	0	1	1	1	1	0	0	0
<i>B. indet</i> MP122	0	1	0	0	0	0	0	0
<i>B. sprucei</i> JB13801	0	0	0	1	1	0	0	0
<i>B. stricta</i> JLC9216	0	0	1	0	0	0	0	0
<i>B. tambensis</i> GEF353	0	1	1	0	0	0	0	0
<i>B. tambensis</i> JLC7116	0	1	1	0	0	0	0	0
<i>B. tambensis</i> JLC13297	0	1	1	0	0	0	0	0
<i>B. trichiata</i> LCB102	0	0	0	1	1	0	0	0
<i>B. vargasii</i> JLC11703	0	0	0	1	1	0	0	0
<i>B. variabilis</i> LCB91	0	0	0	1	1	0	0	0
<i>B. ventricosa</i> GEF332	0	0	1	0	0	0	0	0
<i>B. vestita</i> GEF334	0	0	1	0	0	0	0	0
<i>B. discreta</i> GEF291	0	0	0	0	0	1	0	0
<i>Creosperma hirsutissimum</i> MP205	0	0	1	0	0	0	0	0
<i>Creosperma maculatum</i> MP23	0	1	1	0	0	0	0	0
<i>Creosperma indet</i> MP141	0	1	0	0	0	0	0	0
<i>Creosperma veraguanum</i> MP140	0	1	1	0	0	0	0	0

<i>Gasteranthus indet</i> MP153	0	1	0	0	0	0	0	0
<i>Gasteranthus delphinioides</i> MP101	0	1	1	0	0	0	0	0
<i>Gasteranthus lateralis</i> MP170	0	0	1	0	0	0	0	0
<i>Gasteranthus wendlandianus</i> LCB92	0	1	1	1	0	0	0	0
<i>Reldia minutiflora</i> MP179	0	1	1	1	0	0	0	0
<i>Reldia longipedunculata</i> JLC8835	0	0	1	0	0	0	0	0
<i>Shuaria ecuadorica</i> JLC2009025	0	0	1	0	0	0	0	0

980

981

982

115

983 Dispersal distance multiplayers.

984 Time period 15 Mya

C	N	S	A	B	G	W
1.0	1.0	0.5	0.5	0.5	1.0	0.5
1.0	1.0	1.0	1.0	0.5	1.0	0.5
0.5	1.0	1.0	1.0	0.5	0.5	0.5
0.5	1.0	1.0	1.0	0.5	1.0	0.5
0.5	0.5	0.5	0.5	1.0	0.5	0.1
1.0	1.0	0.5	1.0	0.5	1.0	0.5
0.5	0.5	0.5	0.5	0.1	0.5	1.0

985

986 Time period 90 Mya

987

C	N	S	A	B	G	W
1.0	0.5	0.1	0.1	0.1	0.1	0.5
0.5	1.0	1.0	1.0	0.5	1.0	0.5
0.1	1.0	1.0	1.0	0.5	0.5	0.5
0.1	1.0	1.0	1.0	0.5	1.0	0.5
0.1	0.5	0.5	0.5	1.0	0.5	0.1
0.1	1.0	0.5	1.0	0.5	1.0	0.5
0.5	0.5	0.5	0.5	0.1	0.5	1.0

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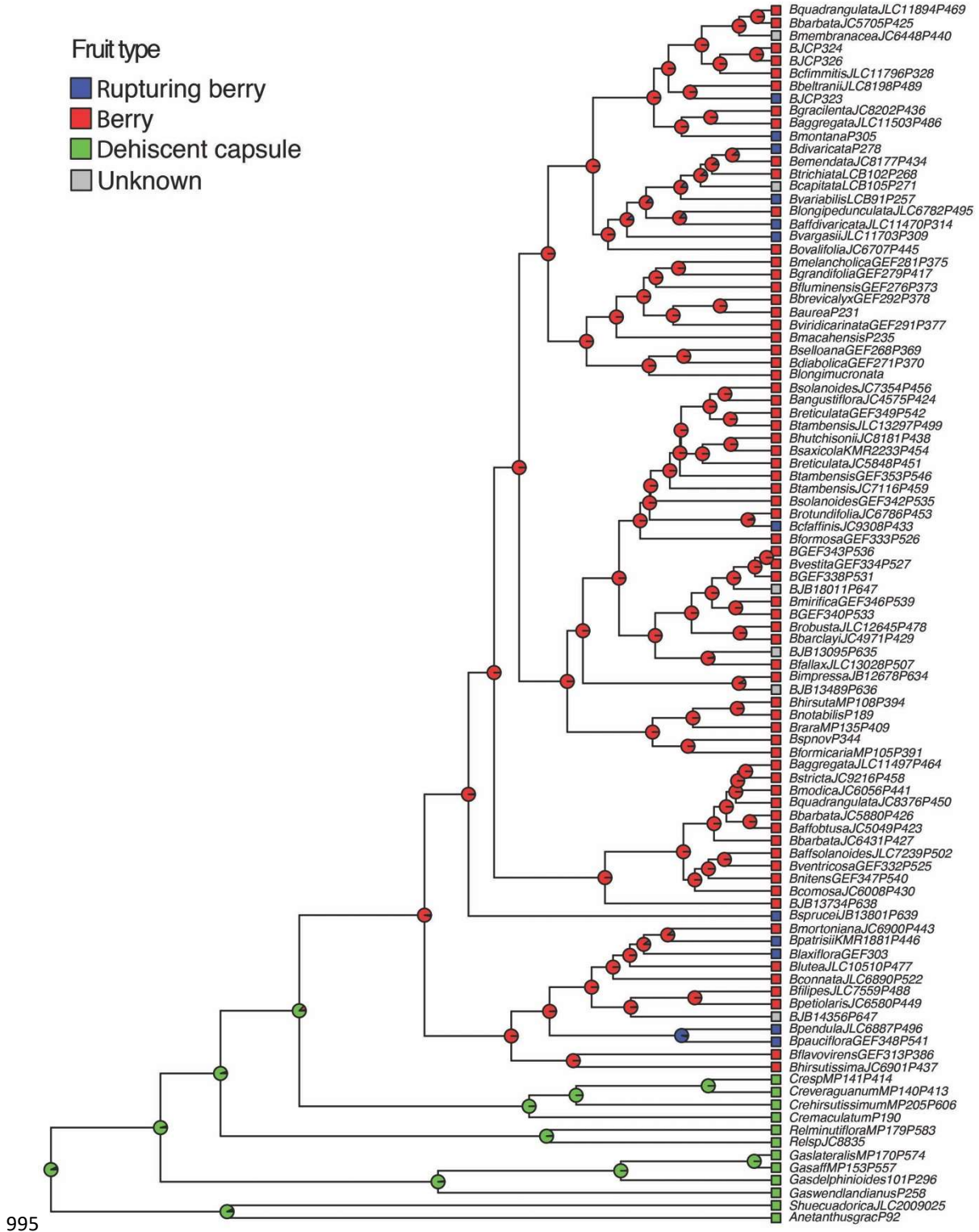
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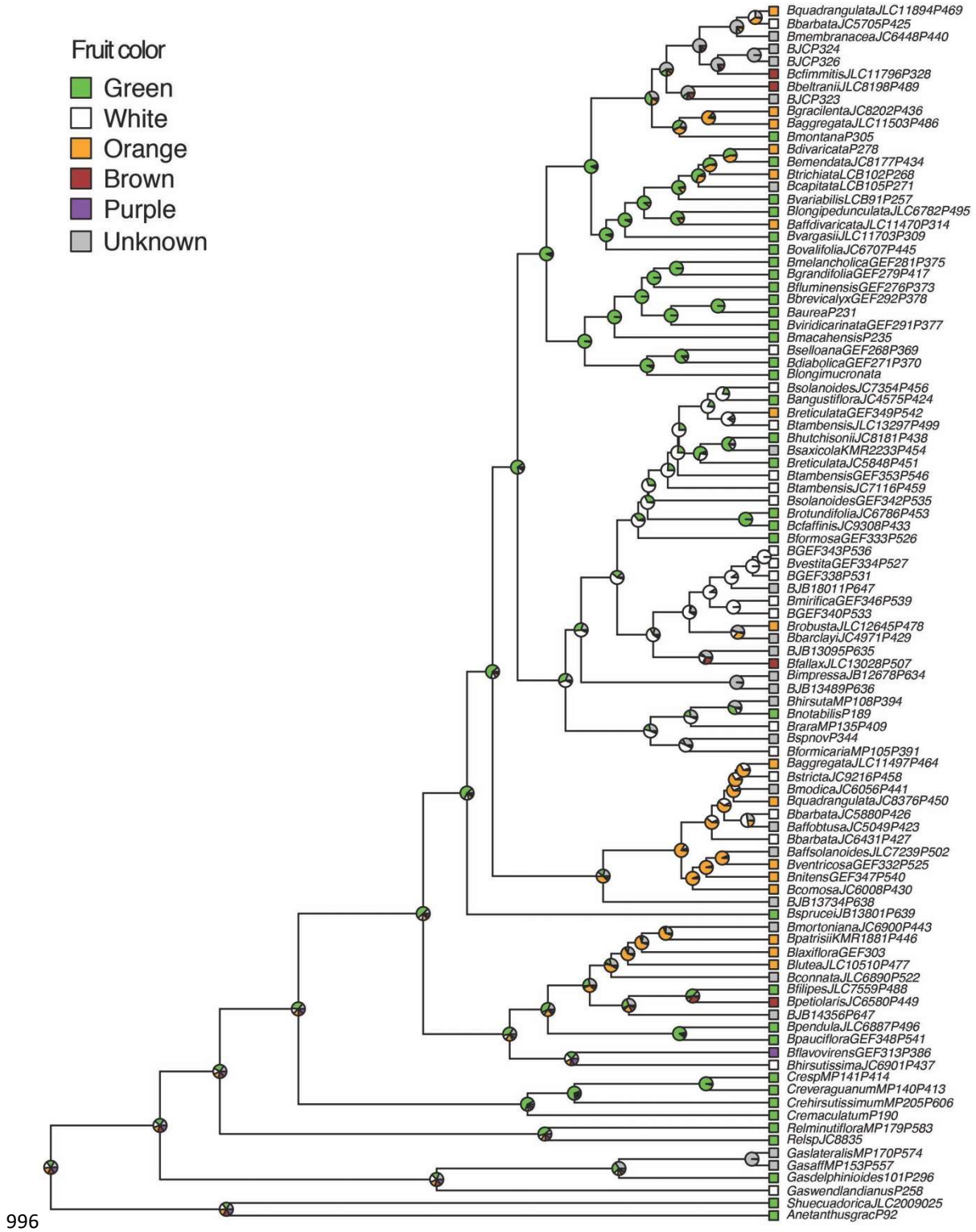
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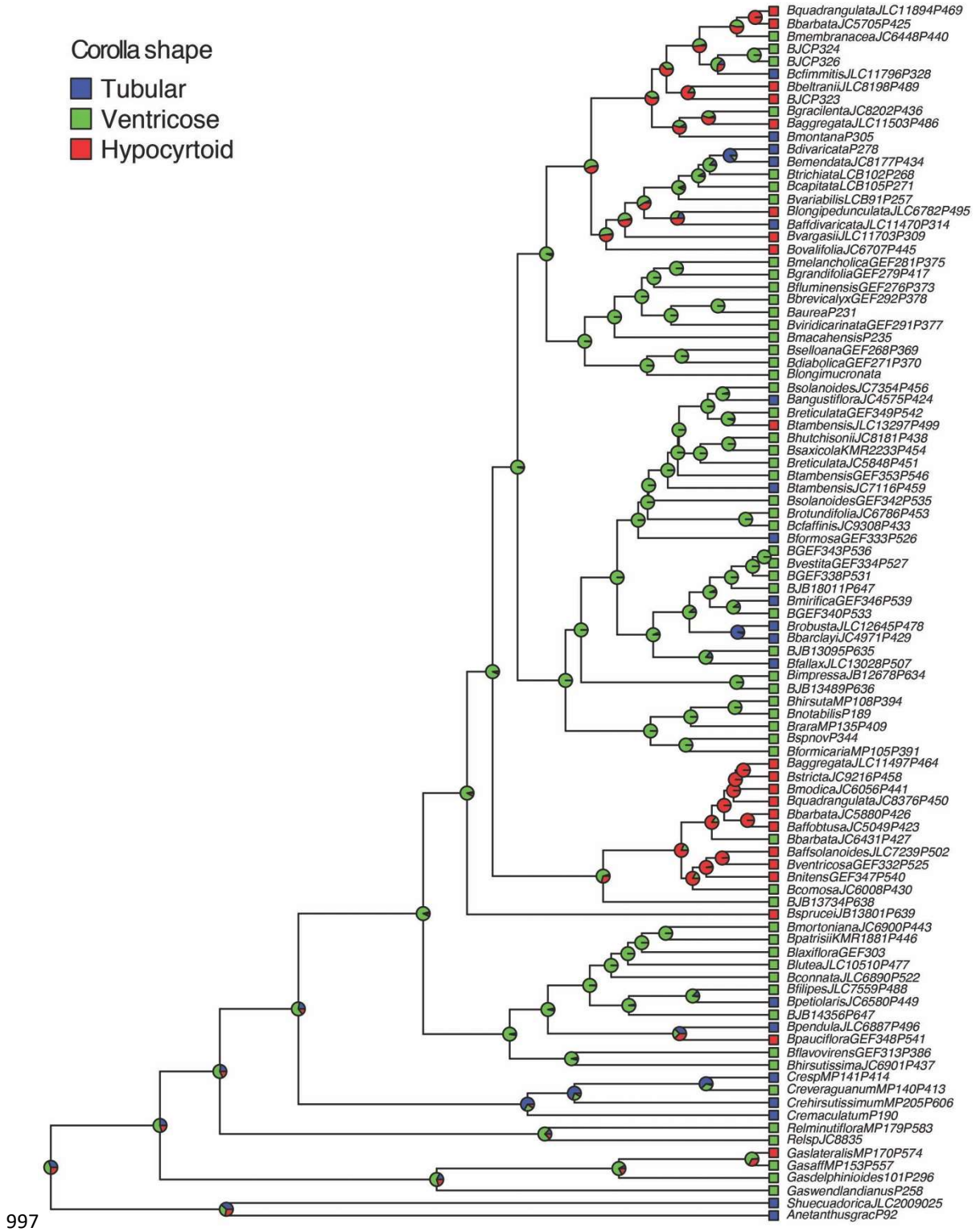
994 Figures S1-S5: Reconstruction Ancestral Characters

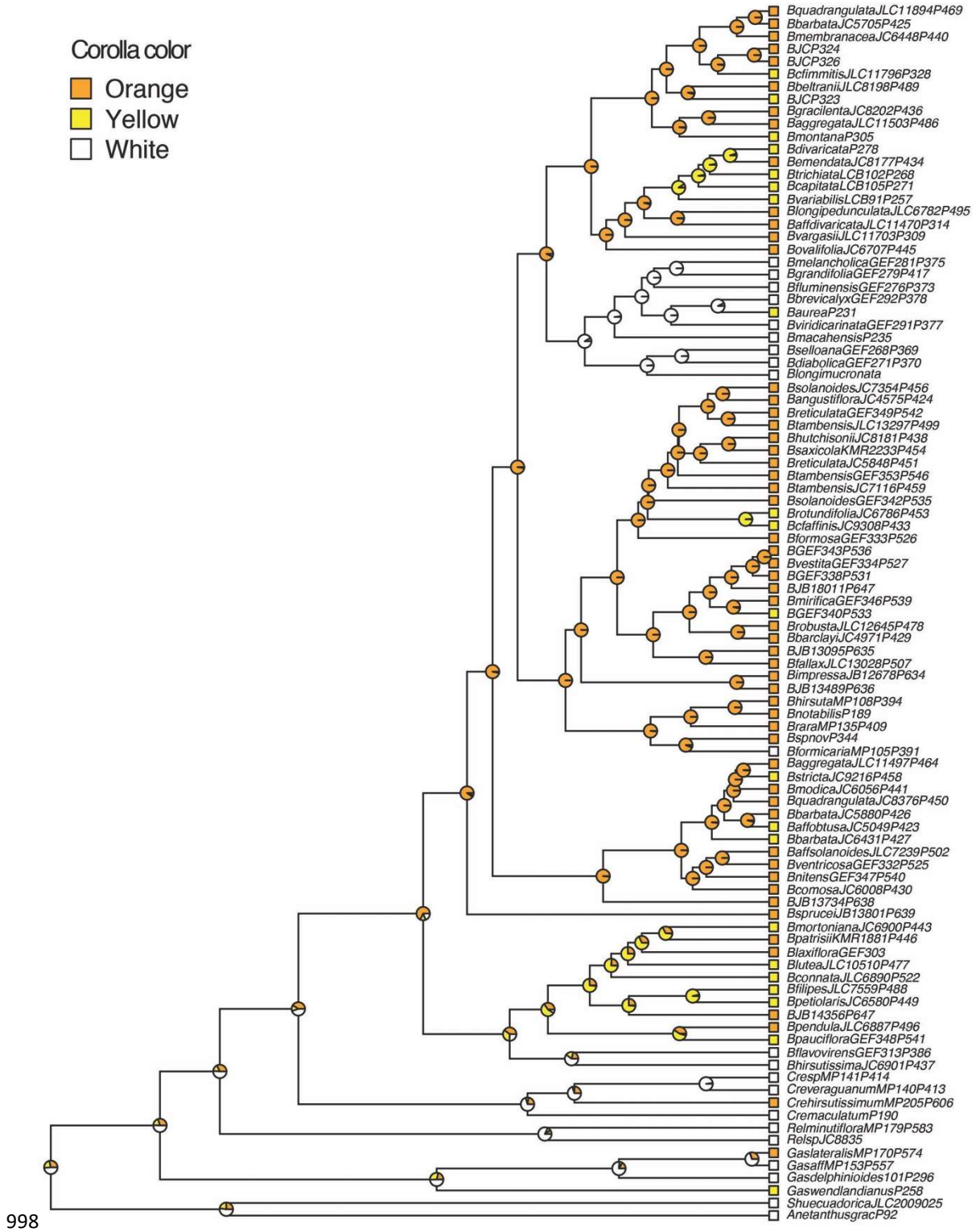


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Capítulo 2

1003

1004Ferreira, G.E.; Araújo, A.O.; Hopkins, M.J.G.; Chautems,
1005A. 2017. A new species of *Besleria* (Gesneriaceae) from the
1006western Amazon rainforest. *Brittonia* 69: 241–245.

129

1007A new species of *Besleria* (Gesneriaceae) from the western Amazon rainforest

1008

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1011

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1018

1019**Abstract.** *Besleria iara*, a new species from the western Amazon lowland rainforest in Brazil

1020and Peru, is described and illustrated. Data are provided on the species' ecology, distribution,

1021and conservation status. This species is a shrub, with hirsute indumentum covering almost the

1022whole plant, orange calyx, and yellow tubular-ventricose corolla. It was found growing in the

1023understory of humid terra firme forest, along the margin of small streams.

1024

1025**Keywords:** Beslerieae, taxonomy, Amazon basin.

1026

1027*Besleria* Plum. ex L. belongs to the Gesneriaceae, a pantropical family with few species
 1028occurring in subtropical and temperate regions. The family contains ca. 150 genera and ca.
 10293500 species (Weber et al., 2013). The genus is placed in the monophyletic tribe Beslerieae
 1030that diverged about 30 million years ago within the subfamily Gesnerioideae (Weber et al.,
 10312013; Perret et al., 2013). *Besleria* is monophyletic, and its sister genus is *Creemosperma*
 1032Benth. (Roalson & Clark, 2006; Clark et al., 2010).

1033*Besleria* comprises 160 to 200 species of terrestrial herbs, shrubs, and small trees that grow in
 1034the understory of rainforests (Berger et al., 2015; Ferreira et al., 2016). The genus occurs
 1035throughout the Neotropics, from the West Indies and Mexico to Andean and Amazonian
 1036Bolivia and the Brazilian Atlantic rainforest (Skog & Feuillet, 2008; Berger et al., 2015). In
 1037Brazil, the genus is distributed disjunctly between the Amazonian and Atlantic rainforests
 1038(BFG, 2015; Araújo et al. 2016; Ferreira et al., 2016). In total, 21 species have been
 1039documented in the country.

1040While studying herbarium material of the genus in the National Museum of Natural History of
 1041the Smithsonian Institution (US), we found an unidentified collection that did not match any
 1042described species. After consulting additional material deposited in other herbaria and based
 1043on observations of the plant in its natural habitat, we concluded that it is a new species, here
 1044described and illustrated.

1045

1046*Besleria iara* G. E. Ferreira & M. J. G. Hopkins, **sp. nov.** Type: Brazil. Amazonas: Benjamin
 1047Constant, sítio Prof. Agno Nonato, trilha prox. ao açude, 8 February 2016, G. E. Ferreira 355
 1048(holotype: INPA; isotype: G). (Figs. 1, 2)

1049

1050*Besleria iara* is similar to *B. aggregata* s.l. in its axillary inflorescences, and flowers with
 1051orange imbricate calyx lobes. It differs by having a long tubular-ventricose yellow corolla (vs.
 1052ventricose-urceolate orange to scarlet), and larger leaf blades, 18–30 × 7.3–11.4 cm, with
 1053serrate margins (vs. 15–19 × 5.5–6.4 cm, with entire margins).

1054

1055*Terrestrial shrub*, 1.5 m tall. *Stems* unbranched, subterete, up to 0.5 cm diam., woody at base,
 1056densely hirsute, internodes 3.0–11.0 cm. *Leaves* opposite, pairs subequal; petioles 1–4 cm
 1057long, green, densely hirsute; leaf blades oblanceolate, 18–30 × 7.3–11.4 cm, chartaceous,
 1058apex attenuate, base long-attenuate, margin sparsely serrate; adaxial surface dark green,
 1059hirsute; abaxial surface pale green, puberulous; secondary veins in 7–11 pairs. *Inflorescence*
 1060axillary, cymose, epedunculate, with 3–7 flowers per node; pedicels terete, 1.2–2.3 cm long,

1061orangish, hirsute. *Calyx* lobes 5, fused at base and imbricate for 3/4 of length, adherent to
 1062corolla base, essentially equal, ovate, 12–14 × 3–5 mm, orange, hirsute, apex obtuse, margin
 1063entire-ciliate. *Corolla* erect with respect to calyx, 18–27 mm long, tubular, slightly ventricose,
 1064yellow, outside puberulous, inside glabrous, tube contracted at base, 5 mm wide at base, 7
 1065mm wide at middle, 5 mm wide at apex; limb regular, lobes 5, patent, yellow, unequal, the 2
 1066larger ones 4 × 4 mm, the 3 smaller ones 2 × 3 mm, obtuse, margin entire, ciliate, pilose.
 1067*Nectary* annular, 1 mm wide, glabrous. *Stamens* 4, included; filaments 8–10 mm long,
 1068epipetal, adnate to base of corolla for 4 mm, glabrous but pilose at insertion; anthers 2 × 2
 1069mm, longitudinally dehiscent; staminode 2 mm long. *Ovary* ovoid, 2–4 × 2–4 mm, pilose;
 1070style included within corolla throat, 9 mm long, pilose; stigma bifid, puberulent. *Fruit* not
 1071seen.

1072*Habitat and distribution.*—*Besleria iara* is currently known only from the Javari River, in the
 1073municipalities of Atalaia do Norte and Benjamin Constant, Amazonas, Brazil, and from
 1074Loreto department, Peru (Fig. 3). It occurs in the understory of lowland Amazonian
 1075rainforests on terra firme, along the margins of small streams, at about 50 m elevation. We
 1076observed few individuals at the type locality. The larger area of distribution is poorly known
 1077from a floristic context. It is expected that additional fieldwork in the region will result in the
 1078discovery of additional populations.

1079*Phenology.*—Flowers recorded from October to February.

1080*Etymology.*—The specific epithet “*iara*” is a reference to the Brazilian indigenous legend of
 1081the water spirit *yîara*, meaning “Lady of the waters” in the Tupí-Guaraní language. *Vîara* is
 1082generally envisaged as a beautiful young lady, similar to a mermaid (Chiaradia, 2008).

1083*Conservation status.*—Endangered (EN) B1ab, according to the IUCN criteria, based on the
 1084extent of occurrence estimated to be less than 5,000 km² from only 4–5 locations and due to
 1085continued habitat loss (IUCN, 2012; IUCN Standards and Petitions Subcommittee, 2016).

1086

1087**Additional specimens examined. BRAZIL. Amazonas:** Município Atalaia do Norte,
 1088localidade de São Joaquim, Rio Javari, fronteira entre Brasil e Peru, 18 Jan 1989, C. A. C.
 1089Ferreira et al. 9933 (CEN, INPA, NY, US); Município Atalaia do Norte, Estirão do Equador,
 1090Rio Javari, 20 Oct 1976, P. I. S. Braga & J. R. Nascimento 3273 (INPA). **PERU. Loreto:** Rio
 1091Javari, 2 hours above Rio Javarzinho, 24 Oct 1976, G. T. Prance et al. 24081 (INPA, MG).

1092

1093*Besleria iara* and *B. aggregata* (Mart.) Hanst. are sympatric and share the same habitat and
 1094vegetative characters. Both species occur in the understory of humid forest, close to streams,

1095 and are shrubs completely covered by indumentum. However, *B. iara* has a yellow, tubular-
 1096 ventricose corolla, ovate calyx lobes with the obtuse apices adherent to the corolla base, wider
 1097 leaf blades (7.3–11.4 cm wide) with sparsely serrate margins, and densely hirsute
 1098 indumentum on the stems, whereas *B. aggregata* has an orange to scarlet, ventricose-urceolate
 1099 corolla, lanceolate calyx lobes with the attenuate apices spreading from the corolla, narrower
 1100 leaf blades (5.5–6.4 cm wide) with entire margins, and sericeous indumentum on the stems
 1101 (Table 1).

1102 *Besleria iara* is also morphologically similar to *B. obtusa* C. V. Morton, known only from the
 1103 type collection (*J. Cuatrecasas 4636*, Colombia, Meta, 1939). Both species have oblanceolate
 1104 leaves and a yellow corolla, but *B. iara* can be distinguished from *B. obtusa* by having a
 1105 longer petiole (1.0–4.0 cm long vs. < 1 cm long), hirsute leaf blades (vs. glabrous with
 1106 tomentose-hirsute midrib), sparsely serrate margins (vs. entire-ciliate), longer pedicels (1.2–
 1107 2.3 cm long vs. 0.5 cm long), ovate calyx lobes with the obtuse apices adherent to the corolla
 1108 (vs. calyx lobes linear-lanceolate with the long-acuminate apices spreading).

1109

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1111

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1121

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- 1156
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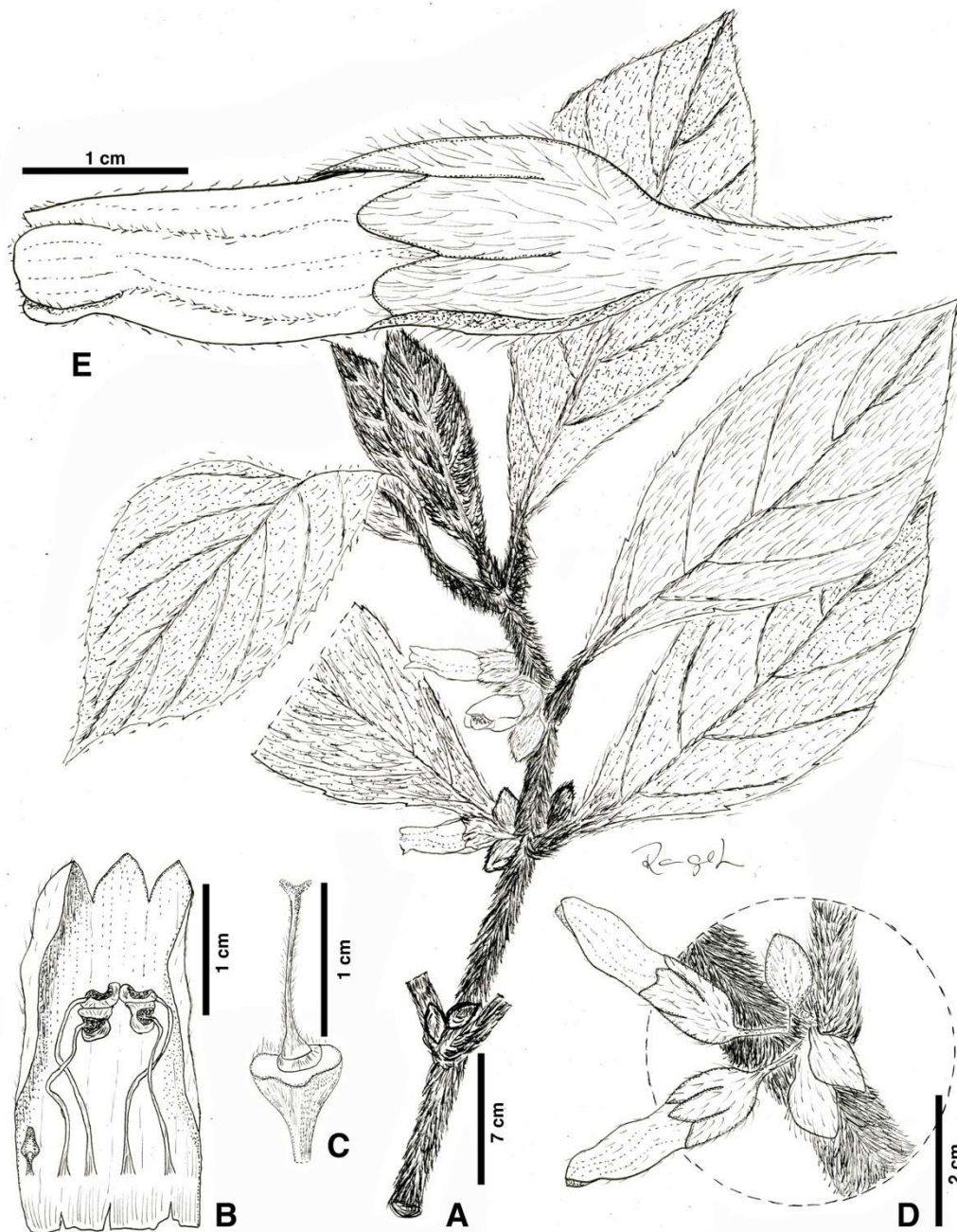
1158 **TABLE 1.** Morphological comparisons of *Besleria iara* and related species.

Traits/Species	<i>B. aggregata</i>	<i>B. iara</i>	<i>B. obtusa</i>
Petiole length [cm]	1.6–3.9	1.0–4.0	<1.0
Leaf blade size [cm]	15–19 × 5.5–6.4	18–30 × 7.3–11.4	18–23 × 5.7–9.5
Leaf blade indumentum abaxial surface	sericeous	puberulous	tomentose-hirsute at midrib
Leaf blade margin	entire	sparsely serrate	entire-ciliate
Number of flowers per axil	1–5	3–7	3–10
Pedicel indumentum	pilose	hirsute	pilose
Pedicel length [cm]	0.5–0.8	1.2–2.3	0.5
Calyx color	orange	orange	-
Calyx lobe length [mm]	14–17	12–14	8–15
Calyx lobe width [mm]	3–4	3–5	1–2.5
Calyx lobe shape	lanceolate	ovate	linear-lanceolate
Calyx lobe apex shape	attenuate	obtuse	long-acuminate
Calyx lobes orientation	spreading	adherent	spreading
Calyx indumentum	pilose	hirsute	pilose
Corolla color	orange to scarlet	yellow	yellow
Corolla length [mm]	16–20	18–27	18–25
Corolla lobe length [mm]	2–3	2–4	5–6

1159

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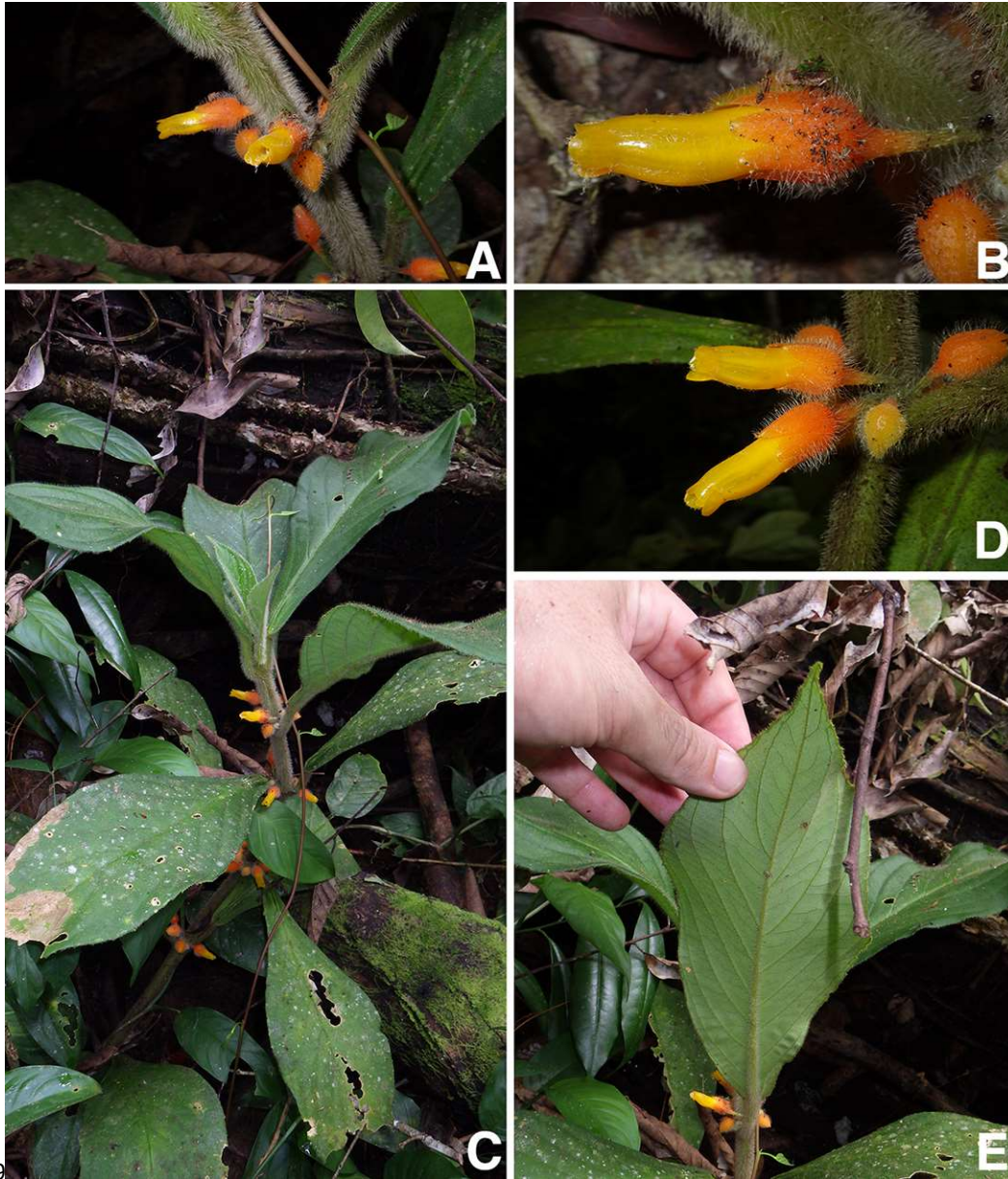
1161FIG. 1. *Besleria iara*. A. Habit. B. Open corolla showing stamens and staminode. C.
1162Gynoecium and nectary. D. Close up of the inflorescence and stem. E. Calyx and Corolla in
1163side view. (A–E from *G.E. Ferreira 355*).



1164

1165

1166**FIG. 2.** Morphology and habitat of *Besleria iara*. **A.** Flowers in frontal and side view and a
 1167portion of the stem. **B.** Flower in side view. **C.** Habit. **D.** Inflorescence. **E.** Detail of the leaf
 1168abaxial surface (A–E from *G.E. Ferreira 355*).

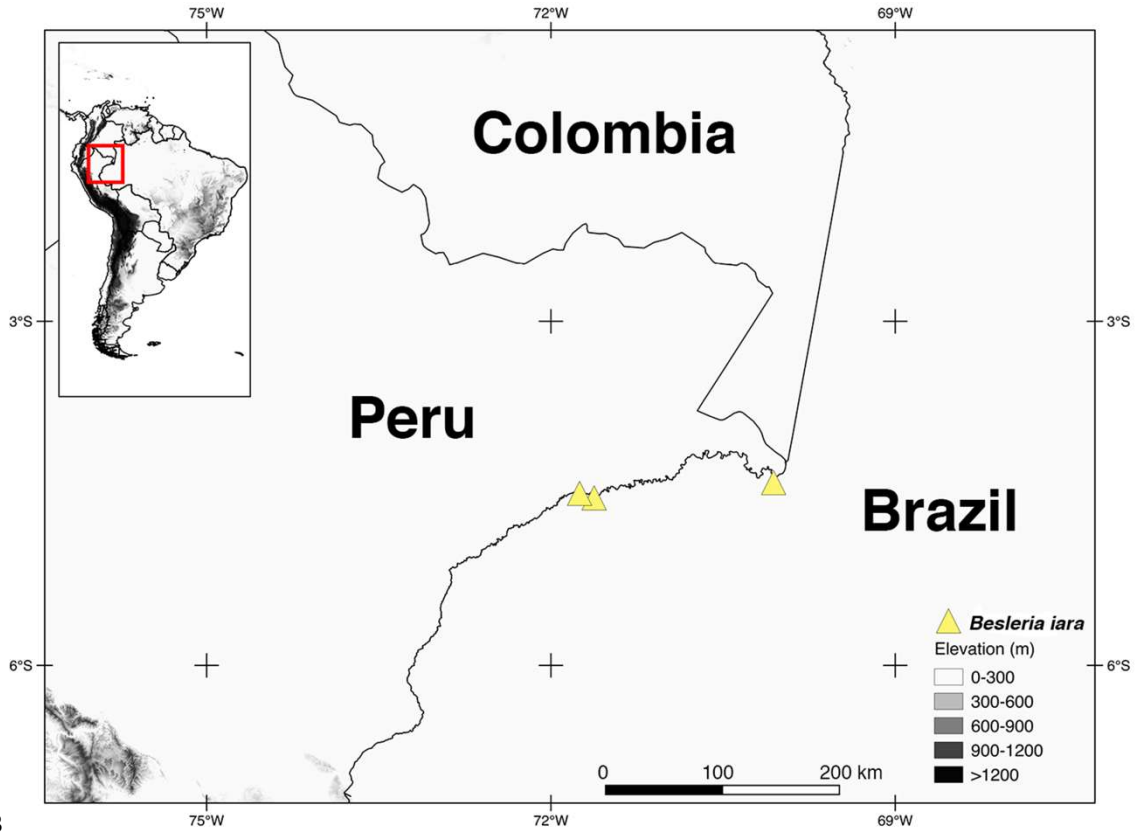


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1171

1172 **FIG. 3.** Distribution of *Besleria iara*.



1173

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1174

Capítulo 3

1175

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1177Chautems, A. 2016. Three new species of *Besleria*

1178(Gesneriaceae) from the southeastern Brazilian Atlantic

1179rainforest. *Phytotaxa* 263: 270–278.

1180

149

1181 **Three new species of *Besleria* (Gesneriaceae) from the southeastern Brazilian Atlantic**
 1182 **rainforest**

1183

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1197

1198 **Abstract**

1199

1200 *Besleria* is a Neotropical genus of terrestrial herbs, shrubs and small trees growing in the
 1201 understory of rainforests, with more than 160 recognized species, and is one of the larger and
 1202 more diverse genera of Gesneriaceae. It belongs to the monophyletic tribe Beslerieae, and
 1203 recent phylogenetic studies indicate that the genus is monophyletic. During field expeditions
 1204 in the Brazilian Atlantic Rainforest, we collected specimens that could not be identified as any
 1205 described species. After morphological analysis and comparison with related species, we
 1206 assigned these specimens to three new species of *Besleria*. In this paper, we describe and
 1207 illustrate *Besleria aurea*, *B. brevicalyx* and *B. diabolica* and provide data on their ecology,
 1208 distribution and conservation status.

1209

12102 Introduction

1211

1212*Besleria* Plumier ex Linnaeus (1753: 619) include 160 to 200 species of terrestrial herbs,
1213shrubs and small trees that grow in the understory of rainforests (Skog & Feuillet 2008,
1214Berger *et al.* 2015). It is placed in the monophyletic tribe Beslerieae, that diverged about 30
1215million years ago within the subfamily Gesnerioideae (Zimmer *et al.* 2002, Perret *et al.* 2013,
1216Weber *et al.* 2013). The genus has a Neotropical distribution, occurring in the Andes and the
1217Amazon rainforest of Bolivia to Colombia, in Central America as far north as Mexico, and
1218some species are endemic to the Brazilian Atlantic rainforest and to Caribbean Islands (Skog
1219& Boggan 2007). In Brazil 18 species are currently known, occurring in the Amazon and
1220Atlantic rainforests (Araujo *et al.* 2015).

1221The revision of *Besleria* by Morton (1939) is the only one in existence to date. Wiehler (1975)
1222segregated two sections of *Besleria*, and placed them into genus *Gasteranthus* Bentham
1223(1846: 233) on the basis of vegetative and fruit characters. According to molecular
1224phylogenetic studies, *Besleria* (excluding *Gasteranthus*) is monophyletic and *Cremosperma*
1225Bentham (1846: 234) is its sister genus (Roalson & Clark 2006, Clark *et al.* 2010). These
1226studies also demonstrated that sections proposed by Morton (1939) were not monophyletic.
1227The circumscription of many species of *Besleria* is still unclear and the genus needs a
1228thorough revision.

1229In the framework of a taxonomic, phylogenetic and biogeographic survey of *Besleria*, we
1230found three undescribed species that are described here.

1231

12323 Material & methods

1233

1234During the examination of herbarium specimens, we found specimens that could not be
1235assigned to any formally described species of *Besleria*. We carried out fieldwork in the
1236Brazilian Atlantic forest to obtain more samples of these unidentified species. We searched
1237for them in the following localities: Descoberto (Minas Gerais), Poço Parado (Rio de Janeiro),
1238and Eldorado (São Paulo), Brazil, between September and November 2014. Living specimens
1239were photographed in the field. We deposited specimens in the G, INPA, HUFABC and SPSF
1240herbaria. Some flowers were preserved in 70% ethanol and used for drawings of floral
1241features. We performed morphological analyses using a stereoscopic microscope. The
1242descriptive terminology follows Beentje (2010). Additional collections from the G, RB,

153

1243CESJ, ESAB, HPL and INPA herbaria were also studied.

1244

12454 **Taxonomy**

1246

1247*Besleria aurea* I.G.Costa & G.E.Ferreira, *sp. nov.* (Fig. 1).

1248

1249*Besleria aurea* is similar to *B. fluminensis* in its axillary inflorescence and having flowers
1250with very long yellow conduplicate calyx lobes, however, it differs by having a yellow corolla
1251(*vs.* yellowish-white), narrowly triangular calyx lobes at the base (*vs.* elliptic), and smaller
1252leaf blades with entire margins (*vs.* with serrate margins).

1253

1254**Type:**—BRAZIL. Rio de Janeiro: Campos dos Goytacazes, Conceição do Imbé, na Serra do
1255Macaco, 16 July 2013, *I.G. Costa 230* (holotype RB!; isotype INPA!).

1256

1257Terrestrial shrub, 1.5 m tall. Stems unbranched, subterete, up to 0.5 cm diam., strigose at the
1258base, internodes 2.0–6.5 cm long. Leaves opposite, pairs subequal; petioles 2.6–6.7 cm long,
1259green, puberulent; leaf blades elliptic to oblanceolate, 15–19 × 5.5–6.4 cm, apex and base
1260attenuate, margin entire, membranaceous; adaxial surface green, glabrous; abaxial surface
1261pale green, pilose, 5–6 pairs of secondary veins. Inflorescence axillary, cymose, epedunculate,
1262with 1–5 flowers per node; pedicels terete, 2.0–2.1 cm long, green, puberulent. Calyx lobes 5,
1263fused and imbricate at base, diverging from the corolla axis, slightly equal, lanceolate, 11–16
1264× 4–6 mm, apex attenuate, margin sparsely denticulate, yellow, puberulent. Corolla oblique in
1265relation to calyx, 16–22 mm long, tube contracted at base, limb regular, 6 mm wide at the
1266base, 4 mm wide at the narrowest point, throat 6.5 mm wide, ventricose, yellow, rarely
1267vinaceous, glabrous outside and inside; lobes 5, patent, slightly equal, obtuse, 3–6 × 2–6 mm,
1268margin entire, orange, glabrous. Nectary annular, 1 mm wide, glabrous. Stamens 4, included;
1269filaments 7–9 mm, epipetalous, adnate, free portion of filaments arising at 5 mm from the
1270base of the corolla, glabrous; anthers 2 × 2 mm, longitudinally dehiscent; staminode 2 mm
1271long. Ovary ovoid, 4 × 4 mm, puberulous; style included in the throat, 11 mm long,
1272puberulous; stigma bifid, puberulous. Fruit not seen.

1273**Distribution and ecology:**—This species is currently found only in the type locality, in
1274Campos dos Goytacazes, in the northern part of Rio de Janeiro state (Fig. 5). This area is
1275rather neglected by plant collectors and new locations for this species are likely to be

154

1276registered. The species was found in the understory of a humid forest covering slopes at the
1277margin of a river, at about 400 m elevation; only a few individuals were observed.

1278**Phenology:**—Flowers are recorded from September to December.

1279**Conservation status:**—Endangered (EN) B1ab(i,iv), according to the IUCN criteria, based
1280on the extent of occurrence estimated to be less than 5,000 km² in only one location (IUCN
12812013).

1282**Taxonomic relationships:**—*Besleria aurea* shares a similar floral morphology with *B.*
1283*fluminensis* Brade (1948: 73), having a yellow calyx with long acuminate lobes. However, it
1284can be distinguished by different corolla colour, calyx lobes shape, leaf blade size and type of
1285the margin (Table 1).

1286**Etymology:**—The name “aurea” refers to the bright yellow colour of both calyx and corolla
1287(Fig. 4A). This species is the only one to have this colour pattern among all currently known
1288Atlantic rainforest *Besleria* species.

1289**Additional specimens examined (paratypes):**—BRAZIL. Rio de Janeiro: Campos dos
1290Goytacazes, Conceição do Imbé, Serra do Macaco, 10 May 2012, *M. Perret et al.* 65 (G!,
1291VIES!); same locality, 27 August 2012, *H. Lorenzi et al.* 7182 (HPL!).

1292

1293***Besleria brevicalyx*** G.E.Ferreira & Chautems, *sp. nov.* (Fig. 2).

1294

1295*Besleria brevicalyx* resembles *B. macahensis* in its short calyx, adherent to the corolla base,
1296however, it differs by its 3-verticillate leaves (*vs.* opposite and decussate), longer yellow
1297pedicel and shorter and green-keeled calyx lobes (*vs.* calyx shorter and purplish).

1298

1299**Type:**—BRAZIL. Minas Gerais: Descoberto, Reserva Biológica da Represa do Grama, trilha
1300do Bananal, 9 November 2014, *G.E. Ferreira et al.* 292 (holotype INPA!; isotypes G!; RB!;
1301HUFABC!).

1302

1303

1304Terrestrial shrub, 0.4–1.8 m tall. Stems branched, subterete, up to 0.4 cm diam., brown,
1305glabrous, sericeous when young, internodes up to 3.0 cm long. Leaves 3-verticillate, equal in
1306a whorl; petioles 2.2–4.1 cm long, green, pubescent; leaf blades oblanceolate, 12.0–20.5 ×
13073.4–5.6 cm, apex attenuate, base long-attenuate, margin distantly serrulate, membranaceous;
1308adaxial surface green, puberulent; abaxial surface pale green, pubescent, 8–10 pairs of
1309secondary veins. Inflorescence axillary, cymose, epedunculate or rarely very short peduncle,

1310with 1–3 flowers per node; pedicels terete, 2.2–3.4 cm long, green, pubescent. Calyx lobes 5,
 1311lobes erect, adherent to the corolla base, dorsally keeled, slightly equal, lanceolate, 4–6 × 3–4
 1312mm, apex acute to mucronate, margin entire, yellow-greenish, outside sparsely puberulous-
 1313glandular, inside glabrous. Corolla horizontal in relation to calyx, 16–18 mm long, tube
 1314contracted at base, limb regular, 6 mm wide at the base, 4 mm wide at the narrowest point,
 1315throat 7 mm wide, ventricose, whitish-yellow, outside puberulous-glandular, inside glabrous;
 1316lobes 5, erect, slightly equal, semiorbicular, 3 × 3 mm, margin entire, white, glabrous. Nectary
 1317annular, 0.2 mm wide, glabrous. Stamens 4, included in the throat; filaments 5–7 mm,
 1318epipetalous, adnate, free portion of filaments arising at 3 mm from the base of the corolla,
 1319glabrous; anthers 1 × 2 mm, longitudinally dehiscent. Ovary ovoid, 3 × 4 mm, puberulous;
 1320style included in the throat, 5–6 mm long, puberulous-glandular; stigma bifid, puberulous.
 1321Fruit not seen.

1322**Distribution and ecology:**—This species occurs in Descoberto, Minas Gerais state (Fig. 5). It
 1323was collected in seasonal dry forest, of the Atlantic rainforest domain, occurring on sandy/
 1324rocky banks of streams (Fig. 4D) at ca. 550–950 m elevation. Only a few plants were found at
 1325each collection point.

1326**Phenology:**—Flowers are recorded from January to October.

1327**Conservation status:**—Endangered (EN) B1ab(i, iv), according to the IUCN criteria, based
 1328on the extent of occurrence estimated to be less than 5,000 km² in only two locations (IUCN
 13292013).

1330**Taxonomic relationships:**—*Besleria brevicalyx* has characteristics similar to those of *B.*
 1331*macahensis* Brade (1948: 74), including fasciculate inflorescence, calyx closely adherent to
 1332the corolla base, calyx lobes 3–4 mm wide, and yellowish-white corolla. However, it differs
 1333from *B. macahensis* by its 3-verticillate leaves (vs. opposite), yellow pedicels (vs. purplish-
 1334yellow), and yellow calyx with green-keeled calyx lobes (vs. purplish-yellow). *Besleria*
 1335*brevicalyx* also has longer pedicels and shorter calyx lobes (Table 1). Additionally, *B.*
 1336*brevicalyx* occurs in Minas Gerais and Espírito Santo in sandy and rocky substrates in
 1337seasonal dry Forest, whereas *B. macahensis* is restricted to Rio de Janeiro state and occurs in
 1338substrates rich in organic matter in the Atlantic rainforest.

1339**Etymology:**—The name “brevicalyx” refers to the very short calyx lobes that are adherent to
 1340the corolla base.

1341**Additional specimens examined (paratypes):**—BRAZIL. Minas Gerais: Descoberto,
 1342Reserva Biológica da Represa do Grama, 18 May 2002, *A.V. Lopes et al.* 43 (CESJ!, G!);
 1343same place, 29 April 2000, *C.L. Faria et al.* 70 (CESJ!, G!).

159

1344

1345 *Besleria diabolica* G.E.Ferreira & Chautems, *sp. nov.* (Fig. 3).

1346

1347 *Besleria diabolica* is similar to *B. melancholica* in having flowers with reflexed, flat calyx
1348 lobes. However, *B. diabolica* differs by its longer leaf blades, usually fewer flowers per axil
1349 and by its narrower, lanceolate calyx lobes, with acute apices.

1350

1351 **Type:**—BRAZIL. São Paulo: Eldorado, Parque Estadual Caverna do Diabo, trilha do Araçá,
1352 nas margens do córrego, 29 September 2014, *G.E. Ferreira et al.* 271 (holotype INPA!;
1353 isotypes G!; HUFABC!; SPSF!).

1354

1355 Terrestrial shrub, 0.8–1.5 m tall. Stems unbranched, subterete, 0.4–0.5 cm diam., green,
1356 hirsute, internodes 1.3–3.2 cm long. Leaves opposite and decussate, pairs subequal; petioles
1357 3.2–5.5 cm long, green, hirsute; leaf blades elliptic to lanceolate, 16.0–22.5 × 3.2–6.0 cm,
1358 apex and base attenuate, margin distantly denticulate and ciliate, membranaceous; adaxial
1359 surface green, hirsute; abaxial surface pale green, hirsute, 6–9 pairs of secondary veins.
1360 Inflorescence axillary, cymose, pedunculate or rarely with a very short peduncle, with 1–3
1361 flowers per node; pedicels terete, 1.2–1.7 cm long, green, hirsute. Calyx lobes 5, fused and
1362 imbricate at base, spreading, subequal, lanceolate, 1.0–1.4 × 0.3–0.4 cm, apex attenuate,
1363 margin entire, yellow, hirsute. Corolla oblique in relation to calyx, 18–24 mm long, tube
1364 contracted at base, limb regular, 6 mm wide at the base, 5 mm wide at the narrowest point,
1365 throat 7 mm wide, ventricose, yellowish-white, glabrous outside and inside; lobes 5, reflexed,
1366 slightly equal, semiorbicular, 2 × 4 mm, margin entire, white, glabrous. Nectary annular, 0.5
1367 mm wide, glabrous. Stamens 4, included in the throat; filaments 5–6 mm, epipetalous, adnate,
1368 free portion of filaments arising in the middle of the corolla tube, glabrous; anthers 1 × 2 mm,
1369 longitudinally dehiscent; staminode 0.4 cm long. Ovary ovoid, 4 × 5 mm, glabrous; style
1370 included in the throat, 11–15 mm long, glabrous; stigma bifid. Fruit not seen.

1371 **Distribution and ecology:**—*Besleria diabolica* is known from Eldorado and Miracatú,
1372 municipalities in the southern part of São Paulo state (Fig. 5). The vegetation type in this
1373 region is Atlantic rainforest of the Atlantic forest domain. The species usually occurs along
1374 banks of streams within forested areas at around 400 m elevation. Based on our own
1375 observations in the vicinity of the “Caverna do Diabo” state park only a few scattered
1376 individuals were seen, indicating a low population density.

1377 **Phenology:**—Flowers are recorded from September to November.

160

1378**Conservation status:**—Endangered (EN) B1ab(i,iv), according to the IUCN criteria, based
1379on the extent of occurrence estimated to be less than 5,000 km² in only two locations (IUCN
13802013).

1381**Taxonomic relationships:**—This new species is somewhat similar to *Besleria melancholica*
1382(Vellozo 1825: 260) Morton (1939: 446) in the shape and position of the calyx lobes, but it
1383can be differentiated by the narrower calyx lobes (3–4 mm vs. 4–7 mm wide), which are
1384lanceolate with acute apices (vs. oblong with obtuse apices). Inflorescences of *B.*
1385*melancholica* may have many flowers, 5–6 (more commonly 2–4), while *B. diabolica* has 1–3
1386flowers per inflorescence (Fig. 4G). Geographically, *B. diabolica* has a different distribution
1387occurring only in southern São Paulo state, whereas *B. melancholica* is restricted to
1388mountainous areas in Rio de Janeiro state.

1389**Etymology:** —The name “diabolica” is a reference to the first place where this species was
1390found, around the “Caverna do Diabo” state park, which is located in the southern region of
1391São Paulo state in Brazil.

1392**Additional specimens examined (paratypes):**—BRAZIL. São Paulo: Eldorado, nas
1393proximidades da Caverna do Diabo, 11 November 2000, *E.R. Salviani & H. Lorenzi 1773*
1394(HPL!, INPA!); Miracatú, perto de Pedro Barros, 30 Ago 1966, *J. Mattos s.n.* (RB!).

1395

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1397

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1404(FAPESP).

1405

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- 1452

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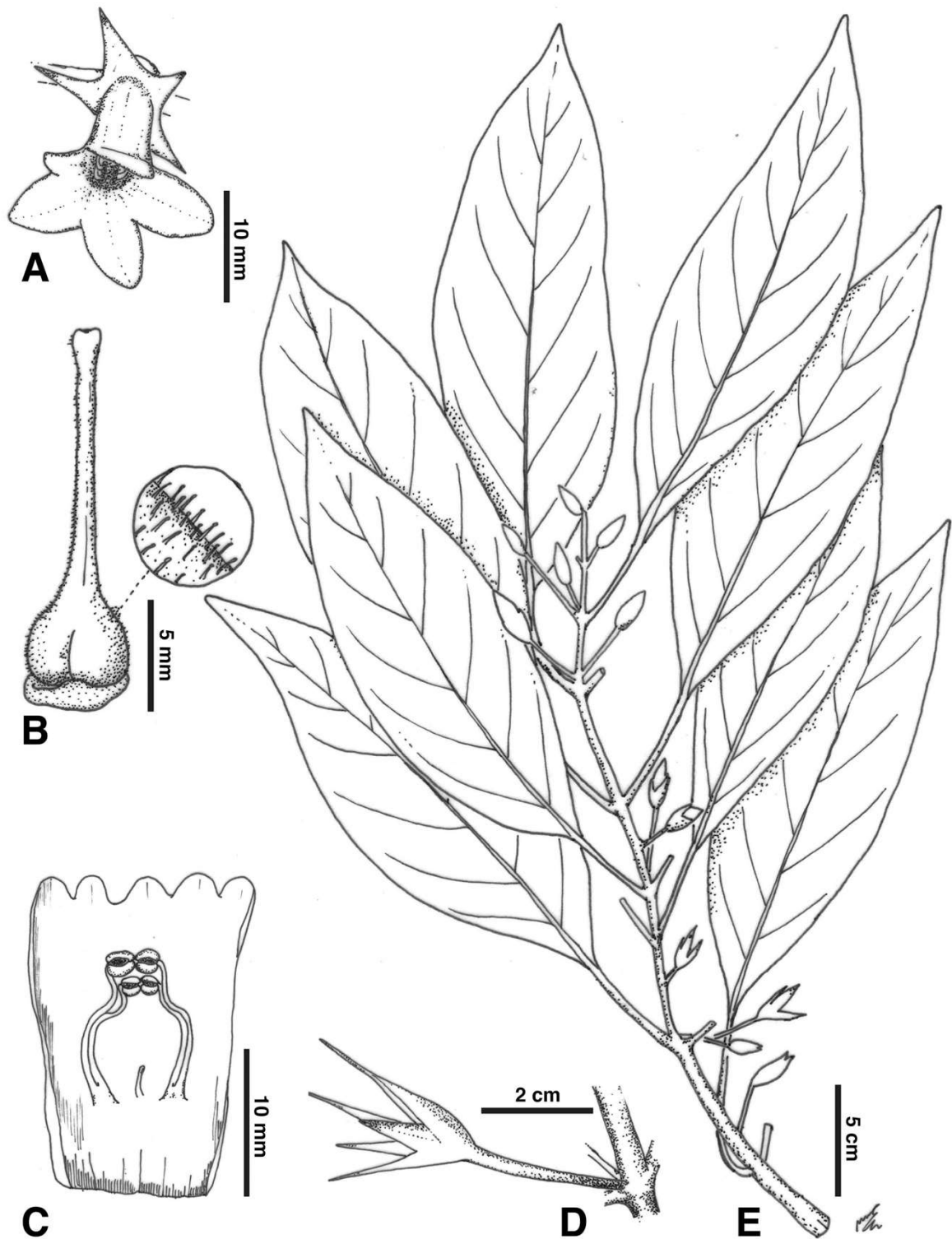
1453 **TABLE 1.** Morphological comparisons of the three new *Besleria* and related species.

Traits/Species	<i>B. aurea</i>	<i>B. brevicalyx</i>	<i>B. diabolica</i>	<i>B. fluminensis</i>	<i>B. macahensis</i>	<i>B. melancholica</i>
Leaf arrangement	opposite	3-verticillate	opposite	opposite	opposite	opposite
Leaf blade size [cm]	15–19 × 5.5–6.4	12.0–20.5 × 3.4–5.6	16.0–22.5 × 3.2–6.0	18–30 × 7–15	11.5–16.0 × 4.2–6.0	11–16 × 3.9–7.1
Leaf blade indumentum, abaxial surface	pubescent	pubescent	hirsute	puberulous	pubescent	glabrous to hirsute
Leaf blade margin	entire	serrulate	distantly denticulate	serrate	entire	entire to serrate
Petiole length [cm]	2.6–6.7	2.2–4.1	3.2–5.5	3.0–18.0	3.0–4.5	2.7–6.5
Number of flowers per axil	2–5	1–3	1–3	2–6	2–6	2–6
Pedicle indumentum	puberulent	pubescent	hirsute	pubescent	pubescent	hirsute
Pedicle length [cm]	2–2.1	2.2–3.4	1.2–1.7	1.3–2.6	1.3–2.6	1.1–2.3
Calyx colour	yellow	yellow-greenish	yellow	yellow–purplish	yellow–purplish	yellow–greenish
Calyx lobes dorsally keeled	yes	yes	no	yes	no	no
Calyx lobes length [mm]	11–16	4–6	10–14	9–11	9–11	13–16
Calyx lobes width [mm]	4–6	3–4	3–4	2–4	3–4	4–7
Calyx lobe shape	lanceolate	lanceolate	lanceolate	elliptic	lanceolate	oblong
Calyx lobe apex	attenuate	acute with mucron	attenuate	acuminate	attenuate	attenuate
Calyx lobe positions	spreading	adherent	spreading	spreading	adherent	spreading
Calyx indumentum	puberulent	glabrous	hirsute	puberulous	glabrous	glabrous to hirsute
Corolla colour	yellow	whitish-yellow	yellowish-white	yellowish-white	yellowish-white	yellowish-white
Corolla length [cm]	1.6–2.2	1.6–1.8	1.8–2.4	1.9–2.1	1.9–2.1	1.6–2.2
Corolla lobe length [mm]	3–6	3	2	5–7	5–7	3–5

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1456 **FIGURE 1.** *Besleria aurea*. A. Calyx and corolla in frontal view. B. Pistil and nectary with a
 1457 close up of the glandular indumentum. C. Corolla opened to show stamens and staminode. D.
 1458 Calyx without corolla and pistil in lateral view. E. Habit (A–E from *I.G. Costa 230*).

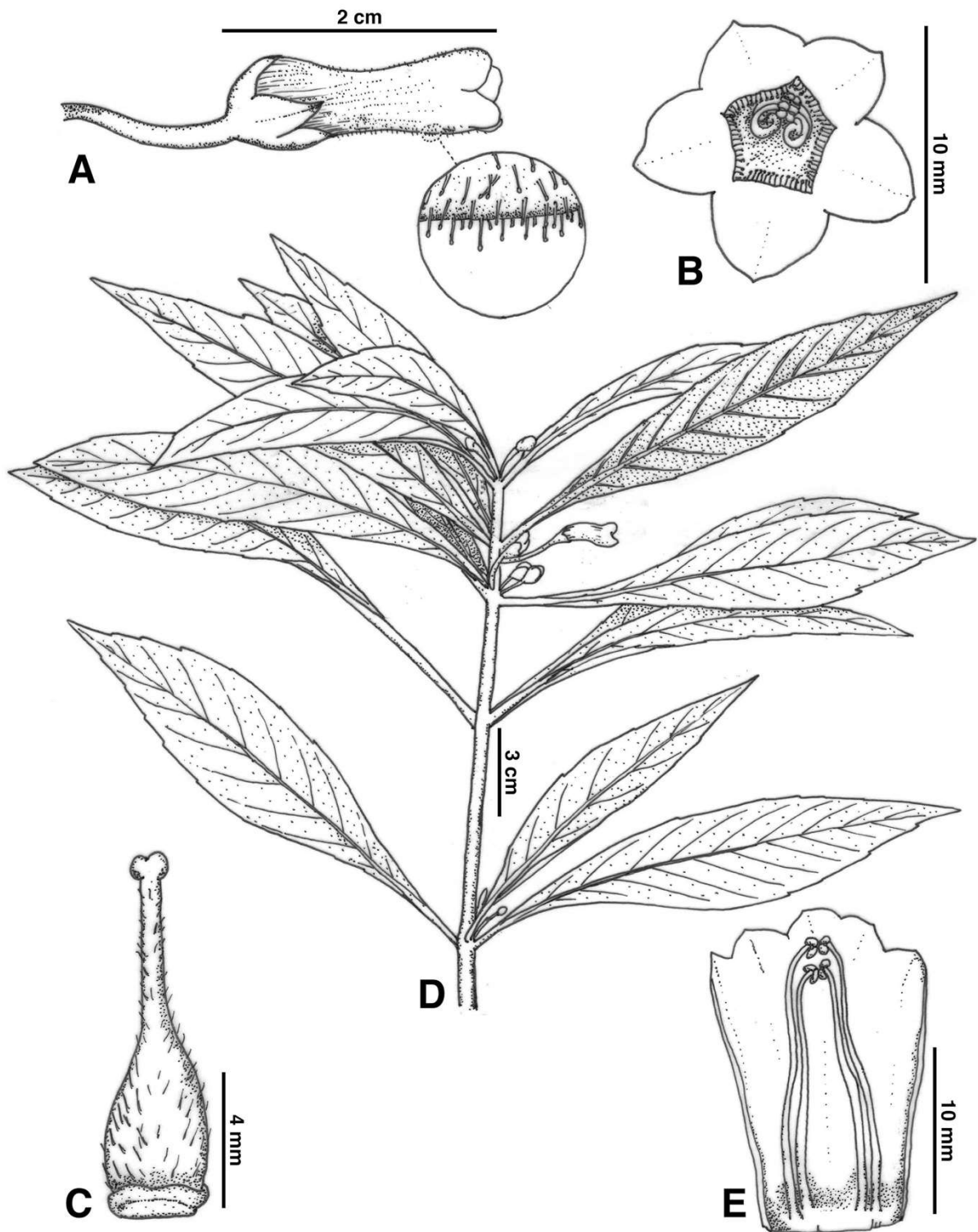


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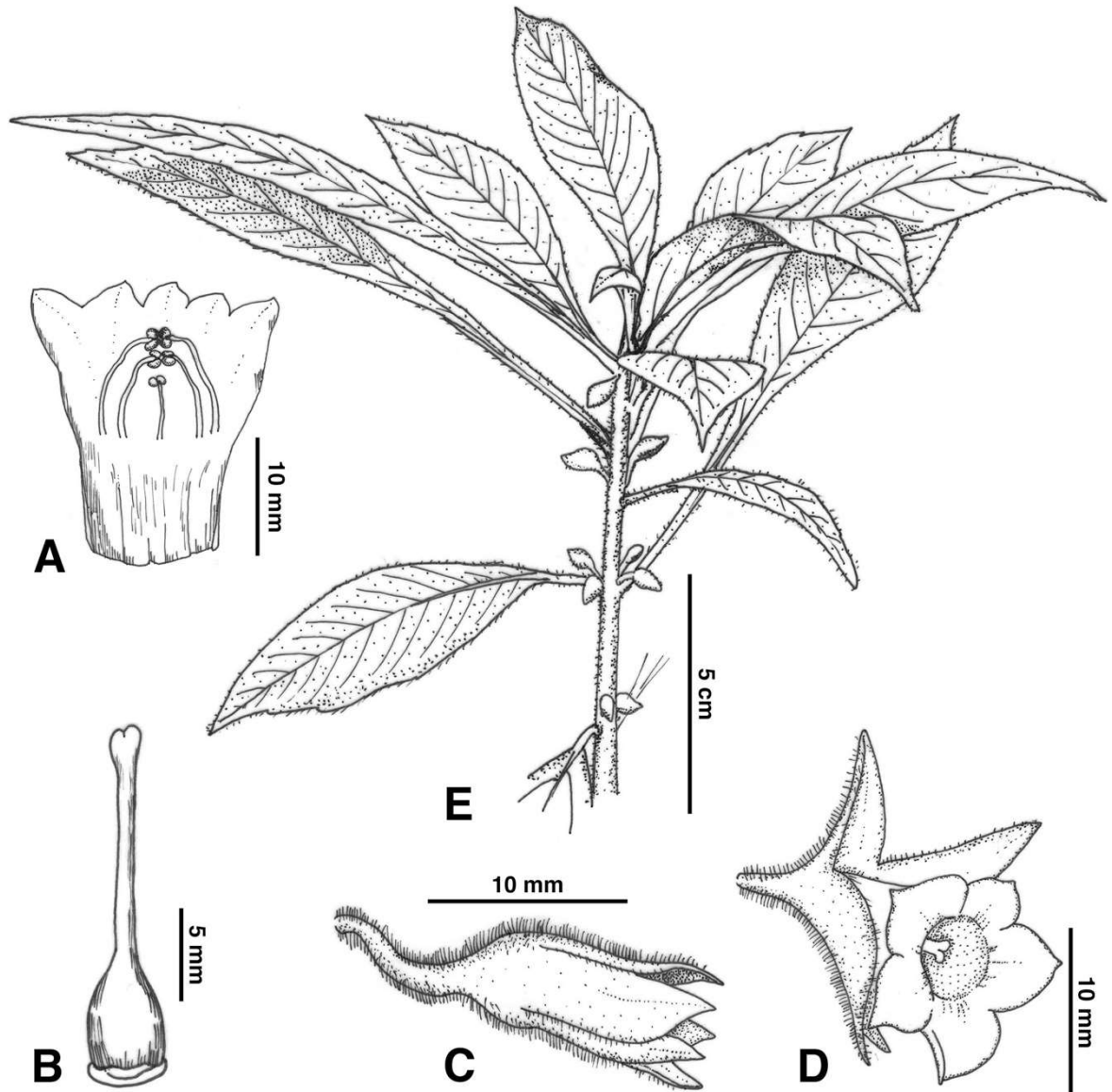
1462 **FIGURE 2.** *Besleria brevicalyx*. A. Calyx and corolla in lateral view with a close up of the
 1463 glandular indumentum. B. Corolla in frontal view. C. Pistil and nectary. D. Habit. E. Corolla
 1464 opened to show stamens (A–E from *G.E. Ferreira et al. 292*).



1465

1466

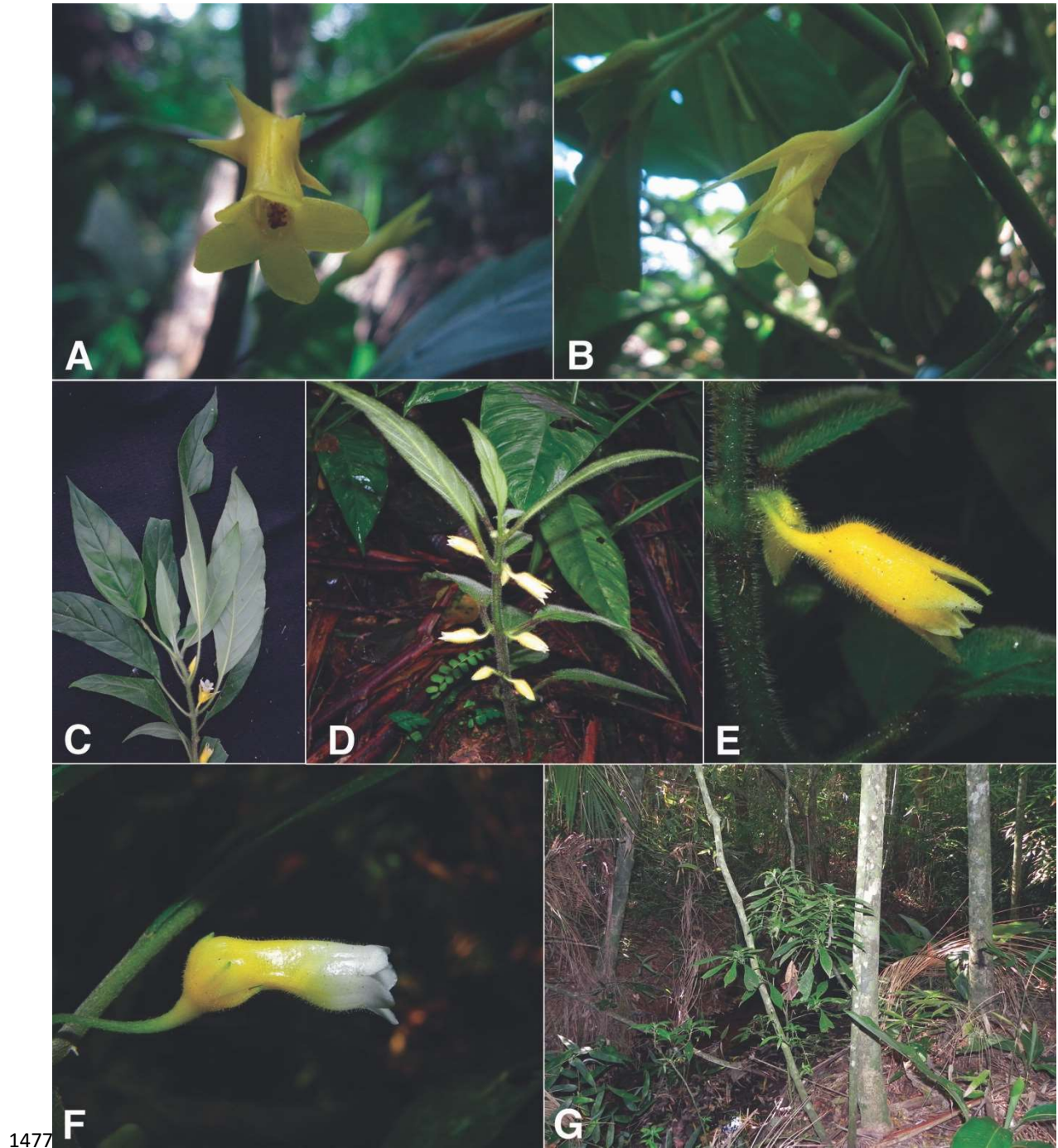
1467 **FIGURE 3.** *Besleria diabolica*. A. Corolla opened to show stamens and staminode. B. Pistil
 1468 and nectary. C. Calyx without corolla in lateral view. D. Calyx and corolla in frontal view. E.
 1469 Habit (A–D from *E.R. Salviani & H. Lorenzi 1773* and E from *G.E. Ferreira et al. 271*).



1470

1471

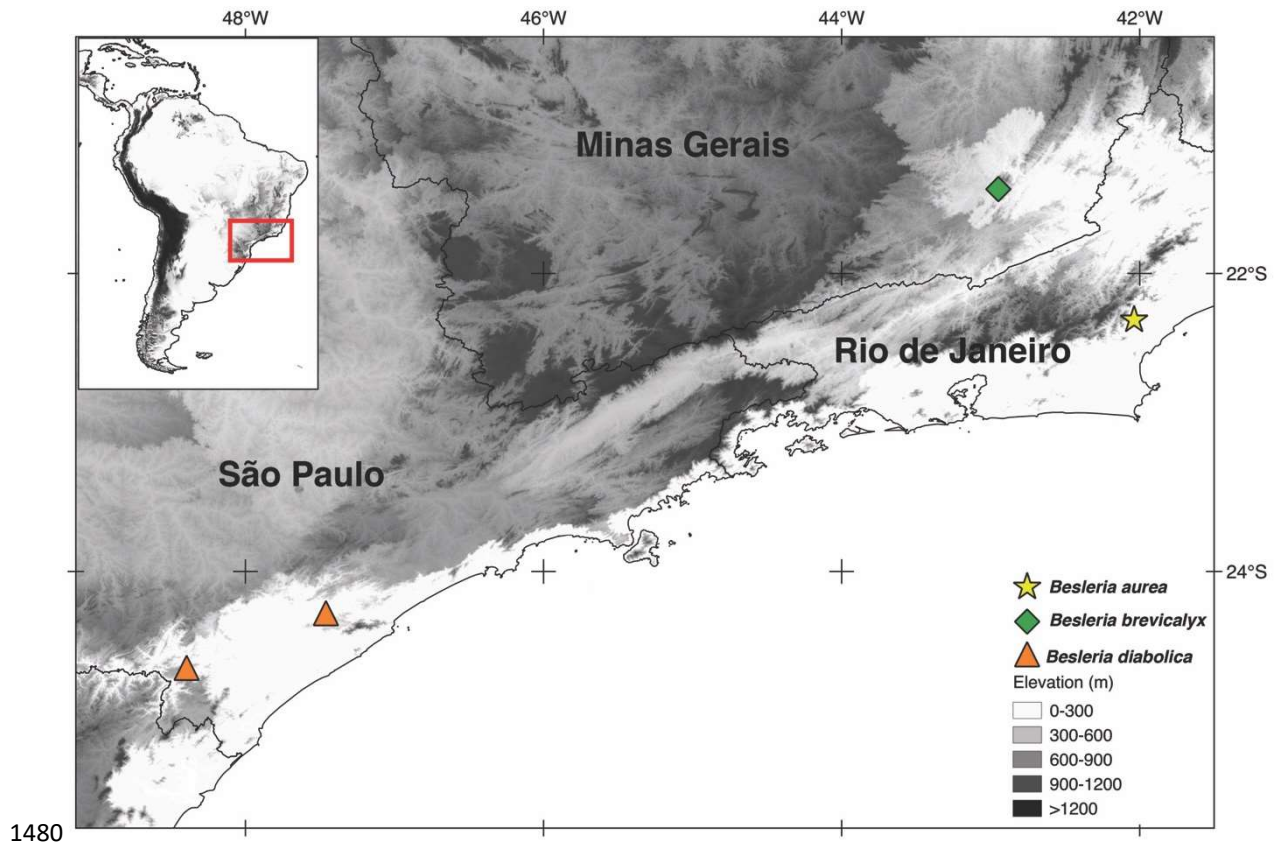
1472 **FIGURE 4.** Morphology and habitat of the new species of *Besleria*. A–B. *Besleria aurea*. A.
 1473 Calyx and corolla in frontal view. B. Calyx and corolla in lateral view. C–D. *Besleria*
 1474 *brevicalyx*. C. Calyx and corolla in frontal view. D. Habit and habitat. F–H. *Besleria*
 1475 *diabolica*. F. Flowering branch. G. Habit. H. Calyx in lateral view. (A–B from *I.G. Costa* 230;
 1476 C–D from *G.E. Ferreira et al.* 292; F from *T. Flores s.n.*, G–H from *G.E. Ferreira et al.* 271).



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1479 **FIGURE 5.** Distribution of the three new species of *Besleria* in eastern of Brazil.



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Capítulo 4

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1484

1485Ferreira, G.E.; Araujo, A.O.; Hopkins, M.J.G.; Chautems,
1486A. A New species and two new records of *Besleria*
1487(Gesneriaceae) from Brazil. Manuscrito formatado para
1488*Systematic Botany*.

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FERREIRA ET AL.: NEW SPECIES AND RECORDS OF BESLERIA

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1496 **A New Species and Two New Records of *Besleria* (Gesneriaceae) from Brazil**

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1522**Abstract**—We describe and illustrate *Besleria discreta*, a new species from the state of
1523Espírito Santo. The new species has been found in a mountainous area in the southern
1524part of the state and can be recognized by leaf blade slightly bullate adaxially and short
1525corolla. We also report the occurrence of two species that had not been recorded in the
1526Amazon rainforest in Brazil: *Besleria concinna* and *Besleria neblinae*. Data on
1527morphology, ecology, distribution and conservation status of the three taxa are also
1528provided.

1529**Keywords**—Atlantic forest, Amazon rainforest, *Besleria discreta*, taxonomy.

1530

1531*Besleria* Plumier ex L. harbors over 160 species and it is one of the largest and most
1532diverse genus among Gesneriaceae (Skog and Feuillet 2008; Möller and Clark 2013;
1533Berger et al. 2015). The genus has a Neotropical distribution, occurring in the Andes and
1534the Amazon rainforest of Bolivia to Colombia, in Central America as far north as Mexico,
1535and some species are endemic to the Brazilian Atlantic rainforest and to the Caribbean
1536Islands (Skog and Boggan 2007; Ferreira et al. 2016). In Brazil, 21 species are currently
1537known, occurring in the Amazon and Atlantic rainforests (BFG 2015). Phylogenetic
1538studies indicate that the genus is monophyletic and belongs to the monophyletic
1539subtribe Besleriinae within tribe Beslerieae (Weber et al. 2013).

1540The genus is common in the understory of rainforests and can be recognized by its
1541terrestrial habit, mostly growing as shrubs, but sometimes as herbs or small trees,
1542stems are usually well developed, sparsely branched, with several pairs of usually large
1543leaves, axillary and pedunculate or ependunculate bractless inflorescences, flowers
1544usually not very conspicuous, calyx formed of equal lobes, more or less developed,
1545tubular corollas, gibbose or ventricose with superior ovary and fleshy fruits that are
1546indehiscent or sometimes partly dehiscent. During systematic and biogeographic studies
1547of *Besleria*, we found some specimens that did not fit into any of the species currently
1548described, and others that were identified as species not yet reported for Brazil. After
1549morphological analysis and comparison with related species, we describe a new species
1550for the genus and two new records for Brazil.

15517 Materials and Methods

1552During the examination of herbarium specimens, we found material that could not be
1553assigned to any formally described species of *Besleria* or that belonged to species
1554unregistered in Brazil. We carried out fieldwork in the Brazilian Atlantic and Amazon

1555rainforests between 2014 and 2015 in order to better identify these species. We
 1556searched for them and found populations in the following localities: Divino de São
 1557Lourenço (Espírito Santo) and Presidente Figueiredo (Amazonas), Brazil. Living
 1558specimens were photographed in the field. We deposited specimens in the G, RB, INPA,
 1559and HUFABC. Some flowers were preserved in 70% ethanol and used for drawings of
 1560floral features. We performed morphological analyses using a stereoscopic microscope.
 1561The descriptive terminology follows Beentje (2010). Additional collections from the F, G,
 1562MO, NY, RB, US, VIES, MBML, and INPA were also studied to prepare the species
 1563distribution map and the identification key. The expected IUCN criteria are provided for
 1564the species (IUCN 2017).

15658 Results

1566TAXONOMIC TREATMENT

1567*Besleria discreta* G.E.Ferreira, sp. nov. TYPE:BRAZIL. Espírito Santo: Divino de São
 1568Lourenço, Patrimônio da Penha, Comunidade Portal do Céu, Vivência Beija-flor, 8 Nov
 15692014, *G.E. Ferreira et al. 291* (holotype: INPA!, isotypes G!, RB!, HUFABC!).

1570

1571*Besleria discreta* resembles *B. brevicalyx* G.E. Ferreira & Chautems in its calyx and corolla
 1572coloration, however, it differs by its leaf blade slightly bullate adaxially, opposite and
 1573decussate leaves (vs. 3-verticillate), obovate leaf blade (vs. oblanceolate), shorter pedicel
 1574of 1.6-2.2 cm (vs. 2.2-3.4 cm), calyx lobes not keeled dorsally (vs. keeled) and shorter
 1575corollas reaching 1.3-1.6 cm (vs. 1.6-1.8 cm).

1576

1577Terrestrial shrub, 0.8–1.0 m tall. **Stems** branched, subterete, up to 0.3–0.6 cm diam.,
 1578green-brownish, glabrous, pubescent when young; internodes 1.5–4.0 cm long. **Leaves**
 1579opposite and decussate, pairs unequal; petioles 1.6–3.4 cm long, green, pubescent; leaf
 1580blades obovate, 10.5–15.0 × 4.0–6.5 cm, apex acuminate, base long-attenuate, margin
 1581distantly serrulate, membranaceous, adaxial surface green, slightly bullate, puberulous;
 1582abaxial surface pale green, sericeous on the veins, 8–10 pairs of secondary veins.
 1583**Inflorescences** axillary, cymose, epedunculate, with 1–3 flowers per node; pedicels
 1584terete, 1.6–2.2 cm long, green-yellowish, puberulous. **Calyx** lobes 5, lobes erect,
 1585adherent to the corolla base, mostly equal, lanceolate, 5–6 × 2–3 mm, apex acute with
 1586short mucro, margin entire, yellow-whitish, outside puberulous, inside glabrous. **Corolla**
 1587horizontal in relation to calyx, ventricose, 13–16 mm long, tube contracted at base, 4 mm

1588wide at the base, 3 mm wide at the narrowest point, throat 6 mm wide, yellow-whitish,
 1589outside pubescent, inside glabrous; limb regular, lobes 5, reflexed, slightly equal, semi-
 1590orbicular, 2 × 2.5 mm, margin entire, white, setose. **Nectary** annular, 0.2 mm wide,
 1591glabrous. **Stamens** 4, included in the throat; filaments 5–7 mm, epipetalous, adnate, free
 1592portion of filaments arising at 3 mm from the base of the corolla, glabrous; anthers 1.5 ×
 15932 mm, longitudinally dehiscent. **Ovary** ovoid, 3 × 4 mm, puberulous; style included in the
 1594throat, 6–7 mm long, puberulous-glandular; stigma bifid, puberulous. **Fruit** not seen.
 1595Figures 1 and 2.

1596**Distribution and Habitat**—This species occurs in Espírito Santo state (Fig. 3). It was
 1597collected in the Brazilian Atlantic rainforest domain, occurring on rocky banks of
 1598streams (Fig. 2D) at ca. 600–1000 m elevation. Only a few plants were found at each
 1599collection point.

1600**Phenology**—Flowers are recorded from August to November.

1601**Etymology**— The name “discreta” refers to the flowers that are among the smallest
 1602known for the genus. It also alludes to the similar coloration of calyx and corolla base
 1603that make the flowers little conspicuous (Fig. 4A).

1604**Conservation Status**—This species is expected to be classified as endangered (EN) B1ab
 1605(i, iv), according to the IUCN criteria, based on the extent of occurrence estimated to be
 1606less than 5000 km² in only two locations (IUCN 2017).

1607**Notes**—*Besleria discreta* is similar to *Besleria brevicalyx* G.E.Ferreira & Chautems; these
 1608species share fasciculate inflorescences, calyx closely adherent to the corolla base, calyx
 1609lobes apex acute with short mucro, and corollas that are yellow at base and white
 1610towards the apex. However, *Besleria discreta* differs from *B. brevicalyx* by its leaf blade
 1611slightly bullate adaxially, phyllotaxy (opposite and decussate leaves vs. 3-verticillate),
 1612shorter pedicels (1.6–2.2 cm long vs. 2.2–3.4 cm long), shape and size of the leaf blades
 1613(obovate, 10.5–15.0 × 4.0–6.5 cm vs. oblanceolate, 12.0–20.5 × 3.4–5.6 cm) and
 1614indumentum on leaf blades and flowers (sericeous vs. pubescent). Additionally, *B.*
 1615*discreta* occurs in Espírito Santo on rocky stream banks in ombrophilous forest, whereas
 1616*B. brevicalyx* is restricted to Minas Gerais state and occurs in sandy substrates on the
 1617ground of a transition area between ombrophilous and seasonal forest (Forzza et al.
 16182014).

1619*B. macahensis* Brade is another similar species but it can be easily differentiated from *B.*
 1620*discreta* by its yellow-purplish pedicel and calyx (vs. green-yellowish pedicel and yellow-

1621whitish calyx), calyx lobe apex attenuate (vs. apex acute with short mucro). *B. discreta*
 1622shares mucronate calyx lobe apex with *B. longimucronata* Hoehne but the shape of the
 1623calyx lobes (lanceolate vs. ovate) and the length of the corolla (1.8–2.8 cm long vs. 1.3–
 16241.6 cm long) differ (Table 1).

1625**Additional Specimens Examined—Brazil.** —ESPÍRITO SANTO: Alegre, Pedra da Carneira,
 162630 Aug 2008, *D.R. Couto 842* (MBML!); Alegre, Monte Cristo, 5 Oct 2009, *D.R. Couto et al.*
 16271267 (VIES!); Cachoeiro de Itapemirim, Burarama-Canta Galo, 30 Aug 2008, *D.R. Couto*
 1628870 (MBML!); Divino de São Lourenço, Patrimônio da Penha, Comunidade Portal do Céu,
 162928 Aug 2011, *D.R. Couto 2059* (VIES!).

1630KEY TO DISTINGUISH *BESLERIA DISCRETA* FROM RELATED SPECIES

16311. Leaves 3-verticillate; growing on sandy substrate and seasonal forests., *Besleria*
 1632**brevicalyx**

16331. Leaves opposite and decussate; growing on humid substrate and rainforest., 2

16342. Pedicel and calyx yellow-purplish, calyx lobe apex attenuate., *Besleria macahensis*

16352. Pedicel and calyx green-yellowish to yellow, calyx lobes apex mucronate or acute
 1636with a shortly mucron., 3

16373. Calyx lobes 8–10 mm long, ovate, apex mucronate; corolla 1.8–2.8 cm long. *Besleria*
 1638**longimucronata**

16393. Calyx lobes 5–6 mm long, lanceolate, apex acute with shortly mucron; corolla 1.3–1.6
 1640cm long. , *Besleria discreta*

1641

1642**New Records—**

1643BESLERIA CONCINNA C.V.Morton Fieldiana, Bot. 28: 525. 1953. TYPE:VENEZUELA. Anzoátegui:
 1644northeast of Bergatín, 9 Mar 1945, *J.A.Steyermark 61465* (holotype: F!, digital image
 1645V0055577F).

1646Terrestrial shrub, 0.5–2.0 m tall. **Stems** unbranched, subterete, up to 0.5–2.0 cm diam.,
 1647green, glabrous at base, hirsute at apex; internodes 3.5–8.0 cm long. **Leaves** opposite,
 1648pairs unequal; petioles 2.6–8.0 cm long, green, hirsute; leaf blades elliptic, 14.0–27.0 ×
 16497.0–11.0 cm, apex acute, base attenuate, margin serrate, membranous, adaxial surface
 1650green, hirsute, abaxial surface pale green, hirsute, 13–16 pairs of secondary veins.
 1651**Inflorescences** axillary, pedunculate, cymose; peduncle 3–4 cm long, with 1–4 flowers;
 1652pedicels terete, 0.8–1.2 cm long, green, hirsute. **Calyx** short-campanulate, tube 2–4 mm
 1653long, lobes 5, erect, subulate-lanceolate, 1.2–2.2 × 0.2–0.4 cm, apex acute, margin entire

1654or sometimes ciliate, green, outside hirsute, inside glabrous. **Corolla** erect in the calyx,
 16551.9–2.1 cm long, ventricose, tube contracted at base, 5 mm wide at the base, 4 mm wide
 1656at the narrowest point, throat 5–6 mm wide, orange, glabrous; limb regular, lobes 5,
 1657patents, slightly equal, rounded, ca. 0.4 × 0.4 cm, margin entire, orange, glabrous.
 1658**Nectary** annular, ca. 0.5 mm wide, glabrous. **Stamens** 4, included, filaments 0.7–1.0 cm,
 1659epipetals, arising ca. 0.2 cm from the base of the corolla, glabrous; anthers ca. 0.1 × 0.2
 1660cm, longitudinally dehiscent. **Ovary** conical, ca. 0.4 × 0.2–0.3 cm, shortly pilose; style
 1661included, ca. 0.5 cm, shortly pilose, stigma bifid. **Fruit** a berry, globose, ca. 0.7 × 0.8 cm,
 1662glabrescent, calyx persistent, seeds numerous, ovoid to widely elliptic, ca. 1.0 × 0.5 mm,
 1663light brown to dark red, longitudinally striate. Figure 4.

1664**Distribution and Habitat**— The species is recorded here for the first time in Brazil at
 1665the Serra dos Surucucus (Roraima state) and Uatumã Biological Reserve (municipality of
 1666Presidente Figueiredo, Amazonas state). This species had been found previously only in
 1667Venezuela (Anzotégui, Miranda, Sucre) (Fig. 3). It grows in the Amazon rainforest, along
 1668the border of the Brazilian Guiana Shield. It occurs between 150–1400 m elevation,
 1669preferentially on rocky substrate next to the waterfalls and in wet places within the
 1670spray zone. Populations with many individuals were found and could be observed at all
 1671stages of development.

1672**Phenology**—Flowers are recorded from September to October, fruits recorded from
 1673November to February.

1674**Conservation Status**— This species is expected to be classified as vulnerable in Brazil
 1675and assessed as (VU) B1ab (i, iv), according to the IUCN criteria, based on the extent of
 1676occurrence estimated to be less than 5000 km² in five locations (IUCN 2017).

1677**Notes**—*Besleria concinna* is similar to *Besleria laxiflora* Benth., however it can be easily
 1678recognized by its hirsute indumentum throughout the plant (vs. glabrous to strigose at
 1679the stem apex), larger leaf blades (14.0–27.0 × 7.0–11.0 cm vs. 8–21 × 3.0–8.5 cm), calyx
 1680lobes longer and hirsute (1.2–2.2 cm long vs. 0.5–1.4 cm long).

1681**Additional Specimens Examined**—**Brazil.** AMAZONAS: Presidente Figueiredo, Rebio
 1682Uatumã, Cachoeira do Paredão, 16 Sep 2015, *G.E.Ferreira et al.* 328 (G!, INPA!, HUFABC!);
 168331 Oct 2006, *J.E.L.S.Ribeiro* 2747 (INPA!); 8 Sep 2006, *J.G.Carvalho-Sobrinho et al.* 1017
 1684(INPA!); Grade PPBio, 23 Sep 2006, *J.G.Carvalho-Sobrinho et al.* 1017 (INPA!); RORAIMA:
 1685Alto Alegre, Serra dos Surucucus, 17 Feb 1969, *G.T.Prance et al.* 9981 (INPA!, NY!, US!); 6
 1686Feb 1973, *G.T.Prance et al.* 13511 (INPA!, NY!, US!).

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1688

1689 *BESLERIA NEBLINAE* Feuillet J. Bot. Res. Inst. Texas, 2: 269. 2008. TYPE: VENEZUELA.

1690 Amazonas: near Cerro de la Neblina, 8 May 1984, A. H. Gentry & B. A. Stein 472535

1691 (holotype: US!; isotype: MO!).

1692 Terrestrial shrub, 0.3–2.0 m tall. **Stems** branched, subterete, up to 0.5 cm diam., green,

1693 villous; internodes 1.0–2.0 cm long. **Leaves** opposite, pairs unequal; petioles 1.5–4.5 cm

1694 long, green, densely villous; leaf blades lanceolate to elliptic, often asymmetric, 9.0–20.0

1695 × 3.0–6.0 cm, apex acute to acuminate, base acute to obtuse, margin serrulate and ciliate,

1696 membranous, adaxial surface green, setose, abaxial surface pale green, setose, 8–12

1697 pairs of secondary veins. **Inflorescences** axillary, cymose, pedunculate, with 2–3

1698 flowers per node; pedicels terete, 3.0–5.0 cm long, green, densely villous. **Calyx** short-

1699 campanulate, tube 1.5 mm long, lobes 5, erect, lanceolate, 5.5–6.0 × 1.2–1.5 cm, apex

1700 attenuate, margin entire or sometimes ciliate, green, outside hirsute to villous, inside

1701 glabrous. **Corolla** horizontal in the calyx, 2.5–3.5 cm long, prominently spurred, spur

1702 5.0–5.5 × 2–3 mm, rounded, tube contracted at base, 4 mm wide at the base, throat 6

1703 mm wide, white to yellowish, puberulent-glandular; limb regular, lobes 5, reflexed,

1704 slightly equal, suborbicular, ca. 0.4 × 0.4 cm, margin entire, whitish-yellow, glabrous.

1705 **Nectary** semi-annular, ca. 0.5 mm wide, glabrous. **Stamens** 4, included, filaments 2.5 cm,

1706 epipetals, arising ca. 0.2 cm from the base of the corolla, glabrous; anthers ca. 0.2 × 0.2

1707 cm, longitudinally dehiscent; staminode ca. 3 mm with sterile anther. **Ovary** ovoid, ca.

1708 0.3 × 0.3 cm, glabrous; style included, ca. 2.0 cm, glabrous, stigma bifid. **Fruit** not seen.

1709 Figure 5.

1710 **Distribution and Habitat**— The species was recorded for the first time in Brazil at the

1711 Pico da Neblina National Park and nearby mountain areas (municipality of São Gabriel

1712 da Cachoeira, Amazonas state); this species was previously recorded only in Venezuela

1713 (Amazonas state – Fig. 3). It was collected in the Amazon rainforest, occurring

1714 preferentially on rocky substrate near very humid places at ca. 100–150 m elevation. No

1715 information about populations with the records.

1716 **Phenology**— Unseasonal flowers recorded in November.

1717 **Conservation Status**— This species is expected to be classified as vulnerable in Brazil

1718 and assessed as (VU) B1ab (i, iv), according to the IUCN criteria, based on the extent of

1719 occurrence estimated to be less than 5000 km² in five locations (IUCN 2017).

1720**Notes**—*Besleria neblinae* somewhat resembles *Besleria gibbosa* (Poepp.) Hanst by its
 1721axillary flowers and white corollas, however it can be differentiated by unequal leaf
 1722pairs and narrower and leaf blades (vs. equal or subequal), and by longer, narrower and
 1723hirsute to villous calyx lobes (vs. glabrous).

1724**Additional Specimen Examined**—**Brazil**. AMAZONAS: São Gabriel da Cachoeira, Sierra do
 1725Padre, 28 Nov 1987, *D.W.Stevenson & J.F.Ramos 1095* (INPA!, NY!).

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173810 Author Contributions

1739GEF, AOA and AC collected, identified and described the species of the article and MGH
 1740assisted in the writing the text.

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- 1767

1768 TABLE 1. Morphological comparisons of the new *Besleria discreta* and related species.

Traits/Species	<i>B. brevicalyx</i>	<i>B. discreta</i>	<i>B. longimucronata</i>	<i>B. macahensis</i>
Leaf arrangement	3-verticillate	Opposite and decussate	Opposite and decussate	Opposite and decussate
Petiole length [cm]	2.2–4.1	1.6–3.4	3.0–12.0	3.0–4.5
Leaf blade size [cm]	12.0–20.5 × 3.4–5.6	10.5–15.0 × 4.0–6.5	10.0–23.0 × 4.0–10.0	11.5–16.0 × 4.2–6.0
Leaf blade indumentum, abaxial surface	Pubescent	Sericeous on the veins	Glabrescent	Pilose
Leaf blade shape	Oblanceolate	Obovate	Elliptic-lanceolate to obovate	Entire
Leaf blade margin	Serrulate	Distantly serrulate	Entire	Entire
Number of flowers per axil	1–3	1–3	2–6	2–6
Pedicele length [cm]	2.2–3.4	1.6–2.2	1.5–4.0	1.3–2.6
Calyx color	Yellow-greenish	Yellow-whitish	Yellow	Yellow-purplish
Calyx lobes length [mm]	4–6	5–6	8–10	7–9
Calyx lobes width [mm]	3–4	2–3	2–4	4–5
Calyx lobe shape	Lanceolate	Lanceolate	Ovate	Lanceolate

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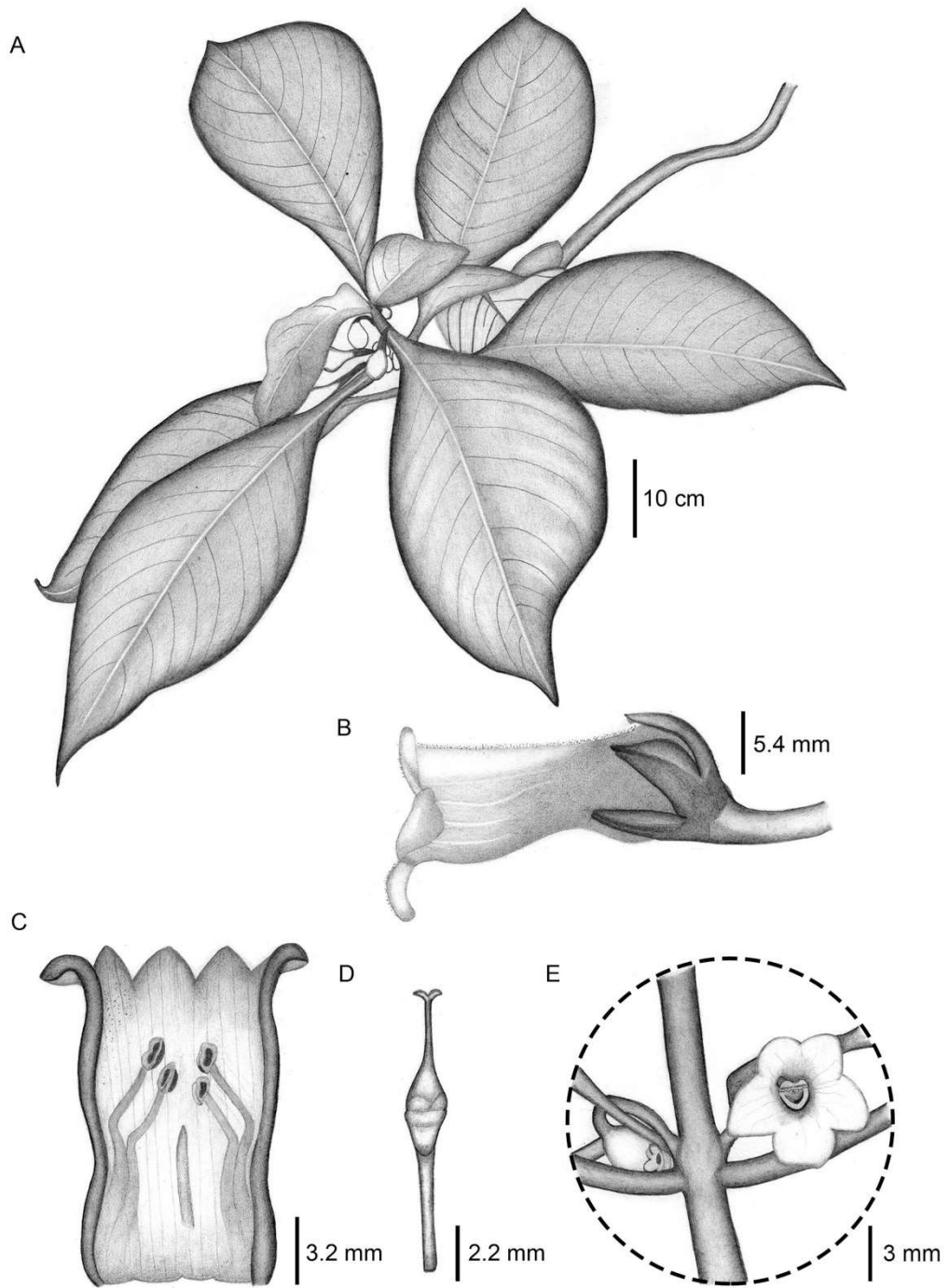
	ate	late		
Calyx lobe apex	Acute with mucron	Acute with mucron	Mucronate	Attenuate
Calyx indumentum	Puberulous-glandular	Puberulent (abaxially)	Puberulent	Glabrous
Corolla length [cm]	1.6–1.8	1.3–1.6	1.8–2.8	1.9–2.1
Corolla lobe length [mm]	3	2	2–4	5–7

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1771FIG. 1. *Besleria discreta*. A. Habit. B. Calyx and corolla in lateral view C. Open corolla
1772showing stamens and staminode. D. Gynoecium and nectary. E. Close up of the
1773inflorescence, stem and corolla (in frontal view). (A–E from *G.E. Ferreira et al. 291*).

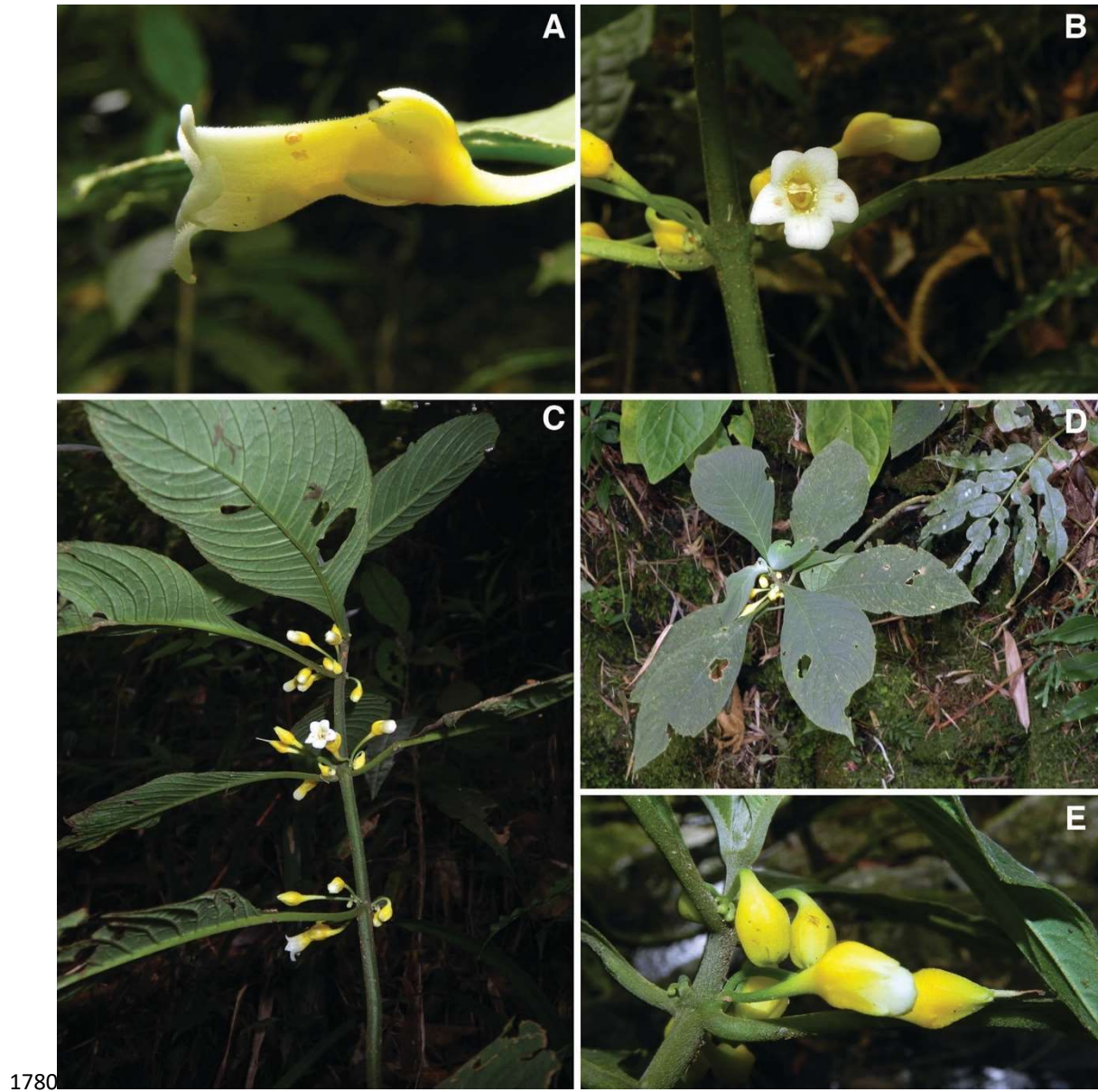


1774

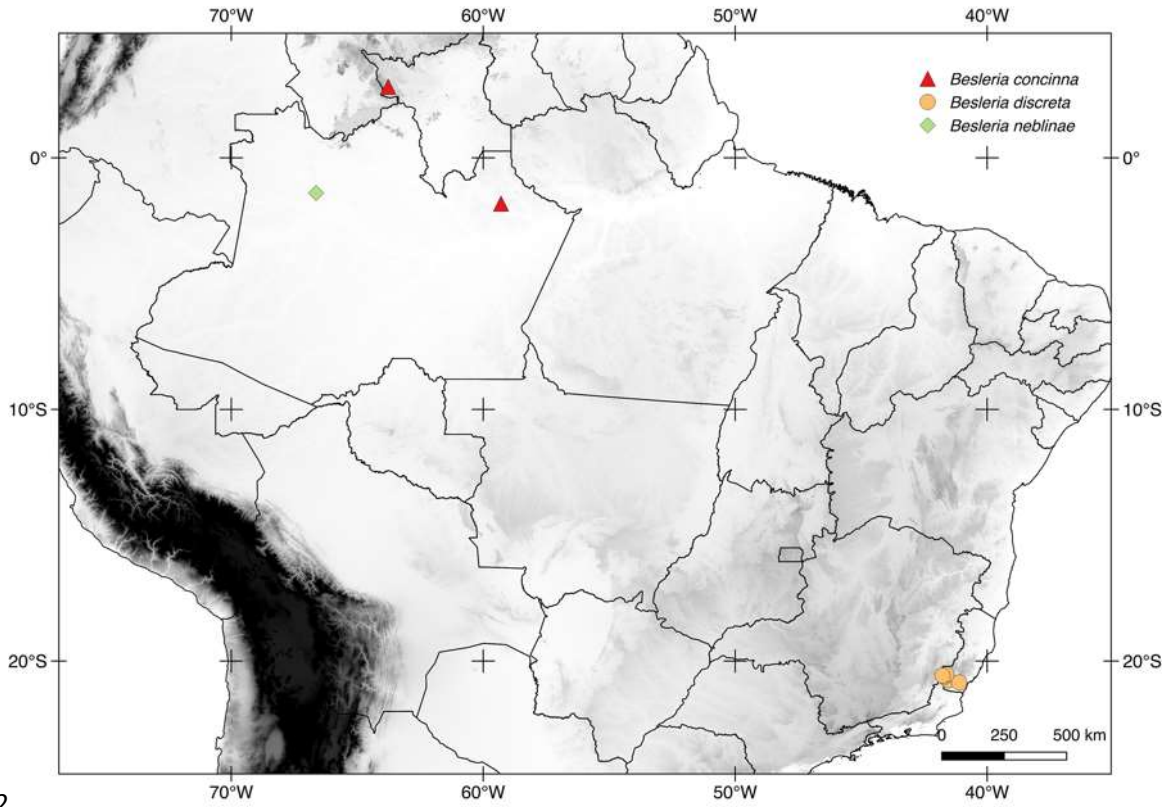
1775

1776

1777FIG. 2. *Besleria discreta*. A. Corolla, calyx and pedicel in lateral view. B. Corolla, in frontal
 1778view. C. Inflorescence, leaf arrangement and venation on the lower surface. D. Habit of a
 1779single plant. E. New branch and floral buds. (A–E from *G.E. Ferreira et al. 291*).



1781 FIG. 3. Distribution of *Besleria concinna*, *B. discreta*, and *B. neblinae*.



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1786

Capítulo 5

1787

1788Ferreira, G.E.; Araujo, A.O.; Hopkins, M.J.G.; Chautems, A.

1789Taxonomic treatment of *Besleria* (Gesneriaceae) from the

1790Brazilian Atlantic Rainforest. Manuscrito formatado para

1791*Phytotaxa*.

1792

1793

213

1794 **Taxonomic treatment of *Besleria* (Gesneriaceae) from southeastern Brazilian Atlantic**
 1795 **Rainforest**

1796

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1808

1809 **Abstract**

1810

1811 In this paper, a taxonomic treatment of species of *Besleria* endemic to the Brazilian Atlantic
 1812 Forest is presented. We recognized the occurrence of 11 species, from about 24 species in
 1813 Brazil. We proposed a dichotomous key, morphological descriptions, illustrations,
 1814 distribution maps and conservations status for the species. The main diagnostic characters
 1815 were the leaf arrangement, inflorescences pedunculate or epedunculate, pedicel length, calyx
 1816 lobes position, shape and colour, corolla length and colour.

1817

1818

1819 **11.1 Introduction**

1820

1821 *Besleria* Plumier ex Linnaeus (1753: 619) is a Neotropical genus of terrestrial herbs, shrubs
 1822 and small trees growing in the understory of rainforests. It includes more than 160 recognized
 1823 species, and is one of the largest and most diverse genera of Gesneriaceae (Berger *et al.* 2015;
 1824 Skog & Feuillet 2008). It belongs to the monophyletic tribe Beslerieae. Preliminary
 1825 phylogenetic studies reveal that the genus is monophyletic and that one of the six clades
 1826 retrieved diversified exclusively in the Brazilian Atlantic Rainforest (Ferreira *et al.* 2018; Perret

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1827 *et al.* 2013; Weber *et al.* 2013; Zimmer *et al.* 2002). The genus has a Neotropical distribution,
 1828 occurring in the Andes and the Amazon rainforest of Bolivia to Colombia, in Central America
 1829 as far north as Mexico, and some species are endemic to the Brazilian Atlantic rainforest and
 1830 to Caribbean Islands (Skog & Boggan 2007). In Brazil 24 species are currently known, occurring
 1831 in the Amazon and Atlantic rainforests (BFG 2017; Ferreira *et al.* 2016, 2017).

1832 The last comprehensive revision of *Besleria* was produced by (Morton 1939). (Wiehler 1975)
 1833 segregated two sections of *Besleria*, and placed them into genus *Gasteranthus* Bentham
 1834 (1846: 233) on the basis of vegetative and fruit characters. According to molecular
 1835 phylogenetic studies, *Besleria* (excluding *Gasteranthus*) is monophyletic *Creemosperma*
 1836 Bentham (1846: 234) is its sister genus (Clark *et al.* 2010; Ferreira *et al.* 2018; Roalson & Clark
 1837 2006). These studies also demonstrated that sections proposed by Morton (1939) were not
 1838 monophyletic. More detailed descriptions were possible through the observation of floral
 1839 characters in living material which contrasted with the descriptions used by Morton (1939),
 1840 based on herbarium material. It was noted that characters used by him to describe the
 1841 infrageneric groups evolved independently along the genus, not being a synapomorphy for
 1842 these groups (Ferreira *et al.* 2018).

1843 In the framework of a taxonomic, phylogenetic and biogeographic survey of *Besleria*, we
 1844 revise here all the 11 species that diversified in the Brazilian Atlantic Rainforest. They all
 1845 group in one of the six clades retrieved by the phylogenetic analysis, named “Atlantic Forest
 1846 clade” (Ferreira *et al.* 2018).

1847

1848 11.2 Material & methods

1849

1850 This study includes the monophyletic group called in a previous study of “Atlantic Forest
 1851 clade”. This clade is represented by shrub to small trees with yellow to yellowish- white
 1852 flowers. It is distributed in the South-eastern Brazilian Atlantic Rainforest, from the states of
 1853 Espírito Santo to Paraná (Ferreira *et al.* 2018).

1854 To undertake this taxonomic revision, all the protologues of the names described for the
 1855 Brazilian Atlantic rainforest were obtained and analysed. All the available herbarium
 1856 collections of the following herbaria were examined: B, F, G, G-DC, M, P, R, S, W, ALCB,
 1857 BAH, BHCB, CAY, CEN, CEPEC, CESJ, COL, ESA, FCAB, FLOR, GZU, HAS,
 1858 HERBAM, HPL, HRCB, HUEFS, HUFU, IAC, INPA, IPA, LABEV, LE, MBM, MBML,
 1859 MG, MO, NY, RB, RBW, RON, SINBIOTA, SP, SPSF, UB, UEC, UPCB, US and VIES,

1860acronyms according to (Thiers n.d.). Additional floristic data were also gathered from
1861GBIF.org (2018) and SpeciesLink (2018).

1862We carried out fieldwork in the Brazilian Atlantic forest to obtain more samples and analyses
1863the living material, between September and November 2014. Living specimens were
1864photographed in the field. Some flowers were preserved in 70% ethanol and used for
1865drawings of floral features. We performed morphological analyses using a stereoscopic
1866microscope. Morphological structures were described following the (Beentje 2010). The main
1867diagnostic features used in this revision are presented in Table 1.

1868 **11.3 Taxonomic treatment**

1869

1870*Besleria* Plumier *ex* Linnaeus (1753: 619)

1871

1872Terrestrial perennial herbs, shrubs or small trees to 5 m tall. Stem terete or quadrangular.
1873Leaves opposite, rarely whorled, membranous to coriaceous. Stomata not in groups. Cymes
1874fasciculate or subumbellate, rarely flowers solitary. Calyx campanulate, urceolate or
1875cylindrical, calyx lobes free or connate, imbricate, rounded or acuminate, entire or serrulate.
1876Corolla yellow, orange, red, or white; tube usually ventricose, hypocyrtoid or cylindrical,
1877sometimes spurred at base and contracted at throat; limb (sub)regular or bilabiate. Stamens
1878with broad, flattened filaments, adnate to corolla base; anthers coherent at first, becoming
1879free; locules confluent at apex. Nectary annular or semi-annular. Fruits fleshy, globose,
1880indehiscent berries or dehiscent through irregular rupturing; pericarp thick, smooth or
1881verrucose, pulp consisting of placental tissue. n = 16 (Berger *et al.* 2015; Weber 2004; Wiehler
18821975).

1883

1884The eleven *Besleria* species of the Atlantic Forest clade are endemic to southeastern Brazil,
1885occurring mainly in the humid forests of the Serra do Mar mountains, only *B. brevicalyx* and
1886*B. meridionalis* occur in the dry forests of Minas Gerais state. The state with the greatest
1887diversity is Rio de Janeiro, with 6 species, followed by São Paulo, with 3 spp., Minas Gerais
1888with two spp. and Espírito Santo and Paraná with one species.

1889

1890

1891

1892 Identification key to *Besleria* species from the Brazilian Atlantic Rainforest

1893

18941., Leaves 3-verticillate ; calyx lobes 4-6 mm

1895long2. *B.*1896*brevicalyx*

18971', Leaves opposite; calyx lobe 5-16 mm

1898long

1899..... 2

19002., Inflorescence pedunculate.....3

19012', Inflorescence sessile to sub-sessile4

19023., Inflorescence 6–12 flowers; calyx lobes oblong, apex

1903rounded11. *B.*1904*selloana*

19053', Inflorescence 1–5 flowers; calyx lobes lanceolate, apex acuminate to rarely mucronate

1906.....6. *B.*1907*grandifolia*

19084., Calyx lobes spreading, diverging from the corolla

1909axis5

19104', Calyx lobes adherent to the corolla

1911base9

19125., Calyx lobes dorsally keeled.....6

19135', Calyx lobes not dorsally keeled.....7

19146., Petiole length 2.6–6.7 cm; leaf blade 5.5–6.4 cm wide, margin entire; corolla yellow,

1915rarely vinaceous1. *B.*1916*aurea*

19176', Petiole length 3.5–18.5 cm; leaf blade 6.5–13.0 cm wide, margin serrate; corolla

1918yellowish-white5. *B.*1919*fluminensis*

19207., Flower solitary in leaf axil; pedicel 3.5–6.0 cm; calyx lobes apex obtuse and

1921mucronate10. *B.*1922*meridionalis*

19237', Flowers 2–6 per leaf axil; pedicel until 2.3 cm; calyx lobe apex? attenuate.....

1924.....8

- 19258., Calyx lobes 3–4 mm wide, lanceolate; from São Paulo.....
 1926.....3. *B. diabolica*
- 19278', Calyx lobes 4–7 mm wide, oblong with obtuse apices; from Rio de Janeiro.....
 1928.....9. *B. melancholica*
- 19299., Pedicel and calyx purplish, calyx lobes apex
 1930attenuate.....8. *B. macahensis*
- 19319', Pedicel and calyx yellow, calyx lobes apex mucronate or acute with a
 1932mucro.....10
- 193310., Calyx lobes 8–10 mm long, ovate; corolla 18–28 mm long
 1934.....7. *B. longimucronata*
- 193510', Calyx lobes 5–6 mm long, lanceolate; corolla 13–16 mm long
 1936.....4. *B. discreta*
- 1937
- 1938
19391. *Besleria aurea* I.G. Costa & G.E. Ferreira (2016: 272). Type:—BRAZIL. Rio de Janeiro:
 1940Campos dos Goytacazes, Conceição do Imbé, na Serra do Macaco, 16 July 2013, *I.G. Costa*
 1941230 (holotype RB!; isotype INPA!).
- 1942
- 1943Terrestrial shrub, 1.5 m tall. Stems unbranched, subterete, up to 0.5 cm diam., strigose at the
 1944base, internodes 2.0–6.5 cm long. Leaves opposite, pairs subequal; petioles 2.6–6.7 cm long,
 1945green, puberulent; leaf blades elliptic to oblanceolate, 15–19 × 5.5–6.4 cm, membranaceous,
 1946apex and base attenuate, margin entire; adaxial surface green, glabrous; abaxial surface pale
 1947green, pilose, 5–6 pairs of secondary veins. Inflorescence axillary, cymose, epedunculate,
 1948with 1–5 flowers per node; pedicels terete, 2.0–2.1 cm long, green, puberulent. Calyx lobes 5,
 1949dorsally keeled, fused and imbricate at base, diverging from the corolla axis, slightly equal,
 1950lanceolate, 11–16 × 4–6 mm, apex attenuate, margin sparsely denticulate, yellow, puberulent.
 1951Corolla oblique in relation to calyx, 16–22 mm long, tube contracted at base, limb regular, 6
 1952mm wide at the base, 4 mm wide at the narrowest point, throat 6.5 mm wide, ventricose,
 1953yellow, rarely vinaceous, glabrous outside and inside; lobes 5, patent, slightly equal, obtuse,
 19543–6 × 2–6 mm, margin entire, orange, glabrous. Nectary annular, 1 mm wide, glabrous.
 1955Stamens 4, included; filaments 7–9 mm long, epipetalous, adnate, free portion of filaments
 1956arising at 5 mm from the base of the corolla, glabrous; anthers 2 × 2 mm, longitudinally
 1957dehiscent; staminode 2 mm long. Ovary ovoid, 4 × 4 mm, puberulous; style included in the
 1958throat, 11 mm long, puberulous; stigma bifid, puberulous. Fruit not seen. (Fig. 1A).

1959**Distribution and ecology:**—This species is so far only known to occur in the type locality, in
 1960the northern Rio de Janeiro state (Fig. 3). This area is rather neglected by plant collectors and
 1961new locations for this species are likely to be registered. The species was found in the
 1962understory of a humid forest covering slopes at the margin of a river, at about 400 m
 1963elevation; only a few individuals were observed.

1964**Phenology:**—Flowers are recorded from September to December.

1965**Conservation status:**—Endangered (EN) B1ab(i,iv), according to the IUCN criteria, based
 1966on the extent of occurrence estimated to be less than 5,000 km² in only one location (IUCN
 19672017).

1968**Taxonomic relationships:**—*Besleria aurea* presents a floral morphology similar to *B.*
 1969*fluminensis* Brade (1948: 73), both displaying a yellow calyx with long attenuate or acuminate
 1970lobes. However, it can be distinguished by the shorter and narrower leaf blades with entire
 1971margin, different corolla colour and long lanceolate calyx lobes.

1972**Specimens examined:**—BRAZIL. Rio de Janeiro: Campos dos Goytacazes, Conceição do
 1973Imbé, Serra do Macaco, 10 May 2012, *M. Perret et al.* 65 (G!, VIES!); same locality, 27
 1974August 2012, *H. Lorenzi et al.* 7182 (HPL!).

1975

1976

1977**2. *Besleria brevicalyx*** G.E.Ferreira & Chautems (2016: 272). Type:—BRAZIL. Minas
 1978Gerais: Descoberto, Reserva Biológica da Represa do Grama, trilha do Bananal, 9 Nov 2014,
 1979*G.E. Ferreira et al.* 292 (holotype INPA!; isotypes G!; RB!; HUFABC!).

1980

1981Terrestrial shrub, 0.4–1.8 m tall. Stems branched, subterete, up to 0.4 cm diam., brown,
 1982glabrous, sericeous when young, internodes up to 3.0 cm long. Leaves 3-verticillate, equal in
 1983a whorl; petioles 2.2–4.1 cm long, green, pubescent; leaf blades oblanceolate, 12.0–20.5 ×
 19843.4–5.6 cm, , membranaceous apex attenuate, base long-attenuate, margin distantly serrulate;
 1985adaxial surface green, puberulent; abaxial surface pale green, pubescent, 8–10 pairs of
 1986secondary veins. Inflorescence axillary, cymose, epedunculate or rarely very short peduncle,
 1987with 1–3 flowers per node; pedicels terete, 2.2–3.4 cm long, green, pubescent. Calyx lobes 5,
 1988lobes erect, adherent to the corolla base, dorsally keeled, slightly equal, lanceolate, 4–6 × 3–4
 1989mm, apex acute to mucronate, margin entire, yellow-greenish, outside sparsely puberulous-
 1990glandular, inside glabrous. Corolla horizontal in relation to calyx, 16–18 mm long, tube
 1991contracted at base, limb regular, 6 mm wide at the base, 4 mm wide at the narrowest point,
 1992throat 7 mm wide, ventricose, whitish-yellow, outside puberulous-glandular, inside glabrous;

1993lobes 5, erect, slightly equal, semiorbicular, 3 × 3 mm, margin entire, white, glabrous. Nectary
 1994annular, 0.2 mm wide, glabrous. Stamens 4, included in the throat; filaments 5–7 mm long,
 1995epipetalous, adnate, free portion of filaments arising at 3 mm long from the base of the
 1996corolla, glabrous; anthers 1 × 2 mm, longitudinally dehiscent. Ovary ovoid, 3 × 4 mm,
 1997puberulous; style included in the throat, 5–6 mm long, puberulous-glandular; stigma bifid,
 1998puberulous. Fruit not seen. (Fig. 1B)

1999**Distribution and ecology:**—This species occurs in the municipality Descoberto, Minas
 2000Gerais state (Fig. 3). It was collected in a transition area between seasonal dry forest
 2001and humid forest, occurring on sandy/ rocky banks of streams at ca. 550–950 m elevation.
 2002Only a few plants were found at each collection point.

2003**Phenology:**—Flowers are recorded from January to October.

2004**Conservation status:**—Endangered (EN) B1ab(i, iv), according to the IUCN criteria, based
 2005on the extent of occurrence estimated to be less than 5,000 km² in only two locations (IUCN
 20062017).

2007**Taxonomic relationships:**—*Besleria brevicalyx* has characteristics similar to those of *B.*
 2008*macahensis* Brade (1948: 74), including fasciculate inflorescence, calyx closely adherent to
 2009the corolla base, calyx lobes 3–4 mm wide, and yellowish-white corolla. However, it differs
 2010from *B. macahensis* by its 3-verticillate leaves (vs. opposite), yellow pedicels (vs. purplish-
 2011yellow), and yellow calyx with green-keeled calyx lobes (vs. purplish-yellow). *Besleria*
 2012*brevicalyx* also has longer pedicels and shorter calyx lobes (Table 1). Additionally, *B.*
 2013*brevicalyx* occurs in Minas Gerais in sandy substrates in less humid forest, whereas *B.*
 2014*macahensis* is restricted to Rio de Janeiro state and thrives on substrates rich in organic matter
 2015in the Atlantic rainforest.

2016**Specimens examined:**—BRAZIL. Minas Gerais: Descoberto, Reserva Biológica da Represa
 2017do Grama, 18 May 2002, *A.V. Lopes et al.* 43 (CESJ!, G!); same place, 29 April 2000, *C.L.*
 2018*Faria et al.* 70 (CESJ!, G!).

2019

2020**3. *Besleria diabolica*** G.E.Ferreira & Chautems (2016: 275). Type:—BRAZIL. São Paulo:
 2021Eldorado, Parque Estadual Caverna do Diabo, trilha do Araçá, nas margens do córrego, 29
 2022Sep 2014, *G.E. Ferreira et al.* 271 (holotype INPA!; isotypes G!; HUFABC!; SPSF!).

2023

2024Terrestrial shrub, 0.8–1.5 m tall. Stems unbranched, subterete, 0.4–0.5 cm diam., green,
 2025hirsute, internodes 1.3–3.2 cm long. Leaves opposite and decussate, pairs subequal; petioles
 20263.2–5.5 cm long, green, hirsute; leaf blades elliptic to lanceolate, 16.0–22.5 × 3.2–6.0 cm,

2027membranaceous, apex and base attenuate, margin distantly denticulate and ciliate; adaxial
 2028surface green, hirsute; abaxial surface pale green, hirsute, 6–9 pairs of secondary veins.
 2029Inflorescence axillary, cymose, epedunculate or rarely with a very short peduncle, with 1–3
 2030flowers per node; pedicels terete, 1.2–1.7 cm long, green, hirsute. Calyx lobes 5, fused and
 2031imbricate at base, spreading, subequal, lanceolate, 10–14 × 3–4 mm, apex attenuate, margin
 2032entire, yellow, hirsute. Corolla oblique in relation to calyx, 18–24 mm long, tube contracted at
 2033base, limb regular, 6 mm wide at the base, 5 mm wide at the narrowest point, throat 7 mm
 2034wide, ventricose, yellowish-white, glabrous outside and inside; lobes 5, reflexed, slightly
 2035equal, semiorbicular, 2 × 4 mm, margin entire, white, glabrous. Nectary annular, 0.5 mm
 2036wide, glabrous. Stamens 4, included in the throat; filaments 5–6 mm long, epipetalous, adnate,
 2037free portion of filaments arising in the middle of the corolla tube, glabrous; anthers 1 × 2 mm,
 2038longitudinally dehiscent; staminode 0.4 cm long. Ovary ovoid, 4 × 5 mm, glabrous; style
 2039included in the throat, 11–15 mm long, glabrous; stigma bifid. Fruit not seen. (Fig. 1C)

2040**Distribution and ecology:**—*Besleria diabolica* is known from Eldorado and Miracatú,
 2041municipalities in the southern São Paulo state (Fig. 3). The vegetation type in this region is
 2042the Atlantic rainforest. The species usually occurs along banks of streams within forested
 2043areas at around 400 m elevation. Based on our own observations in the vicinity of the
 2044“Caverna do Diabo” state park only a few scattered individuals were seen, indicating a low
 2045population density.

2046**Phenology:**—Flowers are recorded from September to November.

2047**Conservation status:**—Endangered (EN) B1ab(i,iv), according to the IUCN criteria, based
 2048on the extent of occurrence estimated to be less than 5,000 km² in only two locations (IUCN
 20492017).

2050**Taxonomic relationships:**—This species is somewhat similar to *Besleria melancholica*
 2051(Vellozo 1825: 260) Morton (1939: 446) in the shape and position of the calyx lobes, but it
 2052can be differentiated by the narrower calyx lobes (3–4 mm vs. 4–7 mm wide), which are
 2053lanceolate (vs. oblong – Table 1). Geographically, *B. diabolica* has a different distribution
 2054occurring only in southern São Paulo state, whereas *B. melancholica* is restricted to
 2055mountainous areas in Rio de Janeiro state.

2056**Specimens examined:**—BRAZIL. São Paulo: Eldorado, nas proximidades da Caverna do
 2057Diabo, 11 November 2000, *E.R. Salviani & H. Lorenzi 1773* (HPL!, INPA!); Miracatú, perto
 2058de Pedro Barros, 30 Ago 1966, *J. Mattos s.n.* (RB!).

20604. *Besleria discreta* G.E. Ferreira (Chapter 4). Type:—BRAZIL. Espírito Santo: Divino de
 2061São Lourenço, Patrimônio da Penha, Comunidade Portal do Céu, Vivência Beija-flor, 8 Nov
 20622014, G.E. Ferreira et al. 291 (holotype INPA!; isotypes G!; RB!; HUFABC!). (Fig. 4).

2063

2064Terrestrial shrub, 0.8–1.0 m tall. Stems branched, subterete, up to 0.3–0.6 cm diam., green-
 2065brownish, glabrous, pubescent when young; internodes 1.5–4.0 cm long. Leaves opposite,
 2066pairs unequal; petioles 1.6–3.4 cm long, green, pubescent; leaf blades obovate, 10.5–15.0 ×
 20674.0–6.5 cm, apex acuminate, base long-attenuate, margin distantly serrulate, membranaceous,
 2068adaxial surface green, slightly bullate, puberulous; abaxial surface pale green, pubescent on
 2069the veins, 8–10 pairs of secondary veins. Inflorescences axillary, cymose, epedunculate, with
 20701–3 flowers per node; pedicels terete, 1.6–2.2 cm long, green, puberulous. Calyx lobes 5,
 2071lobes erect, adherent to the corolla base, mostly equal, lanceolate, 5–6 × 2–3 mm, apex acute
 2072to mucronate, margin entire, yellow-whitish, outside puberulous, inside glabrous. Corolla
 2073horizontal in relation to calyx, 13–16 mm long, tube contracted at base, limb regular, 4 mm
 2074wide at the base, 3 mm wide at the narrowest point, throat 6 mm wide, ventricose, yellow-
 2075whitish, outside pubescent, inside glabrous; lobes 5, reflexed, slightly equal, semi-orbicular, 2
 2076× 2.5 mm, margin entire, white, setose. Nectary annular, 0.2 mm wide, glabrous. Stamens 4,
 2077included in the throat; filaments 5–7 mm long, epipetalous, adnate, free portion of filaments
 2078arising at 3 mm from the base of the corolla, glabrous; anthers 1.5 × 2 mm, longitudinally
 2079dehiscent. Ovary ovoid, 3 × 4 mm, puberulous; style included in the throat, 6–7 mm long,
 2080puberulous-glandular; stigma bifid, puberulous. Fruit not seen. (Fig. 1D)

2081**Distribution and Habitat:**—This species occurs in Alegre, Cachoeiro de Itapemirim and
 2082Divino de São Lourenço, Espírito Santo state (Figure 4). It occurs on rocky banks of streams
 2083at ca. 600–1000 m elevation. Only a small population was found at each collection point.

2084**Phenology:**—Flowers are recorded from August to November.

2085**Conservation status:**—Endangered (EN) B1ab (i, iv), according to the IUCN criteria, based
 2086on the extent of occurrence estimated to be less than 5,000 km² in only two locations (IUCN
 2087Standards and Petitions Subcommittee 2017).

2088**Taxonomic relationships:**—*Besleria discreta* is very similar to *Besleria brevicalyx*, these
 2089species share fasciculate inflorescences, calyx closely adherent to the corolla base, calyx lobes
 2090mucronate, and corollas that are yellow at base and white towards the apex. However, it
 2091differs from *B. brevicalyx* by its opposite and decussate leaves (*vs.* 3-verticillate), shorter
 2092pedicels (1.6–3.4 cm long *vs.* 2.2–4.1 cm long), shape and size of the leaf blades (obovate,
 209310.5–15.0 × 4.0–6.5 cm *vs.* oblanceolate, 12.0–20.5 × 3.4–5.6 cm) and indumentum on leaf

2094blades and flowers (sericeous vs. puberulent to puberulous-glandular). Additionally, *B.*
 2095*discreta* occurs in Espírito Santo on rocky stream banks in ombrophilous forest, whereas *B.*
 2096*brevicalyx* is restricted to Minas Gerais state and occurs in sandy substrates on the ground of a
 2097transition area between ombrophilous and seasonal forest.

2098**Specimens examined:—Brazil.** —Espírito Santo: Alegre, Pedra da Carneira, 30 Aug 2008,
 2099*D.R. Couto 842* (MBML!); Alegre, Monte Cristo, 5 Oct 2009, *D.R. Couto et al. 1267*
 2100(VIES!); Cachoeiro de Itapemirim, Burarama-Canta Galo, 30 Aug 2008, *D.R. Couto 870*
 2101(MBML!); Divino de São Lourenço, Patrimônio da Penha, Comunidade Portal do Céu, 28
 2102Aug 2011, *D.R. Couto 2059* (VIES!).

2103

21045. *Besleria fluminensis* Brade (1948: 73). Type:—BRAZIL. Rio de Janeiro, Angra dos Reis.
 2105Jussaral, 29 Jun 1935, *A.C. Brade 14925* (Holotype RB-0000006911812!; isotypes B!).

2106

2107Terrestrial shrub, 0.85–1.5 m tall. Stems unbranched, quadrangular, 0.4–1 cm diam., green,
 2108hirsute, internodes 1.5–7.5 cm long. Leaves opposite and decussate, pairs subequal; petioles
 21093.5–18.5 cm long, green, hirsute; leaf blades elliptic to lanceolate, 16.0–25.0 × 6.5–13.0 cm,
 2110membranaceous, apex and base attenuate, margin serrate; adaxial surface green, hirsutulous;
 2111abaxial surface pale green, puberulous, 6–9 pairs of secondary veins. Inflorescence axillary,
 2112cymose, epedunculate or rarely with a very short peduncle, with 2–6 flowers per node;
 2113pedicels terete, 1.3–1.6 cm long, green-purplish, pilose. Calyx lobes 5, dorsally keeled, fused
 2114and imbricate at base, spreading, subequal, elliptic, 9–15 × 3–5 mm, apex acuminate, margin
 2115entire, purplish-yellow, puberulous. Corolla oblique in relation to calyx, 19–21 mm long, tube
 2116contracted at base, limb regular, 6 mm wide at the base, 5 mm wide at the narrowest point,
 2117throat 7 mm wide, ventricose, yellowish-white, glabrous outside and inside; lobes 5, reflexed,
 2118slightly equal, semiorbicular, 5–7 × 4 mm, margin entire, white, glabrous. Nectary annular,
 21190.5 mm wide, glabrous. Stamens 4, included in the throat; filaments 5–6 mm long,
 2120epipetalous, adnate, free portion of filaments arising in the middle of the corolla tube,
 2121glabrous; anthers 1 × 2 mm, longitudinally dehiscent; staminode 0.4 cm long. Ovary ovoid, 4
 2122× 5 mm, glabrous; style included in the throat, 11–15 mm long, glabrous; stigma bifid. Fruit
 2123not seen. (Fig. 1E)

2124**Distribution and ecology:—**This species is known from southern Rio de Janeiro state (Fig.
 21256). The species usually occurs along banks of old trails within forested areas at around 400 m
 2126elevation. We found only a single small population located in the type-location, old train
 2127station named Jussaral.

2128**Phenology:**—Flowers are recorded from June to October.

2129**Conservation status:**—Endangered (EN) B1ab(i,iv), according to the IUCN criteria, based
2130on the extent of occurrence estimated to be less than 5,000 km² in only two locations (IUCN
21312017).

2132**Taxonomic relationships:**—*Besleria fluminensis* shares a similar floral morphology with *B.*
2133*aurea*, having a yellow calyx with long acuminate lobes. However, it can be distinguished by
2134different corolla colour, calyx lobes shape, leaf blade size and type of the margin.

2135**Specimens examined:**—BRAZIL. Rio de Janeiro: Angra dos Reis, Jussaral, 2 October 2014,
2136*G.E. Ferreira et al.* 276 (G!, INPA!, HUFABC!); Conceição de Jacareí, Serra de
2137Mangaratiba, Sítio Particular Kalil, 11 September 1985, *N.J. Santos*, 32987 (RB!, US!,
2138INPA!).

2139

21406. *Besleria grandifolia* Schott (1820: 5). Type:—BRAZIL. [Rio de Janeiro], Tinguá, Oct
21411931, *H.W. Schott* 6140 (Lectotype W-0058887!; ILT: W!, F!).

2142

2143Terrestrial shrub, 0.5–(1.5)2.5 m tall. Stems unbranched, subterete, 0.3–1 cm diam., green,
2144pubescent to tomentose at apex, internodes 1.0–6.0 cm long. Leaves opposite and decussate,
2145pairs subequal; petioles 2.0–7.5 cm long, green, hirsute; leaf blades elliptic to oblong-obovate,
21467.0–20.0 × 3.0–9.0 cm, membranaceous, apex acuminate, base acute, margin entire to
2147sparsely denticulate; adaxial surface green, glabrous; abaxial surface pale green, puberulent,
21487–12 pairs of secondary veins. Inflorescence axillary, cymose, with 1–5 flowers per node;
2149peduncle 2.0–5.5 cm long, puberulent to pubescent, pedicels terete, 1.5–2.0 cm long, green,
2150puberulent. Calyx lobes 5, fused and imbricate at base, adherent to the corolla base and free at
2151apex, subequal, ovate-lanceolate, dorsally keeled, 8–10 × 4–6 mm, apex acute to rarely
2152mucronate, margin entire, yellowish, puberulent. Corolla oblique in relation to calyx, 15–20
2153mm long, tube contracted at base, limb regular, 7 mm wide at the base, 5.5 mm wide at the
2154narrowest point, throat 7 mm wide, ventricose, yellowish-white, glabrous outside and inside;
2155lobes 5, reflexed, slightly equal, semiorbicular, 2 × 4 mm, margin entire, white, glabrous.
2156Nectary annular, 0.5 mm wide, glabrous. Stamens 4, included in the throat; filaments 1.0–1.5
2157mm long, epipetalous, adnate, free portion of filaments arising in the middle of the corolla
2158tube, glabrous; anthers 1 × 2 mm, longitudinally dehiscent. Ovary ovoid, 4 × 5 mm, glabrous;
2159style included in the throat, 10–15 mm long, glabrous; stigma bifid. Fruit a berry, globose, ca.
216010.0 × 15.0 mm, glabrescent, calyx and style persistent. (Fig. 1F)

2161**Distribution and ecology:**—This species occurs from Rio de Janeiro to São Paulo states,

2162along Serra da Mantiqueira mountain range. Recently, the species was found in Minas Gerais
 2163state (Fig. 6). The vegetation type in this region is Atlantic rainforest of the Atlantic forest
 2164domain. The species usually occurs along banks of trails and along of small streams within
 2165forested areas at around 400–1200 m elevation.

2166**Phenology:**—Flowers are recorded from October to January and fruits January to March.

2167**Conservation status:**—Least concern (IUCN 2017).

2168**Taxonomic relationships:**—This species is similar to *Besleria selloana* (Klotzsch & Hansten
 21691864: 398) for presenting pedunculate inflorescence, yellow calyx and white-yellowish
 2170flowers, however it is distinguished by the presence of ovate-lanceolate, membranaceous
 2171sepals, acute at the apex.

2172**Specimens selected:**—BRAZIL. Minas Gerais: Passa-Vinte, Usina Hidrelétrica de Paes
 2173Leme., 14 November 2000, *A. Salino 5918* (BHCBI!); Rio Preto, RPPN Mato Limpo, Mata da
 2174Cachoeira Mato Limpo, 29 August 2014, *L.L. Justino 88* (CESJ!); in Minas Gerais, *G.*
 2175*Gardner 4975* (G!, W!, BM!); Rio de Janeiro: Barra do Piraí, 13 November 1986, *V.L.*
 2176*Gomes-Klein 386* (RB!); Ipiabas, na margem da mata próximo ao Rancho Santo Antônio, 25
 2177November 1988, *V.L.G. Klein 568* (RB!); Duque de Caxias, Reserva da Petrobras, Garrão,
 2178Sítio Riacho dos Beija-flores, 30 August 1999, *J.M.A. Braga 5403* (HUEFS!); Baixada
 2179Fluminense, 18 June 1942, *C. Carcerelli 17*, (RB!); Serra do Tinguá, próximo a Xerém., 13
 2180September 1986, *L.P. Gonzaga s.n.* (RB!, INPA!); Trilha ao redor da represa (barragem)
 21815 August 1997, *J.A. Lira Neto 623* (RB!); Rio Pedra Branca, 8 October 1999, *A. Quinet 262*
 2182(RB!); Engenheiro Paulo de Frontin, Estrada Paulo de Frontin-Mendes. Encontrada na beira
 2183da estrada, 10 August 2013, *M.S. Wängler 1405* (RB!); P.N. Itatiaia, Serra da Capelinha,
 21841937, *L. Luiz 80* (RB!); Nova Friburgo, 14 August 1953, *P. Capell S.J. s.n.* (FCAB!); Nova
 2185Iguaçu, Estrada do Ouro, margem do rio Tinguá, 15 January 2002, *M.G. Bovini 2120* (RB!);
 2186Tinguá, 1 October 1946, *A.C. Brade 18624* (RB!, INPA!); Tinguá, Serra do Macuco, 25
 2187September 1983, *J.P.P. Carauta 4493* (RB!); Rebio de Tinguá, estrada para Macuco, 22
 2188October 2002, *L.C. Giordano 2582* (RB!); Reserva Biologica do Tinguá, trilha para a baixada
 2189do Macuco, 22 October 2002, *L.C. Giordano 2583* (RB!); Serra do Tinguá, 29 June 1948, *P.*
 2190*Occhioni 1106* (RB!, CEPEC!); Estrada do Comércio, 23 August 1993, *M.V.L. Pereira, 639*
 2191(RB!); Coleta na Mata, 13 June 1996, *M.V.L. Pereira 649* (RB!); Boa Esperança, próx. ao
 2192entroncamento, 11 December 2001, *S.J. Silva Neto 1555* (RB!); Margem da estrada para a
 2193Represa de Itacolomi, 6 October 1993, *S.J. Silva Neto 307* (RB!, INPA!); Morro do Beco,
 2194beira do primeiro riacho, 17 November 1994, *S.J. Silva Neto 507* (RB!); Estrada entre a
 2195represa do Barrelão e de Reunião, 17 April 1995, *I.M. Silva 352* (RB!); Paty do Alferes,

2196Palmares, beira da estrada em ambiente sombreado, 11 August 2013, *M.S. Wängler 1412*
2197(RB!); Petrópolis, Prope Petrópolis [Serra dos Órgãos], 10 July 1882, *J. Ball s.n.*, (NY!,
2198US!); Petrópolis, 1 October 1931, *A.C. Brade 10531* (GZU!); BR040, estrada vicinal km 87,
21993 October 2014, *G.E. Ferreira et al. 279* (G!, INPA!, HUFABC!); Serra da Estrela, 28 July
22001929, *A.C. Brade s.n.* (GZU!); Serra de Petrópolis, km 34 mais ou menos, March 1952, *A.P.*
2201*Duarte s.n.* (RB!); Petrópolis, July 1944, *O.C. Góes 710* (RB!); Petrópolis, August 1944,
2202*O.C. Góes 879* (RB!); Petrópolis, 1942, *O.C. Góes 99* (RB!); Vale do Bonsucesso, Estrada do
2203contorno, 01 November 1980, *L. Krieger 9562* (CESJ!, INPA!); Petrópolis, 14 October
22041958, *F. Markgraf 3009* (RB!); Petrópolis, Vale Florido, 9 November 1977, *N. Marquete,*
2205*157* (RB!); Araras, Caminho do Capoeirão, 26 September 1977, *G. Martinelli et al. 3066*
2206(RB!); Faz. Inglesa. Floresta sob regime de preservação permanente-IBDF, encosta úmida, 25
2207September 1981, *G. Martinelli et al. 7712* (RB!, US!); Floresta de Preservação Permanete-
2208IBDF, Rocio, 6 October 1983, *G. Martinelli et al. 9604* (RB!, US!, MBM!, INPA!); Serra da
2209Estrela, Raiz da Serra, Estrada velha, 5 September 1977, *L. Mautone 274* (RB!); Petrópolis,
2210Serra dos Órgãos, 07 July 2006, *T.S. Nunes 1750* (HUEFS!); Grotta do Jacó. Na mata
2211secundário perto do rio, 2 November 1968, *D. Sucre 4005*, (RB!, US!, CEPEC!); in Urvalde,
22121879, *H. Wawra, 53*, (W!); Petrópolis, 02 August 2007, *R. Tsuji et al. 2016* (HPL!);
2213Resende, Vale das Flores, na beira do rio das Flores, 7 September 1999, *A. Lobão 455a* (RB!,
2214INPA!); Estrada Resende Visconde de Mauá, 7 December 2006, *V.F. Mansano 06-349*
2215(RB!); Próximo a cachoeira do Alcantilado, Serra da Mantiqueira, 24 July 1994, *L. Rossi*
2216*1532* (SP!, RB!); Resende, *E. Tameirão Neto, 2803* (G!, BHCB!); Serra dos Orgãos, estrada
2217para Petrópolis via Bingem. Refúgio Alpino, 9 November 1973, *D.S.D. Araujo 531* (RB!);
2218Serra de Petropolis, Km 34, *A.P. Duarte, 3464* (CEPEC!); Rio de Janeiro, *J.G. Kuhlmann s.n.*
2219(RB!); Estrada Rio-Petrópolis, União-indústria, 5 April 1972, *D. Sucre 9091* (RB!); Santa
2220Maria Madalena, Serra do Rifa, 25 November 1977, *J.P.P. Carauta 2801* (RB!, INPA!); P.E.
2221Desengano. Sossego, Faz. da Forquilha, próx. ao rio do Norte, 30 June 1987, *C. Farney 1454*
2222(RB!); Distrito de Terra Fria, estrada para a fazenda do Ribeirão vermelho, 20 November
22231990, *A. Fonseca Vaz 827* (RB!, INPA!); Serra dos Orgãos, 1833, *A.-C. Vauthier 555* (G!,
2224P!); Serra de José Vaz, prés de Rezende, 24 February 1874, *A.F.M. Glaziou 7797* (P!); Serra
2225do Coelho, pres de Rezende, 21 November 1876, *A.F.M., Glaziou 8818* (P!); Rio de Janeiro,
222628 August 1882, *A.F.M. Glaziou 14042* (R!, P!); Caxias, Reserva Particular da Petrobrás,
2227Garrão, Sítio Riacho dos Beija-flores, prox. Barragem de Saracuruna, 26 July 2000, *W.G.*
2228*Lima 14* (RB!); Estrada Rio de Janeiro, Rio Tinguá, *G. Pabst 5400* (MBM!); Corcovado
2229Tepuis, Brasílicae, *H.W. Schott s.n.* (W!); Serra d'Estrela [Serra dos Órgãos], 1844, *H.A.*

2230Weddell 779 (P!, G!); Habitat in sylv. umbrosis ad Mandiocea. *C.F.P. von Martius s.n.* (M!);
 2231Brasiliae. In sylvis udis ad scaturigines et rivus in Serra de Estrella [Serra dos Órgãos], *C.F.P.*
 2232*von Martius s.n.* (M!); In Brasilia tropica, *L. Riedel 115* (NY!, US!); São Paulo: Bananal,
 2233Estrada de Acesso à Reserva Florestal, 23 October 1979, *W. Mantovani 154* (SP!); Monteiro
 2234Lobato, Entre Monteiro Lobato e Campos do Jordão, 28 September 1976, *P.H. Davis 2929*
 2235(UEC!); Pindamonhangaba, Eugenio Lefevre, 11 November 1953, *M. Kuhlmann 2903* (SP!,
 2236RB!); Pindamonhangaba, Votorantim, 11 October 2006, *H.O. Yamaki 017* (IAC!).

2237

22387. *Besleria longimucronata* Hoehne (1958: 41). Type:—BRAZIL. São Paulo, Ubatuba,
 2239Estação Experimental, 20 July 1939, *C. Smith s.n. (39?)* (Holotype SP-000744!; Isotype
 2240IAC!)

2241

2242Terrestrial shrub to small tree, 0.5–2.5 m tall. Stems unbranched, terete to quadrangular, 0.5–
 22431.5 cm diam., green, glabrescent at base, pubescent at apex, internodes 2.0–7.0 cm long.
 2244Leaves opposite and decussate, pairs subequal; petioles 3.0–12.0 cm long, green, puberulous;
 2245leaf blades elliptic-lanceolate to obovate, 10.0–23.0 × 4.0–10.0 cm, membranaceous, apex
 2246acuminate, base narrowly cuneate, margin entire; adaxial surface green, glabrescent; abaxial
 2247surface pale green, puberulous, 6–15 pairs of secondary veins. Inflorescence axillary, cymose,
 2248with 2–6 flowers per node; pedunculate, pedicels terete, 1.5–4.0 cm long, pale green,
 2249pubescent. Calyx lobes 5, shortly fused at base, subequal, ovate, 8–10 × 2–4 mm, dorsal veins
 2250prolonging in a mucronate apex, margin entire, yellow, puberulent. Corolla oblique in relation
 2251to calyx, 18–22 mm long, tube contracted at base, limb regular, 7 mm wide at the base, 5.5
 2252mm wide at the narrowest point, throat 7 mm wide, ventricose, yellowish-white, glabrescent
 2253outside and inside; lobes 5, reflexed, slightly equal, semiorbicular, 2 × 4 mm, margin entire,
 2254white, glabrous with a puberulous-glandular ring at the throat. Nectary annular, 0.5 mm wide,
 2255glabrous. Stamens 4, included in the throat; filaments 1.2–1.8 mm long, epipetalous, adnate,
 2256free portion of filaments arising in the middle of the corolla tube, glabrous; anthers 2 × 2 mm,
 2257longitudinally dehiscent. Ovary ovoid, 4 × 5 mm, glabrous to pilose; style included in the
 2258throat, 12–18 mm long, glabrous; stigma bifid. Fruit a berry, globose, ca. 10.0–15.0 × 15.0–
 225920.0 mm, glabrescent, calyx and style persistent, green at maturity.

2260**Distribution and ecology:**—This species occurs along the Serra do Mar mountain range
 2261across the south of Rio de Janeiro to the north of São Paulo states (Fig. 4). The species usually
 2262occurs along banks of trails and along of small streams within forested areas at around 400–
 22631200 m elevation. (Fig. 2A).

2264**Phenology:**—Flowers are recorded from July to October and fruits November to January.

2265**Conservation status:**—Least concern (IUCN 2017).

2266**Taxonomic relationships:**—This species can be easily recognized by its epedunculate
2267inflorescences, ovate and membranaceous sepals with a distinct mucro at the apex (Fig. 4G).

2268**Specimens selected:**—BRAZIL. Rio de Janeiro: Angra dos Reis, Coletada nas proximidades
2269de Nagra dos Reis, 05 May 2006, *R. Tsuji 1936* (HPL!); Mangaratiba, Reserva Ecológico Rio
2270das Pedras, trilha para a Lagoa Seca, 13 August 1999, *J.M.A. Braga 5342* (RB!); Paraty,
2271Estrada Paraty-Cunha km 11, 1 October 2014, *G.E. Ferreira et al. 273* (G!, INPA!,
2272HUFABC!); Estrada Paraty-Cunha, 20, 08, 1987, *M. Kirizawa 1892* (SP!, RB!, INPA!);
2273Estrada entre Paraty e Cunha, 02 February 2000, *E.R. Salviani 1107* (HPL!); Near Parque
2274Nacional da Serra da Bocaina; road Paratí-Cunha, 13 km. from town towards peak, 20
2275October 1991, *H.J. Wiehler 91157* (NY!, US!, SEL!); APA-Cairuçu, trilha em dir. ao Morro
2276da Pedra Rolada, 23 August 1995, *M. Boruche 22* (RB!); Morro da Trindade APA-Cairuçu,
227731 August 1994, *M.G. Bovini 545* (RB!); Trilha do Corisquinho em direção ao rio do
2278Cuscuzeiro, 7 November 1995, *D.P. Campos 3* (RB!); Divisa dos Estados RJ e SP e
2279municípios Parati/Cunha, 19 June 1978, *A.M.V. de Carvalho 2* (RB!, CEPEC!); Estrada para
2280Cunha próximo a um riacho, 2 May 1987, *A. Chautems 230* (G!, RB!); Fazenda Santa Maria,
2281estrada em direção a Praia do Sono, 27 September 1989, *M.F. Freitas 104* (RB!); Estrada
2282Rio-Santos (BR 101), APA-Cairuçu, 13 April 1991, *L.C. Giordano 1086* (RB!); Laranjeiras,
2283caminho para a Praia do Sono, 4 July 1992, *L.C. Giordano 1349* (RB!, F!); São Paulo:
2284Bananal, Serra da Bocaina, Alto Vale do Rio Paca (Bracuí), 29 September 1994, *E.L.M.*
2285*Catharino 2046* (SP!, RB!, UEC!); Estação Ecológica de Bananal, 29 March 2008, *R.T.*
2286*Polisel 618* (SPSF!); Caraguatatuba, P.E.Serra do Mar, Núcleo Caraguatatuba, 07 July 2000,
2287*I. Cordeiro 2265* (SPSF!); SP 99, rumo a São José dos Campos, Serra do Mar, 28 July 1983,
2288*J.R. Pirani 781* (SP!, RB!); Craguatatuba, P.E.Serra do Mar, Núcleo Caraguatatuba, 17 July
22892000, *F.O. Souza 22* (SPSF!); Miracatu, P.E.Jurupará, estrada do Mono, 06 September 1995,
2290*J.B. Baitello, 802* (SPSF!); Picinguaba, Prox. a BR-101, perto da queda d'água, 2 October
22911975, *D.S.D. Araujo 829*, (RB!, US!, CEPEC!); Pouso Alto, 01 August 1993, *C.M.*
2292*Sakuragui 307* (ESA!); Salesópolis, 28 January 2003, *H. Lorenzi 3625* (HPL!); Salesópolis,
2293Parque Nacional da Bocaina, estrada de manutenção da Petrobás, 06 September 1994, *L.*
2294*Rossi, 1666* (SP!, UEC!); São José do Barreiro, Parque Nacional da Serra da Bocaina,
2295Caminho em direção á Cachoeira do Veado, 19 July 1994, *E.L.M. Catharino 1966* (SP!,
2296RB!); São José dos Campos, estrada São José dos Campos-Caraguatatuba, 29 May 1970, *D.*
2297*Sucre 6913* (RB!, CEPEC!, INPA!); São Luís do Paraitinga, Parque Estadual da Serra do Mar,

2298base Itamambuca, 16, October 2007, *L.C. Bernacci 4479* (IAC!); São Sebastião, Parque
 2299Estadual da Serra do Mar, 19 April 2000, *N.M. Ivanauskas 4539* (ESA!, SPSF!); Fazenda
 2300Jaraguá, 30 June 1956, *M. Kuhlmann 3858* (SP!); Boiçucanga, Serra do Mar, 26 July 1983,
 2301*J.R. Pirani 746* (SP!, RB!); Estrada Rio-Santos, a 15 km da cidade no sentido à Bertiooga., 06
 2302October 1979, *G.J. Shepherd, 10448* (UEC!); Parque Estadual da Serra do Mar, Trilha das
 2303Cachoeiras do Ribeirão do Itú, 21 April 2000, *J.P. Souza 3336* (UEC!, ESA!); Ubatuba, Praia
 2304Prumirin, 29 September 2014, *G.E. Ferreira et al. 271* (G!, INPA!, HUFABC!); Trilha e
 2305estrada da almada, 27 August 1994, *M.A. Assis, 288* (RB!, SP!, SPSF!, ESA!, UEC!); Trilha
 2306da Fazenda Capricórnio, em plantação de cacau, 28 August 1994, *M.A. Assis 361* (RB!, SP!,
 2307SPSF!, ESA!, UEC!); Puruba, Restinga, 25 November 1993, *K.D. Barreto 1658* (ESA!, G!,
 2308RB!); Núcleo Picinguaba, 10 November 1993, *F. Barros 2843* (SP!, RB!); Próximo á base
 2309norte do Instituto Oceanográfico, 26 July 1960, *N.D. Cruz 14* (SP!); Serra do Mar above
 2310Ubatuba, 20 August 1976, *P.H. Davis 59755* (UEC!, MBM!); Trilha Praia da Lagoinha-Praia
 2311do Cedro, 06 September 1999, *P. Fiaschi 37* (F!); Trilha da Praia da Caçandoca para a Praia
 2312da Tabatinga, 16 September 2000, *P. Fiaschi 436* (SP!, NY!); Pontal da Lagoinha, km 237 da
 2313Rodovia São Paulo-Ubatuba, 31 August 1980, *E. Forero 7679* (SP!, RB!); Picinguaba,
 2314Parque Estadual da Serra do Mar, trilha para a base do Catarino, 9 November 1989, *A.*
 2315*Furlan, 1090* (RB!); Estação Experimental do Instituto Agrônômia, cerca de 15 km norte de
 2316Ubatuba, 12 August 1977, *P.E. Gibbs, 5657* (MG!, UEC!, MBM!); Mata atlântica da
 2317cachoeira do Macaco contígua á Estação Experimental de Ubatuba, perto do rio, 25 June
 23181986, *M. Kirizawa 1690* (SP!); Estrada Ubatuba-São Luiz de Paraitinga, Serra de Ubatuba,
 231918 August 1987, *M. Kirizawa, 1866* (SP!, RB!); Sertão de Cima, 07 September 1998, *O.S.*
 2320*Ribas 2684* (MBM!, CESJ!, HUEFS!); Praia de Puruba, mata de encosta, 05 September 1996,
 2321*V.C. Souza 12242* (ESA!, G!).

2322

23238. *Besleria macahensis* Brade (1948: 74). Type:—BRAZIL. Rio de Janeiro, Frade de
 2324Macahé, 19 Jun 1937, *A.C. Brade 15851* (Holotype RB-00538587!)

2325

2326Terrestrial shrub, 0.5–1.6 m tall. Stems branched, subterete, up to 0.4–1.0 cm diam., green,
 2327glabrous at base, sericeous when young and at apex, internodes up to 3.0 cm long. Leaves
 2328opposite and decussate, pairs subequal; petioles 3.0–8.0 cm long, green-purplish, glabrescent;
 2329leaf blades oblanceolate to obovate, 11.0–21.0 × 4.0–11.0 cm, membranaceous, apex
 2330acuminate, base attenuate, margin crenulate to denticulate, chartaceous; adaxial surface green,
 2331setose; abaxial surface pale green, lanulose, 6–12 pairs of secondary veins. Inflorescence

2332axillary, cymose, epedunculate or rarely very short peduncle, with 1–3 flowers per node;
 2333pedicels terete, 1.2–3.5 cm long, yellow-purplish, pubescent. Calyx lobes 5, lobes erect,
 2334adherent to the corolla base, slightly equal, lanceolate, 7–9 × 4–5 mm, apex attenuate, margin
 2335entire, yellow-purplish, outside and inside glabrous. Corolla horizontal in relation to calyx,
 233614–16 mm long, tube contracted at base, limb regular, 5 mm wide at the base, 3 mm wide at
 2337the narrowest point, throat 5 mm wide, ventricose, whitish-yellow, outside glabrous, inside
 2338glabrous with a puberulous-glandular ring at the throat; lobes 5, reflexed, slightly equal,
 2339semiorbicular, 3 × 3 mm, margin entire, white, glabrous. Nectary annular, 0.2 mm wide,
 2340glabrous. Stamens 4, included in the throat; filaments 4–7 mm long, epipetalous, adnate, free
 2341portion of filaments arising at 4 mm from the base of the corolla, glabrous; anthers 1 × 2 mm,
 2342longitudinally dehiscent. Ovary ovoid, 2 × 4 mm, puberulous; style included in the throat, 5–6
 2343mm long, glabrous; stigma bifid, glabrous. Fruit a berry, globose, ca. 8.0–12.0 × 12.0–15.0
 2344mm, glabrescent, calyx and style persistent, green-yellowish at maturity. (Fig. 2B).

2345**Distribution and ecology:**—This species is restricted to northern Rio de Janeiro state (Fig.
 2346), where occurs along of small streams within forested areas in substrates rich in organic
 2347matter in the Atlantic rainforest.

2348**Phenology:**—Flowers are recorded from January to October.

2349**Conservation status:**—Endangered (EN) B1ab(i, iv), according to the IUCN criteria, based
 2350on the extent of occurrence estimated to be less than 5,000 km² in only two locations (IUCN
 23512017).

2352**Taxonomic relationships:**—Similar to *Besleria brevicalyx*, it can be differentiate by its
 2353opposite leaves (*vs.* 3-verticillate), yellow-purplish pedicels (*vs.* yellow), and yellow-purplish
 2354calyx (*vs.* yellow with green-keeled calyx lobes). *Besleria macahensis* has shorter pedicels
 2355and longer calyx lobes (Table 1). Additionally, *B. macahensis* is restricted to Rio de Janeiro
 2356state and occurs in substrates rich in organic matter, whereas *B. brevicalyx* occurs in Minas
 2357Gerais and Espírito Santo in sandy substrates in seasonal dry Forest.

2358**Specimens examined:**—BRAZIL. Rio de Janeiro: Macaé, Distrito de Sana, Cabeceira do
 2359Sano, 28 November 2001, *M.G. Bovini*, 2102 (RB!, INPA!); Tapera, próxima a entrada da
 2360Fazenda Crubixaes, 5 December 1985, *C. Farney* 1005 (RB!, US!, INPA!); Estrada Frade-
 2361Tapera, 5.3 Km de Frade, trilha na mata, 4 March 2004, *R.C. Forzza*, 2876 (G!, RB!, INPA!);
 236216 Km depois de Glicério, 24 June 1987, *H.C. de Lima*, 2997 (RB!, INPA!); Santa Maria
 2363Madalena, trilha para o Rio Macapá, 25 July 2012, *J.A. Oliveira*, 181 (RB!, INPA!); São
 2364Fidelis, Poço Parado, Serra do Desengano. Na coleção viva de Mauro Peixoto, 11 October
 23652014, *G.E. Ferreira* 301 (G!, INPA!); Na região do Poço Parado, Desengano, 26 July 2012,

2366H. Lorenzi et al. 7171, (HPL!, INPA!); Poço Parado, au dessus de la casa du Sr. Adenilson, 236711 May 2012, M. Perret et al. 70, G!, VIES!).

2368

23699. *Besleria melancholica* (Vellozo) C.V. Morton (1939: 446) \equiv *Orobanche melancholica* 2370Vellozo (1825: 200). Type:—[illustration] Original plate published after in Vellozo, Fl. 2371Flumin. Icones 6: t. 77. 1827 (Lectotype).

2372

2373Terrestrial shrub, 0.5–3.0 m tall. Stems unbranched, subterete, 0.5–1.0 cm diam., green, 2374hirsute, internodes 2.5–6.5 cm long. Leaves opposite and decussate, pairs subequal; petioles 23752.2–7.5 cm long, green, hirsute; leaf blades elliptic to lanceolate, 12.0–30.0 \times 4.2–8.0 cm, 2376membranaceous, apex acuminate, base attenuate, margin entire to distantly denticulate and 2377ciliate, chartaceous; adaxial surface green, hirsute; abaxial surface pale green, hirsute, 8–13 2378pairs of secondary veins. Inflorescence axillary, cymose, pedunculate or rarely with a very 2379short peduncle, with 2–6 flowers per node; pedicels terete, 0.9–2.0 cm long, green, hirsute. 2380Calyx lobes 5, fused and imbricate at base, spreading, subequal, oblong, 12–18 \times 5–7 mm, 2381apex obtuse, margin entire and ciliate, yellow, hirsute. Corolla oblique in relation to calyx, 238215–22 mm long, tube contracted at base, limb regular, 6 mm wide at the base, 5 mm wide at 2383the narrowest point, throat 7 mm wide, ventricose, yellowish-white, glabrous outside and 2384inside; lobes 5, reflexed, slightly equal, semiorbicular, 2.5 \times 4 mm, margin entire, white, 2385glabrous. Nectary annular, 0.5 mm wide, glabrous. Stamens 4, included in the throat; 2386filaments 4–6 mm long, epipetalous, adnate, free portion of filaments arising in the middle of 2387the corolla tube, glabrous; anthers 1 \times 2 mm, longitudinally dehiscent; staminode 0.4 cm long. 2388Ovary ovoid, 4 \times 5 mm, pilose; style included in the throat, 11–15 mm long, pilose; stigma 2389bifid. Fruit a berry, globose, glabrescent to pubescent, green at maturity, calyx persistent, 2390yellowish. (Fig. 2C).

2391**Distribution and ecology:**—*B. melancholica* is restricted to mountainous areas in Rio de 2392Janeiro state (Fig. 4). The species usually occurs along banks of streams within forested areas 2393between 150 and 1100 m elevation.

2394**Phenology:**—Flowers are recorded from October to February, fruits are recorded from 2395January to March.

2396**Conservation status:**—Least concern (IUCN 2017).

2397**Taxonomic relationships:**—This species shared characters with *B. diabolica* but it can be 2398differentiated by the wider calyx lobes (5–7 mm vs. 3–4 mm), which are oblong with obtuse 2399apices (vs. lanceolate with acute apices (Table 1)).

2400**Specimens selected:**—BRAZIL. Rio de Janeiro, Barra do Piraí, Piabas, 13 October 1986,
 2401*V.L. Gomes-Klein* 383 (RB!); Campos dos Goytacazes, Parque Estadual do Desengano, Trilha
 2402Sossêgo-Boqueirão, 14 May 1989, *M. Leitman* 327 (RB!); Guapimirim, Granja Monte
 2403Olivete, margem do rio Bananal, 17 October 1993, *J.M.A. Braga* 849 (RB!); Trilha das
 2404Andorinhas, 20 December 1995, *J.A. Lira Neto* 183 (RB!); Estação Ecológica Estadual de
 2405Paraíso, margens do rio Paraíso, 8 November 1984, *G. Martinelli* 10293 (RB!); Em subosque
 2406de mata pluvial atlantica, 23 September 2009, *H. Lorenzi* 6750 (HPL!); Macaé, Reserva
 2407Particular do Patrimônio Nacional, Oscar de Jesus, trilha para o Peito do Pombo, 21
 2408November 2002, *M.G. Bovini* 2250 (RB!); Serra do Frade, perto do rio, em um barranco, 18
 2409October 1970, *J.P.P. Carauta*, 1225 (US!); Pico do Frade de Macaé, 22 October 1985, *M.*
 2410*Leitman* 40 (RB!, INPA!, US!); Estrada de Glicério para Tapera, no barranco úmido, 19 July
 24112006, *R. Marquete*, 3747 (RB!, INPA!); Magé, mata de encosta, 17 November 1986, *M.*
 2412*Gomes* 86 (RB) Magé, Centro de Primatologia do RJ, mata das margens dos rios, 8 November
 24131984, *G. Martinelli* 10293 (RB!); Distrito de Santo Aleixo, picada do Córrego das Pedras
 2414Negras, trilha para Pico Grande, 25 September 2007, *M. Nadruz* 1974 (RB!, INPA!); Distrito
 2415de Santo Aleixo, trilha do jequitibá, 26 September 2007, *M. Nadruz* 2009 (RB!); Nova
 2416Friburgo, Reserva Ecológica Municipal de Macaé de Cima, Sitio Sophronites, 21 May 1987,
 2417*A. Chautems* 240 (G!, RB!, CEPEC!); Macaé de Cima, cabeceira do rio das Flores, 24 August
 24181986, *M. Leitman* 127 (US!); Petrópolis, PNSO, trilha da Pedra do Sino, 4 October 2014,
 2419*G.E. Ferreira et al.* 281 (G!, INPA!, HUFABC!); Petrópolis, PNSO, Poço da preguiça, 5
 2420October 2014, *G.E. Ferreira et al.* 285 (G!, INPA!, HUFABC!); Moinho Preto, 16 August
 24211989, *M.C. Marques* 121 (RB!, INPA!); Serra dos Orgãos, Mata sombria, 18 January 1972,
 2422*P. Occhioni* 4778 (US!); Rio de Janeiro, Morro do Queimado, 24 February 1972, *J. Almeida*
 2423/288 (RB!); Tijuca, estrada Vista Chinesa, 5 October 1960, *C. Angeli* 180 (US!); Instituto de
 2424Conservação da Natureza, subida até a Gruta Geonoma, mata secundária, 28 August 1975,
 2425*D.S.D. Araujo* 761 (US!); Floresta da Tijuca, Pico da Tijuca, 30 October 1973, *D.S.D.*
 2426*Araujo* 512 (RB!); Parque Nacional da Serra dos Orgãos, 24 November 1942, *W.D. Barros*
 2427/1153 (RB!); Santa Cruz da Serra, Cachoeira do Pau Grande, 15 November 1993, *M.G.*
 2428*Bovini* 225 (RB!); Est. Dona catarina, 14 January 1943, *A.C. Brade* 17373 (RB!, CEPEC!);
 2429Estrada do Redentor, 06 January 1948, *A.C. Brade* 18771 (RB!, US!, CEPEC!); Tinguá, 1
 2430October 1946, *A.C. Brade s.n.* (RB!); Serra da Carioca, perto da Gruta Geonoma, um pouco
 2431acima do Passo das Pedras, 9 November 1967, *J.P.P. Carauta* 483 (US!); Pedra da Gávea,
 2432lado leste, caminho de São Conrado, 21 October 1973, *J.P.P. Carauta* 1674 (RB!);
 2433Corcovado, 1841, *P. Claussen s.n.* (W!); Morro do Pai Ricardo, 6 March 1978, *A.S. Leão* 38

2434(RB!); Santa Maria Madalena, Trilha para a barragem do Ribeirão Vermelho, 23 October 24352012, *M. Nadruz 2725* (RB!); Silva Jardim, Caminho da caixa d'água, 25 May 1982, *G. 2436Martinelli 8503* (RB!, INPA!); Fazenda Novo Horizonte, 29 April 2001, *F.B. Pereira, 27/90 2437(CESJ!)*; Teresópolis, Parque Nacional da Serra dos Órgãos, margens do Rio Beija-Flor, 02 2438February 1983, *G. Martinelli 9058* (NY!, RB!, US!, INPA!); Parque Nacional da Serra dos 2439Órgãos, estrada entre a pousada e a casa do pesquisador, 21 November 2006, *E.J. Lucas 609 2440(RB!, ESA!, INPA!)*; PNSO, subindo a trilha da Pedra do Sino, relevo ingreme, solo areno- 2441argiloso com afloramentos rochosos, 12 February 2014, *R. Marquete 4381* (RB!); Granja 2442Comarí, 11 February 1964, *H.E. Strang 565* (US!); Tijuca, ad rivulum, in silva grim, 12 2443December 1913, *P. Dusén 14359* (S!, MO!, MBM!); 1833, *C. Gaudichaud Beaupré 432 2444(G!)*; 02 February 1892, *A.F.M. Glaziou 19583* (R!, P!) Gávea, 13 February 1964, *W. 2445Hoehne 5615* (RB!); In umbrosis montis Corcovado, 1818, *J.B.E. Pohl 284/6045* (W!); 2446Habitat in silvis humidiusculis prov. Rio de Janeiro, 1832, *L. Riedel 808* (LE!); Corcovado 2447Tepuis, Brasiliae, s.d., *H.W. Schott s.n.* (W!).

2448

244910. *Besleria meridionalis* C.V.Morton (1939: 446). Type:—BRAZIL. Minas Gerais, Near 2450Papagaio, Oct 1840, G. Gardner 4974 (Holotype K-000601556!; Isotype E-00155041!, G- 245100370733!, FI-009847 on-line image!, FI009848 on-line image!, BM-000992322!, BM- 2452000992323!, P-00606344!, W-1889-0091865!, W-1889-0091866!, W-0050602!)

2453

2454Terrestrial shrub, 0.4–1.0 m tall. Stems unbranched, terete, 0.4–0.6 cm diam., green, hirsute, 2455internodes 1.5–3.5 cm long. Leaves opposite and decussate, pairs subequal; petioles 0.7–3.0 2456cm long, green, hirsute; leaf blades elliptic, 6.0–14.0 × 2.2–7.0 cm, apex acuminate, base 2457cuneate to attenuate, margin entire to serrate toward apex, membranaceous; adaxial surface 2458green, hirsute; abaxial surface pale green, hirsute, 6–9 pairs of secondary veins. Inflorescence 2459axillary, epedunculate, solitary flower; pedicels terete, 3.5–6.0 cm long, green, hirsute. Calyx 2460lobes 5, free at base, spreading, subequal, oblong, 9.2–13 × 4–8 mm, apex obtuse and 2461mucronate, margin entire, yellow at centre and whitish to the edges, pilosulous. Corolla 2462oblique in relation to calyx, 15–19 mm long, tube contracted at base, limb regular, 8 mm wide 2463at the base, 6 mm wide at the narrowest point, throat 7 mm wide, ventricose, yellowish, 2464glabrous outside and inside; lobes 5, reflexed, slightly equal, semiorbicular, 4 × 4 mm, margin 2465entire, white, glabrous. Nectary annular, 0.5 mm wide, glabrous. Stamens 4, included in the 2466throat; filaments 5–6 mm long, epipetalous, adnate, free portion of filaments arising in the 2467middle of the corolla tube, glabrous; anthers 1.5 × 2 mm, longitudinally dehiscent; staminode

253

24680.4 cm long. Ovary ovoid, 4 × 5 mm, glabrous; style included in the throat, 7–10 mm long, 2469glabrous; stigma bifid. Fruit not seen. (Fig. 2D).

2470**Distribution and ecology:**—This species occurs in the southeast of Minas Gerais state (Fig. 24715). It was found in a transition area between seasonal dry forest and humid forest, occurring 2472on banks of streams at ca. 550–950 m elevation.

2473**Phenology:**—Flowers are recorded from October to January, fruits are recorded from January 2474to March.

2475**Conservation status:**— Least concern (IUCN 2017).

2476**Taxonomic relationships:**—*B. meridionalis* present flowers, more specifically calyx lobes 2477similar to *B. diabolica* and *B. melancholica* but this species can be easily differentiated by 2478solitary long pedicellate axillary (Table 1).

2479**Specimens examined:**— BRAZIL. Minas Gerais: Cataguases, 02, June 1993, *E.M. Teixeira* 2480*s.n.* (BHCB!); Descoberto, Serra do Relógio, RPPN Alto da Boa Vista. Ponto 2 da 2481fitossociologia, 09 January 2010, *F.S. Souza et al.* 823 (CESJ!); Serra do Relógio, RPPN Alto 2482da Boa Vista, 09 April 2010, *F.S. Souza et al.* 912 (CESJ!); Reserva Biológica da Represa do 2483Gramma, 22 September 2002, *R.C. Forzza et al.* 2226 (G!, RB!, CESJ!).

2484

248511. *Besleria selloana* Klotzsch & Hanst. (1864: 398). Type:—BRAZIL. São Paulo, Bertioga, 2486na borda da trilha próximo a margem de córrego, 27 Sep 2014, *G.E. Ferreira et al.* 268 2487(Neotype designated here INPA!; Isonotype G!, HUFABC). Sellow, Serra do Cubatão (B, 2488destroyed)

2489

2490Terrestrial shrub, 0.4–2.5 m tall. Stems unbranched, subterete to quadrangular, 0.5–2 cm 2491diam., green to brownish, puberulous to pubescent at apex, internodes 1.5–5.0 cm long. 2492Leaves opposite and decussate, pairs subequal; petioles 2.0–7.0 cm long, green to vinaceous, 2493pubescent; leaf blades ovate to oblong-obovate, 12.0–28.0 × 6.0–11.0 cm, membranaceous, 2494apex acuminate, base acute to obtuse, margin sparsely denticulate to dentate; adaxial surface 2495green, glabrescent; abaxial surface pale green, puberulous, 6–12 pairs of secondary veins. 2496Inflorescence axillary, cymose, with 6–12 flowers per node; peduncle 2.0–7.0 cm, puberulous, 2497pedicels terete, 2.0–3.0 cm long, green, puberulent. Calyx lobes 5, fused and imbricate at 2498base, adherent to the corolla base, subequal, ovate-oblong, 0.8–1.0 × 0.3–0.5 cm, apex 2499rounded, margin entire, yellow, puberulent. Corolla oblique in relation to calyx, 17–22 mm 2500long, tube contracted at base, limb regular, 6 mm wide at the base, 5 mm wide at the 2501narrowest point, throat 7 mm wide, ventricose, yellowish-white, glabrous outside and inside;

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2502lobes 5, reflexed, slightly equal, semiorbicular, 3 × 4 mm, margin entire, white, glabrous.
 2503Nectary annular, 0.5 mm wide, glabrous. Stamens 4, included in the throat; filaments 1.0–1.5
 2504mm, epipetalous, adnate, free portion of filaments arising in the middle of the corolla tube,
 2505glabrous; anthers 1 × 2 mm, longitudinally dehiscent. Ovary ovoid, 4 × 5 mm, glabrous to
 2506pilose; style included in the throat, 10–15 mm long, pubescent; stigma bifid. Fruit a berry,
 2507globose, white, ca. 10.0 × 15.0 mm, glabrescent, calyx and style persistent. (Fig. 2E–F).

2508**Distribution and ecology:**—This species occurs in the coast of Paraná until São Paulo state
 2509(Fig. 6) in the Brazilian Atlantic Rainforest generally close to small streams or in humid
 2510banks at ca. 100–950 m elevation. Large populations are easy to find in places of occurrence
 2511of the species, with young individuals.

2512**Phenology:**—Flowers are recorded from October to January and fruits January to March.

2513**Conservation status:**—Least concern (IUCN 2017).

2514**Taxonomic relationships:**—*B. selloana* is similar to *B. grandifolia* for presenting
 2515pedunculate inflorescence, yellow calyx and white-yellowish flowers, however it is
 2516distinguished by the presence of calyx lobes ovate-oblong with apex obtuse-rounded.

2517**Specimens examined:**—BRAZIL. Paraná: Antonina, Rio Pequeno, 31 October 1973, *G.*
 2518*Hatschbach et al. 32987* (B!, G!, W!, RB!, US!, MBM!, HEPH!, BHCB!) Guaraqueçaba,
 2519Tagaçaba de Cima, 19 November 1993, *R.X. Lima 178* (UPCB); Bertiooga, 10 October 1989,
 2520*E.C.C. Telles s.n.* (ESA!); Biritiba Mirim, Estação Biológica de Boracéia, 06 April 1984, *A.*
 2521*Custodio Filho 2378* (SP!); same place, 19 April 1986, *A. Custodio Filho 2569* (SPSF!);
 2522Cubatão, Parque Estadual da Serra do Mar, s.d., *O.T., Aguiar 263* (MBM!); Raiz Nova da
 2523Serra, December 1898, *G. Edwall CGG4349* (SP!); Sitio Piassaguera, 12 August 1896, *A.*
 2524*Loefgren CGG3326* (SP!); Iguape, 8 km to Iguape from the junction with the São Paulo-
 2525Registro road, 06 September 1976, *P.H. Davis et al. 60546* (SP!, UEC!); Juititaba, Fundação
 2526Caramuru, September 1998, *G. Hashimoto 21780* (MBM!); Mauá, Rodoanel Mário Covas,
 2527Trecho Sul, 05 December 2007, *R.T. Shirasuna 757* (SP!); Miracatu, Parque Estadual de
 2528Jurupará, Estrada do Morro, caminho para o Parque, 06 September 1995, *J.B. Baitello 802*
 2529(SP!); Fazenda Iterei, Serra de Paranapiacaba, trilha Capoeirinha, 19 April 1994, *J.R. Pirani*
 2530& *R.F.J. Garcia 3115* (SP!, RB!, UEC!); Serra do Cafezal. Área da futura duplicação da BR-
 2531116, 03 January 2012, *V.C. Souza 36044* (ESA!, INPA!); Mogi das Cruzes, Serra do Mar,
 2532Picada Mogi-Bertiooga, parte elevada, 28 August 1983, *M. Kirizawa et al. 1017* (SP!);
 2533Serra do Mar, 16 September 1983, *M. Kirizawa et al. 1057* (SP!, RB!); na descida da serra, 12
 2534April 1972, *E. Pereira 5955* (RB!, CEPEC!); Serra do Mar. Picada Mogi-Bertiooga, parte
 2535elevada, 28 July 1983, *M. Kirizawa 101* (RB!); Paranapiacaba, alto da serra, beira da mata,

253624 June 1968, *A.M. Giuliatti 175* (IPA!); Alto da Serra, 26 May 1948, *A.O. Netto s.n.* (RB!);
 2537Serra do Mar, Reserva Gebiet alto da Serra, ca. 800 m, 29 October 1927, *H. Zerny s.n.* (W!);
 2538Pedro de Toledo, Parque Estadual da Serra do Mar, 22 September 1988, *O.T. Aguiar 263*
 2539(MBM!, SPSF!), Salesópolis, Estação Biológica de Boracéia, 3 September 1994, *R.S.*
 2540*Bianchini et al. 485* (RB!); Estação Biológica de Boracéia, 21 November 1940, *L. Silva s.n.*
 2541(SP!, IAC!); Santo André, 03 November 1993, *A.A. Binelli s.n.* (ESA!); E.B. do Alto da Serra
 2542de Paranapiacaba, 18 September 1992, *I. Cordeiro et al. 918* (SP!); Vila de Paranapiacaba,
 2543trilha do Rio Mogi, nos limites da Estação Biológica do Instituto de Botânica, 13 October
 25442009, *E.K.O. Hattori 881* (BHCB); São Paulo, antiga São Paulo-Santos, na descida da Serra,
 254514 October 1961, *G. Pabst & E. Pereira 5782* (B!); Alto de Serra, in silva prim., ad terram, 4
 2546October 1912, *P. Dusén 14223* (MO!); Rodovia São Paulo-Santos, 22 October 1966, *J.*
 2547*Lindeman & H. Haas 3101* (MBM); Caeté Distrito de Caeté, SP-55, 13 November 1998, *E.*
 2548*Melo 2536* (MO!, HUEFS!).

2549

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2551

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 2559*Estado de São Paulo* (FAPESP).

2560 **11.5 References**

- 2561 **B561** Berger, A., Clark, J.L. & Weber, A. (2015) *Besleria macropoda* (Gesneriaceae): Lectotypification,
 2562distribution, functional epiphyllly and discordant fruit morphology of a rare Costa Rican endemic.
 2563*Phytotaxa* 233: 139–152. <https://doi.org/10.11646/phytotaxa.233.2.2>
- 2564 **B564** T.B.F.G. (2017) Flora do Brasil 2020 em construção. *Jardim Botânico do Rio de Janeiro*. Available
 2565from: <http://floradobrasil.jbrj.gov.br/> (August 15, 2017)
- 2566 **C566** Neill, J.L., Neill, D.A., Weber, A., Gruhn, J.A. & Katan, T. (2010) *Shuaria* (Gesneriaceae), an arborescent
 2567new genus from the Cordillera del Cóndor and Amazonian Ecuador. *Systematic botany* 35: 662–674.
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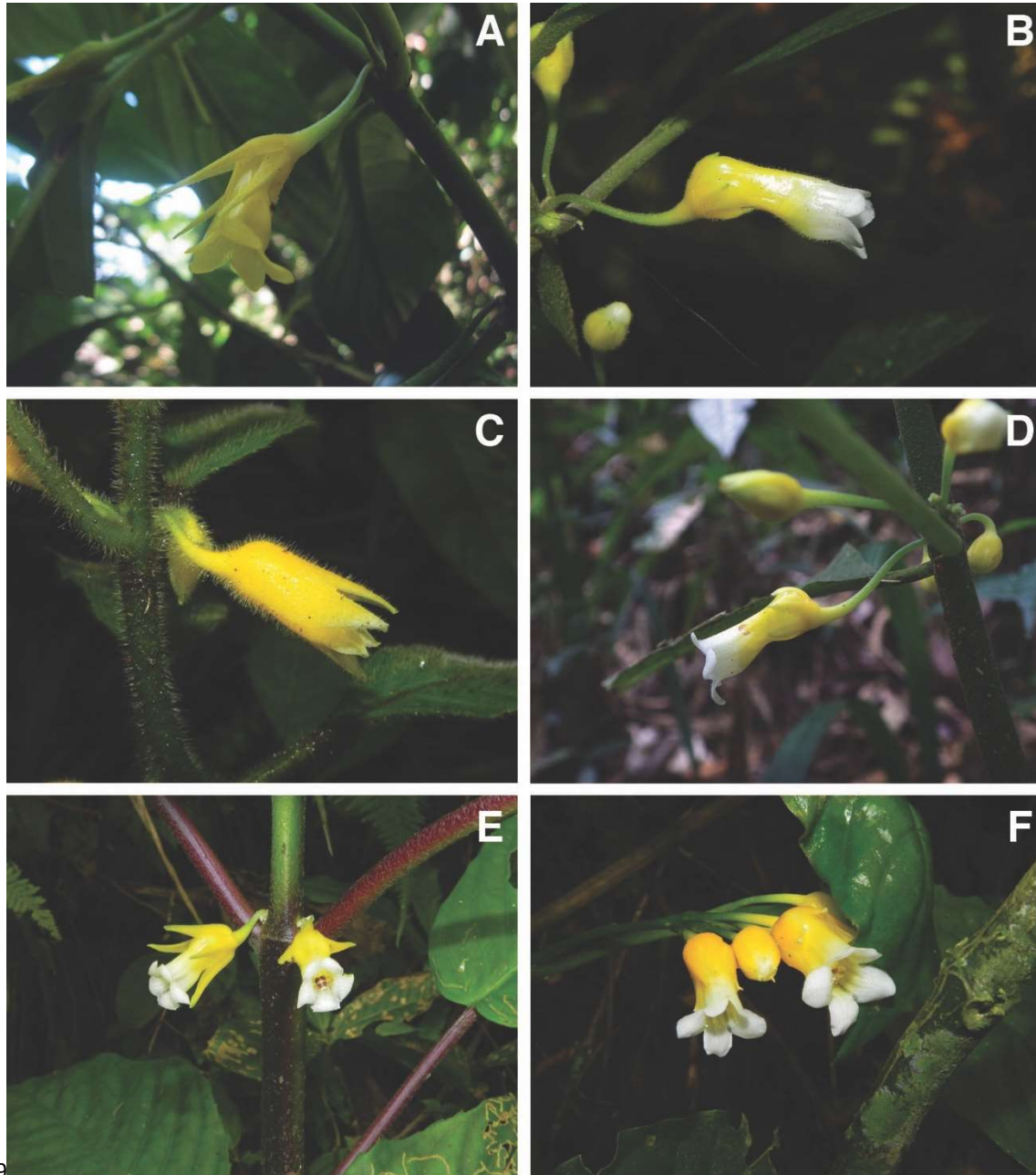
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2601the Gesnerioideae (Gesneriaceae) based on nrDNA ITS and cpDNA trnL-F and trnE-T spacer region
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- 2603
- 2604**TABLE 1.** Morphological comparisons of the *Besleria* species.

Traits/ Species	<i>B. aurea</i>	<i>B. brevicalyx</i>	<i>B. diabolica</i>	<i>B. discrota</i>	<i>B. fluminensis</i>	<i>B. grandifolia</i>	<i>B. longimucronata</i>	<i>B. macahensis</i>	<i>B. melancholica</i>	<i>B. meridionalis</i>	<i>B. sellonana</i>
Leaf arrangement	opposite	3-verticillate	opposite	opposite	opposite	opposite	opposite	opposite	opposite	opposite	opposite
Petiole length [cm]	2.6–6.7	2.2–4.1	3.2–5.5	1.6–3.4	3.5–18.5	2.0–7.5	3.0–12.0	3.0–4.5	2.7–6.5	0.7–3.0	2.0–7.0
Leaf blade size [cm]	15–19 × 5.5–6.4	20.5 × 3.4–5.6	22.5 × 3.2–6.0	10.5–16.0 × 4.0–6.5	16.0–25.0 × 6.5–13.0	7.0–20.0 × 3.0–9.0	10.0–23.0 × 4.0–10.0	11.5–16.0 × 4.2–6.0	11–16 × 3.9–7.1	6.0–14.0 × 2.2–7.0	– × 28.0–6.0–11.0
Leaf blade indumentum, abaxial surface	pubescent	pubescent	hirsute	sericeous	puberulous	puberulent	glabrescent	pubescent	glabrous to hirsute	hirsute	glabrescent
Leaf blade shape	elliptic to obovate	oblong-ovate	elliptic to lanceolate	elliptic to obovate	elliptic to lanceolate	elliptic to obovate	elliptic-lanceolate to obovate	entire	elliptic to lanceolate	elliptic	oblong-ovate
Leaf blade margin	entire	serrulate	distally denticulate	distally serrulate	serrulate to sparsely denticulate	entire to sparsely denticulate	entire	entire	entire to serrate	entire to serrate	sparsely denticulate

Traits/ Species	<i>B. aurea</i>	<i>B. brevicalyx</i>	<i>B. diabolica</i>	<i>B. discretata</i>	<i>B. fluminensis</i>	<i>B. grandifolia</i>	<i>B. longimucronata</i>	<i>B. macahensis</i>	<i>B. melancholica</i>	<i>B. meridionalis</i>	<i>B. sellaana</i>
Number of flowers per axil	2–5	1–3	1–3	1–3	2–6	1–5	2–6	2–6	2–6	1 rarely	6–12
Peduncle	no	no	no	no	no	yes	no	no	no	no	yes
Pedicel indumentum	puberulent	pubescent	hirsute	pubescent	pubescent	puberulent	pubescent	pubescent	pubescent	pubescent	pubescent
Pedicel length [cm]	2–2.1	2.2–3.4	1.2–1.7	1.6–2.2	1.3–2.6	1.5–2.0	1.5–4.0	1.3–2.6	1.1–2.3	3.5–6.0	2.0–3.0
Calyx colour	yellow	yellowish	yellow	yellowish	yellowish	yellowish	yellowish	yellowish	yellowish	yellowish	yellowish
Calyx lobes dorsally keeled	yes	yes	no	no	yes	no	no	no	no	no	no
Calyx lobes length [mm]	11–16	4–6	10–14	5–6	9–15	8–10	8–10	7–9	13–16	9–13	8–10
Calyx lobes width [mm]	4–6	3–4	3–4	2–3	3–5	4–6	2–4	3–4	4–7	4–8	3–5
Calyx lobe	lanceolate	lanceolate	lanceolate	lanceolate	elliptic	ovate-lanceolate	ovate-lanceolate	lanceolate	oblong	oblong	ovate-lanceolate

Traits/ Species	<i>B. aurea</i>	<i>B. brevicalyx</i>	<i>B. diablica</i>	<i>B. discrota</i>	<i>B. fluminensis</i>	<i>B. grandifolia</i>	<i>B. longimucronata</i>	<i>B. macahensis</i>	<i>B. melancholica</i>	<i>B. meridionalis</i>	<i>B. sellosana</i>
shape	olate	olate	olate	olate		late		late			oblong
Calyx lobe apex	attenuate	acute with mucron	attenuate	acute with mucron	acuminate	acuminately mucronate	mucronate	attenuate	attenuate	obtuse and shortly mucronate	obtusely rounded
Calyx lobe positions	spreading	adherent	spreading	adherent	spreading	adherent	adherent	adherent	spreading	spreading	adherent
Calyx indumentum	puberulent	puberulous-glandular	hirsute	puberulent	puberulous	puberulent	puberulent	glabrous	glabrous to hirsute	short hairs on dorsal vein	puberulent
Corolla colour	yellowish white	whitish yellow	yellowish white	yellowish white	yellowish white	yellowish white	yellowish white	yellowish white	yellowish white	yellowish white	wish white
Corolla length [cm]	1.6–2.2	1.6–1.8	1.8–2.4	1.3–1.6	1.9–2.1	1.5–2.0	1.8–2.8	1.9–2.1	1.6–2.2	1.5–1.9	1.7–2.2
Corolla lobe length [mm]	3–6	3	2	2	5–7	2	2–4	5–7	3–5	1.5–2	3–4

2605 **FIGURE 1.** A. *Besleria aurea*. B. *Besleria brevicalyx*. C. *Besleria diabolica* D. *Besleria*
 2606 *discreta*. E. *Besleria fluminensis*. F. *Besleria grandifolia*. A from I.G. Costa 230; B from G.E.
 2607 *Ferreira et al.* 292; C from G.E. *Ferreira et al.* 271; D from G.E. *Ferreira et al.* 291; E from
 2608 G.E. *Ferreira et al.* 276 and F from G.E. *Ferreira et al.* 279.



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2612 **FIGURE 2.** A. *Besleria longimucronata*. B. *Besleria macahensis*. C. *Besleria melancholica*
 2613 D. *Besleria meridionalis*. E. *Besleria selloana*. F. fruits of *Besleria selloana*. A from G.E.
 2614 *Ferreira et al.* 273; B from M.Perret *et al.* 70; C from G.E. *Ferreira et al.* 285; D from
 2615 P.Viana *s.n.* and E-F from G.E. *Ferreira et al.* 268.



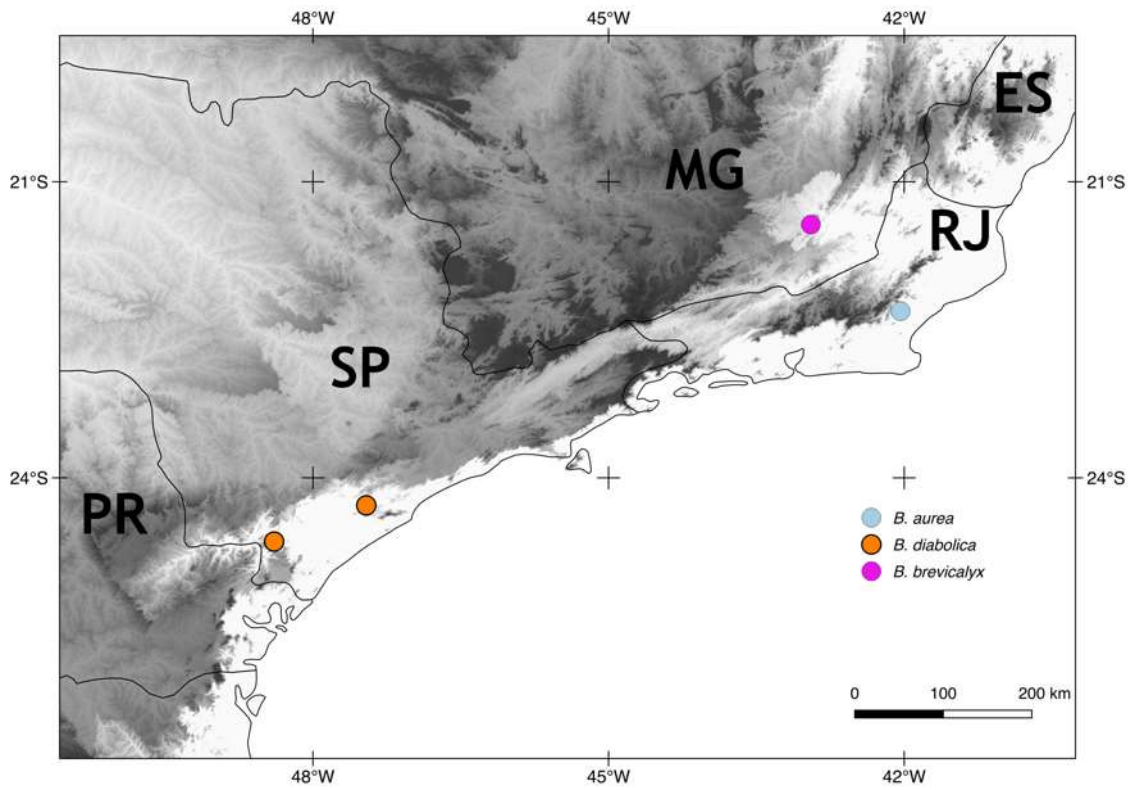
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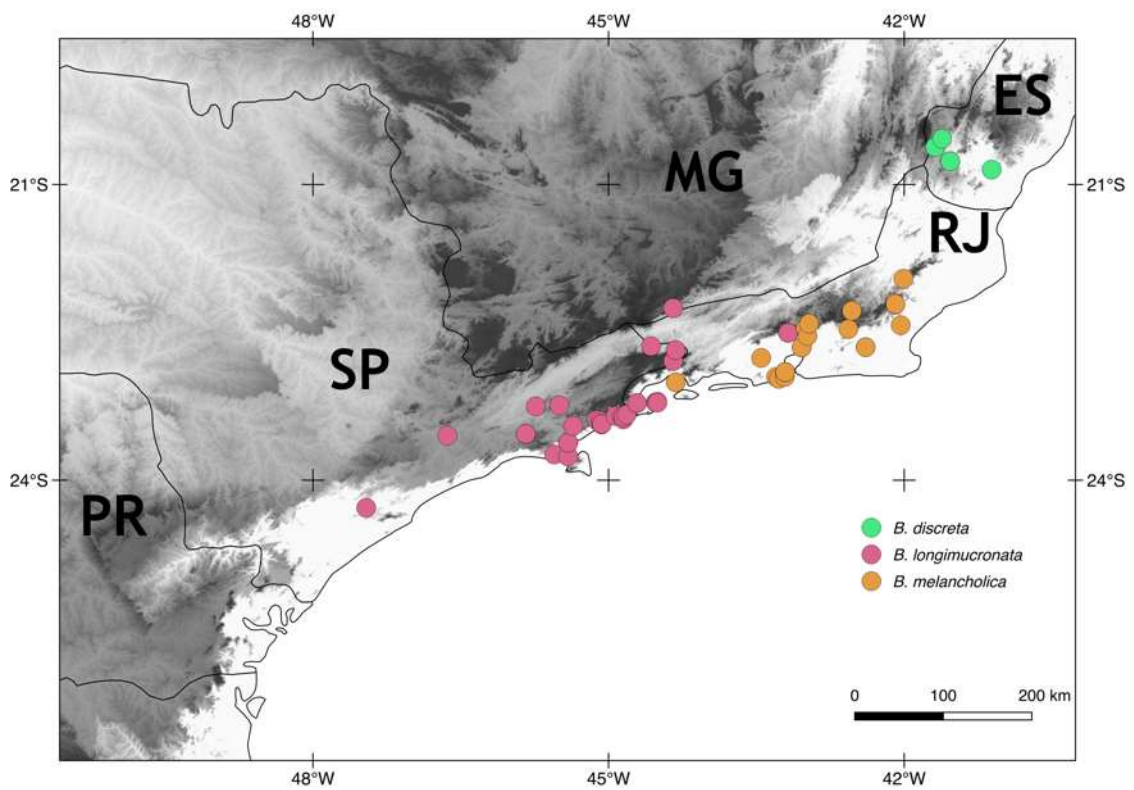
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2619 **FIGURE 3.** Distribution of *Besleria aurea*, *B. brevicalyx* and *B. diabolica* in Southeastern of
 2620 Brazil.



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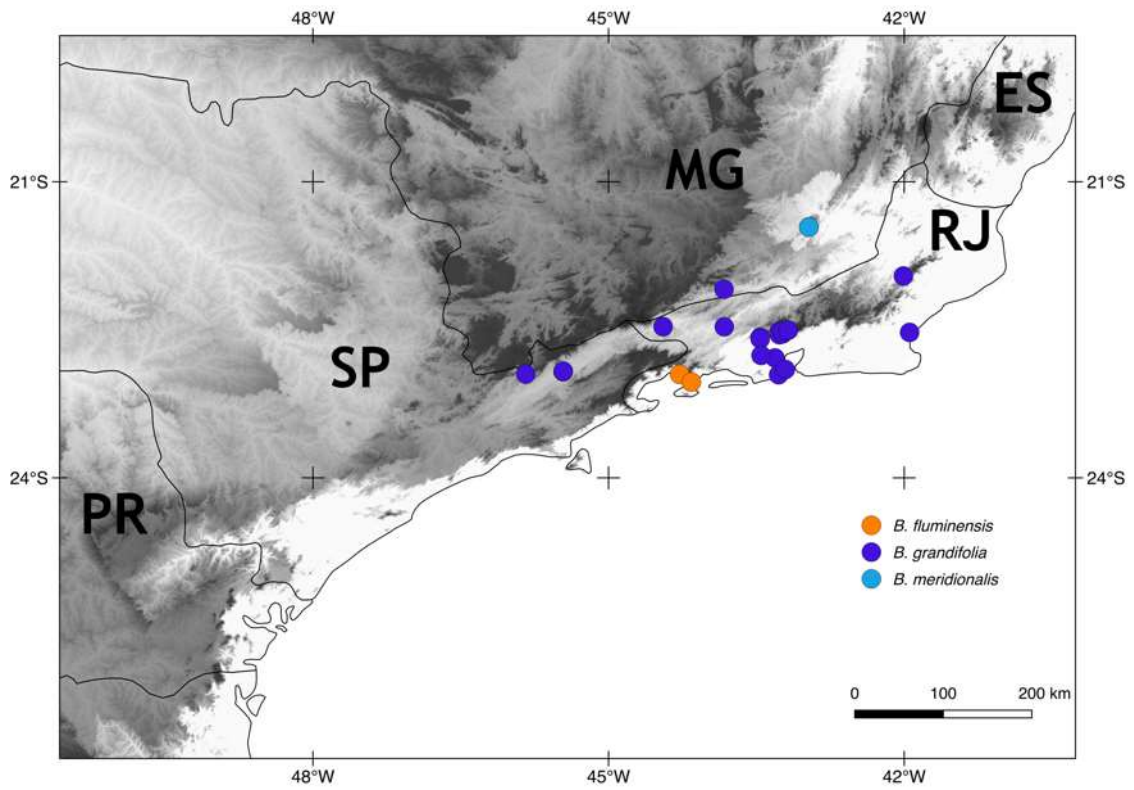
2622 **FIGURE 4.** Distribution of *Besleria discreta*, *B. longimucronata* and *B. melancholica* in
 2623 Southeastern of Brazil.



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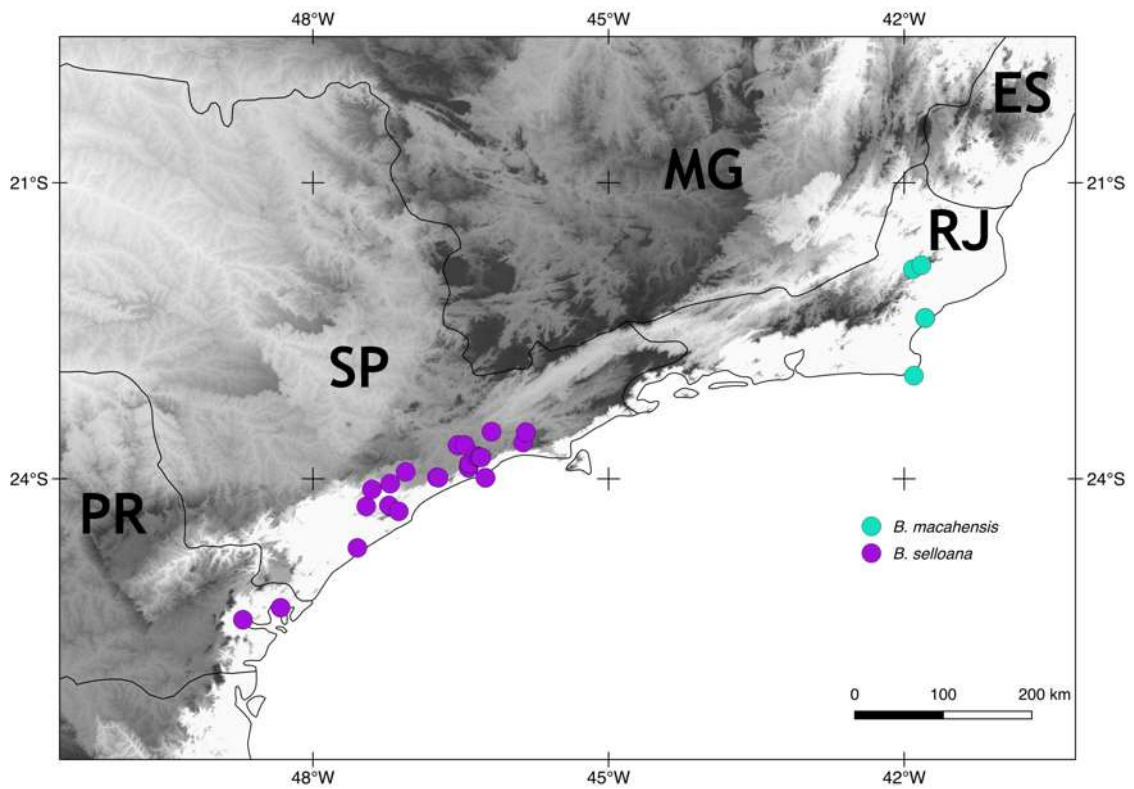
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2625 **FIGURE 5.** Distribution of *Besleria fluminensis*, *B. grandifolia* and *B. meridionalis* in South-
2626 eastern of Brazil.



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2628 **FIGURE 6.** Distribution of *Besleria macahensis*, and *B. selloana* in South-eastern of Brazil.



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2630 CONCLUSÕES GERAIS

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2632 Nossos resultados fornecem a filogenia do gênero *Besleria* melhor resolvida até o
2633 momento. A maioria dos seis principais clados identificados em *Besleria* não haviam sido
2634 reconhecidos em estudos filogenéticos e taxonômicos anteriores. Essas linhagens são mais
2635 facilmente caracterizadas por sua distribuição geográfica do que por características
2636 morfológicas.

2637 Nossas análises temporais e de reconstrução de área ancestral sugerem que *Besleria*
2638 começou a diversificar no início do Mioceno, provavelmente no norte dos Andes. A história
2639 biogeográfica de *Besleria* e sua expansão na América do Sul e Central foram amplamente
2640 influenciadas pelos principais eventos geológicos e paleogeográficos que ocorreram nos
2641 neotrópicos durante o Mioceno.

2642 Foram identificadas 24 espécies de *Besleria* ocorrendo em florestas tropicas da
2643 Amazônia e da Mata Atlântica brasileira, onde 11 espécies são endêmicas do bioma Mata
2644 Atlântica. Cinco destas espécies são novas para a ciência e duas são novas ocorrências para o
2645 Brasil.

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