

OTÁVIO LUIS MARQUES DA SILVA

**Revisão taxonômica, filogenia e  
biogeografia de *Astraea* Klotzsch  
(Euphorbiaceae)**

Tese apresentada ao Instituto de Botânica da Secretaria do Meio Ambiente, como parte dos requisitos exigidos para a obtenção do título de DOUTOR em BIODIVERSIDADE VEGETAL E MEIO AMBIENTE, na Área de Concentração de Plantas Vasculares em Análises Ambientais.

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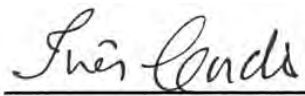
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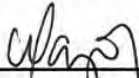
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**(Presidente)**



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**Prof. Dr. Renato de Mello-Silva**



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**Prof. Dr. Jefferson Prado**



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**Profa. Dra. Lucia Rossi**





Dedico este trabalho à minha orientadora, Dra. Inês Cordeiro  
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In Memoriam à Aracy M. Fevereiro e Waki Kodama

*"A tarefa não é tanto ver aquilo que ninguém viu, mas pensar o que  
ninguém ainda pensou sobre aquilo que todo mundo vê"*

(ARTHUR SCHOPENHAUER)

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## RESUMO

*Astraea* pertence à tribo Crotonaeae (Crotonoideae, Euphorbiaceae), juntamente com *Croton*, *Brasilicroton*, *Acidocroton*, *Sagotia* e *Sandwithia*. Distribui-se ao longo de toda a região Neotropical, mas algumas de suas espécies são ruderais e também são encontradas nos Paleotrópicos. Descrita como um gênero por Klotzsch em 1841, *Astraea* tradicionalmente era reconhecida como uma seção do grande gênero *Croton* (*C. sect. Astraea*). E como tal, era uma das mais bem definidas morfológicamente. As monografias mais completas de *C. sect. Astraea* são as de Müller Argoviensis para o Prodrômus de Candolle e a Flora Brasiliensis, no século XIX. Nestes trabalhos são reconhecidas diversas variedades para *C. lobatus* (= *A. lobata*), a espécie tipo do gênero e a mais complexa e amplamente distribuída de suas espécies. Em consequência dos estudos filogenéticos recentes, *Croton sect. Astraea* foi reconhecida como um gênero distinto. Por terem sido incluídas em filogenias de Crotonaeae apenas como grupo externo, pouco se sabia sobre as relações entre as espécies de *Astraea*. Com base em cerca de 5.200 exsicatas de mais de 90 herbários, apresentamos uma delimitação mais restrita de *A. lobata* e rearranjos no gênero que resultaram no reconhecimento de 13 espécies (*A. cincta*, *A. comosa*, *A. digitata*, *A. gracilis*, *A. klotzschii*, *A. lobata*, *A. macroura*, *A. manihot*, *A. paulina*, *A. praetervisata*, *A. subcomosa*, *A. surinamensis* e *A. trilobata*). As análises filogenéticas com dois marcadores plastidiais (*trnL-trnF* e *psbA-trnH*) e um nuclear (ITS), incluindo múltiplas amostras para muitas das espécies, confirmaram o monofiletismo de *Astraea*. Tais análises reconheceram três clados principais suportados por características morfológicas e/ou distribuição geográfica. Baseados na hipótese filogenética, realizamos estimativas de tempo de divergência dos clados e reconstrução de áreas ancestrais, bem como otimização de caracteres morfológicos para avaliar a história evolutiva de *Astraea*. Também apresentamos insights sobre a evolução de Crotonaeae na região Neotropical e a posição de *Brasilicroton*, *Sagotia* e *Sandwithia* na tribo.

**PALAVRAS-CHAVE:** *Astraea lobata*, Crotonoideae, Crotonaeae, *Brasilicroton*, Flora Neotropical, *Sagotia*, *Sandwithia*.

## ABSTRACT

*Astraea* belongs to tribe Crotoneae (Crotonoideae, Euphorbiaceae) along with *Croton*, *Brasilicroton*, *Acidocroton*, *Sagotia* e *Sandwithia*. The genus is distributed mostly throughout the Neotropical region, but some of its species are weedy and also found along the Paleotropics. Described as a genus by Klotzsch in 1841, *Astraea* was traditionally recognized as one of the morphologically best-defined sections within the giant *Croton* (*C. sect. Astraea*). As such, *C. sect. Astraea* was one of the morphologically best-defined groups within *Croton*. The last comprehensive monographs of *Astraea* are those made by Müller Argoviensis in De Candolle's Prodrumus and Flora Brasiliensis during the 19<sup>th</sup> century. In these works, many varieties are recognized for *Croton lobatus* (= *A. lobata*), the type species of *Astraea* and the most complex and widespread of its species. As consequence of recent phylogenetic studies, *C. sect. Astraea* was recognized as a distinct genus. *Astraea* has been included in studies mostly as outgroup and, therefore, little is known about the relationships among its species. Based on ca. 5,200 specimens from more than 90 herbaria, we present a more precise morphological delimitation for the complex *A. lobata* and rearrangements within the genus, which resulted in the recognition of 13 species (*A. cincta*, *A. comosa*, *A. digitata*, *A. gracilis*, *A. klotzschii*, *A. lobata*, *A. macroura*, *A. manihot*, *A. paulina*, *A. praetervisa*, *A. subcomosa*, *A. surinamensis* e *A. trilobata*). The phylogenetic analysis with two plastid (*trnL-trnF* and *psbA-trnH*) and one nuclear (ITS) regions, including more than one sample for many of the species, confirmed the monophyly of *Astraea*. These analyses also recognized three main clades based on morphological characters or geographical distribution. Based on the phylogenetic hypothesis, we also performed divergence time estimates and reconstructions of ancestral ranges and morphological characters states to evaluate the evolutionary history of *Astraea*. We also present insights into the evolution of Crotoneae in the Neotropical region and discuss the alternative positions of *Brasilicroton*, *Sagotia* and *Sandwithia*.

**KEYWORDS:** *Astraea lobata*, Crotonoideae, Crotoneae, *Brasilicroton*, Neotropical Flora, *Sagotia*, *Sandwithia*.

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INTRODUÇÃO GERAL

## UMA BREVE CONTEXTUALIZAÇÃO SOBRE A REGIÃO NEOTROPICAL

A região Neotropical causava, já desde o século XIX, grande fascínio entre naturalistas como Alexander von Humboldt e Karl Friederich Philip von Martius, que se depararam com a grande riqueza dos cerrados, incluindo a beleza cênica e endemismos dos campos rupestres, além das exuberantes formações florestais como as Florestas Amazônica e Atlântica (Zanella 2011).

Toda a diversidade fitogeográfica encontrada na região Neotropical pode ser compartimentalizada em dois grupos principais: de um lado as formações úmidas, sem estações bem definidas, como a Floresta Amazônica e a Mata Atlântica, e do outro as formações mais secas, com uma sazonalidade bem demarcada, como o Cerrado e a Caatinga. Ainda, é importante ressaltar a presença de formações florestais dentro das formações secas – como as Florestas Estacionais Semidecíduais ao longo do domínio da Mata Atlântica, e de vegetações abertas ao longo das formações úmidas, como é o caso das campinaranas ao longo da Floresta Amazônica, os campos de altitude, principalmente, na porção setentrional da Mata Atlântica, e as restingas ao longo de toda a costa brasileira (Carvalho & Almeida 2011).

Tamanha diversidade na paisagem Neotropical reflete-se em uma enorme diversidade biológica: Antonelli & Sanmartin (2011) estimam que existam de 90 a 110 mil espécies de plantas com sementes na região Neotropical, o que corresponde a cerca de 35% do total destas espécies conhecidas no mundo inteiro e, potencialmente, tanto quanto ou até mais que toda a diversidade dos paleotrópicos combinada. Burnham & Graham (1999) elegeram três fatores principais envolvidos na alta diversificação da biota neotrópica: o soerguimento dos Andes, o intercâmbio biótico entre as América do Norte e do Sul, antes e após o fechamento do Istmo do Panamá e as flutuações climáticas do Quaternário. Além desses fatores, também devem ser consideradas a heterogeneidade de solos, bem como as diferenças altitudinais (Fine *et al.* 2005, Givinish *et al.* 2000), além da invasão de biomas ou de novas áreas por determinados grupos (Pennington *et al.* 2004, Gonçalves *et al.* 2007, Salsis-Lagoudakis *et al.* 2008).

No continente americano, o Brasil se destaca como o país com a mais rica flora (Ulloa-Ulloa *et al.* 2017) e também pela notável heterogeneidade das paisagens encontradas em seus domínios fitogeográficos (Amazônia, Cerrado, Floresta Atlântica, Caatinga e Campos Sulinos). Tal heterogeneidade comporta uma flora riquíssima, com cerca de 30 mil espécies nativas, e uma elevada diversidade filogenética, com 229 famílias e 2.746 gêneros (BFG 2015). A distribuição desta riquíssima flora também é heterogênea, com grupos e/ou espécies endêmicos de um domínio fitogeográfico, p.ex., *Hevea* (Euphorbiaceae) restrito à Amazônia, e *Diplusodon* (Lythraceae) restrito ao Cerrado (Fiaschi & Pirani 2009), enquanto em outros casos observa-se uma distribuição que se estende por dois ou mais domínios, por vezes de forma disjunta, como é o caso dos padrões Campo rupestres-Restingas (Alves *et al.* 2017) ou entre os núcleos de florestas tropicais decíduas

sazonais (Pennington et al. 2006), especialmente entre os núcleos Caatinga, Paranaense, Misiones e Piedmont (Fiasch & Pirani 2009).

Ainda, o Brasil, juntamente com Austrália, China e Nova Guiné, está entre os países onde o maior número de novas espécies são descritas anualmente (Christenhusz & Byng 2016), e, mesmo considerando o viés causado pelas grandes dimensões do território brasileiro, e que tal delimitação é meramente política, a flora brasileira apresenta um alto grau de endemismo, com cerca de 18 mil espécies encontradas apenas no território brasileiro, que correspondem a mais de 50% das espécies que ocorrem no país (BFG 2015).

## EUPHORBIACEAE: UM GRANDE DESAFIO TAXONÔMICO E FILOGENÉTICO

Entre as famílias mais representativas da flora brasileira encontram-se algumas megadiversas como Fabaceae, Orchidaceae e Asteraceae, e outras, como Bromeliaceae, que possuem seu centro de diversidade na região Neotropical. Entre estas, encontra-se Euphorbiaceae, com 934 espécies (638 endêmicas) em 64 gêneros. Nos domínios fitogeográficos brasileiros, a família está sempre entre as mais representativas, exceto nos Pampas. Enquanto nos domínios mais úmidos Euphorbiaceae contribui com 2,2 a 2,4% da diversidade de espécies, nos mais secos varia de 2,7 a 5,0%, alcançando a maior diversidade relativa de espécies na Caatinga e, absoluta no Cerrado, com 386 espécies (BFG 2015).

Entre os principais gêneros de Euphorbiaceae na flora brasileira (Flora do Brasil 2020, em construção) estão *Croton* L. (311 espécies / 247 endêmicas), *Manihot* Mill. (99/88), *Dalechampia* L. (72/50), *Euphorbia* L. (64/31), *Acalypha* L. (49/30), *Cnidoscolus* Pohl (42/37), *Mabea* Aubl. (25/3), *Bernardia* Houst. ex Mill. (23/19), *Caperonia* A.St.-Hil. (18/12), *Tragia* L. (16/13), *Microstachys* A.Juss. (15/9), *Jatropha* L. (14/7), *Algernonia* Baill. (11/10), *Sapium* Jacq. (11/2), *Hevea* Aubl. (11/4), *Gymnanthes* Sw. (10/3), *Actinostemon* Mart. ex Klotzsch (9/4) e *Stillingia* Garden (9/7).

A riqueza de Euphorbiaceae no Brasil é apenas uma parte de uma família de superlativos, a maior de Malpighiales com quase sete mil espécies e cerca de 250 gêneros, com distribuição quase cosmopolita, porém especialmente concentrada ao longo dos trópicos (Wurdack *et al.* 2005, Xi *et al.* 2012). Destaca-se também por sua extraordinária diversidade morfológica, com hábito herbáceo a arbóreo, por vezes cactiforme, látex colorido, transparente ou leitoso, e indumento bastante variado, com tricomas simples, malpiguiáceos, escamiformes, dendríticos, estrelados, glandulares ou urticantes. As folhas são geralmente alternas, mas também podem ser opostas ou mais raramente verticiladas, pecioladas ou sésseis, com estípulas inconspícuas, bem desenvolvidas ou ausentes e frequentemente com glândulas no ápice do pecíolo ou na base do limbo; o limbo é geralmente simples (folhas compostas somente em alguns gêneros como *Hevea* e *Manihot*), as margens são inteiras a variavelmente serreadas. As inflorescências podem ser terminais e/ou axilares, cimosas,



geralmente em tirso, com pseudantos característicos nos gêneros *Dalechampia* e *Euphorbia*. As flores são unissexuais (em espécies monoicas ou dioicas), geralmente actinomorfas, podendo ser aclamídeas, monoclamídeas ou, mais raramente, diclamídeas, e frequentemente com nectários florais. As flores estaminadas podem possuir de um a vários estames, com filetes livres ou conados e anteras geralmente rimosas; os grãos de pólen na família são em geral tricolporado, mas também são comuns os grãos de pólen inaperturados com padrão de ornamentação crotonóide. As flores pistiladas possuem ovário súpero, tricarpelar e trilobular, cada lóculo com apenas um óvulo, provido de prolongamento nucelar e obturador placentário; os estiletos podem ser inteiros ou variavelmente ramificados, com regiões estigmáticas ou estigmas diferenciados. Os frutos, conhecidos como tricocas, são cápsulas com deiscência septicida e loculicida, na maioria das vezes compostos por três mericarpos (cocas) bivalvados, com exocarpo liso a variadamente ornamentado e carpóforo persistente; cada mericarpo porta uma única semente, com variados formatos e ornamentação da testa, podendo possuir carúncula ou arilo, com endosperma abundante e embrião reto, com cotilédones achatados e amplos (Webster 1994, 2014, Radcliffe-Smith 2001).

Entre as espécies de Euphorbiaceae, três podem ser destacadas por sua grande importância econômica: *Hevea brasiliensis* (Willd. ex A.Juss.) Müll.Arg., a seringueira, principal fonte de borracha natural (Souza & Lorenzi 2012); *Ricinus communis* L., a mamona, cujo óleo extraído das sementes é amplamente utilizado na indústria (Ogunniyi 2006), como lubrificante, fonte de biodiesel (Scholz & Silva 2008), matéria prima para próteses humanas (Ereno 2003), além de usos medicinais (Scarpa & Gueci 1982); e *Manihot esculenta* Crantz, a mandioca, que é uma das mais importantes fontes de amido para a alimentação humana (Souza & Lorenzi 2012). Além destas, algumas espécies dos gêneros *Croton* L., *Acalypha* L. e *Euphorbia* L. são utilizadas como ornamentais, enquanto muitas outras possuem propriedades medicinais tradicionalmente conhecidas (Mwine & van Damme 2011). Várias espécies arbóreas pioneiras dos gêneros *Croton* L. e *Alchornea* Sw. são utilizadas na recuperação de áreas florestais degradadas, enquanto várias herbáceas são invasoras de culturas e pastagens, especialmente nos gêneros *Croton* e *Euphorbia* (Souza & Lorenzi 2008). *Triadica sebifera* (L.) Small, uma espécie asiática arbórea, tornou-se uma agressiva invasora na América do Norte (Pattinson & Mack 2008).

Euphorbiaceae tem sido considerada um grande desafio para a taxonomia, principalmente por sua ampla variação morfológica, o que ocasionou diferentes posicionamentos nos diversos sistemas de classificação e divergências nas delimitações propostas para a família (Bentham & Hooker 1880, Cronquist 1968, Hutchinson 1973, Takhtajan 1980, Dahlgren 1980, Cronquist 1981). Ao longo dos anos foram propostos diversos tratamentos taxonômicos para a família e muitas classificações infrafamiliares (Baillon 1858, Bentham & Hooker 1880, Hutchinson 1969, Müller-Argoviensis 1866, Pax 1890, Webster 1975, 1994, 2014).

Dentre estes tratamentos, merecem destaque os de Webster (1975, 1994, 2014), os quais, baseados em dados morfológicos, subdividiram Euphorbiaceae em 5 subfamílias: Oldfieldioideae, Phyllanthoideae,

Acalyphoideae, Crotonoideae e Euphorbioideae. Posteriormente, no trabalho de Chase *et al.* (2002), já com base em dados moleculares, o monofiletismo da família não foi sustentado, uma vez que seus representantes emergiram em diferentes clados não diretamente relacionados. Assim, os autores propuseram o reconhecimento apenas das subfamílias unioviladas (Acalyphoideae, Crotonoideae e Euphorbioideae) em Euphorbiaceae. Os outros dois clados recuperados por Chase *et al.* (2002) correspondem às outras duas subfamílias de Euphorbiaceae, as quais foram elevadas ao nível de família (Oldfieldioideae = Picrodendraceae e Phyllanthoideae = Phyllanthaceae).

Wurdack *et al.* (2005), ao analisarem as relações infrafamiliares de Euphorbiaceae, concluíram que Euphorbioideae é a única subfamília monofilética e devido à ausência de estudos mais informativos, apenas reconheceram duas linhagens originalmente pertencentes a Acalyphoideae como novas subfamílias: Peroideae e Cheilosoideae.

Uma relação surpreendente emergiu no trabalho de Davis *et al.* (2007): espécies de Rafflesiaceae, família conhecida pelos seus representantes holoparasitas, entre elas a maior flor do mundo (*Rafflesia arnoldii* R.Br.), emergiram como um clado entre os representantes de Euphorbiaceae. Esta relação foi novamente recuperada por Wurdack & Davis (2009), que propuseram o reconhecimento de Peroideae como uma família (Peraceae) e mantendo, dessa forma, Rafflesiaceae como uma família e Euphorbiaceae monofilética, incluindo apenas as subfamílias Cheilosoideae, Acalyphoideae, Crotonoideae e Euphorbioideae (Figura 1).

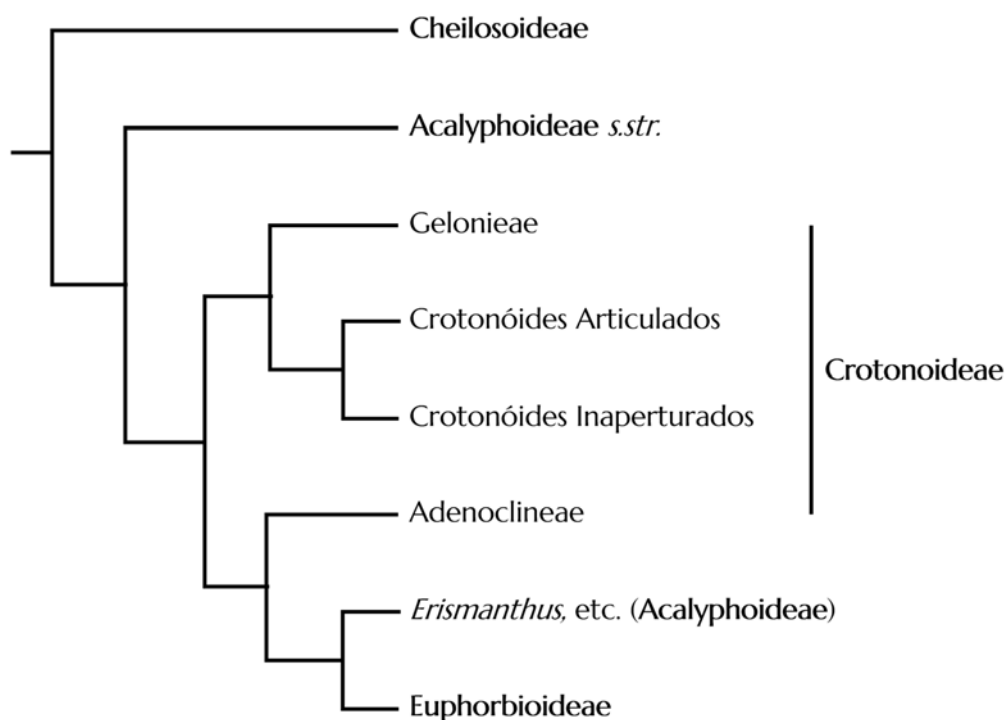


Figura 1: Relações filogenéticas dentro de Euphorbiaceae, adaptado de Wurdack *et al.* (2005). Peroideae é omitida devido ao reconhecimento como uma família distinta após os trabalhos de Davis *et al.* (2007) e Wurdack & Davis (2009).

Sun *et al.* (2016), com uma densa amostragem do clado das Rosídeas, corroboraram as relações de Euphorbiaceae com Peraceae e Rafflesiaceae, mas não o monofiletismo de Euphorbiaceae: Cheilosoideae ficou separada das demais Euphorbiaceae, sendo Rafflesiaceae mais próxima de Euphorbiaceae. Além de corroborar o não monofiletismo de Acalyphoideae e Crotonoideae, estes autores reconheceram os mesmos clados de Wurdack *et al.* (2005): Acalyphoideae *s.s.*, Erismantheae, Euphorbioideae, os crotonóides articulados e os inaperturados, Gelonieae e Adenoclineae *s.l.* Assim como em Wurdack *et al.* (2005) as relações entre estes sete clados ainda permaneceram incerta.

## ASPECTOS SISTEMÁTICOS DE CROTONOIDEAE

Dentre as atuais quatro subfamílias de Euphorbiaceae, Crotonoideae, que não é monofilética, inclui 12 tribos (Radcliffe-Smith 2001, Webster 2014) e cerca de 1.900 espécies de acordo com o checklist de Radcliffe-Smith (2001). Cabe ainda ressaltar que a maioria das tribos que compõem Crotonoideae, como Aleuritideae e Codieae, foram apontadas como parafiléticas na hipótese filogenética mais recente de Wurdack *et al.* (2005).

Wurdack *et al.* (2005), que reconheceram Crotonoideae como não monofilética, ressaltaram a necessidade de mais estudos para a resolução da delimitação da subfamília, e, sendo assim, apenas reconheceram quatro grandes clados para a subfamília (Figura 1):

- (1) **Adenoclineae**, indicado como mais próximo de Euphorbioideae do que dos demais clados de Crotonoideae;
- (2) **Gelonieae**, o grupo mais basal entre Crotonoideae *sensu stricto*, incluindo gêneros do Velho Mundo;
- (3) os **Crotonóides articulados**, nome dado devido à prevalência de laticíferos articulados em gêneros importantes como *Hevea*, *Cnidoscolus* e *Manihot*; e
- (4) os **Crotonóides Inaperturados**, o mais diverso entre estes clados.

Os representantes dos crotonóides inaperturados compartilham os grãos de pólen desprovidos de aberturas, com uma ornamentação característica, conhecida como padrão crotonóide (Wurdack *et al.* 2005, Nowicke 1994). Outra característica do clado é a presença de pétalas ao menos nas flores estaminadas (exceto nos gêneros *Benoistia* H.Perrier & Leandri e *Neoboutonia* Müll.Arg.).

Nos crotonóides inaperturados, Wurdack *et al.* (2005), com base em dados das regiões *trnL-trnF* e *rbcl*, reconheceram dois subclados (C1 e C2) que carecem de sinapomorfias morfológicas aparentes, mas com uma grande deleção no espaçador *trnL-trnF* caracterizando o clado C2, portanto com bom suporte molecular para o reconhecimento deste clados, apesar da baixa resolução no backbone do clado C2. Além disso, ambos

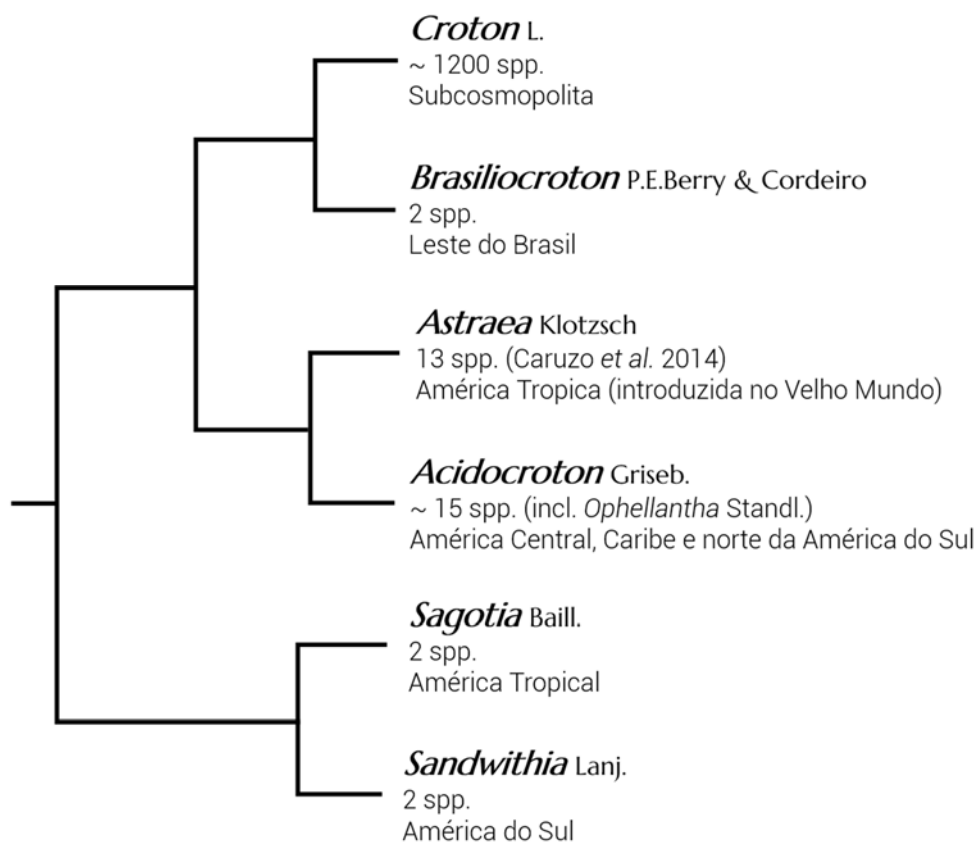
apresentam um padrão biogeográfico, a maioria dos representantes do clado C2 ocorre no Velho Mundo, com raras exceções de gêneros amazônicos, como *Pausandra* Radlk. e *Dodecastigma*, Ducke, ao passo que no clado C1 a maioria das espécies ocorre no Novo Mundo, com apenas *Asteaea*, *Croton* e *Jatropha* contando com representantes no Velho Mundo.

No clado C1, estão inclusas apenas duas tribos, Jatropeae e Crotoneae. Jatropeae atualmente possui três gêneros: *Jatropha*, com mais de 180 espécies, ocorrendo tanto no Velho quanto no Novo Mundo; e *Vaupesia* R.E.Schult. e *Joannesia* Vell., com uma e duas espécies, respectivamente, restritas ao Novo Mundo. Outros pequenos gêneros (com uma a três espécies) anteriormente incluídos em Jatropeae por Webster (1994) agora encontram-se em outros grupos de Crotonoideae: *Leeuwenbergia* Letouzey & Hallé e *Annesijoa* Pax & K.Hoffm. (África) no clado C2, na tribo Ricinodendreae, enquanto *Deutzianthus* Gagnep. (incluindo *Loerzingia* Airy-Shaw) e *Oligoceras* Gagnep. (Ásia) foram transferidos para Aleuritideae subtribo Grosserinae (Webster 2014).

## CROTONEAE: MUITO MAIS DO QUE O GIGANTESCO *CROTON*

Crotoneae incluía originalmente (Webster 1994) apenas o grande gênero *Croton* e pequenos gêneros satélites como *Julocroton* Mart., *Eremocarpus* Benth. e *Moacroton* Croizat. *Mildbraedia* Pax (3-4 espécies, África) e *Paracroton* Miq. (= *Fahrenheitia* Rchb.f. & Zoll.; 4 espécies, Ásia) também já foram incluídos em Crotoneae. Entretanto, os pequenos gêneros satélites foram incluídos em *Croton* para manter o monofiletismo de *Croton* (Berry et al. 2005, Wurdack et al. 2005). O posicionamento de *Mildbraedia* e *Paracroton* em Crotoneae já era questionado por Webster (1994), e na hipótese filogenética de Wurdack et al. (2005) estes últimos emergiram no clado C2. No tratamento mais recente para a família (Webster 1994), estes dois gêneros foram acomodados em uma nova subtribo, Paracrotoninae G.L. Webster (within Aleuritideae), caracterizada pelo androceu com os estames dos verticilos externos possuindo filetes livres enquanto nos verticilos internos os filetes são conados.

Em sua atual circunscrição (Wurdack et al. 2005), Crotoneae compreende mais de 1.200 espécies e seis gêneros, a maior entre as tribos de Crotonoideae. Essa delimitação resulta da transferência de gêneros de outras tribos de Crotonoideae, e ao posicionamento de *Brasiliocroton* P.E. Berry & Cordeiro como irmão de *Croton* nas análises de Berry et al. (2005) e Wurdack et al. (2005), que separou uma das seções de *Croton*, *C. sect. Astraea* (Klotzsch) Baill., a qual foi elevada ao nível genérico (= *Astraea* Klotzsch).



**Figura 2:** Relações filogenéticas entre os gêneros da tribo Crotoneae de acordo com as hipóteses filogenéticas de Wurdack et al. (2005), Berry et al. (2005) e Riina et al. (2014).

De acordo com as hipóteses filogenéticas mais recentes (Wurdack *et al.* 2005, Berry *et al.* 2005, Riina *et al.* 2014; Figura 2), *Sagotia* Baill. e *Sandwithia* Lanj., gêneros amazônicos com duas espécies cada são irmãos dos demais gêneros de Crotoneae, que foram dois clados. Um destes clados inclui *Croton* e *Brasiliocroton*, e possui como sinapomorfia morfológica os nectários extraflorais acropeciulares ou basilaminares, apesar destes não serem observados em algumas espécies ou mesmo seções inteiras de *Croton* (Riina *et al.* 2014). O outro clado, por sua vez, compreende *Astraea* e *Acidocroton* Griseb., sem sinapomorfias morfológicas aparentes.

Em sua delimitação original, *Acidocroton* compreendia cerca de 15 espécies restritas ao Caribe (principalmente às Grandes Antilhas), porém Webster (1994), com base em semelhanças florais, nele sinonimizou *Ophellantha* Standl., um gênero contendo 3 espécies com ocorrência na América Central e no norte da América do Sul, considerando-as como uma seção de *Acidocroton*. Apesar de similares em caracteres florais, as espécies destes dois gêneros são bastante diferentes vegetativamente: as estípulas transformadas em espinhos, comuns aos dois gêneros, são pouco desenvolvidas em *Ophellantha*, enquanto em *Acidocroton* estas são bem desenvolvidas, e muito mais evidentes, uma vez que as folhas são muito menores (em relação às de *Ophellantha*) e organizadas em braquiblastos. Por estas disparidades vegetativas, a inclusão de *Ophellantha* em *Acidocroton* não foi reconhecida por Govaerts et al. (2000), porém o mais recente tratamento abrangente sobre Euphorbiaceae (Webster 2014), que é fortemente baseado em Webster (1994), continua reconhecendo *Ophellantha* como uma seção de *Acidocroton*.

## *ASTRAEA*

Histórico e relações com *Croton*—A espécie mais antiga de *Astraea* foi originalmente descrita em *Croton*, *C. lobatus* L. [= *Astraea lobata* (L.) Klotzsch], na obra clássica *Species Plantarum* de Linnaeus (1753). O epíteto faz referência às folhas profundamente lobadas, que diferenciam a maioria das espécies de *Astraea* daquelas de *Croton*.

Como gênero, *Astraea* foi proposto quase cem anos depois por Klotzsch (1841), que separou *Croton* em diversos gêneros, como *Cleodora* Klotzsch e *Geiseleria* Klotzsch. Em *Astraea*, Klotzsch reconheceu oito espécies (*A. manihot* Klotzsch, *A. jatropa* Klotzsch, *A. palmata* Klotzsch, *A. lobata*, *A. diversifolia* Klotzsch, *A. divaricata* Klotzsch e *A. prunifolia* Klotzsch), mas apenas uma delas, *A. lobata*, uma nova combinação baseada em *Croton lobatus*, é um nome validamente publicado, uma vez que os demais não foram acompanhados por uma diagnose (o que os torna *nomina nuda*), e, apesar de materiais tipos não serem exigidos naquela época (Art. 30, McNeill *et al.* 2012) a ausência de tais materiais dificultam a determinação da identidade dos táxons propostos por Klotzsch (1841).

Pouco tempo depois da publicação de Klotzsch, Baillon (1858) propôs que *Astraea* fosse reconhecido como uma seção de *Croton*. Desde então, o grupo foi tradicionalmente reconhecido como *Croton* sect. *Astraea* por compartilhar com *Croton* tricomas estrelados, inflorescências espiciformes bissexuadas, com flores pistiladas monoclamídeas e proximais, e flores estaminadas diclamídeas e em sua maioria distais, com os estames encurvados no botão. Pax (1890) chegou a propor que o grupo fosse reconhecido como um subgênero de *Croton*, mas a posição de Baillon (1858) prevaleceu ao longo dos anos.

As monografias do grupo elaboradas por Müller Argoviensis para o *Prodromus de Candolle* (Müller Argoviensis 1866) e para a *Flora Brasiliensis* (Müller Argoviensis 1873) foram de grande importância, e incluíram, além de um tratamento mais amplo para o grupo, novas espécies e o rearranjo dos diversos nomes publicados até o momento, com diversas sinonimizações. Após os trabalhos de Müller Argoviensis, os avanços na taxonomia do grupo foram representados, basicamente, por descrições de novas espécies. Um resumo do histórico do grupo é apresentado na Tabela I enquanto que o histórico taxonômico mais detalhado é apresentado junto da revisão de *Astraea*, no Capítulo IV.

Webster (1993) já indicava *Croton* sect. *Astraea* como uma das seções mais bem delimitadas de *Croton*, e inclusive excluiu *Croton bonplandianus* (tratado como *C. pauperulus* na *Flora Brasiliensis*) da Seção, em virtude de suas glândulas proeminentes na base das folhas, estiletos bifidos e sementes lisas, interpretando o receptáculo glabro das flores estaminadas, característico de *Croton* sect. *Astraea*, como resultado de evolução paralela. A exclusão de *Croton* sect. *Astraea* de *Croton* foi indicada por Wurdack *et al.* (2005), e definitivamente proposta por Berry *et al.* (2005). O reconhecimento de *Astraea* como um gênero resultante dos estudos

filogenéticos acima citados é suportado também por características morfo-anatômicas indicadas por De Paula *et al.* (2011, Tabela II).

**Tabela I:** Histórico taxonômico resumido de *Astraea*.

Período (anos)	Descrição
Pré-Muelleriano (1753-1865)	Compreende o período anterior à primeira revisão mais abrangente de <i>Astraea</i> . Durante este período, o grupo foi reconhecido como parte de <i>Croton</i> até 1841, quando Klotzsch propôs o gênero <i>Astraea</i> , mas que não foi bem aceito. A partir de 1858, o grupo foi tradicionalmente reconhecido como uma seção de <i>Croton</i> ( <i>Croton</i> sect. <i>Astraea</i> ). Apesar de não ser reconhecido como um gênero segregado de <i>Croton</i> , Klotzsch sempre descrevia as espécies em <i>Astraea</i> . Esse período inclui a descrição de diversos nomes por uma grande variedade de autores, de diferentes regiões. O período termina com o trabalho de Müller Argoviensis na <i>Linnaea</i> , em 1865, no qual o autor apresenta algumas novidades taxonômicas para <i>Croton</i> sect. <i>Astraea</i> , preliminares do tratamento do gênero para o <i>Prodromus</i> de Candolle. Ao final do período temos 22 nomes aceitos.
Muelleriano (1866-1873)	Compreende o período no qual foram publicadas duas grandes revisões abrangentes do grupo por Müller Argoviensis: uma para o <i>Prodromus</i> de Candolle, em 1866, e outra para a <i>Flora Brasiliensis</i> , em 1873. Por serem os primeiros trabalhos a organizar o grupo, este período é marcado por diversas sinonimizações e novidades nomenclaturais, mas também por publicações de espécies novas. Apesar de ser o período mais curto no histórico taxonômico de <i>Astraea</i> , pode ser considerado como um dos mais importantes pelas grandes contribuições de Müller Argoviensis para a taxonomia do grupo. Ao final desse período, são reconhecidos 28 táxons, com um elevado número de táxons infraespecíficos em alguns casos como <i>Croton lobatus</i> e <i>Croton klotzschii</i> .
Pós-Muelleriano (1874-2004)	Compreende o período após os importantes tratamentos de Müller Argoviensis no <i>Prodromus</i> de Candolle e na <i>Flora Brasiliensis</i> . Durante este período o grupo foi tratado como uma seção de <i>Croton</i> , apesar da proposta de Pax para reconhecer o grupo como um subgênero de <i>Croton</i> . Novos táxons foram descritos e o período termina com a publicação do <i>World Checklist of Selected Plant Families</i> de Euphorbiaceae, por Govaerts em 1999, com 18 táxons reconhecidos, sem o grande número de variedades e formas do período anterior.
Contemporâneo (2000-dias atuais)	Compreende o período em que o projeto de pesquisa está sendo desenvolvido e inicia-se após o reconhecimento do grupo como um gênero novamente, com base nas hipóteses filogenéticas publicadas a partir de 2005. Após este trabalho, a maioria dos trabalhos publicados visa apenas transferir as espécies de <i>Croton</i> sect. <i>Astraea</i> para <i>Astraea</i> . Um destes trabalhos, o de Van Ee (2011), ainda fornece informações importantes sobre aspectos nomenclaturais do grupo. Nenhum trabalho mais amplo foi publicado até o momento, e o grupo conta com 13 táxons (12 espécies de <i>Astraea</i> + <i>Croton palmatus</i> ).

**Tabela II:** Diferenças morfo-anatômicas nas flores pistiladas e estaminadas de *Croton* e *Astraea* apontados por De-Paula *et al.* (2011).

Caráter	<i>Croton</i>	<i>Astraea</i>
Margem dos lobos do cálice das flores pistiladas	sem coléteres	com coléteres
Indumento das pétalas das flores estaminadas	com tricomas filiformes	com tricomas moniliformes
Nectários das flores pistiladas	vascularizado e anular	não-vascularizado e segmentado
Nectários das flores estaminadas	vascularizado e segmentado	não-vascularizado e segmentado

Assim, de acordo com Berry *et al.* (2005) e Webster (2014), as espécies de *Astraea* podem ser reconhecidas pelo hábito herbáceo a arbustivo, folhas alternas, 3-5-lobadas (raramente inteiras), estipuladas e pecioladas, inflorescências em tirsos espiciformes, bissexuadas e terminais, com cúpulas basais bissexuais ou exclusivamente pistiladas e apicais estaminadas; estiletes cilíndricos, delgados e bastante ramificados, flores estaminadas com perianto imbricado e receptáculo geralmente glabro e sementes quadrangulares, com testa rugosa e carúncula proeminente.

**Problemas nomenclaturais**—Como todas as espécies propostas por Klotzsch (1841) na publicação de *Astraea* (com exceção de *A. lobata*) não possuíam indicação de basônimo, material-tipo ou descrição original, seus nomes foram considerados *nomina nuda*. Como os epítetos de *A. divaricata*, *A. tomentosa* e *A. prunifolia* já haviam sido utilizados em *Croton*, estes nomes foram erroneamente interpretados como novas combinações de espécies de *Croton*, sem existir, entretanto, qualquer relação entre elas (Van Ee 2011).

Outro aspecto importante a ser considerado em relação aos problemas nomenclaturais de *Astraea* é que os materiais originais de Klotzsch se encontravam no herbário do Museu e Jardim Botânico de Berlim (B), que foi parcialmente destruído durante a II Guerra Mundial. Também os nomes propostos por Muller Argoviensis (1866), na primeira grande monografia do grupo, foram baseados em exsicatas deste mesmo herbário. A destruição destes materiais dificultou o estabelecimento da identidade dos nomes envolvidos.

Uma série de trabalhos nomenclaturais envolvendo as espécies de *Astraea* foram publicados (Berry *et al.* 2005, Caruzo & Cordeiro 2007, Zuloaga *et al.* 2007, Van Ee 2011, Caruzo *et al.* 2014), e atualmente todos os epítetos originalmente descritos em *Croton* já se encontram combinados em *Astraea*, em alguns casos, já com as devidas lectotipificações (Caruzo & Cordeiro 2007, Van Ee 2011, Caruzo *et al.* 2014).

O monofiletismo de *Astraea* tem bastante suporte nos estudos filogenéticos realizados com *Crotoneae* (Wurdack *et al.* 2005, Berry *et al.* 2005, Van Ee *et al.* 2011, Riina *et al.* 2014). Entretanto, devido à baixa amostragem do gênero nestes trabalhos, não existiam informações sobre a relação filogenética entre suas espécies. Além disso, as espécies amostradas nestes trabalhos (*A. lobata*, *A. klotzschii* e *A. praetervisata*) não representam toda a diversidade e distribuição geográfica do gênero.

Caruzo *et al.* (2014) estimaram que *Astraea* seria composto por 13 espécies concentradas na América do Sul, principalmente no Brasil, sendo *A. lobata* a única espécie encontrada ao longo de toda a região Neotropical, mas também, como invasora, no Velho Mundo. Porém, são reconhecidas, no início desta tese, 12 táxons: *A. aureomarginata*, *A. cincta*, *A. comantha*, *A. comosa*, *A. douradensis*, *A. gardneri*, *A. hauthalii*, *A. jatrophae*, *A. lobata*, *A. macrourea*, *A. praetervisata* e *A. subcomosa*.



## JUSTIFICATIVA E OBJETIVOS

No Brasil, Euphorbiaceae é amplamente representada por um grande número de espécies encontradas nos mais variados tipos de vegetação. A família apresenta uma extraordinária diversidade morfológica e ampla distribuição geográfica, e mesmo com os recentes esforços para elucidar as relações entre seus representantes, ainda há muito a ser estudado. A região Neotropical concentra grande parte da diversidade de Euphorbiaceae, e um dos maiores grupos da família, Crotonae, tem seu maior centro de diversidade nesta região. Dentro da tribo, *Croton* concentra a maioria dos estudos pelo seu tamanho e diversidade, enquanto seu gênero irmão, *Brasiliocroton*, foi recentemente descrito e os pequenos gêneros amazônicos (*Sagotia* e *Sandwithia*) já foram revisados. *Astraea* e *Acidocroton*, por sua vez, ainda carecem de estudos sistemáticos. *Astraea* também necessita de uma melhor circunscrição de suas espécies, principalmente as de ampla distribuição e com grande número de sinônimos, como *Astraea lobata*. Como reflexo da incerteza dos limites de suas espécies, dados sobre distribuição geográfica são ineficientes. Assim, frente à falta de informações claras sobre as espécies de *Astraea* e a necessidade de sua melhor delimitação, o presente trabalho teve como objetivos:

- (1) revisar e reavaliar a circunscrição do gênero *Astraea* Klotzsch, com principal ênfase em suas espécies;
- (2) inferir uma filogenia para o gênero com base em dados moleculares;
- (3) entender a biogeografia do gênero com base na filogenia inferida, e
- (4) levantar padrões de evolução de caracteres morfológicos.

Neste trabalho as seguintes hipóteses foram testadas:

**Hipótese A:** *Astraea* possui 12 espécies distribuídas principalmente na América do Sul: *A. aureomarginata*, *A. cincta*, *A. comantha*, *A. comosa*, *A. douradensis*, *A. gardneri*, *A. hauthalii*, *A. jatropa*, *A. lobata*, *A. macroua* (= *A. klotzschii*), *A. praetervisata* e *A. subcomosa*.

**Hipótese B:** *Astraea lobata*, em sua atual delimitação morfológica, corresponde a um aglomerado de táxons distintos morfológicamente e com distribuição geográfica característica, por vezes não proximamente relacionados filogeneticamente.

**Hipótese C:** *Astraea*, com uma amostragem taxonômica completa, incluindo toda a variação morfológica do gênero não avaliada nos recentes estudos envolvendo a tribo *Crotonae*, pertence à esta tribo e é o gênero irmão de *Acidocroton*.

**Hipótese D:** *Astraea* teria se originado na América Central e Caribe, onde seu gênero irmão, *Acidocroton*, é encontrado, e, após o fechamento do Istmo do Panamá, teria expandido sua distribuição geográfica até o leste e sul da América do Sul, onde alcançou a maior diversidade de espécies.

## REALIZAÇÃO E APRESENTAÇÃO DA TESE

**Levantamento bibliográfico**—Consultas a bibliotecas virtuais como o *Biodiversity Heritage Library* (<http://www.biodiversitylibrary.org/Default.aspx>) e o *Botanicus.org* (<http://botanicus.org/>) foram realizadas para reunir os protólogos de todos os nomes relacionados a *Astraea*. A listagem de nomes em *Astraea* foi elaborada por meio consultados ao *World Checklist and Bibliography of Euphorbiaceae (and Pandaceae)* (Govaerts et al. 2000), além de bases de dados online, como o *Tropicos.org* (<http://tropicos.org/>), *International Plant Names Index – IPNI* (<http://www.ipni.org/>) e o *World Checklist of Selected Plant Families* (<http://apps.kew.org/wcsp/home.do>).

**Visita aos herbários**—As coleções de *Astraea* disponíveis nos 93 herbários incluídos neste trabalho (Tabela III) foram consultadas pessoalmente ou através de imagens em alta resolução disponibilizadas pelos próprios herbários ou através de consulta ao *Jstor Global Plants* (<http://plants.jstor.org/>). As informações de todas estas exsicatas foram incluídas em um banco de dados associado a uma biblioteca de imagens contendo uma imagem de cada uma destas exsicatas, organizadas através de identificadores digitais (*tags*) para herbário, procedência e identificação taxonômica.

Um total de aproximadamente 5.200 exsicatas foram consultadas, representando 3.175 coleções (i.e., o número de registros excluindo duplicatas). Destas, 554 (17%) foram consultadas apenas pelo exame de imagens em alta resolução, enquanto das demais 2.621 coleções examinadas pessoalmente, 1.391 (44%) foram consultadas apenas nos seus respectivos herbários e 1.230 (39%) estão no acervo ou foram enviadas ao Herbário Maria Eneida P.K. Fidalgo (SP), a caráter de empréstimo, para um estudo mais minucioso.

Devido a uma delimitação morfológica imprecisa de muitas espécies antes da finalização desta tese, além da necessidade de publicação formal de alguns dos novos nomes aqui propostos, durante a visita aos herbários não foi possível fornecer a identificação para muitos dos materiais analisados, motivo pelo qual todos estes foram solicitados por empréstimo. A disponibilização destes materiais por grande parte dos herbários consultados foi de extrema importância para os resultados aqui apresentados e, portanto, há um compromisso de anexar as determinações corretas no momento da devolução destas coleções ou quando os nomes forem publicados, não somente para os herbários que os emprestaram, mas também para aqueles dos quais foi possível apenas examinar as imagens das coleções. Com a digitalização de coleções concluída ou em andamento em diversos herbários, bases de dados mais abrangentes como o *SpeciesLink* (<http://www.splink.org.br/index>) ou o *JABOT* (<http://jabot.jbrj.gov.br/v2/consulta.php>) poderão ser atualizadas com os resultados desta tese, contribuindo para trabalhos futuro que possam vir a usufruir de tais resultados.

**Tabela III:** Lista de herbários e instituições que tiveram coleções de *Astraea* incluídas neste trabalho. Os acrônimos são apresentados de acordo com Thiers (2018, constantemente atualizado). Os herbários marcados com \* tiveram suas coleções analisadas por meio de imagens e ‡ indica que o herbário não está indexado no Index Herbariorum.

Herbário	Instituição (Localização)
A*	Harvard University (E.U.A.: Cambridge)
ALCB	Universidade Federal da Bahia (Brasil: Bahia. Salvador)
AMD*	National Herbarium of the Netherlands (Holanda: Leiden)
ASE	Universidade Federal de Sergipe (Brasil: Sergipe: Aracajú)
B*	Botanischer Garten und Botanisches Museum Berlin-Dahlem (Alemanha: Berlin)
BHCB	Universidade Federal de Minas Gerais (Brasil: Minas Gerais. Belo Horizonte)
BHZB	Fundação Zoo-Botânica de Belo Horizonte (Brasil: Minas Gerais. Belo Horizonte)
BM*	The Natural History Museum (Inglaterra: Londres)
BOTU	Universidade Estadual Paulista (Brasil: São Paulo. Botucatu)
BR*	Botanic Garden Meise (Bélgica: Meise)
C*	University of Copenhagen (Dinamarca: Copenhagen)
CEN	EMBRAPA Recursos Genéticos e Biotecnologia (Brasil: Distrito Federal. Brasília)
CEPEC	Centro de Pesquisas do Cacau (Brasil: Bahia. Itabuna)
CESJ	Universidade Federal de Juiz de Fora (Brasil: Minas Gerais. Juiz de Fora)
CGMS	Universidade Federal do Mato Grosso do Sul (Brasil: Mato Grosso do Sul. Campo Grande)
COL*	Universidad Nacional de Colombia (Colômbia: Bogotá)
CTES	Instituto de Botánica del Nordeste (Argentina: Corrientes)
CVRD	Companhia Vale do Rio Doce (Brasil: Espírito Santo. Sooretama)
DAV*	University of California (E.U.A.: Davis)
E*	Royal Botanic Garden Edinburgh (Escócia: Edinburgo)
EAC	Universidade Federal do Ceará (Brasil: Ceará. Fortaleza)
ESA	Escola Superior de Agricultura Luiz de Queiroz (Brasil: São Paulo. Piracicaba)
F*	Field Museum of Natural History (E.U.A.: Chicago)
FHI*	Forestry Research Institute of Nigeria (Nigeria: Ibadan)
FLAS*	Florida Museum of Natural History (E.U.A.: Gainesville)
FSU*	Florida State University (E.U.A.: Tallahassee)
FTG*	Fairchild Tropical Botanic Garden (E.U.A.: Miami)
FUEL	Universidade Estadual de Londrina (Brasil: Paraná. Londrina)
G	Conservatoire et Jardin botaniques de la Ville de Genève (Suíça: Genebra)
GH*	Harvard University (E.U.A.: Cambridge)
HAL*	Martin-Luther-Universität (Alemanha: Halle)
HB	Herbarium Bradeanum (Brasil: Rio de Janeiro. Rio de Janeiro)
HBG*	Universität Hamburg (Alemanha: Hamburgo)
HCF	Universidade Tecnológica Federal do Paraná (Brasil: Paraná. Campo Mourão)
HEPH	Jardim Botânico de Brasília (Brasil: Distrito Federal. Brasília)
HNBU*	Institut de l'Environnement et de Recherche Agricola (Burkina Faso: Ouagadougou)
HRB	Instituto Brasileiro de Geografia e Estatística (Brasil: Bahia. Salvador)
HRCB	Universidade Estadual Paulista (Brasil: São Paulo. Rio Claro)

Herbário	Instituição (Localização)
HUEFS	Universidade Estadual de Feira de Santana (Brasil: Bahia. Feira de Santana)
HUEM	Universidade Estadual de Maringá (Brasil: Paraná. Maringá)
HUFU	Universidade Federal de Uberlândia (Brasil: Minas Gerais. Uberlândia)
IAC	Instituto Agrônômico de Campinas (Brasil: São Paulo. Campinas)
IBGE	Instituto Brasileiro de Geografia e Estatística (Brasil: Distrito Federal. Brasília)
IEB*	Instituto de Ecología, A.C. (México: Michoacán. Pátzcuaro)
INPA*	Instituto Nacional de Pesquisas da Amazônia (Brasil: Amazonas. Manaus)
IPA	Empresa Pernambucana de Pesquisa Agropecuária (Brasil: Pernambuco. Recife)
JPB	Universidade Federal da Paraíba (Brasil: Paraíba. João Pessoa)
K	Royal Botanic Gardens (Inglaterra: Kew)
L*	Naturalis Biodiversity Center (Holanda: Leiden)
LE*	V. L. Komarov Botanical Institute (Rússia: São Petersburgo)
LINN*	Linnean Society of London (Inglaterra: Londres)
M*	Botanische Staatssammlung München (Alemanha: Munique)
MA	Real Jardín Botánico (Espanha: Madrid)
MAC	Instituto do Meio Ambiente (Brasil: Alagoas. Maceió)
MBM	Museu Botânico Municipal (Brasil: Paraná. Curitiba)
MBML	Museu de Biologia Mello Leitão (Brasil: Espírito Santo. Santa Teresa)
MEXU*	Universidade Autónoma de México (México: Cidade de Mexico)
MICH*	University of Michigan (E.U.A.: Ann Arbor)
MO	Missouri Botanical Garden (E.U.A.: Saint Louis)
MPU*	Université de Montpellier (França: Montpellier)
NY	The New York Botanical Garden (E.U.A.: Bronx)
OUPR	Universidade Federal de Ouro Preto (Brasil: Minas Gerais. Ouro Preto)
P	Muséum National d'Histoire Naturelle (França: Paris)
PACA*	Instituto Anchieta de Pesquisas (Brasil: Rio Grande do Sul. São Leopoldo)
PAMG	Empresa de Pesquisa Agropecuária de Minas Gerais (Brasil: Minas Gerais. Belo Horizonte)
PEUFR	Universidade Federal Rural de Pernambuco (Brasil: Pernambuco. Recife)
R	Museu Nacional (Brasil: Rio de Janeiro. Rio de Janeiro)
RB	Jardim Botânico do Rio de Janeiro (Brasil: Rio de Janeiro. Rio de Janeiro)
RSA*	Rancho Santa Ana Botanic Garden (E.U.A.: Claremont)
S*	Swedish Museum of Natural History (Suécia: Estocolmo)
SJRP	Universidade Estadual Paulista (Brasil: São Paulo. São José do Rio Preto)
SP	Instituto de Botânica (Brasil: São Paulo. São Paulo)
SPF	Universidade de São Paulo (Brasil: São Paulo. São Paulo)
SPSF	Instituto Florestal (Brasil: São Paulo. São Paulo)
TCD*	Trinity College (Irlanda: Dublin)
TOGO*	Université du Lomé (Togo. Lomé)
TUB*	Universität Tübingen (Alemanha: Tübingen)
U*	Naturalis Biodiversity Center (Holanda: Leiden)
UB	Universidade de Brasília (Brasil: Distrito Federal. Brasília)

Herbário	Instituição (Localização)
UC*	University of California (E.U.A.: Berkeley)
UEC	Universidade Estadual de Campinas (Brasil: São Paulo. Campinas)
UESC <sup>‡</sup>	Universidade Estadual de Santa Cruz (Brasil: Bahia. Ilhéus)
UFG	Universidade Federal de Goiás (Brasil: Goiás. Goiânia)
UFP	Universidade Federal de Pernambuco (Brasil: Pernambuco. Recife)
UFRN	Universidade Federal do Rio Grande do Norte (Brasil: Rio Grande do Norte. Natal)
US*	Smithsonian Institution (E.U.A.: Washington)
USF*	University of South Florida (E.U.A.: Tampa)
USZ	Museo de Historia Natural Noel Kempff Mercado (Bolívia: Santa Cruz de la Sierra)
VIC	Universidade Federal de Viçosa (Brasil: Minas Gerais. Viçosa)
VIES	Universidade Federal do Espírito Santo (Brasil: Espírito Santo. Vitória)
W*	Naturhistorisches Museum Wien (Áustria: Viena)
WAG*	Naturalis Biodiversity Center (Holanda: Leiden)
WIS*	University of Wisconsin (E.U.A.: Madison)

**Trabalho de campo**—As localidades para as quais foram realizadas viagens de campo foram selecionadas com base nas coleções disponíveis nos herbários consultados. Nessas viagens foram coletados espécimes e amostras em álcool e FAA 50% para estudos morfológicos e anatômicos, além de material vegetal (preferencialmente folhas jovens) para extração de material genético.

Durante as viagens também foi dada especial atenção à observação de variações morfológicas nas populações encontradas, crucial para a delimitação de algumas espécies, e foi feito o registro fotográfico das plantas em seu hábitat natural. O material coletado foi herborizado segundo técnicas tradicionais (Fidalgo & Bononi 1989), e encontra-se incluído no Herbário Maria Eneida P. K. Fidalgo (SP), no Instituto de Botânica (São Paulo, SP), com duplicatas enviadas a diferentes herbários de acordo com a região coletada. As localidades visitadas, com datas e espécies coletadas em cada ocasião, estão listadas na Tabela IV.

**Estudo filogenético e biogeográfico**—Todo o trabalho de bancada para a elaboração das diferentes hipóteses filogenéticas apresentadas ao longo desta tese foi realizado no Laboratório de Biomedicina da Escola de Artes, Humanidades e Ciências da Universidade de São Paulo (EACH-USP) sob supervisão do Dr. Pedro Dias. O material genômico utilizado foi obtido de amostras desidratadas em sílica gel ou de materiais herborizados depositados no herbário SP ou então cedidos pela Dra. Ricarda Riina (Real Jardín Botánico, Madrid, Espanha).

**Tabela IV:** Viagens de campo realizadas durante a realização do presente trabalho com datas das viagens e espécies de *Astraea* coletadas

Localidade	Data	Espécies coletadas
Brasil Central (Noroeste de Minas Gerais, Goiás, Distrito Federal e Mato Grosso do Sul)	I-2014	<i>Astraea lobata</i> <i>Astraea paulina</i> <i>Astraea surinamensis</i>
Espírito Santo (Vitória, Linhares e Águia Branca)	VI-2014	<i>Astraea macroura</i> <i>Astraea surinamensis</i>
Interior da Bahia	VIII-2014	<i>Astraea paulina</i> <i>Astraea surinamensis</i>
Litoral Norte da Bahia (Mata de São João)	X-2014	<i>Astraea klotzschii</i>
Paraná (Campo Mourão e Maringá)	XII-2014	<i>Astraea cincta</i>
Bolívia (Santiago de Chiquitos)	I-2015	<i>Astraea cincta</i> <i>Astraea paulina</i>
Interior de São Paulo (Campinas, Piracicaba, Rio Claro e Botucatu)	I-2015	<i>Astraea paulina</i>
Sul da Bahia (Ilhéus, Itacaré, Marau e região)	I-2015	<i>Astraea digitata</i> <i>Astraea gracilis</i> <i>Astraea klotzschii</i> <i>Astraea surinamensis</i>
São Paulo (P.E. do Juquery)	VI-2015	<i>Astraea manihot</i> <i>Astraea 'douradensis'</i> (ver Cap. II)
Mato Grosso do Sul (Campo Grande e região)	III-2016	<i>Astraea cincta</i> <i>Astraea lobata</i> <i>Astraea surinamensis</i>
Minas Gerais: Caldas e região	III-2016	<i>Astraea manihot</i>
Minas Gerais (Grão Mogol, Diamantina e região) e Espírito Santo (Teófilo Otoni e Nova Venécia)	IV-2016	<i>Astraea cincta</i> <i>Astraea comosa</i> <i>Astraea gracilis</i>
Paraná (Londrina, Campo Mourão e Jaguariaíva)	X-2016	<i>Astraea cincta</i>
Minas Gerais (Serra do Cipó, Serra do Caraça, Ouro Preto e região)	XII-2016	<i>Astraea comosa</i> <i>Astraea manihot</i>
São Paulo (Santo Antônio do Pinhal e região)	I-2017	<i>Astraea manihot</i>
Goiás (Chapada dos Veadeiros, Niquelândia e região) e Distrito Federal	II-2017	<i>Astraea paulina</i>
Nordeste (Sergipe, Maceió, Pernambuco, Paraíba e Rio Grande do Norte)	VII-2017	<i>Astraea klotzschii</i> <i>Astraea surinamensis</i>

Para compor o grupo externo do estudo filogenético, foram selecionados acessos disponíveis no GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>) para todos os representantes de Crotonae: um acesso para cada um dos pequenos gêneros *Brasiliocroton*, *Sagotia* e *Sandwithia* (que possuem apenas duas espécies, cada), dois acessos para *Acidocroton* (representando as duas seções atualmente reconhecidas, uma delas correspondendo ao antigo gênero *Ophellantha*) e 21 acessos para *Croton*, representando os quatro subgêneros atualmente reconhecidos (Tabela V, mais informações no Capítulo V). Para o enraizamento das árvores foi utilizado um acesso de *Jatropha*, representando Jatrophaeae, a tribo irmã de Crotonae.

Já em relação ao grupo interno, foram amostradas todas as espécies de *Astraea*, com algumas representadas por mais de um acesso, com o objetivo de testar o monofiletismo do gênero e dos táxons reconhecidos na revisão taxonômica. A seleção de mais de um acesso por espécie, quando possível, foi guiada por fatores geográficos (como a ampla distribuição de *A. lobata* ou *A. paulina*, por exemplo) ou morfológicos (como no caso de *Astraea surinamensis*, um novo táxon proposto nesta tese, removido de *Astraea lobata*).

Dos três marcadores moleculares utilizados (*trnL-trnF*, *psbA-trnH* e *ITS*), o *ITS* e *trnL-trnF* foram eleitos para o estudo pela sua ampla utilização nos estudos com Euphorbiaceae e Crotonae (Wurdack *et al.* 2005, Berry *et al.* 2005, Caruzo *et al.* 2011, Riina *et al.* 2014), enquanto o *psbA-trnH* foi escolhido por ser um forte candidato para DNA barcoding (Kress *et al.* 2005, Lahaye *et al.* 2008), além de ter apresentado boa variabilidade para *Croton* sect. *Cleodora* (Caruzo *et al.* 2011). Dificuldades para a amplificação ocorreram principalmente na amplificação do *trnL-trnF* de amostras provenientes de materiais herborizados, provavelmente devido à degradação do DNA extraído. Outra grande dificuldade foi a amplificação do *ITS* para a única amostra representando *Astraea aureomarginata* incluída neste trabalho: mesmo após cinco tentativas de sequenciamento (direto e reverso, com produto purificado em alta concentração [ $> 100 \mu\text{g}/\mu\text{l}$ ]) uma mesma região das leituras apresentava múltiplos picos. Para explicar tal situação foram consideradas as possibilidades de poliploidia ou hibridização, porém, infelizmente, nenhuma destas hipóteses puderam ser testadas durante o desenvolvimento da tese.

Apesar da ampla utilização dos marcadores selecionados nos estudos de grupos relacionados, as análises de distância com estes marcadores realizados após a geração das sequências revelaram, entre os marcadores plastidiais, pouca variação para o *psbA-trnH* e uma grande variação para o *trnL-trnF*. Entretanto, a alta variação encontrada para o *trnL-trnF* não se reflete em um alto sinal filogenético, com poucos clados bem sustentados recuperados nas análises bayesiana e de máxima verossimilhança. A grande variação e alto sinal filogenético encontrado para o *ITS* nas análises citadas acima baseou a escolha deste conjunto de dados para as análises de tempo de divergência, reconstrução de áreas ancestrais e mapeamento de estado de caracteres morfológicos apresentados no Capítulo V. As análises de tempo de divergência e reconstrução de áreas ancestrais foram desenvolvidas no Real Jardín Botánico de Madrid (Espanha) com a supervisão da Dra. Ricarda

Riina e colaboração da Dra. Isabel Sanmartín durante o período de estágio de pesquisa no exterior (setembro a outubro de 2017).

**Tabela V:** Espécies de Crotonae selecionadas para compor o grupo externo do estudo filogenético neste trabalho.

Espécie	Sub-Grupo
<i>Acidocroton spinosus</i> (Standl.) G.L. Webster	<i>Acidocroton</i> sect. <i>Ophellantha</i>
<i>Acidocroton verrucosus</i> Urb. / <i>Acidocroton trichophyllus</i> Urb.	<i>Acidocroton</i> sect. <i>Acidocroton</i>
<i>Brasiliocroton mamoninha</i> P.E.Berry & Cordeiro	<i>Brasiliocroton</i>
<i>Croton alchorneicarpus</i> Croizat	<i>Croton</i> subg. <i>Adenophyllii</i> sect. <i>Cyclostigma</i>
<i>Croton astroites</i> Dryand	<i>Croton</i> subg. <i>Geiseleria</i> sect. <i>Lasiogyne</i>
<i>Croton cuneatus</i> Klotzsch	<i>Croton</i> subg. <i>Geiseleria</i> sect. <i>Cuneati</i>
<i>Croton cupreatus</i> Croizat	<i>Croton</i> subg. <i>Geiseleria</i> sect. <i>Cupreati</i>
<i>Croton echinocarpus</i> Baill.	<i>Croton</i> subg. <i>Adenophyllii</i> sect. <i>Cyclostigma</i>
<i>Croton echioides</i> Baill.	<i>Croton</i> subg. <i>Adenophyllii</i> sect. <i>Adenophyllii</i>
<i>Croton glandulosus</i> L.	<i>Croton</i> subg. <i>Geiseleria</i> sect. <i>Geiseleria</i>
<i>Croton gossypifolius</i> Vahl.	<i>Croton</i> subg. <i>Adenophyllii</i> sect. <i>Cyclostigma</i>
<i>Croton gracilipes</i> Baill.	<i>Croton</i> subg. <i>Adenophyllii</i> sect. <i>Adenophyllii</i>
<i>Croton heterocalyx</i> Baill.	<i>Croton</i> subg. <i>Geiseleria</i> sect. <i>Cleodora</i>
<i>Croton jacobinensis</i> Baill.	<i>Croton</i> subg. <i>Adenophyllii</i> sect. <i>Lasiogyne</i>
<i>Croton manampetsae</i> Leandri	<i>Croton</i> subg. <i>Croton</i>
<i>Croton nobilis</i> Baill.	<i>Croton</i> subg. <i>Croton</i>
<i>Croton palanostigma</i> Klotzsch	<i>Croton</i> subg. <i>Adenophyllii</i> sect. <i>Luntia</i>
<i>Croton piptocalyx</i> Müll.Arg.	<i>Croton</i> subg. <i>Quadrilobi</i> sect. <i>Sampatik</i>
<i>Croton rottlerifolius</i> Baill.	<i>Croton</i> subg. <i>Geiseleria</i> sect. <i>Cleodora</i>
<i>Croton sapiifolius</i> Müll.Arg.	<i>Croton</i> subg. <i>Quadrilobi</i> sect. <i>Quadrilobi</i>
<i>Croton schiedeanus</i> Schldl.	<i>Croton</i> subg. <i>Geiseleria</i> sect. <i>Eluteria</i>
<i>Croton trichotomus</i> Geiseler	<i>Croton</i> subg. <i>Croton</i>
<i>Croton troncosoi</i> Ahumada	<i>Croton</i> subg. <i>Geiseleria</i> sect. <i>Lamprocroton</i>
<i>Croton velutinus</i> Baill.	<i>Croton</i> subg. <i>Geiseleria</i> sect. <i>Barhamia</i>
<i>Sagotia racemosa</i> Baill. / <i>Sagotia brachysepala</i> (Müll.Arg.) Secco	<i>Sagotia</i>
<i>Sandwithia guyanensis</i> Lanj.	<i>Sandwithia</i>



## ORGANIZAÇÃO DA TESE

Para facilitar a publicação dos resultados desta tese, optou-se pela organização em forma de capítulos. De modo a primeiro apresentar os esforços para uma melhor delimitação das espécies de *Astraea*, e depois os resultados sistemáticos – a revisão taxonômica e o estudo filogenético do gênero. Os manuscritos são apresentados aplicando apenas a formatação de citações e referências exigidas por cada periódico para manter um padrão visual ao longo de toda a tese. A sequência dos capítulos foi organizada da seguinte forma:

- I. **Disentangling *Astraea lobata*: three new taxa in *Astraea* based on previous varieties of *Croton lobatus* (Euphorbiaceae).** Este manuscrito, já publicado no periódico *Phytotaxa*, propõe o reconhecimento de três novas espécies em *Astraea*: *A. digitata*, *A. gracilis* e *A. manihot*, com base na elevação a nível específico e combinação das variedades *digitatus*, *gracilis* e *manihot* de *Croton lobatus* propostas por Müller Argoviensis. Neste trabalho as lectotipificações dos nomes envolvidos foram realizadas, juntamente com comentários sobre distribuição geográfica e diferenciação entre estas espécies.
- II. **A report of infestation by phytoplasmas in *Astraea* (Euphorbiaceae) and its taxonomic implications in *Astraea douradensis*.** Neste trabalho, também já publicado no periódico *Phytotaxa*, tratamos de *Astraea douradensis*, uma espécie descrita por Steyemark (como *Croton douradensis*). Este táxon apresentava características diagnósticas bastante evidentes que, no entanto, são resultantes de infecção por fitoplasmas. Este trabalho se baseia na observação de populações com indivíduos infectados durante as viagens de campo realizadas e também na detecção, por método de amplificação de fragmentos genômicos, dos agentes infecciosos responsáveis pelas alterações morfológicas descritas para *A. douradensis*. Como consequência, *A. douradensis* foi reconhecida como sinônimo de *A. paulina*. Também reportamos a ocorrência de tal infestação em outra espécie do gênero, *A. manihot*.
- III. **What and where is *Astraea lobata* (Euphorbiaceae)? A redefinition of a widespread weedy species with the recognition of two new taxa.** Neste manuscrito é proposta uma nova delimitação para *Astraea lobata*, a espécie tipo de *Astraea*. Tal delimitação é baseada no tipo nomenclatural depositado no herbário BM, analisado pessoalmente. Dois novos nomes, *A. surinamensis* e *A. trilobata*, são apresentados baseados em nomes previamente considerados sinônimos de *Astraea lobata*. Destes dois últimos táxons, *A. trilobata* é excepcional entre as espécies do gênero por possuir poucos registros na região Neotropical, mas ser amplamente distribuída na África Tropical. A segregação destes dois novos táxons também é avaliada em um contexto filogenético, baseado em sequências de *trnL-trnF*, *psbA-trnH* (plastidiais) e *ITS* (nuclear). Uma breve discussão sobre um novo

posicionamento de *Brasiliocroton* (como irmão de *Croton* + [*Acidocroton* + *Astraea*] e não somente de *Croton*) é apresentada.

- IV. **Taxonomic revision of *Astraea* (Euphorbiaceae).** Aqui é apresentada a monografia de *Astraea* reunindo todos os avanços no conhecimento do grupo apresentados nos capítulos anteriores e outros trabalhos disponíveis na literatura, como aqueles abordando anatomia e micromorfologia. Os resultados apresentados neste capítulo se baseiam majoritariamente em materiais herborizados, mas populações de quase todas as espécies puderam ser observadas em seu hábitat natural. São reconhecidas 13 espécies para o gênero (*A. cincta*, *A. comosa*, *A. digitata*, *A. gracilis*, *A. klotzschii*, *A. lobata*, *A. macroura*, *A. manihot*, *A. paulina*, *A. praetervisata*, *A. subcomosa*, *A. surinamensis* e *A. trilobata*) e o tratamento inclui chave de identificação para estas espécies, com descrições morfológicas, comentários taxonômicos e nomenclaturais, listas completas de sinônimos, nomes populares encontrados em exsicatas (e aplicações etnobotânicas, em alguns casos), além de informações sobre distribuição geográfica, hábitat e fenologia, avaliação do status de conservação, pranchas de fotografias, mapas de distribuição e ilustrações a nanquim para todas as espécies não previamente ilustradas na literatura. Vinte lectótipos e três neótipos são designados.
- V. **Phylogeny and biogeography of *Astraea* with insights into the evolutionary history of Crotonaeae (Crotonoideae, Euphorbiaceae).** Neste trabalho, as relações filogenéticas internas de *Astraea* e com os demais gêneros da tribo Crotonaeae são avaliadas através de inferência Bayesiana e por máxima verossimilhança com base em três marcadores (*trnL-trnF*, *psbA-trnH* e *ITS*). Com uma ampla amostragem de *Astraea*, cobrindo todas as espécies do gênero e com mais de um acesso para aquelas de ampla distribuição (como, por exemplo, *A. lobata*, *A. paulina* e *A. klotzschii*), o monofiletismo de *Astraea* é corroborado e três clados principais são reconhecidos. As análises apontam que *Astraea* divergiu de *Acidocroton* muito antes da sua recente diversificação, e a hipótese de origem do gênero na América Central e Caribe foi refutada na análise biogeográfica do gênero no contexto de Crotonaeae, que aponta para uma série de eventos de especiação simpátrica no leste do Brasil e posterior ocupação do norte da América do Sul, América Central e Caribe. A recente diversificação de *Astraea* no leste do Brasil se reflete no não agrupamento dos múltiplos acessos amostrados para algumas das espécies, porém as relações filogenéticas apresentadas neste capítulo reforçam o reconhecimento dos novos táxons propostos nos capítulos I e III. Ainda, identificamos a ausência ou extrema redução das pétalas nas flores pistiladas como uma possível sinapomorfia de Crotonaeae e discutimos as relações de *Brasiliocroton* com os demais gêneros da tribo, assim como o posicionamento de *Sagotia* e *Sandwithia*, com uma amostragem mais ampla de *Croton* e sob a luz das análises de tempo de divergência e reconstrução de áreas e estados de caracteres ancestrais.

Ainda, no Anexo I apresentamos um manuscrito contendo a atualização da sinopse publicamente anteriormente (Caruzo & Cordeiro 2007) para *Astraea* no estado de São Paulo, enquanto o Anexo II contém o histórico taxonômico completo e detalhado de *Astraea*.

Ressalta-se que, de acordo com o Art. 30.8 do Código Internacional de Nomenclatural para Algas, Fungos e Plantas (McNeill et al. 2012, ver também Prado & Bicudo 2002), as propostas nomenclaturais apresentadas neste trabalho somente serão válidas pela publicação dos respectivos manuscritos.

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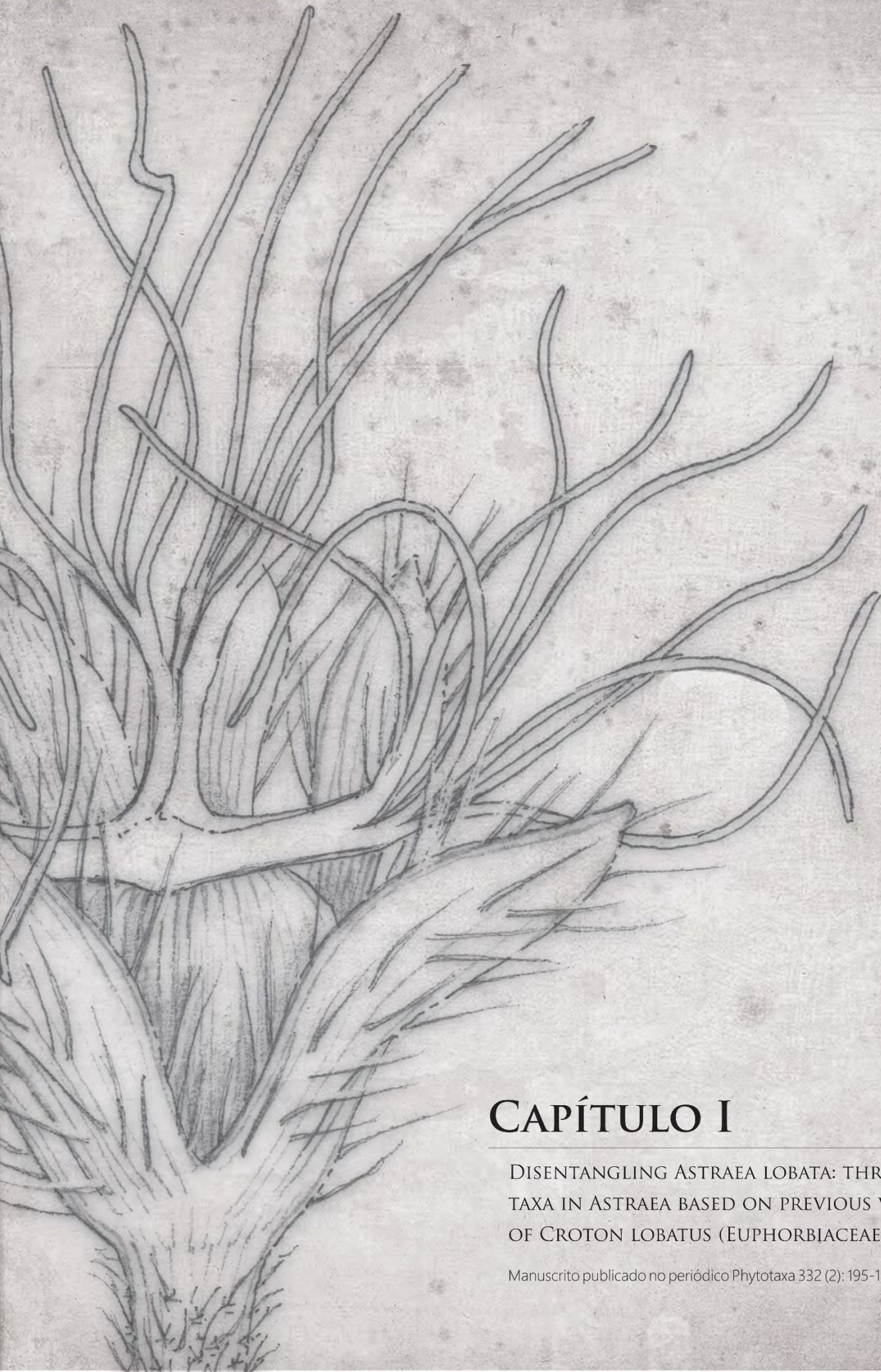
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## CAPÍTULO I

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DISENTANGLING *ASTRAEA LOBATA*: THREE NEW  
TAXA IN *ASTRAEA* BASED ON PREVIOUS VARIETIES  
OF *CROTON LOBATUS* (EUPHORBIACEAE)

Manuscrito publicado no periódico *Phytotaxa* 332 (2): 195-198.



**DISENTANGLING *ASTRAEA LOBATA*: THREE NEW TAXA IN *ASTRAEA* BASED ON PREVIOUS VARIETIES OF *CROTON LOBATUS* (EUPHORBIACEAE)**Otávio Luis Marques da Silva <sup>1,2</sup> & Inês Cordeiro <sup>1</sup><sup>1</sup>*Instituto de Botânica, Secretaria do Meio Ambiente, Cx. Postal 3005, 01061-970, São Paulo, SP, Brazil*<sup>2</sup>*author for correspondence, email: otaviolmarques@gmail.com*

Within *Astraea* Klotzsch (1841: 194), *Astraea lobata* (Linnaeus 1753: 1005) Klotzsch (1841: 194) may be considered the most taxonomically complex species due to its wide geographical distribution and the several varieties that have been proposed for this species by Müller Argoviensis (1866, 1874<sup>1</sup>). In his concept, Müller Argoviensis (1866) united under *Croton lobatus* Linnaeus (1753: 1005) plants with 3–5-partite leaves almost as long as the petioles, subulate stipules, the bracts not well developed and ovaries with varied indumentum. In De Candolle's Prodrômus, Müller Argoviensis (1866) recognized eight varieties, maintaining this concept in the Flora Brasiliensis (Müller Argoviensis 1874<sup>1</sup>) with few modifications. Morphological characters and geographical distribution support the recognition of some of these varieties as species distinct from *A. lobata*. As part of an undergoing taxonomic revision of *Astraea*, these distinct taxa must be validly published for further studies on this genus. Therefore, in this note we propose these novelties with commentaries about morphology and geographic distribution, along with photos to illustrate them and lectotypifications when necessary.

These decisions are made based on the study of more than 3000 specimens from 78 herbaria, along with fieldwork for observation of populations. However, due to nomenclatural problems involving Müller Argoviensis' concept of *Croton lobatus* var. *lobatus* in contrast with the original concept of *Croton lobatus* presented by Linnaeus (1753: 1005) and based on previous works (Martyn 1728), comparisons between these new species and *A. lobata* will not be presented here until further problems are solved (Silva *et. al.*, in prep.).

***Astraea digitata* (Müll.Arg.) O.L.M.Silva & Cordeiro, *comb. et stat. nov.* *Croton lobatus* var. *digitatus* Müller Argoviensis (1866: 668). *Croton digitatus* Salzmann ex Schlechtendal (1846: 240), *nom. illeg.* Lectotype (designated here):—BRAZIL. Bahia: unknown locality, unknown date, *P. Salzmann* 492 (G00312450!); remaining syntype:—BRAZIL Bahia: unknown locality, unknown date, *J. Lhotsky* s.n. (G00312449!).**

*Astraea digitata* is characterized by leaves with long simple trichomes on the abaxial surface (Fig. 1A), more concentrated at the base, pistillate flowers with calyx lobes hirsute on the outer surface (Fig. 1B–C) and the

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<sup>1</sup> Publicando erroneamente. O correto é 1873.



calyx of staminate flowers with one simple trichome on the outer surface of each lobe (Fig. 1D). Both *A. digitata* and *A. gracilis* occur on edges of humid forests, but the indumentum of several structures is remarkably different in these two species.

This species is found in northeastern Brazil, in the states of Bahia and Pernambuco, in the Atlantic Forest domain, growing both in shaded or sunny environments, usually along forest edges, or disturbed sites, such as cocoa plantations and secondary forests.

*Croton digitatus* Salzm. ex Schtdl. is an illegitimate name as it is a later homonym—the epithet was first used by Geiseler (1807) and afterwards also by Steudel (1821) and Don in Sweet (1839). According to Schlechtendal (1846), it would be distinguished from *Croton lobatus* by inflorescence length and seed shape. The author cited a collection (*P. Salzmann s.n.*) from Bahia for this name, and when Müller Argoviensis (1866) published *Croton lobatus* var. *digitatus*, he added Salzmann's collection number 492 and another syntype, namely Lhotsky's collection without number. Since Salzmann's collections are cited both in the protologue of *Croton digitatus* and *Croton lobatus* var. *digitatus*, we choose them to represent the species. We select the specimen deposited at G as lectotype because it is the only specimen with the number indicated by Müller Argoviensis on it, and also presents a good conservation state, with enough material to recognize the species, and is in the herbarium where most of collections for De Candolle's Prodrômus are deposited. Four other specimens collected by Salzmann were found, either unnumbered or with a different number, which may also serve as good references for *A. digitata*: three specimens without number deposited at E (326421!), HAL (136204!) and K (missing barcode and accession number) and another one with the number 422 at W (missing barcode and accession number).

***Astraea gracilis* (Müll. Arg.) O.L.M. Silva & Cordeiro, comb. et stat. nov.** *Croton lobatus* var. *manihot* lus *gracilis* Müller Argoviensis (1866: 668). *Croton lobatus* var. *gracilis* (Müll.Arg.) Müller Argoviensis (1873: 273). Lectotype (designated here):—BRAZIL. Rio de Janeiro: 'in pascuis montanis prope Sebastianopolis', unknown date, *C.F.P. von Martius s.n.* (G00312451!, isolectotypes M0089080!, M0089081!, M0089082!); remaining syntypes:— BRAZIL. Rio de Janeiro, unknown date, *C. Gaudichaud-Beaupré 1129* (G00312452!), *M.K. Guillemette 167*<sup>2</sup> (G00312453!, isosyntypes NY00594296!, NY504207!).

*Astraea gracilis* may be identified by its 3–5-partite leaves and lack of indumentum on the abaxial leaf surface (Fig. 1F), on the outer surface of the calyx lobes and on the ovary and fruit. This species is found in eastern Brazil, with most materials collected from Rio de Janeiro, where it grows along the edges of deciduous or evergreen forests, usually on shaded environments or in disturbed places such as and roadsides within the

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<sup>2</sup> Publicado erroneamente. O correto é J.B.A. Guillemine – este erro é corrigido no Capítulo IV, na revisão taxonômica de *Astraea*

Atlantic Forest domain. *Astraea gracilis* is quite similar to *A. digitata* due to its herbaceous habit (Fig. 1E), but the lack of indumentum of leaves and calyx of both pistillate (Fig. 1H) and staminate (Fig. 1G) flowers distinguishes these species.

Martius' collection was chosen as lectotype as duplicates are found in several herbaria, and the duplicate deposited at G was chosen because of its good conservation state, including both pistillate and staminate flowers and fruits. Furthermore, G is original herbarium of the author. Another collection, *C. Gaudichaud-Beaupré 1729* (probably a mis-transliteration of 1129), was also found in NY (00885197!) and may serve as additional reference for *A. gracilis*.

***Astraea manihot* (Müll.Arg.) O.L.M. Silva & Cordeiro, comb. et stat. nov.** *Croton lobatus* var. *manihot* Müller Argoviensis (1866: 668). *Astraea manihot* Klotzsch (1841: 194), *nom. nud.* *Croton manihot* (Klotzsch) Baillon (1864: 361), *nom. inval.* Lectotype (designated here):— BRAZIL. Minas Gerais: Dourado, 01 June 1846, *J.F. Widgren s.n.* (S17-36790!); remaining syntype:— BRAZIL. Unknown locality, unknown date, *F. Sellow s.n.* (BR00583982!, isosyntypes K!, P00634915!, TUB009126!).

*Astraea manihot* usually has 5(–7)-partite leaves (Fig. 1K), although it is not uncommon to observe only 3-partite leaves near the inflorescences. It also has long-pedicellate pistillate flowers (Fig. 1L), calyx lobes that do not surpass the fruit in length (Fig. 1N), as well as staminate cymules with up to 10 flowers each (Fig. 1M). The shrubby habit (Fig. 1J), along with the long-pedicellate pistillate flowers (vs. short-pedicellate to sessile in *A. digitata* and *A. gracilis*) and multiflowered staminate cymules of *A. manihot* (vs. with 2–4 flowers in *A. digitata* and *A. gracilis*) easily distinguishes it both from *A. digitata* and *A. gracilis*.

This species is found in southeastern Brazil, especially in the state of Minas Gerais, with few collections registered also for Paraná and Santa Catarina states. It grows in dry open or humid shaded environments, including edges of deciduous or evergreen forests, gallery forests in cerrado, disturbed areas, such as secondary forest, and *Eucalyptus* plantations.

As most of Klotzsch's names that accompanied his original description of *Astraea*, *Astraea manihot* Klotzsch lacks a diagnosis, and, although Klotzsch in Seemann (1853) cites that specimens of all species of *Astraea* were preserved at the Royal Herbarium at Berlin (B), all original specimens are now destroyed. Baillon (1864) combined this name under *Croton*, as *Croton manihot* (Klotzsch) Baill. In addition, this name is based on a *nomen nudum* and even considering that Baillon cited three collections, he still gave no diagnosis. Therefore, only Müller Argoviensis' name is valid and consequently is the one we transfer to *Astraea*.



**Figure 1:** Morphological characters of *Astraea digitata*, *A. gracilis* and *A. manihot*. **A–D:** *Astraea digitata*. **A.** abaxial surface of leaf, **B.** pistillate flowers, **C.** immature fruit, **D.** cymules with staminate flowers in bud. **E–I:** *Astraea gracilis*. **E.** herborized branch with inflorescences, **F.** abaxial surface of herborized leaf, **G.** staminate cymule, **H.** pistillate flower, **I.** herborized inflorescences with immature fruits. **J–N:** *Astraea manihot*. **J.** habit with inflorescences, **K.** abaxial surface of leaf, **L.** pistillate flower, **M.** staminate cymules with one mature flower, **N.** immature fruits with mature staminate flowers. Photos: O.L.M. Silva.

According to the protologue of *Croton lobatus* var. *manihot* Müll.Arg., the original materials seen by the author would be in B (*F. Sellow*) and S (*J.F. Widgren*). Once Sellow's collection at B is destroyed, Widgren's collection at S was chosen as lectotype, although Sellow's isosyntypes may be found in other herbaria. Specimens from Minas Gerais also collected by *J.F. Widgren*, but numbered as 364, were found at BR (BR00583842!, BR00583843!, BR00583844!) and S (S17-36787!, S17-36789!) and they may serve as additional reference for *Astraea manihot*.

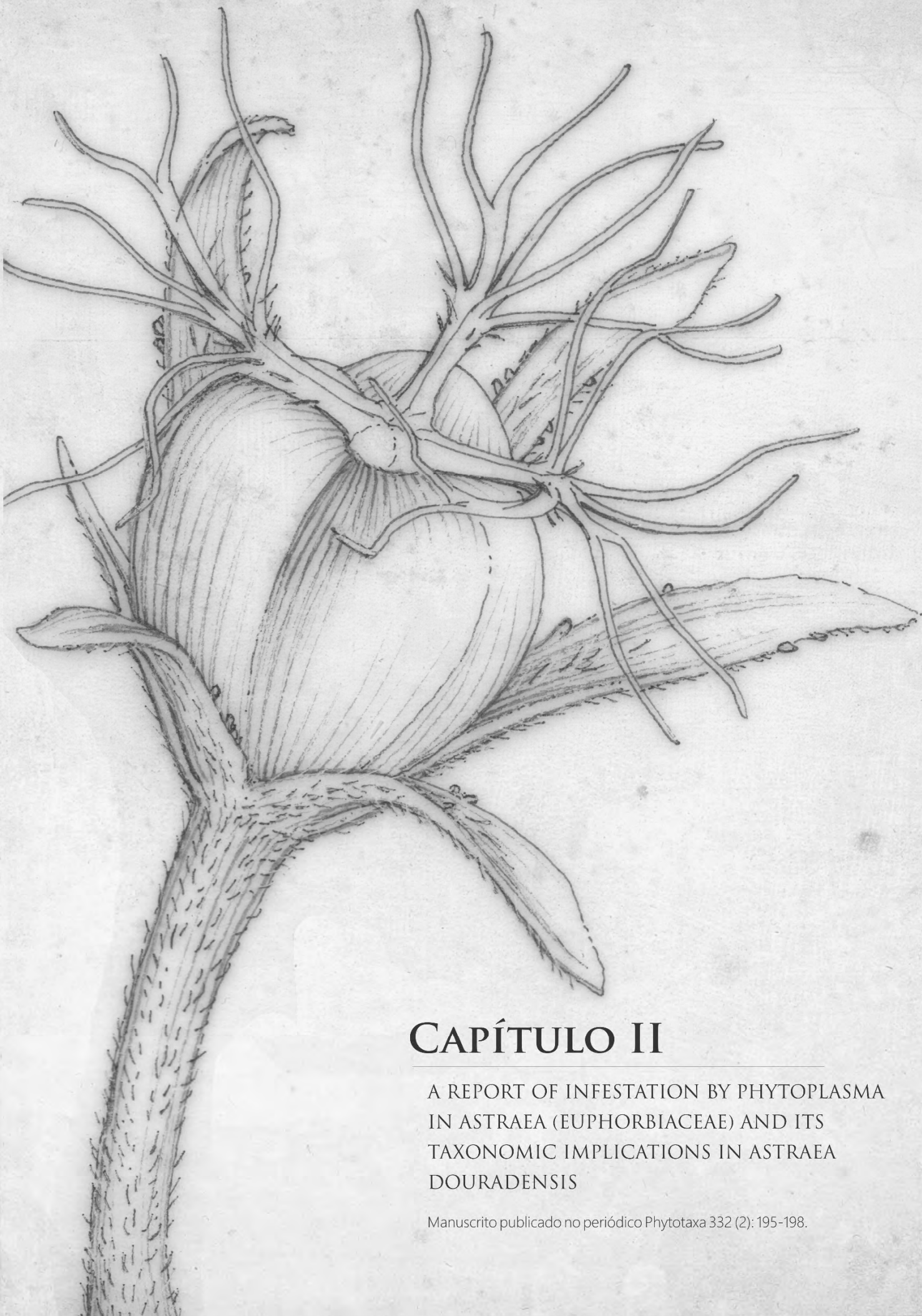
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## CAPÍTULO II

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A REPORT OF INFESTATION BY PHYTOPLASMA  
IN ASTRAEA (EUPHORBIACEAE) AND ITS  
TAXONOMIC IMPLICATIONS IN ASTRAEA  
DOURADENSIS

Manuscrito publicado no periódico Phytotaxa 332 (2): 195-198.

## A REPORT OF INFESTATION BY PHYTOPLASMAS IN *ASTRAEA* (EUPHORBIACEAE) AND ITS TAXONOMIC IMPLICATIONS IN *ASTRAEA DOURADENSIS*

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Phytoplasmas infestations are widely documented in angiosperms, especially in ornamental species (Chaturverdi *et al.* 2010). Infestations by these phloem-limited plant pathogenic bacteria may induce several symptoms such as loss of floral meristem determinacy and abnormal flower development, including virescence of floral organs and phyllody, i.e., replacement of floral organs by leaf-like structures (Lee *et al.* 2000, Chaturverdi *et al.* 2010). However, symptoms may also vary according to the plant host and other factors, such as localization of phytoplasmas in host tissues (Bertaccini 2007). Some species may be infested but remain asymptomatic by seasonal dormancy and they may act as reservoirs for the further spread of the phytoplasmas, involving insect vector (Dermastia *et al.* 2017). Developments in the detection methods of phytoplasmas have contribute to a better understanding of these intriguing bacteria, and nowadays identification of these organisms rely mostly in molecular methods such as polymerase chain reaction of selected phytoplasma-specific gene regions (Dermastia *et al.* 2017). Our current understanding about phytoplasmas includes how the phenotype linked to the infestation by phytoplasma are triggered: Kitazawa *et al.* (2017) present results which suggest that these changes in floral organs are caused by the interactions of phylogen (a virulence factor conserved in phytoplasmas) with ABCE-class MADS domains transcription factor (MTFs), which is known as key regulator of floral organs development in angiosperms.

This report is part of an ongoing taxonomic revision of *Astraea* Klotzsch (1841: 194), based on more than 3,500 herbarium specimens (including nomenclatural types) from more than 80 herbaria, along with fieldwork for observation of populations. In this work, we report the occurrence of infestation by phytoplasmas in *Astraea paulina* Didrichsen (1857: 138) and *Astraea manihot* (Müller Argoviensis 1866: 668) Silva & Cordeiro (2017: 299) and its taxonomic implication in *Astraea douradensis* (Steyermark 1958: 4) Caruzo in Caruzo *et al.* (2014: 127).

In the protologue of *Croton douradensis*, Steyermark (1958), indicates that this species is characterized by staminate flowers with pubescent receptacle and pistillate flowers with a 6-lobed calyx, with one lobe

unequal to the others. Our analysis of the holotype of *Astraea douradensis* (E.Y. Dawson 14973, R 104976), along with the illustrations provided in Steyermark (1958), show that there are additional diagnostical characters which may easily distinguish it from other species of *Astraea*, such as long-pedicellate (more than 1 cm long) pistillate flowers, with patent calyx lobes and cylindrical ovary (Fig. 1A), besides staminate cymules with up to 10 flowers each (Fig. 2B). However, there are very few collections which could be identified as *Astraea douradensis* following these characters, and therefore it is considered a rare species. Additionally, field notes in G. Martinelli 5306 (CEPEC, HUEFS, NY, RB, SPF), mention that only one individual was observed, given some indication of its local rareness.

In G. Martinelli 5306 and all other collections of *Astraea douradensis* (G. Hatschbach 56805 [FUEL!, HUEFS!, MBM!], B.M.T. Walter 1824 [CEN!, EAC!, RB!, UB!] and R.M. Harley 22681 [CEPEC!, NY!, SPF!, UEC!]), it is possible to observe an unusual growth in male cymules, with an uncommon paniculiform branching pattern of staminate cymules (Fig. 3C), and malformation of the ovary resulting in a laminar, leaf-like structure, with filiform appendages at the apex (Fig. 4E), which resembles the branched styles characteristic of *Astraea*. Stamens are also transformed into leaf-like, laminar structures (Fig. 1D). These morphological traits are consistent with what is reported for infestation by phytoplasma in plants (Lee *et al.* 2000, Chatuverdi *et al.* 2010).

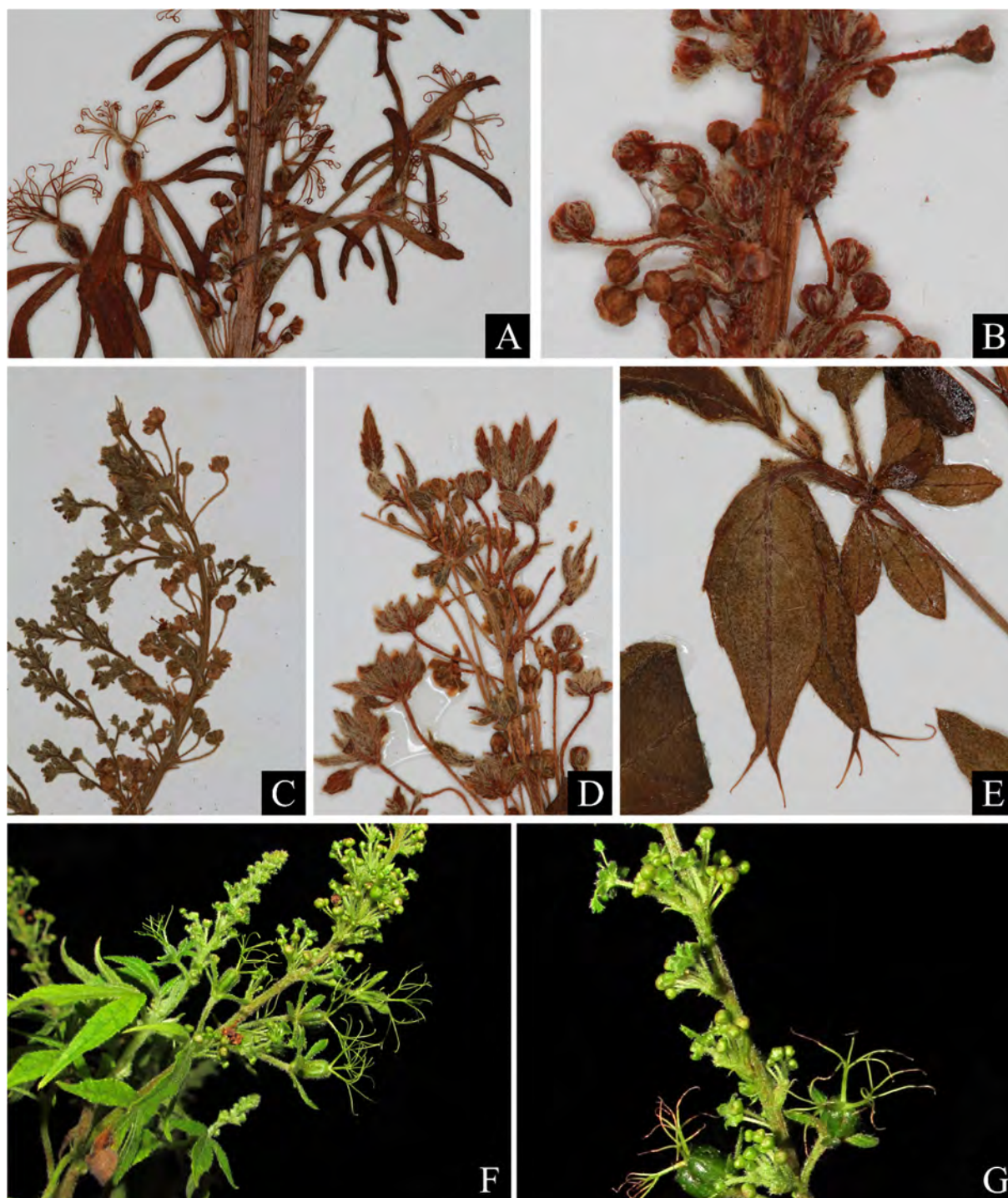
It is noteworthy that the isotype of *Astraea douradensis*, deposited at RSA (catalogue number 2661!), does not show long-pedicellate pistillate flowers, with patent calyx lobes and cylindrical ovary, and the staminate cymules possess up to 5 flowers each. Lacking the diagnostic characters of *A. douradensis*, that specimen resembles *A. paulina*, a widespread species found within the belt of seasonal woodlands in South America, comprehending the Caatinga, Cerrado and Chaco phytogeographic domains, named as “dry diagonal” by Prado & Gibbs (1993). Localities from where specimens with the morphological characteristics of *A. douradensis* were found are within the distribution range of *A. paulina* and there are numerous collections of *A. paulina* from these localities. Additionally, *A. paulina* also occurs in gallery forests within cerrado vegetation, congruent to what is described by Steyermark (1958) for *A. douradensis*. Considering that the diagnostical characters present in the holotype of *A. douradensis* and specimens identified as such are result of infestation by phytoplasmas and the overlapping in morphological traits, distribution range and habitat with *A. paulina*, we conclude that *A. douradensis* should be treated as a synonym of *A. paulina*:

***Astraea paulina*** Didrichsen (1857: 138). Type:—BRAZIL. São Paulo: Itú, February 1834, N.T. Lund s.n. (holotype C, isotype G00312455!).

= *Astraea douradensis* (Steyerm.) Caruzo in Caruzo *et al.* (2014: 127). *Croton douradensis* Steyermark (1958: 4).

Type:—BRAZIL. Goiás: in gallery forest along stream 17 km east of Formoso, region of the southern Serra Dourada at 48° 40' W, 13° 40' S, 19 May 1956, E.Y. Dawson 14973 (holotype R!, isotypes F!, RSA!).





**Figure 1:** Morphological traits related to infestation by phytoplasmas in *Astraea*. **A.** pistillate flowers with long pedicels, patent calyx and cylindrical ovary from *G. Martinelli 5306* (SPF). **B.** Staminate cymules with up to 10 flowers from *G. Martinelli 5306* (HUEFS). **C.** Unusual growth of staminate cymules from *B.M.T. Walter 1824* (RB) **D.** Staminate flowers with stamens transformed into leaf-like, laminar structures from *G. Martinelli 5306* (HUEFS). **E.** Ovary transformed into laminar, leaf-like structures, with filiform appendages at the apex from *G. Hatschbach 56805* (HUEFS). **F–G.** Inflorescences of individuals from Franco da Rocha, São Paulo (*O.L.M. Silva 235* [SP]), showing pistillate flowers with patent calyx and cylindrical ovaries, and staminate cymules with multiple flowers, bearing stamens transformed into leaf-like, laminar structures. (photos: O.L.M. Silva).



It is important to notice that another species of *Astraea* may show the same morphological traits as result of infestation by phytoplasmas. During our fieldwork, we found individuals of *Astraea manihot* in São Paulo (southeastern Brazil, O.L.M. Silva 235, SP 475344!) possessing all the malformations reported above (Fig. 1F–G).

Leaf samples from individuals of *Astraea manihot* from São Paulo were submitted to DNA extraction with the DNeasy Plant Mini Kit and we could trace phytoplasmas in these samples through polymerase chain reaction (PCR). In PCR we amplified genomic fragments of 1.2 kb with the primers 16F2n/16R2 (Lee & Gundersen 1996) in reactions with 20 ng of total DNA, 200 µM of each dNTP and 0.4 to 1.0 µM of each primer. PCR program consisted of an initial denaturation at 94 °C for 2 min, followed by 35 cycles of denaturation at 94 °C for 1 min, annealing at 55 °C for 2 min and extension at 72 °C for 3 min, and final extension at 72 °C for 3 min. PCR products were analyzed through electrophoresis in 1 % agarose gel colored with Sybr Safe (Invitrogen) and visualized in UV light transilluminator.

Although morphologically similar, *Astraea manihot* may be distinguished from *A. paulina*, in their healthy form, by having pedicels of pistillate flowers with up to 1 cm long (vs. subsessile pistillate flowers, with pedicels up to 0.3 cm long in *Astraea paulina*, while in infested plants we observe pedicels with 1.5–3 cm long) and leaves (3–)5(–7)-partite (vs. entire or 2–3-partite leaves in *Astraea paulina*). Therefore, special attention is required when identifying individuals of *Astraea* presenting the suite characteristics linked to *A. douradensis*. Nonetheless, as far as we know, within *Astraea*, only *A. manihot* and *A. paulina* are susceptible to infestation by phytoplasmas.

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## CAPÍTULO III

WHAT AND WHERE IS *ASTRAEA LOBATA*  
(EUPHORBIACEAE)? A REDEFINITION OF A  
WIDESPREAD WEEDY SPECIES WITH THE  
RECOGNITION OF TWO NEW TAXA

Manuscrito a ser submetido ao período Botanical Journal of the Linnaean Society

## WHAT AND WHERE IS *ASTRAEA LOBATA* (EUPHORBIACEAE)? A REDEFINITION OF A WIDESPREAD WEEDY SPECIES WITH THE RECOGNITION OF TWO NEW TAXA

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**Abstract**—*Astraea lobata* (L.) Klotzsch is, taxonomically, the most complex species within *Astraea* Klotzsch (Euphorbiaceae) due to its wide geographic distribution range and broad morphological variation, which is reflected in the high number of synonyms associated with this name. In this paper, we present a more restrict definition of *A. lobata* and recognize two new taxa previously hidden under this species: *A. surinamensis* and *A. trilobata*. We used molecular data from the ITS (nrDNA), *trnL-trnF* and *psbA-trnH* (cpDNA) regions to test the new delimitation of *Astraea lobata* and to understand its relationship with the two new taxa and other representative *Astraea* clades. Additionally, we present comments about morphology and distribution of these three taxa, and briefly discuss relationships among *Crotoneae* genera in the light of an increased sampling of *Astraea* species.

**Keywords** — *Crotoneae*, nomenclatural notes, taxonomy

## INTRODUCTION

*Astraea* Klotzsch is a genus of ca. 15 species of herbs and shrubs (Caruzo *et al.*, 2014; Silva & Cordeiro, 2017; Silva *et al.*, 2017) which, according to the recent molecular phylogenies, is a monophyletic group within tribe Crotoneae (Euphorbiaceae: Crotonoideae) and is sister to a clade formed by *Croton* L. and *Brasilicroton* (Wurdack, Hoffman & Chase 2005; Berry *et al.* 2005; Riina *et al.* 2014). Most species of *Astraea* are centered in South America (Caruzo *et al.*, 2014) with the exception of the weedy *A. lobata*. This species is widespread in the Neotropics (from southern Florida, Mexico and West Indies to northern Argentina) and it has also been documented for the Old World as an alien species (Gaikwad, Gore & Garad 2012; Caruzo *et al.*, 2014; Das, Kar & Datta 2016).

In the original description of *Astraea*, almost all names proposed by Klotzsch (1841) are *nomina nuda* because they lack a diagnosis. Also, there is no reference to any type material that could guide us to establish their identity. The only valid name from Klotzsch (1841) is *A. lobata*, which is a combination based on *Croton lobatus* published in Linnaeus' (1753) *Species Plantarum*. Müller Argoviensis (1866; 1873) proposed numerous varieties for *C. lobatus* reflecting the high morphological variability across its geographic range. In fact, several of Müller Argoviensis' varieties were based on specimens from different regions along the Neotropics, leading to the interpretation that there is a geographic component behind them. This morphological variability is also translated into a difficult taxonomy as suggested by the 33 synonyms currently recognized under *A. lobata* (Govaerts, Frodin & Radcliffe-Smith, 2000).

Many of the varieties of *Croton lobatus* proposed by Müller Argoviensis (1866) were described based on material collected in eastern Brazil, and three of them (*C. lobatus* var. *digitatus*, *C. lobatus* var. *gracilis* and *C. lobatus* var. *manihot*) were recently considered as distinct species and transferred to *Astraea* (as *A. digitata*, *A. gracilis* and *A. manihot*, respectively; Silva & Cordeiro, 2017). This work aims to publish nomenclatural and taxonomic novelties and validate names that related to *Astraea lobata* that will be necessary for later works within a more comprehensive taxonomic revision and phylogenetic framework of the entire genus.

## MATERIALS AND METHODS

**Taxonomy**—Herbarium specimens analyzed for the purpose of this study include collections of *Astraea* from more than 90 herbaria - A, ALCB, AMD, ASE, B, BHCB, BHZB, BM, BOTU, BR, C, CEN, CEPEC, CESJ, CGMS, COL, CTES, CVRD, DAV, E, EAC, ESA, F, FHI, FLAS, FSU, FTG, FUEL, G, GH, HAL, HB, HBG, HCF, HEPH, HNBU, HRB, HRCB, HUEFS, HUEM, HUFU, IAC, IBGE, IEB, INPA, IPA, JPB, K, L, LE, LINN, M, MA, MAC, MBM, MBML, MG, MEXU, MICH, MO, MPU, NY, OUPR, P, PACA, PAMG, PEUFR, R, RB, RSA, S, SJRP, SP, SPF, SPSF, TCD,

TOGO, TUB, U, UB, UC, UEC, UESC, UFG, UFP, UFRN, US, USF, USZ, VIC, VIES, W, WAG and WIS (abbreviations according to Thiers 2018, continuously updated). The analysis of more than 5,000 specimens was complemented with collecting trips for observation of Brazilian populations in the field. For nomenclatural matters, we obtained protologues from the Biodiversity Heritage Library (<http://biodiversitylibrary.org>) and high-resolution images mostly from JStor Global Plants website (<http://plants.jstor.org/>) when we were unable to physically examine type specimens.

As this work stands as part of the ongoing taxonomic revision of *Astraea* (Silva & Cordeiro [Capítulo IV]), we do not present here morphological descriptions nor a complete review of nomenclatural matters for any of the studied taxa. We propose two new taxa (See Results and Discussion) based on names previously synonymized under *Astraea lobata* in its current delimitation (hereafter referred as *A. lobata* s.l.). And then test these two new taxa and the recircumscribed *A. lobata* (hereafter referred as *A. lobata* s.s.) using a phylogenetic approach through the analysis of DNA sequence data from the nuclear ITS (nrDNA) and the plastid *trnL-trnF* and *psbA-trnH* regions.

**Taxon sampling for phylogenetic analysis**—We selected four samples of *Astraea lobata* s.s. from Mexico, Central America (Costa Rica: Guanacaste), and South America (Argentina and Brazil) to represent its geographic range. Also, based on morphological characters, we segregated two new taxa (see Results and Discussion), previously recognized as synonyms of *A. lobata* s.l. by Govaerts *et al.* (2000): *A. surinamensis* is represented by three samples from the Brazilian states of Rio Grande do Norte (RN), Bahia (BA), Espírito Santo (ES) and Mato Grosso do Sul (MS), while *A. trilobata* is represented by one sample from Ivory Coast. In addition, we included samples for three other species of *Astraea* from eastern Brazil (*A. comosa*, *A. macrourea* and *A. praetervisita*) to represent the remaining species of the genus. As outgroup (Nixon and Carpenter 1993), we included species from all other genera of *Crotoneae* based on previous studies about this tribe (Berry *et al.*, 2005; Riina *et al.*, 2014): one representative of each one of the small genera (*Brasiliocroton*, *Sagotia* and *Sandwithia*), two of *Acidocroton* (one representing *Acidocroton* sect. *Acidocroton* and the other representing *Acidocroton* sect. *Ophellantha*), and four of the giant genus *Croton*, representing each of the four subgenera recognized by van Ee *et al.* (2011). All trees were rooted using a species of *Jatropha*, which corresponds to *Jatrophaeae*, the sister tribe of *Crotoneae* (Wurdack *et al.*, 2005). Species and voucher information are presented on Table I.

**Molecular procedures**—DNA was extracted from leaves dried in silica-gel or samples from herbarium specimens using Invisorb® Spin Plant Mini Kit, according to manufacturer's protocol (with minor modification such as an overnight incubation for chemical lysis and 30 minutes incubation before elution). We used one nuclear region, ITS (including ITS1, the 5.8S gene and ITS2) and two plastid intergenic spacers, *trnL-trnF*

(hereafter referred as *trnL-F*) and *psbA-trnH* (hereafter referred as *psbA*), based on its usefulness in phylogenetics of Crotonae (Berry *et al.*, 2005; Caruzo *et al.*, 2011; van Ee *et al.*, 2011; Riina *et al.*, 2014) and availability of sequences in GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>) for outgroups. For ITS, we used the primers CCTTATCATTTAGAGGAAGGAG and TATGCTTAAAYTCAGCGGGT (Wurdack, K.J. pers. com., Cullmann Program) designed specifically for angiosperms to avoid amplification of non-target sequences (complemented by visual inspection on 1% agarose gel, see below); for *trnL-F* we used *c* (CGAAATCGGTAGACGCTACG) and *f* (ATTTGAACTGGTGACACGAG) primers designed by Taberlet *et al.* (1991) for amplifying the entire region, and when the DNA was highly degraded the amplification of *trnL-F* was performed in two steps using *c* and *d* (GGGGATAGAGGGACTTGAAC), and *e* (GGTCAAGTCCCTCTATCCC) and *f* primers (*d* and *e* primers were also designed by Taberlet *et al.* [1991]). For *psbA-trnH* we used the *psbA* (GTTATGCATGAACGTAATGCTC) primer, designed by Sang, Crawford & Stuessey (1997), and *trnH2* (CGCGCATGGTGGATTCACAATCC) primers, designed by Tate & Simpson (2003).

Polymerase chain reactions (PCR) were performed following previous studies, with annealing temperatures of 50°C for ITS, 61°C for *trnL-F* and 62°C for *psbA-trnH*. Additionally, in some reactions we used the same annealing temperature of 50°C for all three regions (according to the protocol modified by L. Brito *et al.*, pers. com., University of São Paulo). PCR products were run in 1% agarose gel to corroborate the existence of a single band, especially with those from ITS, and purified using Wizard® SV Gel and PCR Clean Up System (Promega), and then sequenced on ABI 3370 automatic sequencer with the same primers mentioned above.

**Sequence assembling and alignment**—All sequences newly generated for this study were analyzed and assembled using *phred/phrap/consed* packages (Ewing & Green, 1998; Ewing *et al.*, 1998; Gordon, Abajian & Green, 1998), and *phred 20* was considered as minimum quality for base calling. For multiple sequence alignment, we used Clustal Ω (Sievers *et al.*, 2011) with successive 10, 100 and 1000 iterations, followed by bidimensional alignment in RNASalsa (Stocsits *et al.*, 2009). We performed manual editing in the case of the plastid spacer based on similarity criterion (Simmons, 2004). For bidimensional alignment, we used sequences of *Suregada boiviniana* Baill. (Crotonoideae: Gelonioae; voucher data on Table I) to build constraints to guide the alignment based on the secondary structure of the putative RNA sequences.

Table I. Voucher information for the samples used in this work. Sequences newly generated for this study are labeled as NG.

Terminal	Taxon	Specimen	Origin	<i>trnLF</i>	<i>psbA</i>	ITS
<i>Acidocroton</i> sect. <i>Acidocroton</i>	<i>Acidocroton tricophyllus</i> <i>Acidocroton verrucosus</i>	HABJ 81844 (MICH) G.L. Webster 8463	Holguin, Cuba Jamaica	EF408087 -	- -	- AY971344
<i>Acidocroton</i> sect. <i>Acidocroton</i>	<i>Acidocroton spinosus</i>	A.H. Gentry 74385 D.E. Breedlove 46994	Jalisco, Mexico Chiapas, Mexico	AY971344 -	- -	- AY971263
<i>A. comosa</i>	<i>Astraea comosa</i>	O.L.M. Silva 318	Santa Bárbara, MG, Brazil	NG	NG	NG
<i>A. klotzschii</i>	<i>Astraea klotzschii</i>	O.L.M. Silva 229	Ilhéus, BA, Brazil	NG	NG	NG
<i>A. lobata</i>	<i>Astraea lobata</i>	O.L.M. Silva 119	Aquidauana, MS, Brazil	NG	NG	NG
<i>A. lobata</i>	<i>Astraea lobata</i>	R. Riina 1890	Salta, Argentina	NG	NG	NG
<i>A. lobata</i>	<i>Astraea lobata</i>	U. Chavarria 2199	Bagaces, Costa Rica	NG	NG	NG
<i>A. lobata</i>	<i>Astraea lobata</i>	C.A. Maya-Lastra 621	Múgica, Mexico	NG	NG	NG
<i>A. praetervisia</i>	<i>Astraea praetervisia</i>	J.R. Pirani 2938	Ilhéus, BA, Brazil	NG	NG	NG
<i>A. surinamensis</i>	<i>Astraea surinamensis</i>	O.L.M. Silva 217	Ilhéus, BA, Brazil	NG	NG	NG
<i>A. surinamensis</i>	<i>Astraea surinamensis</i>	O.L.M. Silva 117	Campo Grande, MS, Brazil	NG	NG	NG
<i>A. surinamensis</i>	<i>Astraea surinamensis</i>	B.W. van Ee 549	Puerto Rico	EU497699	HM044809	EU497727
<i>A. trilobata</i>	<i>Astraea trilobata</i>	J. Koning 4937	Ivory Coast	NG	NG	NG
<i>Brasiliocroton</i>	<i>Brasiliocroton mamoninha</i>	Lobo 340 J.R. Pirani 4947	? Linhares, ES, Brazil	AY794691 -	- HM044810	- EU586944
<i>C. gracilipes</i>	<i>Croton gracilipes</i>	M. Nee 47412	Bolivia	EU586962	HM044823	EU586909
<i>C. nobilis</i>	<i>Croton nobilis</i>	B.W. van Ee 938	Toliar, Madagascar	HM044778	HM044831	HM044797
<i>C. rottlerifolius</i>	<i>Croton rottlerifolius</i>	R. Riina 1534 M.B.R. Caruzo 56	São Paulo, Brazil São Paulo, Brazil	HM044781 -	- HM044838	HM044801 -
<i>C. sapiifolius</i>	<i>Croton sapiifolius</i>	Lima 667 ?	? ?	EF408150 -	HM044841 -	- EF421754
<i>Sagotia</i>	<i>Sagotia racemosa</i>	Smith 253	Madre de Dios, Peru	AY794687	-	AY971264
<i>Sandwithia</i>	<i>Sandwithia guyanensis</i>	Ek 906 E.Y. Kataoka 347	? Manaus, AM, Brazil	AY794688 -	- -	- NG
<i>Jatropha</i>	<i>Jatropha integerrima</i>	K.J. Wurdack D047 Strain JCGLD-01	Cultivated Cultivated	AY794685 -	- -	- EU340795
	<i>Jatropha podagrica</i> <i>Suregada boiviniana</i>	PS0176MT01 Rakotomalaza 1292	Cultivated ?	- AY794663	GQ434947 DQ006183	- DQ006006



**Phylogenetic reconstruction**—We built two different datasets, one for ITS (nuclear) and the other with the two plastid spacers combined (*trnLF* and *psbA*). For both Bayesian inference and maximum likelihood (ML) we examined nuclear and chloroplast data separately to check for topological incongruence between the datasets.

Bayesian phylogenetic analyses were conducted in MrBayes v3.2.5 (Ronquist & Huelsenbeck, 2003), with substitution models estimated through functions implemented since version 3.2 (Ronquist *et al.*, 2012). We performed four independent runs, each with four simultaneous chains (one cold and three heated), for ten million generations, and sampling every 100<sup>th</sup> generation. Runs were analyzed with Tracer v.1.5 (Rambaut *et al.*, 2018) to check convergence and stationarity through effective sample size (ESS values >200). The consensus tree was built after a burn-in set to 25%, with the extended majority rule (Felsenstein, 2004).

ML searches were conducted in RaXML (Stamatakis, 2014), adopting the GTR+G evolutionary model, with ten thousand bootstrap replicates. For support estimates we adopted  $\geq 75$  to  $< 95\%$  BS or  $\geq 0.75$  to  $< 0.95$  PP as moderately supported and  $\geq 95$  BS or 0.95 PP as strongly supported.

Sequences newly generated were deposited in GenBank (see Table I for accession numbers) and alignment files submitted to MrBayes and RaXML, are available as supplementary files.

## RESULTS AND DISCUSSION

**The ‘real’ *Astraea lobata*: what and where is it?**—*Astraea lobata* is the only validly published name by Klotzsch (1841) in the original description of *Astraea*, because it was based on *Croton lobatus* L. Although Linnaeus’ original description (diagnosis) for *C. lobatus* is not detailed, the previous work of Martyn (1728), cited by Linnaeus (1753), has a detailed description, commentaries and even an illustration of this taxon. According to the information in Martyn (1728) and analyzing the specimen cited by Linnaeus (1753; Herb. Clifford: 445, BM647404!), *A. lobata* s.s. has pubescent younger portions of the branches, with stellate-porrect trichomes bearing a central ray not surpassing 1.5 mm, calyx of the pistillate flower strongly accrescent in the fruit, surpassing it in length, and ovary with stellate trichomes.

The type locality of *Astraea lobata* was still considered unknown by van Ee (2011), who properly designated the above-mentioned collection (BM647404) as its lectotype. Therefore, no locality is given in that lectotypification. The type locality was indicated as “*Vera Cruce*” by Linnaeus (1753), and as the

state of Veracruz, in the Atlantic coast of Mexico by Smith, Downs & Klein (1988: 68). The state of Veracruz is also accepted by Webster (2001) and Caruzo & Cordeiro (2007). Van Ee's (2011) questions this type locality due to the possibility that the type specimen represents a cultivated plant according to observations from Martyn (1728: 46; "*Circa Veram Crucem frequens est, teste Houstono, qui semina ejus anno 1730 in Europam misit*"). Since there is no mention of the origin of the specimen in the lectotype, Van Ee (2011) advocates that Linnaeus (1753) could be citing Martyn (1728) instead of the origin of the plant in its description of *C. lobatus*. Given that Houston indicates the species as frequent in Veracruz and considering that Linnaeus (1753) used Martyn's work as the basis for the description of *Croton lobatus*, we think it is logical to consider the state of Veracruz, Mexico, as the type locality for *A. lobata* s.s.

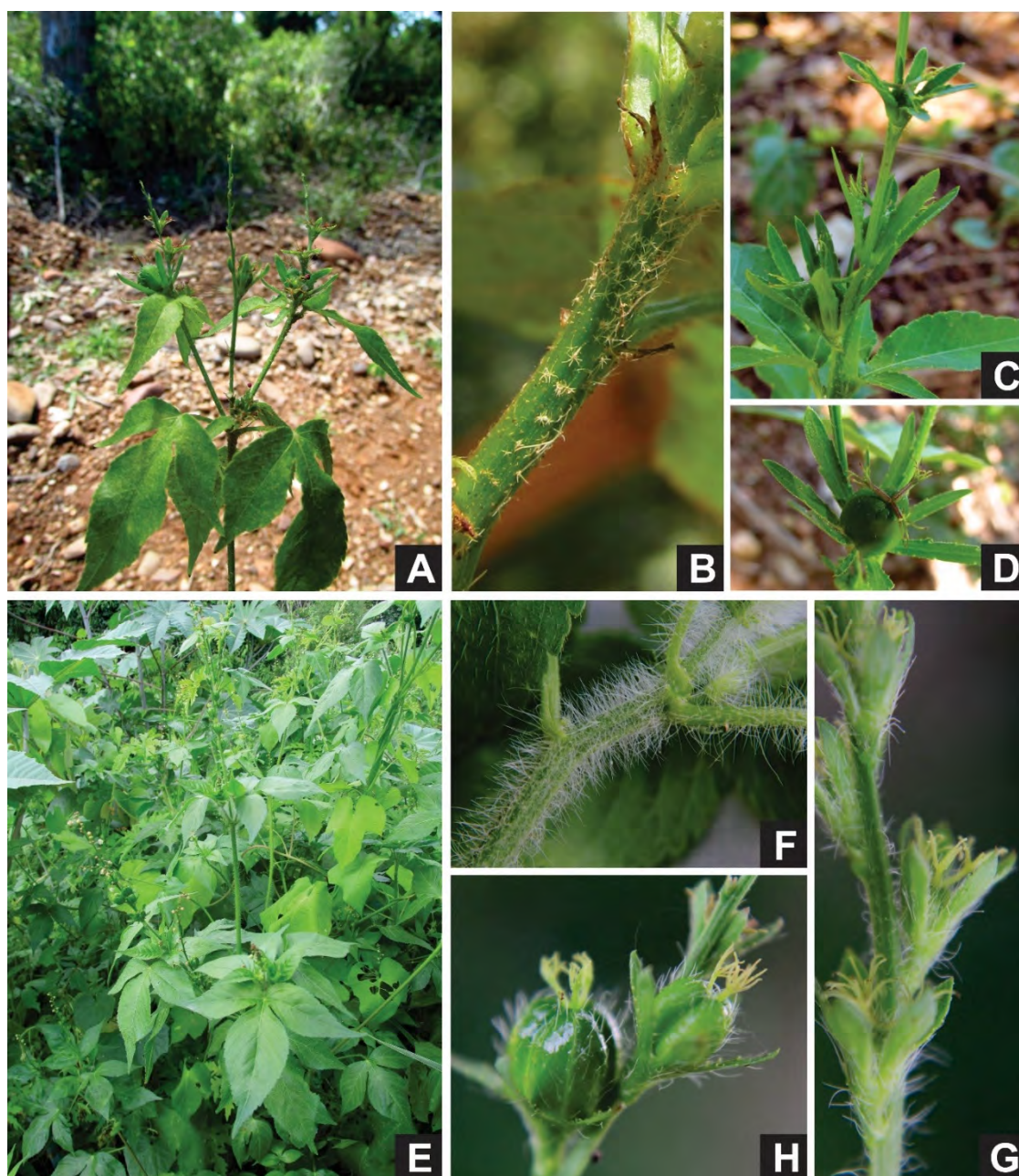
Even in our more restrictive delimitation of *Astraea lobata* (s.s.), the species still has a wide geographical distribution: it is found mostly in Mexico, Central America, southern Florida, part of the West Indies (Bahamas, Cuba, Haiti, Dominican Republic and Puerto Rico), and South America (Colombia, Ecuador, Peru, Bolivia, south-western Brazil, Paraguay and northern Argentina). However, there are very few collections of *Astraea lobata* s.s. in the Old World – so far, the species has been only reported for India and Philippines.

The type of trichomes found on the young portions of branches and the size of the calyx are the main traits guiding our delimitation of *Astraea lobata*. However, after analyzing more than 500 specimens with such characteristics, we found differences from the type collection in some traits such as density of the indumentum of young portion of stems, type of trichomes (simple or stellate) on the ovary and the size of the calyx in fruit (surpassing [ $> 1$  cm long] or not [ $< 1$  cm long] the fruit when fully developed). We interpreted these variations as phenotypic plasticity since they can be found in specimens from the same locality, within a population or even in a same individual (although in rare cases). Considering this morphological plasticity, we propose to characterize *A. lobata* s.s. using the following diagnostic characters: herbs (Fig. 1A), up to 1.5 m tall, young portion of branches sparsely to densely pubescent, with simple, stellate or stellate-porrect trichomes bearing a central ray not surpassing 1.5 mm in length (Fig. 1B); leaves 3-5-partite, glabrous or pilose on the adaxial surface and pubescent on the abaxial surface; thyrses up to 15(-20) cm long, with 3-6 pistillate flowers at the base, male cymules with 1-3 flowers each, pistillate flowers with 5-7(-9)-lobed calyx (Fig. 1C) and fruit glabrous to sparsely pilose (Fig. 1D), with short simple, stellate or stellate-porrect trichomes. Another important characteristic is that the fruit of *A. lobata* s.s. is opaque (Fig. 1D), while most other species of *Astraea* have lustrous fruits (see Fig. 1H). However, this trait is better observed in live plants rather than in dried specimens.

**Two new taxa segregated from *Astraea lobata* s.l. based on morphological characters**—A large number of the specimens identified in herbaria as *A. lobata* present indumentum on younger portions of branches composed by stellate-porrect trichomes bearing a central ray longer than 2 mm (usually 4+ times longer than the lateral rays). These trichomes were interpreted in some cases (Müller Argoviensis 1866, 1874) as simple trichomes – and in fact the long central ray gives the appearance of an indumentum made of simple, elongated, erect trichome (hirsute indumentum) when not observed under a stereoscope (Fig. 1F). Along with these distinct trichomes, the fruit is sparsely covered with simple elongated (> 1 mm long) trichomes (Fig. 1H).

Miquel (1845) described *Cnidoscolus surinamensis* based on a specimen with the indumentum on young portions of stems and fruits as mentioned above, placing it within *Cnidoscolus* Pohl perhaps due to the spiny appearance of the trichomes. *Cnidoscolus surinamensis*, as the epithet states, was described from Suriname, where no collections of *Astraea lobata* s.s. has been found so far. Furthermore, Miquel's name was also previously synonymized under *A. lobata* by Müller Argoviensis (1866; 1873) and Govaerts *et al.* (2000). Based on morphological characters (type of trichomes on younger portions of branches and fruit), we recognize specimens matching the type of *Cnidoscolus surinamensis* (A. Kappler 1573), as a distinct taxon, ***Astraea surinamensis*** (Miq.) O.L.M. Silva & Cordeiro (Fig. 1E-G), comb. nov. (basonym: *Cnidoscolus surinamensis* Miq., *Linnaea* 18: 749 [1845]). *Astraea surinamensis* is mostly found in the Lesser Antilles (from U.S. Virgin Islands to Trinidad and Tobago) Panama, northern South America (Venezuela, Guyana, Suriname and French Guiana), and most of Brazil. However, the distribution range of this species overlaps that of *A. lobata* s.s. in Central America and western South America, although there are only a few collections of *A. surinamensis* from those areas. Like *A. lobata* s.s., *A. surinamensis* also occurs in the Old World, where it is represented only by a few records along western tropical Africa (Benin, Cameroon, Ivory Coast, Niger, Nigeria and Sudan).

Although *Astraea* has the tropical America as its natural distribution range, it is represented, as an alien species, by a large number of specimens in the Old World, especially along western tropical Africa, which do not fit either *A. lobata* or *A. surinamensis*. Some of the names currently under *A. lobata* s.l. were described based on African specimens, as *Croton trilobatus* Forssk., the earliest name among them, published in the *Flora Aegyptiaco-Arabica* (Forsskal & Niebuhr, 1775). *Croton trilobatus* Forssk. and all other names based on African specimens were synonymized by Müller Argoviensis' (1866) treatment for De Candolle's *Prodromus* under *C. lobatus* var. *riparius* (Kunth) Müll.Arg., based on *C. riparius* Kunth, described for northwestern South America (Humboldt *et al.*, 1817).



**Figure 1:** Morphological characters useful to distinguish *Astraea lobata* s.s. from *Astraea surinamensis*. A-D: *Astraea lobata*. A. habit with inflorescences. B. detail of younger portion of stems. C. pistillate flowers. D. immature fruit. E-G: *Astraea surinamensis*. E. habit with inflorescences. F. detail of younger portion of stems. G. pistillate flowers. H. immature fruits. Photos: O.L.M. Silva.

*Croton trilobatus* Forssk. was described based on a specimen from the southern Arabian Peninsula, collected in 1763 in Wadi Surdud (=“Uadi Surdûd”), Yemen, according to Hepper & Friis (1994). The diagnosis given in the protologue is not enough to establish its identity, and no type specimen could be found despite the efforts of Christensen (1922) and Hepper & Friis (1994). However, specimens analyzed from Yemen (S.M. Botta s.n. [P5478220!], A. Defflers 191, 227 and 230 [P!], A.G. Miller 3059

and 5379 [E (photo!)], and G. Schweinfurth 237 [G!, P!] and 904[G!]) match the diagnostic characteristics of *C. lobatus* var. *riparius* mentioned above. Therefore, we advocate that Forsskal's name should be treated as the earliest name for this taxon, which is widely distributed in tropical Africa, but it is also known from northwestern South America, and from a few collections from the Caribbean (Jamaica and Saint Vincent and the Grenadines).

*Astraea trilobata* (Forsskl.) O.L.M. Silva & Cordeiro, comb. nov. (basionym: *Croton trilobatus* Forssk., Fl. Aegypt.-Arab.: 163 [1775]) is therefore characterized by the indumentum on the abaxial surface of leaves, which is sparsely to densely pubescent with stellate trichomes, and by the tomentose ovary (becoming pubescent or densely pubescent in fruit) with stellate or stellate-porrect trichomes. Also, young portions of branches are pubescent to densely pubescent, with stellate and stellate-porrect trichomes bearing a central ray, longer than the lateral ones, similar to those present in *A. surinamensis*., but not surpassing 2 mm in length. In Table II we present a comparison among *A. lobata*, *A. surinamensis* and *A. trilobata*.

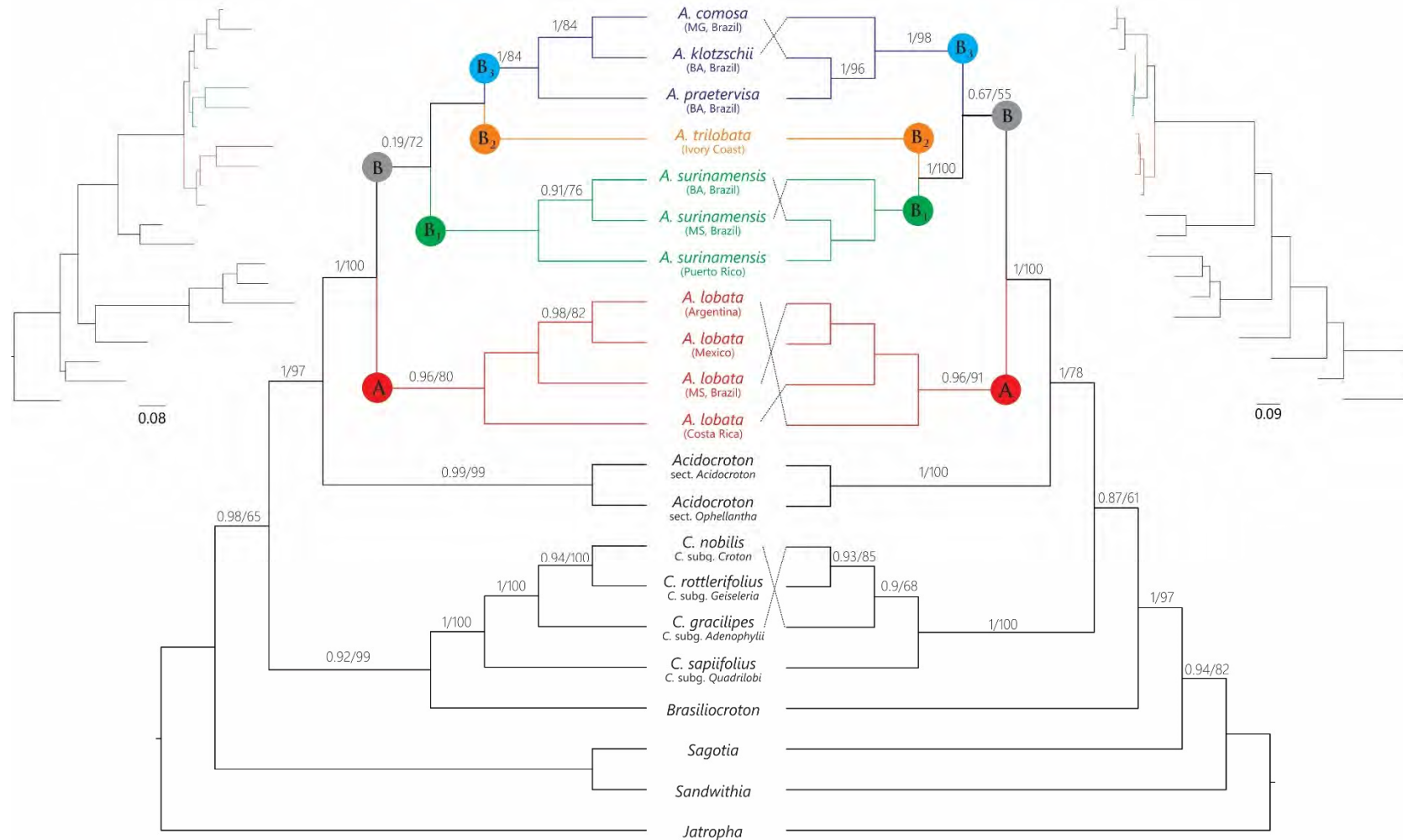
**Table II.** Main distinguishing characters and distribution ranges of *Astraea lobata* s.s., *A. surinamensis* and *A. trilobata*.

	<i>A. lobata</i>	<i>A. surinamensis</i>	<i>A. trilobata</i>
Trichomes on younger portion of branches	simple, stellate or stellate-porrect, the central ray < 1 mm long (same size or twice longer than lateral rays)	stellate-porrect, the central ray > 2 mm long (4+ times longer than lateral rays)	stellate-porrect, the central ray > 1.5 mm long (3+ times longer than lateral rays)
Length (mm) of calyx lobes in mature fruit	2.5-6(-7), up to 15(-20) in fruit	2-3, up to 6-7 in fruit	(1.5-)3-4, up to 5-7 in fruit
Fruit surface	opaque	lustrous	lustrous
Fruit indumentum	glabrous to sparsely pilose	pilose to pubescent	pubescent to tomentose
Fruit trichomes	short (< 1 mm long) simple, stellate or stellate-porrect, the central ray < 1.5 mm long (same size or twice longer than lateral rays)	long (> 1 mm long) simple	short (< 1 mm long) stellate or stellate-porrect, the central ray > 1.5 mm long (2-3 times longer than lateral rays)
Distribution	Mexico, Central America, southern Florida, West Indies (Bahamas, Cuba, Haiti, Dominican Republic and Puerto Rico), and western South America (Colombia, Ecuador, Peru, Bolivia, SW Brazil, Paraguay and N Argentina). A few specimens in the Old World.	Lesser Antilles (from U.S. Virgin Islands to Trinidad and Tobago) Panama, N South America (Venezuela, Guyana, Suriname and French Guiana), and most of Brazil. A few specimens in Central America, W South America, and Africa	widely distributed in tropical Africa, a few collections in NW South America, and the Caribbean (Jamaica Saint Vincent and the Grenadines).

**Relationships of *Astraea* within Crotonaeae**—The resulting nuclear and plastid phylogenetic trees (Fig. 2) recovered a well supported monophyletic *Astraea* (1 PP, 100 BS). Although the monophyly of the genus was reported in previous studies (Berry *et al.*, 2005, van Ee *et al.*, 2011; Riina *et al.*, 2014), their taxon sampling was not comprehensive, once they used *Astraea* samples only as outgroups. The closer relationship of *Astraea* with *Acidocroton* is also corroborated with strong support (1 PP, 78-97 BS), as well as the monophyly of *Acidocroton* (including *Ophellantha* as a section) with high support (0.99-1 PP, 99-100 BS).

The plastid tree corroborates the position of *Sagotia* and *Sandwithia* as sister to the remaining Crotonaeae, as recovered by Wurdack *et al.* (2005) based on *trnLF* and *rbcl*. In Wurdack *et al.* (2005), the clade with *Sagotia* and *Sandwithia* was recovered with high support (98 BS and  $\geq 0.95$  PP), while the clade containing the remaining members of Crotonaeae showed moderate (72 BS) to high ( $\geq 0.95$  PP) support. In our study, the clade with *Sagotia* and *Sandwithia* is recovered, but with low support, whereas the clade with the other genera of Crotonaeae is recovered with moderate (65 BS) to high support (0.98 PP). However, due to difficulties (large gaps and repeated portions) aligning the *psbA* sequences of these genera, they were excluded from the *psbA* matrix and, therefore, it is likely that the low support of the clade of *Sagotia* and *Sandwithia* in our plastid tree could be an effect of missing data. On the other hand, the inclusion of an ITS sequence of *Sandwithia* allowed us to evaluate the position of this genus in the ITS tree. In that topology, *Sandwithia* is recovered as the first diverging genus within Crotonaeae, while *Sagotia* is recovered as most closely related to the remaining genera of the tribe, in a clade with moderate (82 BS) to high (0.94 PP) support.

*Croton* is also recovered as monophyletic with high support (1 PP, 100 BS) on both the ITS and plastid tree, as in previous studies (Berry *et al.*, 2005; Riina *et al.*, 2009; Caruzo *et al.*, 2011; van Ee *et al.*, 2011; Riina *et al.*, 2014). Regarding the position of *Brasiliocroton*, it is recovered as sister to *Croton* in the plastid tree with high support (0.92 PP, 99 BS), corroborating other Crotonaeae phylogenetic studies (Berry *et al.*, 2005; Wurdack *et al.*, 2005; van Ee *et al.*, 2011; Riina *et al.*, 2014). However, in our ITS tree, this genus emerged as sister to a clade formed by *Croton*, *Astraea* and *Acidocroton* but with moderate (0.87 PP) to low support (61 BS). It is noteworthy that the relationship of *Brasiliocroton* as sister to *Croton* has low to moderate support in the hypotheses by Wurdack *et al.* (2005) based on *trnLF* and *rbcl* (68 BS and  $\leq 0.95$  PP, respectively), Berry *et al.* (2005) based solely on ITS (57 BS), and van Ee *et al.* (2011) based on ITS and *EMB2765* (75-90 BS on both).



**Figure 2:** Extended majority consensus tree obtained from Bayesian analysis of plastid (left) and ITS (right) datasets. Values above branches correspond to Bayesian posterior probabilities / maximum likelihood bootstrap percentages. Values below 50 BS and/or 0.50 PP were omitted. On the upper corners, the same trees are presented as phylograms and the scale bar indicates the mean number of nucleotide substitutions per site.



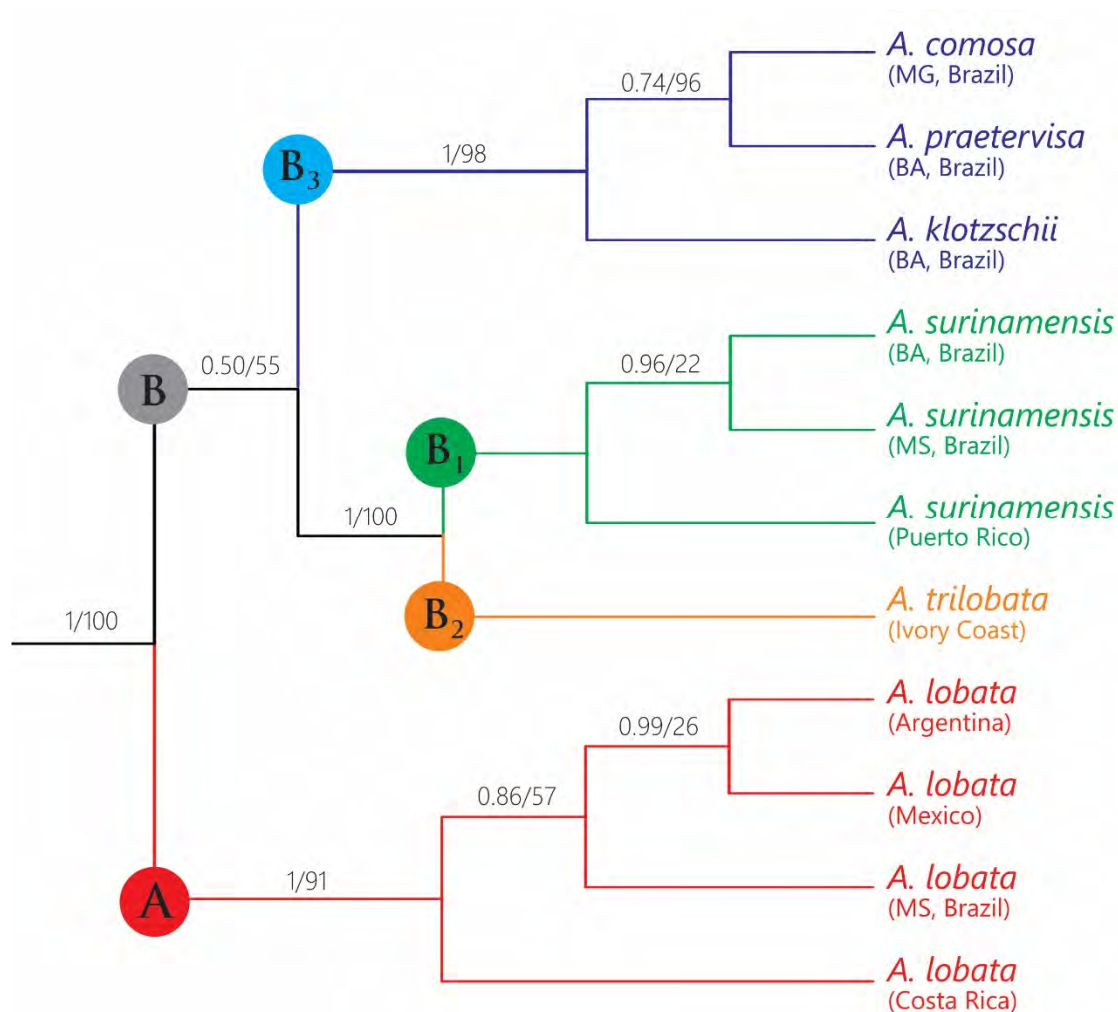
*Brasiliocroton* shares with *Sagotia* and *Sandwithia* (sisters to the remaining *Crotoneae*) the strictly arboreal habit and paniculiform inflorescences. *Acidocroton*, and *Astraea* are predominantly herbaceous to shrubby whereas habit in *Croton* varies from herbs, and shrubs to trees (rarely lianescent). These three genera share thyrse with a spiciform appearance due to the strong reduction of the central axis of cymules in the thyrse.

The presence of nectaries at the junction of petiole and leaf blade are only observed in *Croton* and *Brasiliocroton* and was previously suggested as a putative morphologic synapomorphy for the clade containing these genera (Riina *et al.*, 2014). However, since these nectaries are not present in many species (or even entire sections) of *Croton*, the alternative relationship of *Brasiliocroton* recovered on the ITS tree suggests that this trait could be result of convergent evolution. Nevertheless, a wider sampling of *Croton* and *Astraea* using additional informative genetic markers, along with ancestral character states reconstruction for morphological traits, is needed to better evaluate the position of *Brasiliocroton*, as well as the incongruence between the ITS and the plastid phylogenies in tribe *Crotoneae*.

**Molecular phylogenetics gives additional support to *Astraea lobata* s.s. *Astraea surinamensis* and *Astraea trilobata***—Samples of *Astraea lobata* s.s. were recovered in clade A (Figure 2) with high to moderate support both in the ITS (0.96 PP, 91 BS) and the plastid (0.96 PP, 80 BS) trees. The remaining species of *Astraea* sampled in this study were recovered in a distinct clade (clade B), however, with low support (0.19-0.67 PP, 55-72 BS). In the ITS tree, samples of *A. surinamensis* (clade B1) and the only accession of *A. trilobata* (clade B2) emerged as a highly supported clade (1 PP, 100 BS), whereas in the plastid tree *A. trilobata* is recovered sister to the remaining species of *Astraea* sampled (clade B3), but with low support (0.19 PP) in the Bayesian tree, or as sister to *A. surinamensis*, *A. comosa*, *A. klotzschii* and *A. praetervis*a in the ML tree, although this clade and the one containing *A. surinamensis* plus the remaining species are low supported (72 and 32 BS, respectively).

Regarding the relationships within *Astraea*, the incongruence between nuclear and plastid trees are mainly restricted to the position of *A. trilobata*, as mentioned above. There are also low supported incongruent relationships among accessions of the same species in *A. lobata* s.s. and *A. surinamensis*. Because all the incongruent nodes were low supported, we concatenated the ITS and plastid datasets to further explore relationships within *Astraea* (Fig. 3). In the concatenated tree, clade A (containing samples of *A. lobata* s.s.) was recovered with high support (1 PP, 91 BS), but clade B (with *A. surinamensis*, *A. trilobata* and the other species of *Astraea* sampled) was still low supported (0.50 PP, 55 BS). The position of *A. trilobata* as sister to *A. surinamensis* is recovered, however, with low support. The low supported sister relationship of these two species might be the result of low sequence divergence of the regions selected in this study.





**Figure 3:** Extended majority consensus tree obtained from Bayesian analysis of concatenated plastid and ITS datasets. Values above branches correspond to Bayesian posterior probabilities / maximum likelihood bootstrap percentages. Values below 50 BS and/or 0.50 PP were omitted. The relationships among the remaining Crotonaeae genera are omitted.

From a morphological point of view, the distinction of *Astraea lobata* s.s. (clade A) from the remaining species of *Astraea* (clade B) is supported by its opaque fruit, since all other species sampled have lustrous fruits (Fig. 2). Within clade B, *A. trilobata* and *A. surinamensis* share a unique character, the stellate-porrect trichomes bearing a central ray much longer than the lateral ones (Fig. 2), which easily distinguish *Astraea trilobata* and *Astraea surinamensis* from the remaining species in clade B and from *A. lobata* s.s. The type of trichomes in adaxial surface of leaves and fruits distinguish *A. surinamensis* (simple) and *A. trilobata* (). Conclusions regarding putative synapomorphies of internal clades within *Astraea* need a wider sampling of the genus combined to a more comprehensive character states mapping.

## CONCLUSIONS

With a more restricted morphological delimitation for *Astraea lobata* (s.s.) we identified two new taxa, *A. surinamensis* and *A. trilobata* based on morphological characters. We also evaluated these three taxa in a phylogenetic context, which supported the recognition of the two later since they are more closely related to the remaining species of *Astraea* we included in this hypothesis. This relationship is supported by the lustrous fruits observed in *A. surinamensis*, *A. trilobata* and the remaining species of *Astraea* we sampled, while in *A. lobata* s.s. we observed opaque fruits. However, a more comprehensive framework with a larger sampling of *Astraea* is necessary to evaluate potential synapomorphies within the genus. We also presented different positions for *Brasiliocroton*, *Sagotia* and *Sandwithia*, but more studies, with a comprehensive sampling of *Crotoneae* are mandatory to evaluate these novelties.

## ACKNOWLEDGEMENTS

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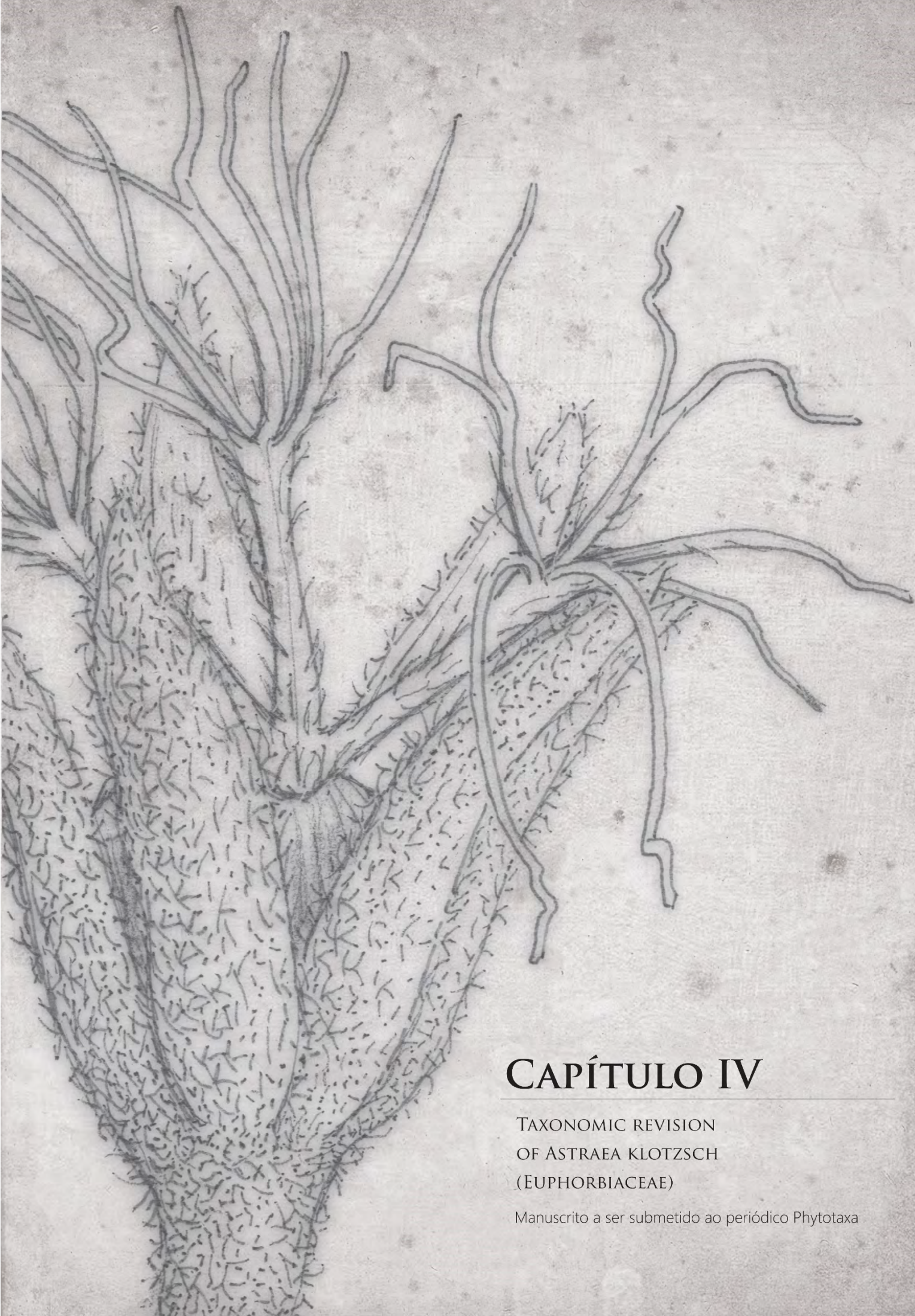
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## CAPÍTULO IV

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TAXONOMIC REVISION  
OF *ASTRAEA* KLOTZSCH  
(EUPHORBIACEAE)

Manuscrito a ser submetido ao periódico Phytotaxa



**TAXONOMIC REVISION OF *ASTRAEA* KLOTZSCH (EUPHORBIACEAE)**

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**Abstract**—*Astraea* is a genus within Crotonae (Euphorbiaceae: Crotonoideae) widely distributed in the Neotropical region. However, the highest diversity of the genus is found in eastern Brazil, and some weedy species also occur along the Paleotropics. With recent advances in the taxonomic and systematic knowledge of *Astraea*, in this work we present the taxonomic revision of the genus, recognizing 13 species based on morphological characters. Species of *Astraea* may be recognized by the usually deeply lobed / partite leaves, lacking basilaminar or acropetiolar nectaries; spiciform inflorescence with bisexual cymules at the base and staminate cymules towards the apex; pistillate flowers with a segmented nectary and styles multifid; staminate flowers with imbricate calyx, petals bearing dense moniliform trichomes at the basal portion of their margin and ca. 15 stamens; and seeds usually tetragonal and verrucose, bearing a caruncle. We present a full review of morphology and geographical distribution of the genus, along with data gathered from literature and fieldwork on ecology, genetics, phytochemistry and medicinal uses. With an identification key to the 13 species recognized in this work, we present, for each species, descriptions, illustrations, photographs besides etymology and vernacular names, geographical distribution and ecology, conservation status, and comments on taxonomic and nomenclatural matters, with 20 lectotypes and 3 neotypes here designated.

**Keywords**—Crotonae, Crotonoideae, Neotropics, taxonomy

## INTRODUCTION

*Astraea* Klotzsch (1841: 194), is a small genus belonging to Crotonaeae (Crotonoideae, Euphorbiaceae), and has been traditionally treated in the most important monographs for the family (Müller Argoviensis 1866, 1873) as a section of the giant *Croton* Linnaeus (1753: 1004), as *C. sect. Astraea* (Klotzsch) Baillon (1858: 363). This is due to the presence of stellate trichomes, flowers arranged in spiciform thyrse, with pistillate or bisexual proximal cymules and staminate distal cymules and inflexed stamens in bud (Berry et al. 2005). Despite these strong similarities with *Croton*, the combination of deeply lobed leaves, without glands at the junction of the petiole and the leaf blade, staminate flowers with imbricate aestivation and glabrous receptacle and tetragonal and strongly carunculate seeds made it one of the best-defined section within *Croton* (Webster 1993).

*Astraea* belongs to the tribe Crotonaeae, one of the largest within Euphorbiaceae, and is currently placed in the “Inaperturate Crotonoids” clade of subfamily Crotonoideae (Wurdack et al. 2005). The tribe had strong changes in its composition after the current phylogenetic framework presented by Wurdack *et al.* (2005) and now includes, besides the giant *Croton* and the recently described *Brasilicroton* Berry & Cordeiro in Berry et al. (2005: 357), genera previously placed in not closely related tribes: *Acidocroton* Grisebach (1859: 42), including *Ophellantha* Standley (1924: 97), and *Sagotia* Baillon (1860: 53) from Codieae, and *Sandwithia* Lanjouw (1932: 184) from Aleuritideae. The tribe is found mainly throughout the Neotropical region, but species of *Croton* and *Astraea* may be found in the Old World, including native and invasive species (van Ee et al. 2011, Silva et al. [Capítulo III]).

*Astraea* is positioned as sister to *Acidocroton* in the current phylogenetic framework by Wurdack et al. (2005) and Berry et al. (2005) and the monophyly of the genus is also fully supported in these works. Potential morphological synapomorphies includes the presence of agglomerate of colleters at the junction of the petiole and leaf blade (Vitarelli et al. 2015) and moniliform trichomes at the base of the petals of staminate cymules (De-Paula et al. 2010a).

The current morphological delimitation of the genus presented by Webster (2014) excludes three species proposed by Müller Argoviensis as part of *Croton* sect. *Astraea*: *C. humilis* Linnaeus (1759: 1276), whose staminate flowers possess 25–35 stamens (while in *Astraea* staminate flowers have 11–15 stamens), *C. panduraeformis* Müller Argoviensis (1866: 671) and *C. bonplandianus* Baillon (1864: 339), which have bifid styles and nectaries at the junction of lamina and petiole (while in *Astraea* the styles are 6–8-fid and there is no nectaries at the junction of lamina and petiole). Nevertheless, Froembling (1896) previously indicated the exclusion of *C. humilis* based on anatomical features. These exclusions are also supported by the recent phylogenetic sectional classification presented in van Ee et al. (2011), in which these species are placed in *C. sect. Adenophyllii* Grisebach (1859: 40).

Recent advances on the taxonomy and systematics of *Astraea* presented more precise delimitation of *A. lobata*, the type species of the genus (Silva et al. [Capítulo III]), new taxa (Silva & Cordeiro 2017, Silva et al. [Capítulo III]), re-evaluation of the identity of some species (Silva et al. 2017) and ultimately a better knowledge of the phylogenetic and biogeographic framework of the genus based on molecular data (Silva et al. [Capítulo V]). These works brought more refined morphological delimitation to the species of *Astraea* and a deeper understanding of relationships among them and the evolution of the genus within Crotonaeae (Silva et al. [Capítulo V]).

In this work, the current taxonomic and systematic knowledge of *Astraea* is gathered and presented as an update to the last monographs of Müller Argoviensis (1866, 1873) for *Croton* sect. *Astraea* from more than one century ago. Herein, we present a taxonomic revision of *Astraea*, with an identification key, morphological descriptions, comments on distribution and ecology (including distribution maps), nomenclatural notes, conservation status and taxonomic comments, besides line drawings and photographs, for all species of the genus.

## MATERIAL AND METHODS

The delimitation of *Astraea* adopted in this work follows the previous works with *Croton* sect. *Astraea* by Müller Argoviensis (1866, 1873) and Webster (1993, 2014). In this delimitation, the genus is morphologically characterized by usually deeply lobed or partite leaves, lacking basilar or acropetal nectaries; spiciform thyrse with bisexual (rarely unisexual) cymules at the base and staminate cymules towards the apex; pistillate flowers with a segmented nectary and styles multifid; staminate flowers with imbricate calyx, petals bearing dense moniliform trichomes at the basal portion of their margin and ca. 15 stamens; and seeds generally tetragonal and verrucose, bearing a caruncle.

This study is based on the observation of about 100 type specimens, along with approximately 5,200 herbarium specimens, from more than 90 herbaria: A, ALCB, AMD, ASE, B, BHCB, BHZB, BM, BOTU, BR, C, CEN, CEPEC, CESJ, CGMS, COL, CTES, CVRD, DAV, E, EAC, ESA, F, FHI, FLAS, FSU, FTG, FUEL, G, GH, HAL, HB, HBG, HCF, HEPH, HNBU, HRB, HRCB, HUEFS, HUEM, HUFU, IAC, IBGE, IEB, INPA, IPA, JPB, K, L, LE, LINN, M, MA, MAC, MBM, MBML, MEXU, MICH, MO, MPU, NY, OUPR, P, PACA, PAMG, PEUFR, R, RB, RSA, S, SJRP, SP, SPF, SPSF, TCD, TOGO, TUB, U, UB, UC, UEC, UESC, UFG, UFP, UFRN, US, USF, USZ, VIC, VIES, W, WAG and WIS (abbreviations according to Thiers 2018), which covers sufficiently the native distribution range of the genus.



We adopted the Morphological Species Concept (MSC) as defined by Regan (1926): “a species is a community, or a number of related communities, whose distinctive morphological characters are, in the opinion of a competent systematist, sufficiently definite to entitle it, or them, to a specific name”.

Type specimens were analyzed mostly through images available at the JSTOR Global Plants website ([plants.jstor.org/](http://plants.jstor.org/)) along with searches on digitalized specimens available on Global Biodiversity Information Facility (GBIF; [www.gbif.org/](http://www.gbif.org/)). Additional online databases consulted include those from C ([www.daim.snm.ku.dk/search-in-types](http://www.daim.snm.ku.dk/search-in-types)), G ([www.ville-ge.ch/musinfo/bd/cjb/chg/index.php?lang=en](http://www.ville-ge.ch/musinfo/bd/cjb/chg/index.php?lang=en)), K ([apps.kew.org/herbcat/navigator.do](http://apps.kew.org/herbcat/navigator.do)), LINN, P ([science.mnhn.fr/institution/mnhn/item/search](http://science.mnhn.fr/institution/mnhn/item/search)), US ([collections.nmnh.si.edu/search/botany/](http://collections.nmnh.si.edu/search/botany/)) and W ([herbarium.univie.ac.at/database/search.php](http://herbarium.univie.ac.at/database/search.php)). Type collections deposited at BM, G, K and P were physically analyzed. For lectotypifications, whenever possible specimens of these herbaria were chosen since they keep most of the type collections of *Astraea*, especially G, the herbarium where Müller Argoviensis worked during the production of the treatments of *Croton* sect. *Astraea* for De Candolle’s Prodrômus (Müller Argoviensis 1866) and Flora Brasiliensis (Müller Argoviensis 1873).

Descriptions were mostly based on the large amount of herbarium specimens and complemented by observation of living plants from South American populations. Measures were taken randomly from specimens, but always considering the smallest and longest measures among the available material and from mature structures. Terminology for morphologic characters is mostly based in Bentje (2010) and Stearn (1992), with specific terminology for trichomes types based on Webster et al. (1996), and Hickey (1973) for leaf venation.

Geographic distribution is given according to the World Geographical Scheme for Recording Plant Distributions (TDWG2, Brummit [2001]), following the model “LEVEL 1. Level 2: Level 3 (Level 4, in 5-letter abbreviation)”, followed by commentaries about distribution range of each species. Specimens were georeferenced through original coordinates obtained from herbarium labels (converted to decimal degrees when necessary through *conversor* [available at: [slink.cria.org.br/conversor](http://slink.cria.org.br/conversor)]) or, in cases in which this data were unavailable, by approximate coordinates from municipalities or localities. For Brazilian localities and municipalities, coordinates were obtained from *geoLoc* (available at: [slink.cria.org.br/geoloc](http://slink.cria.org.br/geoloc)) using IBGE as source, and for municipalities and localities from other countries we conducted searches in Google Earth and Global Gazetteer version 2.3 (available at: [www.fallingrain.com/world/index.html](http://www.fallingrain.com/world/index.html)). Maps were elaborated in Quantum GIS v. 2.18 (Quantum GIS development team 2017) using shape and vector files from the Americas Base Map (Bletter et al. 2004).

Conservation status for each species was evaluated according to the criteria adopted by the International Union for the Conservation of Nature (IUCN 2012), with the extent of occurrence and area of occupancy calculated through Kew’s GeoCAT tool (available at: [geocat.kew.org/](http://geocat.kew.org/)) adopting Extent of Occurrence (EOO)

for the weedy species, and Area of Occupancy (AOO), based on 2 km cell width, for the remaining species. To calculate EOO and AOO we excluded collections which could not be properly georeferenced.

Vernacular names were extracted from herbarium labels, and one specimen per municipality is cited in the selected specimens examined section, and for the widely distributed *Astraea lobata*, *Astraea surinamensis* and *Astraea trilobata* specimens are arranged by major geographical area (Africa, Antilles, Central America, North America and South America) to facilitate reading. Appendix I shows a complete list of specimens included in this work.

## TAXONOMY

### Taxonomic history of *Astraea*

The taxonomic history of *Astraea* may be divided into four main phases: (i) Pre-Müllerian, (ii) Müllerian, (iii) Post-Müllerian and (iv) Contemporaneous.

The Pre-Müllerian phase comprehends the period from 1753 (description of *Croton lobatus* by Linnaeus) to 1865 (the preliminary treatment for the group by Müller-Argoviensis). An important event during this phase is the splitting of *Croton* in *Astraea* and many other genera by Klotzsch (1841), but the work of Baillon (1858) recognized Klotzsch's genera as sections of *Croton* rather than splitting this genus, was the one traditionally used until nowadays. During this phase, many names were newly described within the group, by several authors and from different localities, resulting in 22 accepted names by the end of this phase.

The Müllerian phase comprehend the period in which the two main taxonomic treatments for the group were published by Müller Argoviensis, starting in 1866, with the treatment for De Candolle's Prodrômus and ending in 1873 with the treatment of the group for Flora Brasiliensis. Since these two works were the first attempts to organize the group, this phase is marked by several synonymizations and nomenclatural novelties, with relatively few new species. Although very short in time, this is a very important phase due to the valuable contributions to the group by Müller Argoviensis, resulting in 28 taxa, with an elevated number of infraspecific taxa recognized for *Croton lobatus* and *C. klotzschii*.

By the beginning of the Post-Müllerian phase, in 1890, Pax proposed the recognition of the group as a subgenus of *Croton*, with 12 species (10 in Brazil, and two in the Antilles), but, as mentioned above, Baillon's (1858) scheme with sections was still the more broadly accepted. New species were described, and the group was reorganized by Govaerts, in 2000, with the World Checklist of Selected Plant Families, resulting in 18 taxa recognized, without the several infraspecific taxa proposed by Müller Argoviensis, which were considered as synonyms mostly under *Croton lobatus* and *C. klotzschii*.

The Contemporaneous phase starts with the recent phylogenetic studies published by Berry et al. (2005) and Wurdack et al. (2005), which recognized the group as distinct genus once again, but now based on molecular evidence *Croton humilis*, *C. bonplandianus* (treated as *C. pauperulus* in the Flora Brasiliensis) and *C. panduriformis*, which were included in *Croton* sect. *Astraea* by Müller Argoviensis (1866), were excluded from *Astraea*. It is noteworthy that Webster (1993) proposed the exclusion of *C. humilis* and *C. panduriformis* from *C. sect. Astraea* based on morphology and doubted the inclusion of *C. bonplandianus* within the section. Following this new framework, most of publications after 2005 aimed to nomenclatural transfers from *Croton* to *Astraea*, and van Ee (2011) also provided important contributions regarding nomenclatural matters for the group. Anatomical studies (Sá-Haiad et al. 2009; De-Paula et al. 2010a,b; Vitarelli et al. 2015) also have successfully shed light into the relationship of *Astraea* with *Croton* and *Brasilicroton*.

## Morphology

**Habit**—species of *Astraea* may be annual or biannual herbs or perennial shrubby. *Astraea lobata* and other invasive species have mostly herbaceous habit, but it is not uncommon to observe a slightly secondary (woody) growth in basal portion of the stems. *Astraea cincta* is the only species which has a well-developed underground system (probably xylopodiferous). The remaining species of *Astraea* have subshrubby to shrubby habit. According to Raunkier's (1934) classification for life forms, *Astraea cincta* is classified as hemicryptophyte due to the position of meristems very close to the soil, while the remaining species are all classified as phanerophytes.

**Branches**—in transversal section, branches from species of *Astraea* may be cylindrical or slightly costate, with variations within some species, most likely related to different developmental stages. It is noteworthy that the ramification of branches, when in reproductive state, follow a pattern in which three lateral branches originate right below the first inflorescence. These lateral branches develop as normal branches (i.e., with leaves), and shortly develop another inflorescence, repeating this ramification pattern. Indumentum is variable, both regarding type of trichomes (simple, stellate or stellate-porrect) and density of trichomes (glabrous to tomentose). This variation in indumentum is of great utility to distinguish species.

**Leaves**—species of *Astraea* are always alternate, stipulate and petiolate. Stipules are always lateral, and vary in form (deltoid, subulate or glanduliform) and indumentum. When subulate, they may be entire or lobed and it is common to observe secretory structures (probably colleters) at its tip(s). Indumentum of stipules generally follows branches, but sometimes are hard to classify due to its reduced size. Regarding petioles, leaves may be short or long-pedicellate but never sessile, and indumentum of this structure may also help on distinguishing species since it follows branches indument. At the apex of the petioles, in the joining with the leaf blade, clusters of colleters are observed, and were assigned as a possible synapomorphy for *Astraea* by Vitarelli et al. (2015).

Leaf blade may be entire or deeply lobed/partite, or sometimes hastate. Lobed and partite leaves usually have three or five lobes but some leaves with two or seven lobes, may be found in uncommon cases. Finding leaves with different number of lobes in a same branch, or even with both and entire leaves, is not uncommon in *Astraea*, as in *A. klotzschii* and *A. paulina*, for example. Lobes are generally elliptic, varying from wider or narrower forms. Venation usually is camptodromous in entire leaves and actinodromous in lobed leaves. Leaf margin varies from entire to crenate or serrate, with conspicuous or inconspicuous teeth, among species and within a single species, and secretory structures at the apex of each protrusion of the margin are present and usually spread throughout the margin. Apex of leaf blade is mostly attenuate or long-attenuate, but it may also be rounded, obtuse or acute, while base may be rounded, obtuse, cordate or acute, with variations.

Generally, leaves are discolor, with the abaxial surface lighter than the adaxial one, sometimes enhanced by the usually denser indumentum on the adaxial surface. Indumentum is diversified, varying from glabrous to tomentose, with simple, stellate or stellate-porrect trichomes. Along primary and secondary veins and near leaf base different density of trichomes may be found, and in some cases trichomes found in these portions are different from the ones on the leaf blade.

**Inflorescences and flowers**—flowers in *Astraea* are always arranged in terminal bisexual thyrses, although unisexual inflorescences may be observed in rare cases. Along the proximal portion of the thyrses, the cymules may have one pistillate flowers (i.e., unisexual cymules) or one pistillate accompanied by staminate flowers (i.e., bisexual cymules), while the distal portion is composed only by staminate cymules, with two to ten flowers per cymules. The rachis may be canaliculated sometimes, glabrous or with an indumentum pilose to tomentose, with simple, stellate or stellate-porrect trichomes. Bracts may be linear, deltoid or subulate and may surpass the length of flowers in some individuals of *A. comosa* or *A. manihot*. Inflorescence size and number of cymules may vary among species, with inflorescences of up to 20 cm in *Astraea lobata* to more than 50 cm in *A. comosa*, *A. manihot* and *A. praetervisita*.

Flowers, as in all Euphorbiaceae, are always unisexual. The pistillate ones are generally short-pedicellate and always monochlamydeous, with a gamosepalous calyx with valvar aestivation and usually five or six lobes (rarely seven to nine), equal in size, although unequal lobes are not uncommon. Calyx lobes are usually elliptic to slightly obovate, and present colleters along their margin, usually more concentrated near the base. In some species, the calyx is slightly campanulate due to large nectaries, which are disposed around the ovary in the same number of calyx lobes. It is noteworthy that these nectaries could be interpreted as a single 5-segmented nectary due to the proximity among segments, but ontogenetic studies of De-Paula et al. (2011a) showed that they are initiated separately during flower development and correspond to secretory staminodes. The ovary also follows the pattern found in Euphorbiaceae (superous, trilocular and tricarpelar, with only one ovule per locule) and possesses three styles which are united only at the base and entire for up to half of their length

and then multifid (with six to eight tips each), usually in a dichotomic pattern, without clearly defined stigmas, but with an internal stigmatic region.

Staminate flowers, in contrast to the pistillate ones, are always long-pedicellate and dichlamydeous. The calyx is gamosepalous, green or sometimes reddish, with five generally usually elliptic or oblong lobes with imbricate aestivation, while the corolla is dialipetalous, also with imbricate aestivation, with five free sepals, elliptic or oblong, white or pinkish, and bear dense moniliform trichomes along the basal to middle portion of the margin. The nectaries have the same configuration as in pistillate flowers, but as the number of calyx lobes is constant in staminate flowers, the number of nectaries is always 5. Nectaries and stamens rest on a glabrous or sparsely pilose receptacle, which is usually slightly convex. Stamens are inflexed in bud and vary from 10 to 15, with two whorls of five stamens plus the central whorl with one to five stamens. Variation in number of stamens within this third whorl is not constant within species and may vary among flowers from a single individual. Therefore, number of stamens does not have taxonomic value to distinguish species. Filets are usually white, glabrous or with a few trichomes at the base and inflexed in early stages (becoming erect later), while anthers are white to yellowish, tetrasporangiate and introrse.

**Fruits and seeds**—Fruits follow the pattern found in Euphorbiaceae: capsules with three bivalvate mericarps with dehiscence both septically and loculicidally. In rare cases, malformation leading to fruits with two or four mericarps may be observed. Generally, fruits are subglobose and may be lustrous or opaque. Even when pistillate flowers are sessile, the fruits are long-pedicellate once pedicels are accrescent in fruit. Styles are persistent, but may easily fall when preparing herbarium specimens, and become darker after fecundation. As the pedicels, the calyx is always accrescent in fruits and may be strongly accrescent (doubling in size) in some species. Seeds are tetragonal or rounded in cross sections, with verrucose, tuberculate or smooth testa and caruncle may be small or well-developed.

### Anatomy and micromorphology

In the classical work by Froembling (1896), seven taxa were included: *Croton comosus* var. *major* (= *Astraea comosa*), *C. klotzschii* var. *latifolius* (= *A. klotzschii*), *C. lobatus* var. *manihot* (= *A. manihot*), *C. lobatus* var. *gracilis* (= *A. gracilis*), *C. lobatus* var. *digitatus* (= *A. digitata*), *C. lobatus* var. *lobatus* (= *A. lobata*) and *C. paulinus* (= *A. paulina*). Despite the difficulty to verify the identity of each taxon sampled by Froembling (1896) since none of the materials are numbered or possess any other more exact verifier, in this work he suggested the exclusion of *C. humilis* from *C. sect. Astraea* (included in the group by Müller Argoviensis [1866]) and the recognition of *Astraea* as a distinct genus instead as a section of *Croton* based on the intra-axillary phloem and oil-cells observed in *Croton* and not observed in *Astraea*.

A series of more recent anatomical and micromorphological investigations involving *Astraea* were published, presenting details on leaf structure (Sá-Haiad et al. 2009), foliar secretory structures (Vitarelli et al. 2015) and morphology and development of perianth and floral nectaries (De-Paula et al. 2011a) and anthers and ovules (De-Paula et al. 2011b).

Regarding leaf structure, Sá-Haiad et al. (2009), characterized the leaves in *Astraea* as dorsiventral and amphistomatic (and in *A. klotzschii* the cell layer adjacent to the epidermis on the abaxial surface exhibits a tendency to a palisade configuration), with paracytic stomata on abaxial surface at the same level as ordinary epidermal cells, laticifers non-articulated accompanying the vascular bundles (and just below the epidermis on the adaxial surface in *A. surinamensis*), idioblasts with lipophilic content absent, leaf margin with palisade and spongy tissue differentiated and with colleters (interpreted as nectaries by the authors), midrib biconvex, with 8–10 collenchyma layers interrupted by the palisade parenchyma and vasculature composed by an arch of collateral bundles near the abaxial surface and one or two small bundles next to the adaxial side, and petiole with a circular outline, but with a depression on the adaxial side, collateral bundles arranged in a ring, with two to four small satellite bundles on the adaxial side and two to six colleters at the boundary between leaf blade and adaxial side of the petiole. These traits related by Sá-Haiad et al. (2009) are based on four distinct taxa of *Astraea*, two of them misidentified as *A. jatropa* (= *A. manihot*) and *Astraea lobata* (= *A. surinamensis*), while the taxon unidentified (*Astraea* sp.) is *A. comosa*.

Vitarelli et al. (2015) identified the “extrafloral nectaries” on leaf margins or “long cylindrical extrafloral nectaries with round apices” at the junction of blade and petioles from Sá-Haiada et al. (2009) as colleters of the standard type, composed of a short stalk, a parenchymatous axis with or without vascularization, and elongated, vacuolated thin-walled cell with cellulosic walls, containing druses, and covered by a palisade secretory epidermis with a thick cuticle. According to these authors, in *Astraea* these colleters are found, besides along the leaf margin, in acropetiolar, basilaminar or basipetiolar clusters, but acropetiolar cluster are also reported in *Croton alabamensis*. Vitarelli et al. (2015) also reported articulated and anastomosed laticifers for *Astraea paulina* (identified as *A. lobata* by the authors). This species was not sampled by Rudall (1994) and Sá-Haiad et al. (2009), who both identified non-articulated laticifers for *A. comosa*, *A. klotzschii*, *A. manihot* and *A. surinamensis*.

Details available for perianth, nectaries, anthers and ovules development by De-Paula et al. (2011a, b) were based on two species of *Astraea*: *A. klotzschii* and *A. paulina* (identified as *A. praetervisa* and *A. lobata*, respectively, in their work). For the development of flowers, on the other hand, De-Paula et al. (2011a) found a set of features in *Astraea* which distinguish it from *Croton*, including the presence of colleters in the sepal margin of pistillate flowers and of moniliforms trichomes on the base of petals of staminate flowers, non-vascularized nectaries in both pistillate and staminate flowers, filamentous structures alternating with the sepals (interpreted as reduced petals in *Croton*) highly reduced and non-secretory and also present alternate with

the nectaries and receptive portion of stigmas formed by elongated non-secretory cells. In this work, the authors also gave details about the different vasculature pattern of pistillate and staminate flowers of *Astraea* when compared to *Croton*, such as the arc configuration of the bundles within the pedicel of staminate flowers in *Astraea*, while in *Croton* they observed a ring configuration of these bundles.

Considering anther and ovule development, De-Paula et al. (2011b) could not find any difference between *Croton* and *Astraea*, indicating features which are common to Euphorbiaceae, such as dicotyledonous type of anther wall formation, a secretory tapetum, a mixed origin of the outer ovule integument, and epidermal origin of the inner ovule integument, the occurrence of many archesporial cells inside the ovules and a megagametophyte of the *Polygonum*-type. However, the authors highlighted that *Astraea*, as well as *Croton*, presents features not previously reported to Euphorbiaceae, such as styloidal crystals in the tapetum, and idioblasts with a druse in the endothecium, simultaneous and successive microsporogenesis and a functional micropylar megaspore, which could represent autapomorphies for Crotonaeae.

## Palinology

Sá-Haiad (2008) studied four species of *Astraea* (*A. comosa*, *A. klotzschii*, *A. manihot* and *A. surinamensis*) and found that these species share medium (32.5–50.0  $\mu\text{m}$ ) pollens spheroidal, apolar, inaperturate, with the exina presenting the crotonoid pattern, with 5–7 ornamentation subunits and the nexine slender than the sexine. Sá-Haiad (2008) indicates that interspecific differences remain basically on the traits of the subunits: prismatic (with the distal portions triangular) and smooth in *A. comosa*, bacular (with the distal portion conical) in *A. klotzschii*, prismatic (with the distal portion triangular) and granulate in *Astraea manihot* and bacular (with the distal portion conical), strongly granulate and with most of the elements acuminate in *A. surinamensis*. Additional studies are in development with a more comprehensive sampling of *Astraea* and could show characters of interest within the group (L. Ribeiro & D.S. Carneiro-Torres, pers. comm., Feira de Santana State University).

## Genetics

**Chromosome numbers**—The only data available for species of *Astraea* is the one presented by Miller & Webster (1966). These authors presented a chromosome number of  $n=9$  for the group, and Berry et al. (2005) indicate that this would be a unique chromosome number for the tribe, although no data is available for *Acidocroton*, *Sagotia* and *Sandwithia*. The specimen used for this work (*G. L. Webster 12461*), was identified as *Croton lobatus* and is in fact *A. lobata* following its original delimitation discussed by Silva et al. (Capítulo III).

## Ecology

**Habitat**—The genus is found in different vegetation types, but mainly within two phylogeographic domains: Cerrado and Atlantic Forest. Within Cerrado, species may be found in open cerrado vegetation (*Astraea cincta*), in gallery forest (*A. paulina*, for example) or in rocky grasslands (*campo rupestres*; *A. comosa*, for example), while in Atlantic Forest the genus colonized humid dense forests (*A. gracilis* and *A. digitata*), although the species are restricted to forest edges, and seashore plain vegetation (*A. klotzschii* and *A. praetervisita*, for example) or found in neighboring rocky outcrops (as *A. gracilis*, for example). Along the South American Dry Diagonal (Prado and Gibbs 1993, Pennington et al. 2000, Särkinen et al. 2011), some species also are found in seasonally dry forest, as is the case of *A. paulina* and *A. manihot*, the latter also found in montane dense forests.

Due to the heliophile nature of the genus, even the species which can be found in shaded environments in montane or humid forests are still more frequently along borders of these formations. There is no specific preferences or restrictions for soils or other abiotic factors which could be indicated for the entire genus, but some species may have strict habitats as *Astraea comosa* in rocky grasslands (*campos rupestres*) or *A. cincta* in open cerrado vegetation. There are also ruderal species, as *A. lobata* and *A. surinamensis*, which are found in disturbed environments.

**Phenology**—There is not a well-defined flowering season for the genus. For most species, flowers and fruits are recorded at the same time and throughout the year. An exception is *Astraea cincta*, the only species within the genus with a xylopodiferous underground system and characteristic from open cerrado vegetation, has its flowering usually triggered by fire.

**Pollination and animal-plant interactions**—Inflorescences in *Astraea* may be linked to anemophily, once they are long spiciform thyrses, with small flowers and pistillate flowers bearing branched and exposed styles. On the other hand, the low number of anthers and presence of nectaries in both pistillate and staminate flowers indicates that pollination may also be mediated by insects. No observation of pollinators was found in the literature, but during fieldwork we observed small insects visiting flowers, as, for example, bees, beetles and ants. There are no secretory structures in vegetative organs, except for the colleters at the junction of the petiole with the leaf blade and along the leaf margin. However, these structures secrete complex sugars usually involved in lubrication of the meristems and not in attracting pollinators (Rudall 2007).

## Phytochemistry and Medicinal uses

Species of *Croton* are largely known for their traditional uses in South America and Africa (Salatino et al. 2007). In *Astraea*, medicinal uses are mostly known for the African *A. trilobata* (usually referred as *Croton*



*lobatus*). Weniger et al. (2004) reported *in vitro* activity of methanolic extracts from aerial parts of *A. trilobata* in *Plasmodium falciparum* resistant strains, which cause malaria in humans. Nevertheless, herbarium labels indicate that this species is also commonly used in Africa, in the traditional medicine, to treat many other diseases as pregnancy troubles and dysentery. Chabert et al. (2006) elucidated and characterized ten different chemical constituents of *A. trilobata*, including sterols, diterpenes, triterpenes, esters and the novel triglyceride lobaceride.

### Geographic distribution

*Astraea* is mostly found throughout the Neotropical region, but also in temperate Americas and along western Tropical Africa, with few collections in Asia and Oceania. The highest diversity of species is found in Brazil, where the distribution range of *Astraea* follows, in part, that of seasonally dry tropical forests (Fig. 1), but some species are also found along the Atlantic Forest or in neotropical savannas (Cerrado). The occurrence of *Astraea* in Africa, Amazon Basin, Antilles and Central and North America is almost entirely due to widely distributed ruderal species (*A. lobata*, *A. surinamensis* and *A. trilobata*).

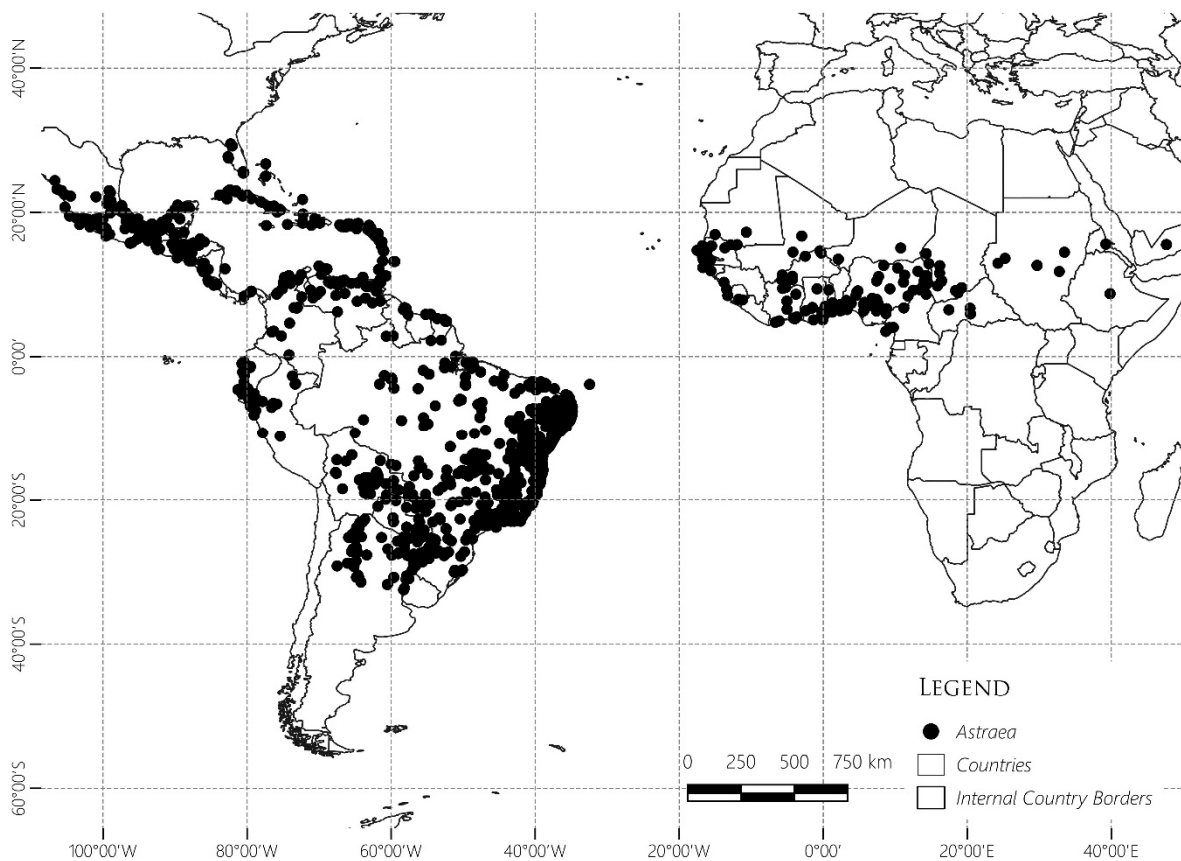


Figure 1: Geographical distribution of *Astraea*. Occurrence points in Asia and Oceania are omitted

## Phylogenetic relationships within the genus

The current phylogenetic knowledge on *Astraea* is based on the recent phylogenetic studies on *Crotoneae* by Berry et al. (2005), Wurdack et al. (2005) and Riina et al. (2014). However, in these studies the genus is sampled by only 2 or 3 species, but they are always recovered in a clade with high support. Recent advances confirmed the monophyly of *Astraea*, with the 13 species recognized in this work recovered in a well supported clade (Capítulo V).

## Phytopathology

Silva et al. (2017) verified that species of *Astraea* are susceptible to infestation by phytoplasma. These authors indicated that pistillate flowers with pedicels with more than 1 cm long, patent calyx lobes and cylindrical ovary are malformations caused by such infestation. Other malformations include the transformation of stamens and carpels into leaf-like structures. So far, this infestation was recorded only in individuals of *A. paulina* and *A. manihot*, but plants with such morphological traits should be avoided in our identification key because it may lead to misidentification.

## TAXONOMIC TREATMENT

*Astraea* Klotzsch (1841: 194)

Type: *Astraea lobata* (L.) Klotzsch (basionym: *Croton lobatus* L.)

**Annual or biannual herbs** to perennial shrubs, monoecious, with inconspicuous translucent or whitish latex, rarely with a well-developed (xylopodiferous) underground system. Indumentum with simple, stellate or stellate-porrect trichomes. **Leaves** alternate, petiolate, simple; leaf blade entire, hastate or (2-)3-5(-7)-partite, heterophyllous in some cases; margin entire, crenate or serrate, rarely cartilaginous, with colleters distributed along the margin; venation actinodromous (in partite leaves) or camptodromous (in entire leaves); stipules subulate or deltoid, rarely glanduliform, when subulate entire or partite; petioles with an cluster of colleters at the junction with the leaf blade (basilaminar). Inflorescences terminal, thyrse, with lateral branches congested giving a spiciform appearance; proximal cymules unisexual, with only one pistillate flower, or bisexual, with one pistillate flower and 2-10 staminate flowers; distal cymules unisexual, with 2-10 staminate flowers; bracts subulate or linear, generally persistent; bracteoles generally linear. **Staminate flowers** long-pedicellate, dichlamydeous, actinomorphic; calyx gamosepalous, rotaceous, with imbricate aestivation, lobes 5, almost free from each other, equal to each other, oblong-elliptic to ovate, margin entire; corolla dialipetalous, petals 5, oblong-elliptic to ovate, reflex, equal to each other, margin entire, densely barbate, especially near the base, with moniliform trichomes; receptacle glabrous to glabrescent; nectaries 5, opposite to the sepals; stamens

11–15, with two whorls of 5 stamens and the inner whorl with 1–5 stamens, filets free, glabrous or glabrescent, curved in bud; anther basifixed, dehiscent longitudinally; pistillode absent. **Pistillate flowers** monochlamydeous, actinomorphic; calyx gamosepalous, campanulate, with imbricate aestivation, generally accrescent in fruit, lobes 5–6(–9), united only at the base, ovate or oblong-elliptic to narrow-elliptic, margin entire or rarely serrate, with colleters distributed along the margin; nectaries 5–6(–9), opposite to the sepals; staminodes absent; ovary globose, 3-locular, ovules 1 per locule, styles 3, 6–8-fid each, united only at the base, stigma not differentiated. **Fruit** capsule, globose, trigonous, smooth, short to long-pedicellate, dehiscent both septicidally and loculicidally, with persistent collumela and calyx accrescent in fruit; seeds tetragonal or rounded in cross section, testa smooth to slightly or strongly verrucose; caruncle vestigial or strongly developed.

### Identification key to the Species

1. Hemicryptophytes, with a well-developed (xylopodiferous) underground system. Leaf margin cartilaginous. Seeds rounded in cross section ..... *A. cincta*
- 1' Phanerophytes, without a well-developed (xylopodiferous) underground system. Leaf margin not cartilaginous. Seeds tetragonous in cross section
  2. Stipules glanduliform, inconspicuous (< 0.5 mm long) ..... *A. praetervis*
  - 2' Stipules deltoid or subulate (sometimes lobed), conspicuous (1–15[–30] mm long)
    3. Calyx of pistillate flowers 4–9 mm long, surpassing 10 mm long in the mature fruit
      4. Pistillate flowers with margin of calyx lobes irregularly serrate. Fruit opaque ..... *A. lobata* p.part.
      - 4' Pistillate flowers with margin of calyx lobes entire. Fruit lustrous ..... *A. gracilis* p.part.
    - 3' Calyx of pistillate flowers 1.5–5 mm long, up to 9 mm long in the mature fruit
      5. Young portion of stems and petioles with stellate-porrect trichomes bearing a central ray > 1.5 mm in length (central ray 3+ times longer than the lateral ones). Fruits with erect simple or stellate-porrect trichomes bearing a central ray > 1.5 mm in length (central ray 2+ times longer than the lateral ones)
        6. Adaxial surface of leaves with mostly simple long (> 1 mm) trichomes (stellate or stellate-porrect trichomes restricted to the base or along the proximal portion of primary veins). External surface of the calyx (in pistillate flowers) with simple trichomes. Ovary and fruit with mostly simple trichomes ..... *A. surinamensis*
        - 6' Adaxial surface of leaves with stellate and stellate-porrect trichomes. External surface of the calyx (in pistillate flowers) with stellate or stellate-porrect trichomes (except for the margin, with simple trichomes). Ovary and fruit with stellate or stellate-porrect trichomes ..... *A. trilobata*
      - 5' Young portion of stems and petioles without stellate-porrect trichomes, or, if present, bearing a central ray not surpassing 1 mm in length (central ray almost the same size of the lateral ones). Fruits

glabrous or with simple, stellate or stellate-porrect trichomes, the later with the central ray up to 1 mm in length (central ray almost the same size of the lateral ones)

7. Young portion of stems tomentose

8. Leaves 3-partite (rarely entire). Meridional Espinhaço Range (central Minas Gerais).....

..... *A. comosa*

8' Leaves mostly entire (rarely entire and 3-partite). Septentrional Espinhaço Range (northern Minas Gerais and Southern Bahia) and Chapada Diamantina .....

..... *A. subcomosa*

7' Young portion of stems pilose to pubescent

9. Abaxial surface of leaves with long (> 1 mm) simple trichomes along the proximal portion of the primary veins. Calyx of pistillate flowers with long (> 1 mm) simple trichomes on the external surface .....

..... *A. digitata*

9' Abaxial surface of leaves with short (< 1 mm) simple or stellate trichomes along the primary veins or, if glabrous, margin ciliate (also with short simple trichomes). Calyx of pistillate flowers glabrous or with short (< 1 mm) simple or stellate trichomes on the external surface

10. Pistillate flowers long-pedicellate (pedicels with 3–5 mm long). Staminate flowers 6–8(–10) per cymule .....

..... *A. manihot*

10' Pistillate flowers sessile or short-pedicellate (pedicels with up to 2.5 mm long). Staminate flowers up to 5(–7) per cymule

11' Abaxial surface of leaves with predominantly stellate or stellate-porrect trichomes

12. Leaves mostly entire (sometimes 2–3-partite). Plants from humid forests or seashore vegetation (*restingas*) .....

..... *A. macroura*

12' Leaves mostly 3-partite (sometimes entire or 2-partite). Plants from gallery forest or rocky grasslands (*campos rupestres*) on cerrado or seasonally dry tropical forests .....

..... *A. paulina* p.part.

11. Abaxial surface of leaves with mostly simple trichomes (stellate trichomes, if present, restricted to the base), or, if glabrous, margin ciliate (also with simple trichomes)

13. Stipules deltoid. Leaves predominantly entire (or sometimes 2–3-partite). Plants from seashore vegetation (*restingas*) or rocky grasslands (*campos rupestres*) .....

..... *A. klotzschii*

13' Stipules subulate. Leaves 3–5-partite. Plants from disturbed environments, humid forest, rocky grasslands (*campos rupestres*) or seasonally dry forests, sometimes growing in rocky outcrops - not in seashore vegetation (*restingas*)

14. Staminate cymules with 1–3 flowers. Fruits opaque. Plants from Central America, Caribbean and western South America (up to southern and western Brazil), growing in disturbed environments .....

..... *A. lobata* p.part.

14' Staminate cymules with 3–5 flowers. Fruit lustrous. Plants from eastern South America and along the northeastern-southwestern diagonal of dry vegetation, growing in edges of forests, rocky grasslands (*campos rupestres*) or rocky outcrops

15. Leaves membranaceous. Plants from edges of humid forests, seasonally dry forests or rocky outcrops..... ***A. gracilis* p.part.**

15' Leaves chartaceous. Plants from gallery forests or rocky grasslands (*campos rupestres*) within cerrado..... ***A. paulina* p.part.**

1. ***Astraea cincta*** (Müll.Arg.) Caruzo & Cordeiro (2007: 573). *Croton cinctus* Müller Argoviensis (1873: 235).

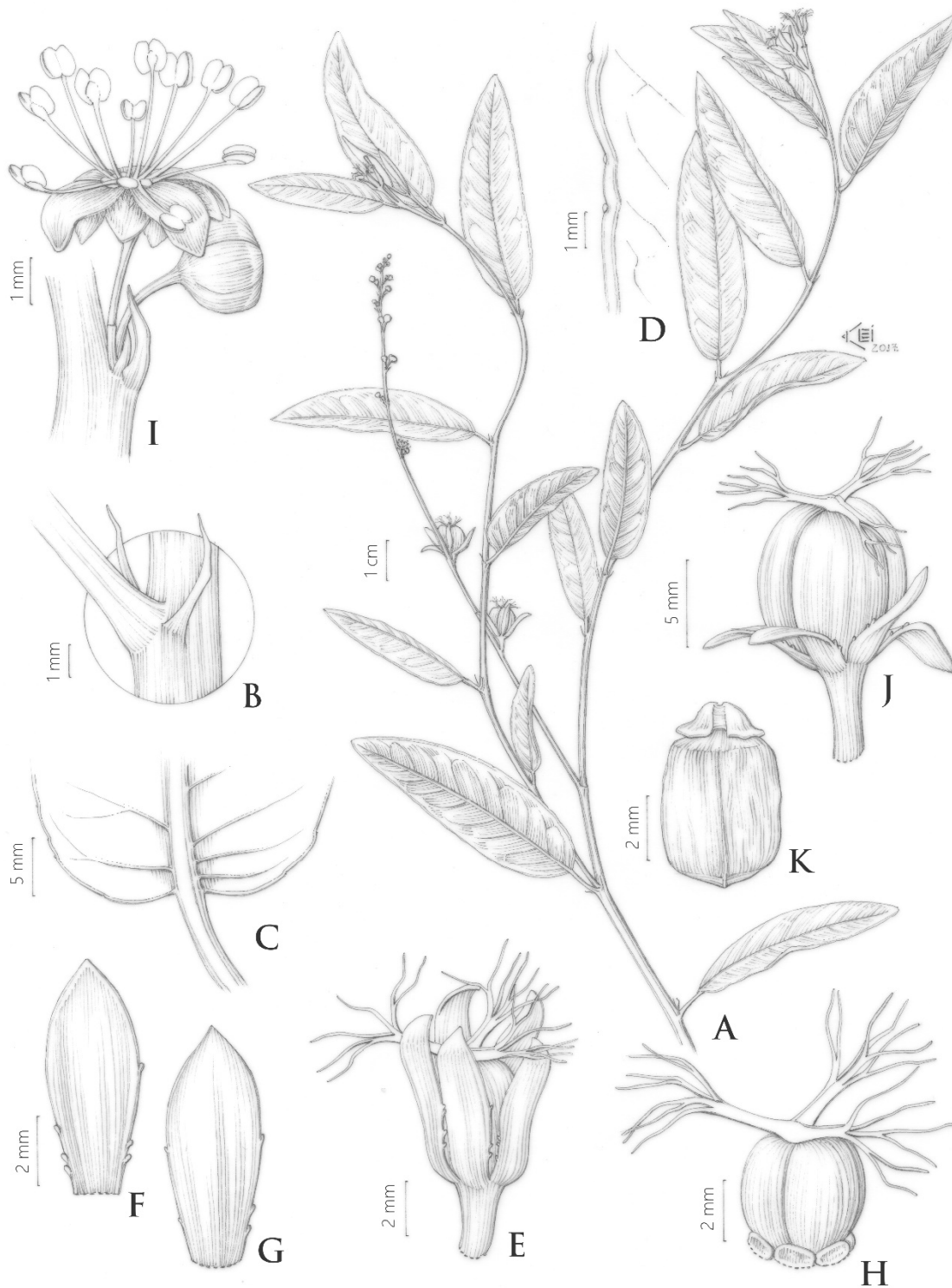
*Oxydectes cincta* (Müll.Arg.) Kuntze (1891: 613). Lectotype (designated here):—BRAZIL. Mato Grosso do Sul: 'in campis siccis ad Rio Pardo', 1826, L. Riedel 608 (LE [on 2 sheets, photo!], isotypes B+ [photo F24476!], G00434508!). Figs. 2–4.

*Astraea aureomarginata* (Chodat & Hassl.) Berry in Zuloaga *et al.* (2007: 238). *Croton aureomarginatus* Chodat & Hassler (1905: 496). Lectotype (designated here):—PARAGUAY: 'Ipe hu, Sierra de Maracayu', October 1898–99, E. Hassler 5010 (G00306936!, isotype B+ [photo F24470!]), **syn. nov.**

*Astraea hauthalii* (Kuntze) Berry in Zuloaga *et al.* (2007: 238). *Oxydectes hauthalii* Kuntze (1898: 289). *Croton hauthalii* (Kuntze) Schumann (1900: 348). Lectotype (designated by Berry in Zuloaga *et al.* 2007):—PARAGUAY: 'Cordillera bei Ibitimi', unknown date, R. Hauthal 14 (G, isotype B+ [photo F5112! and NY5112!]), **syn. nov.**

*Croton rumicifolius* Chodat & Hassler (1905: 496). Lectotype (designated here):—PARAGUAY: 'In campis pr. flumen Capibary', September 1898–99, E. Hassler 4386 (G! [on 7 sheets], isolectotypes B+ [photo F!, G! and NY!{2 photos}], BM000504276 [photo!], F767142 [photo!], GH00047403 [photo!], K000254428!, MO1574152 [photo!], MPU014858 [photo!], NY00262946 [photo!], P00634393!, P00634920!, S10570 [photo!], UC950981 [photo!], W [photo!]) , **syn. nov.**

**Perennial shrubs or subshrubs**, hemicryptophytes, up to 0.5 m high, with erect or procumbent branches (up to 0.5–1(–2) m long when procumbent), with a well-developed underground system, branches glabrous. **Leaves** entire, hastate or 3–5(–7)-partite, entire leaves ovate, oblong or elliptic (rarely wide-elliptic), 2.5–8 x 1–3.5 cm, hastate leaves with laterall lobes up to 1 x 0.5 cm, partite leaves with medium lobe oblanceolate to narrow-elliptic, (1.5)2–4(–5.5) x 0.5–1(–1.5) cm, and lateral lobes oblanceolate to narrow-elliptic, (1–)2–2.5(–3.5) x (0.3)0.5–1 cm, chartaceous, apex obtuse, rounded, attenuate or acute, with an apiculate colleter, base rounded, cordate, obtuse or slightly truncate, margin entire, crenate or serrate, with inconspicuous or conspicuous teeth, cartilaginous, glabrous, adaxial surface glabrous, abaxial surface glabrous, venation camptodromous (when entire or hastate) or actinodromous (when partite); petioles (1–)2.5–8(–10) cm long,



**Figure 2:** Line drawing of *Astraea cincta* A. flowering branch, B. detail of stipules, C. abaxial surface of leaf base, D. detail of leaf margin, E. pistillate flower, F. calyx lobe of a pistillate flower – internal face, G. calyx lobe of a pistillate flower – external face, H. gynoecium and floral nectaries (calyx removed), I. staminate cymules with one mature flower, J. immature fruit, K. seed – ventral face. Illustration by Klei Sousa, based on O.L.M. Silva 238 (SP).

glabrous; stipules subulate, entire or 2–3-partite, medium lobe up to 7(–8) mm long and lateral lobes up to 2 mm long, glabrous. **Thyrse** 10–20(–30) cm long, rachis glabrous; basal cymules with 5–8 pistillate flowers, accompanied by 1–2(–3) staminate flowers; distal cymules with 1–2(–3) staminate flowers; bracts triangular to

subulate, 2–5(–7) mm long, glabrous or with scarce short (< 0.5 mm) simple trichomes; **Staminate flowers** with pedicel up to 3 long, glabrous; calyx glabrous. **Pistillate flowers** with pedicels 2–6 mm long, up to 10(–15) mm in fruit, glabrous or pilose, with simple short (< 0.5 mm) trichomes, calyx lobes 5–6(–7), sometimes with one or two lobes poorly developed and shorter and narrower than the others, lobes narrow to wide-oblong, 2.5–6(–8) mm long, up to 10(–15) mm in fruit and (1–)2–4 mm wide, glabrous on the external face, except sometimes for the pilose calyx base, with short (< 0.5 mm) simple trichomes, margin entire or strongly serrate, cartilaginous, glabrous, apex acute, obtuse, attenuate or rounded; ovary 1–3(–4) x 1–3(–4) mm, glabrous. **Fruits** opaque, 7–10(–12) x 7–10(–12) cm, glabrous; seeds rounded in cross section, 5–6(–8) x 4–5.5(–6) mm, caruncle 1.5–2.5 x 3.5–4.5 mm.

**Nomenclatural notes:**—Caruzo & Cordeiro (2007) called the specimen at G as holotype of *Croton cinctus*, although no herbarium is mentioned in the protologue of this name (Müller Argoviensis 1873). Following the International Code of Nomenclature for algae, fungi and plants (McNeill et al. 2012) and Prado et al. (2015), this cannot be considered an inadvertent lectotypification as this was published after 1 January 2001 (Art. 9.19). Therefore, the lectotype for this name is here designated as a specimen recently found in LE.

In the case of *Astraea aureomarginata*, Berry in Zuloaga et al. (2007) indicated the collection *Hassler 5010* deposited at G as the holotype of this name, although no direct mention of this herbarium is presented in the protologue of *Croton aureomarginatus* (Chodat & Hassler 1905). Also, a duplicate of this collection was found at B, although this was destroyed during the Second World War (Merrill 1943). As the indication of the specimen at G as the holotype of *A. aureomarginata* occurred after 1 January 2001, this does not represent an inadvertent lectotypification. Nevertheless, in support of this view, Berry designated a specimen at G as the lectotype of *A. hauthalii*, which has the exact same scenario, with a specimen at B destroyed. Therefore, we formally designate the specimen at G as the lectotype of *A. aureomarginata* in this work due to the reasons mentioned above.

Specimens of the type collection of *Croton rumicifolius* are distributed in many herbaria, and usually mounted to represent leaf blade diversity. Therefore, we choose the specimen at G as the lectotype once this herbarium holds most of Hassler's collections and better represent the leaf shape diversity of this species, with seven herbarium sheets (however, mounted with the same catalogue number in G).

**Etymology and vernacular names:**—the epithets *cinctus* and *aureomarginatus* refer to aspects of the leaf margin, thickened in the case of *cinctus* or thickened and golden in the case of *aureomarginatus*. *Oxydectes hauthalii* was proposed in honor of Rudolf J.F. Hauthal, a German geologist and paleontologist who explored Argentina and Paraguay from 1901 to 1902 and collected the type specimen of this name. The epithet *rumicifolius* is probably due to the irregularly lobed leaves. No vernacular names are registered for this species.

**Geographical distribution:**—SOUTHERN AMERICA. *Brazil*: Brazil South (BZS-PR), Brazil Southeast (BZL-MG), Brazil West-central (BZC-GO, BZC-MT, BZC-MS); *Southern South America*: Paraguay (PAR); *Western South America*: Bolivia (BOL).

*Astraea cincta*, in the delimitation proposed in this treatment, is found in Brazil, Bolivia and Paraguay (Fig. 3). In both Bolivia and Paraguay, it is found in the eastern region of these countries, close to the frontier with Brazil, while in Brazil the species is found in the states of Goiás, Mato Grosso, Mato Grosso do Sul, São Paulo, Paraná and, in a disjunct pattern, in Minas Gerais, along the southern portion of the Espinhaço range. This disjunct distribution pattern is also documented for other species from dry forest and caatingas along the South American Dry Diagonal. Prado and Gibbs (1993) indicate that this may be a vestige from a once more



Figure 3: Geographical distribution of *Astraea cincta*.



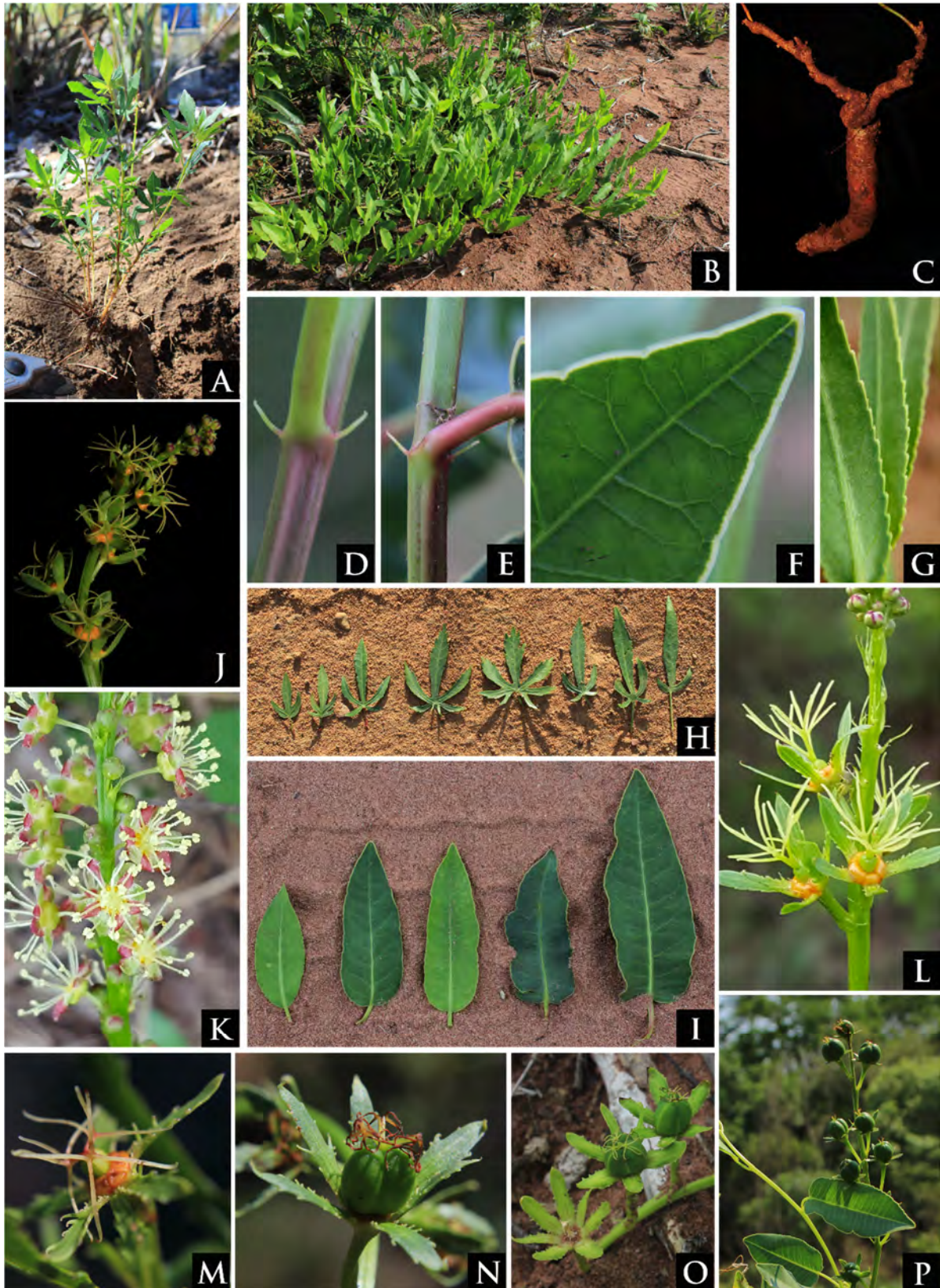
extensive formation which reached its maximum extent during the dry climatic period of the Pleistocene. The species grows on open cerrado formations, sometimes with sparse trees or shrubs and dense to sparse grass coverage. Elevation varies mostly from 607–660 meters above sea level, reaching a maximum of 1017–1100 meters above sea level in Serra do Cabral, Minas Gerais. Occurrence in plain terrain with sandy soils are registered for Bolivia and Brazil, but while during fieldwork we observed the species also occurring in red latosols in Bolivia and Brazil, while in Minas Gerais, it was found growing nearby rock outcrops among “campo rupestre” vegetation.

**Phenology:**—Flowering and fruiting are recorded from November to early April, but probably occur throughout the year. According to herbarium labels and field observations (M.G. Caxambu, pers. comm.), fire seems to act as trigger to reproductive growing of this species.

**Conservation status:**—With the synonymization of *Astraea aureomarginata* and *A. hauthalii*, the geographic distribution of *A. cincta* now encompasses not only central-southwestern Brazil, but also eastern Bolivia and Paraguay, reaching a wider area of occupancy (104.000 km<sup>2</sup>). Although Martinelli & Moraes (2013) only considered the occurrence of *A. cincta* in the states of Goiás, Mato Grosso do Sul and Paraná, they reached the same conclusion about the conservation status of this species: Endangered (B2ab[iii]), due to an area of occupancy < 500 Km<sup>2</sup> and the anthropic pressure caused by grazing resulting in loss of quality of habitat and number of populations. *Astraea hauthalii* was treated in Bolivia (as *Croton rumicifolius*) as Endangered (B2ab[iii]) by its narrow distribution, few populations and threat of its habitat due to livestock activities (Mamani et al. 2010).

**Taxonomic comments:**—According to Chodat & Hassler (1905), *Astraea aureomarginata* is distinguished from *A. cincta* by its long-petiolate (7–12 mm long) leaves, with whitish and undulate margin (vs. reddish and crenate in *A. cincta*) and sepals also with whitish margin (instead of reddish as in *A. cincta*). Through analysis of the type specimen of *A. aureomarginata* (E. Hassler 5010 at G!) we also concluded that *A. aureomarginata* would be a more robust form of *A. cincta* with woody branches that can reach up to 2 m long in its caespitose habit. During fieldwork in Corguinho municipality in Mato Grosso do Sul state in western Brazil we came across a small natural population in which we were able to observe individuals with a more robust form (Fig. 4B), which linked to *A. aureomarginata*, along with more delicate habit as in *A. cincta*, with mixed patterns of leaf margin type (Fig. 4I) and color and sepal margin color. Reinforcing this, during fieldwork to other localities where we found populations of *A. cincta*, we could observe individuals with undulate and whitish leaf margin and whitish sepal margins. Therefore, we synonymized *A. aureomarginata* under *A. cincta*.

Chodat & Hassler (1905) described *Croton rumicifolius* along with *C. aureomarginatus*, indicating that these two species are “similar”, with no further detailed comparison. Instead, the authors compared *C. rumicifolius* in details with *C. jatropha* (= *Astraea manihot* in this treatment) but this species lacks the characteristic



**Figure 4:** Morphological characters of *Astraea cincta*. **A–B.** habit. **C.** well-developed (xylopodiferous) underground system. **D–E.** variation of petiole color. **F–G.** variation in leaf margin type. **H–I.** variation in leaf shape. **J.** inflorescence. **K.** staminate flowers. **L–M.** pistillate flowers. **N–P.** immature fruits. **A, H, M and N:** populations from Serra do Cabral, MG (O.L.M. Silva 263); **B, D, E, F, I and O:** population from Corguinho, MS (O.L.M. Silva 238); **C, J, K, L and P:** populations from Campo Mourão, PR (O.L.M. Silva 304, 308); **G:** population from Santiago de Chiquitos, Bolivia. Photos: O.L.M. Silva.

underground system and leaf margin of *C. rumicifolius*. Following the description in the protologue of *C. rumicifolius*, this species is distinguished from both *C. aureomarginatus* and *C. cinctus* by its lobed/partite leaves and serrate leaf margin (Fig. 4G). Five years earlier, Kuntze (1898) described *Oxydectes hauthalii*, which resembles *C. rumicifolius* by its lobed/partite leaves but has crenate leaf margin. Berry in Zuloaga et al. (2007)

transferred *Oxydectes hauthalii* to *Astraea* (= *A. hauthalii*) and included *C. rumicifolius* as its synonym with no further discussion. The type collection of *C. rumicifolius* (*E. Hassler 4386*) has several isotypes deposited in many herbaria, and with all those specimens it is possible to observe all the variation in leaf shape and margin within a putative population. This variation was also observed in fieldwork to Santiago de Chiquitos, in Bolivia, where we could observe entire, hastate, 3- and 5-lobed/partite leaves, with crenate to serrate margin.

The type collection of *Astraea cincta* (*L. Riedel 608*) is annotated as from Rio Pardo [= Pardo River], a locality assigned to the state of São Paulo by Müller Argoviensis (1873). However, according to Riedel's itinerary on Flora Brasiliensis, this locality should be considered as from Mato Grosso do Sul. The type collection of *Croton aureomarginatus* (*E. Hassler 5010*), in turn, was collected in eastern Paraguay (in Ypehú), while the type collection of *C. rumicifolius* is from Ybytymí, southwestern Paraguay. Apart of all the collections concentrated in southwestern Brazil, eastern Bolivia and eastern Paraguay, we found population from central Minas Gerais in southeastern Brazil. These specimens from Minas Gerais are remarkable by their usually deeply (5–)7-partite leaves (Fig. 4H), a leaf shape found only in some collections from Paraguay as *E. Hassler 9509* (P 4830249!).

The high overlapping in leaf shape and margin among specimens analyzed so far, allied to conservation (indumentum of different structures) or plasticity (in shape and margin of pistillate calyx lobes) in other floral characters, it is impractical to recognize these different taxa. Therefore, we synonymize *A. aureomarginata* and *A. hauthalii* under *A. cincta*, the earliest name among them, recognizing one heterophyllous species with well-developed, woody underground system (probably xylopodiferous; Fig. 4C) and leaves with a thickened margin (Fig. 4F-G), along with seeds rounded in cross-section (Fig. 3K), characteristics exclusive to this taxon within *Astraea*.

**Selected specimens examined:**—BOLIVIA. **Santa Cruz. Chiquitos:** Santiago de Chiquitos, Ca. 0,5km from San Juanamo (near Santiago de Chiquitos) on road towards Motacu, 650 m, 18° 19' 10" S, 59° 37' 39" W, 15 November 2007, *J.R.I. Wood 23907* (UB, USZ). BRAZIL. **Goiás:** Caiapônia, Estrada entre Caiapônia e Jataí, margem esquerda junto a fonte de água sulfurosa, 14 October 1968, *Sidney 1532* (UB); Chapadão do Céu, Parque Nacional das Emas. Cerrado. 29 km do portão Jacuba, 11 October 2006, *J. Paula-Souza 8344* (SPF); Jataí, Balsano, 1 November 1950, *A. Macedo 2692* (US). **Mato Grosso:** Barra do Garças, Área da fenologia - coletas pós-fogo. Parque Estadual da Serra Azul, 15° 51' 00" S, 52° 16' 00" W, 30 September 2005, *M. Sanchez 2037* (SP). **Mato Grosso do Sul:** Campo Grande, 06 August 1936, *F.C. Hoehne s.n.* (SP 35784); Corguinho, MS-352, no sentido Taboco - Ciplândia, cerca de 10 km após a entrada para o Instituto Quinta do Sol, 265 m, 19° 50' 57.74" S, 55° 16' 06.86" W, 8 March 2016, *O.L.M. Silva 238* (SP); Costa Rica, Estrada do Alto Araguaia, Camapuã próximo a Costa Rica, 19° 05' 00" S, 53° 52' 10" W, 17 May 1978, *J. Guimarães 203* (HRB, RB); Maracajú, Rod. BR-267, 20 km O de

Maracajú, 25 October 1988, *G. Hatschbach 52613* (MBM); Sidrolândia, Assentamento Capão Bonito II, 29 September 2007, *A. Pott 14554* (CGMS, SP). **Minas Gerais:** Buenópolis, Serra do Cabral. Região do Cuba (no Rancho do Sr. Paulo Menezes), 17° 56' 19" S, 44° 15' 17" W, 10 November 2007, *L. Pangaio 1302* (HB, R); Curvelo, Estrada Curvelo-Corinto, Km 40, 02 October 1965, *A.G. Ferreira 32* (SP); Jaboticatubas, São José de Almeida, 26 February 2001, *A.F. Silva 64* (BHCB); Joaquim Felício, Próximo à Pedra Branca, 1017 m, 17° 42' 30.78" S, 44° 11' 45.52" W, 2 April 2016, *O.L.M. Silva 263* (SP); Morada Nova de Minas, Cerrado recorde acima do cerrado virgem da fazenda Boa Vista; a 18.2 km da cidade, 620 m, 18° 35' 00" S, 45° 22' 00" W, 12 November 1991, *R.F. Vieira 946* (CEN). **Paraná:** Campo Mourão, Cerrado ao lado da Agricase na rodovia Avelino Piacentini, margem esquerda (sentido Campo Mourão - Peabiru) acesso pela Rua Alfonso Germano Hruschka, 526 m, 24° 00' 36.17" S, 52° 21' 47.34" W, 19 October 2017, *O.L.M. Silva 308* (SP). **PARAGUAY. Alto Parana:** Ea. Santa Elena, Pira Pyta, 25° 17' 00" S, 54° 35' 00" W, 11 October 1990, *A. Schinini 27179* (CTES, MO). **Caaguazú:** Caaguazú, 12 km N de Caaguazú, camino a Yhú, 25° 21' 00" S, 56° 00' 00" W, 19 October 1994, *A. Krapovickas 45759* (CTES). **Canendiyú:** Maracayú Natural Reserve administered by Fundación Moisés Bertoni: Aguará ñú, 24° 11' 01" S, 55° 16' 48" W, 22 September 1999, *E.M. Zardini 51037* (MO). **San Pedro:** Santa Rosa del Aguaray - Santa Bárbara, 23° 50' 32" S, 56° 23' 39" W, 26 May 1997, *E.M. Zardini 46655* (MO).

**2. *Astraea comosa*** (Müll.Arg.) van Ee (2011: 17). *Croton comosus* Müller Argoviensis (1866: 667). *Croton comosus* var. *major* Müller Argoviensis (1866: 667). *Oxydectes comosa* (Müll.Arg.) Kuntze (1891: 611). Lectotype (designated here):—BRAZIL. Minas Gerais: Serra do Caraça, unknown date, *P. Claussen s.n.* (G-DC00312460!, isoelectotype G00434502! [on 2 sheets]); remaining syntype:—BRAZIL. Minas Gerais, Serra do Caraça, unknown date, *G. Casaretto 2745* (G00312459!). Figs. 5–6.

*Croton comosus* var. *minor* Müller Argoviensis (1866: 667). *Croton digitifolius* Baillon (1864: 340), *nom. nud.* Lectotype (designated by van Ee 2011):—BRAZIL. Minas Gerais: Villa Rica [= Ouro Preto], unknown date, *J.B.E. Pohl s.n.* [3911] (G-DC00312458!; isoelectotype B† [negative not found in F, W]).

**Perennial shrubs**, phanerophytes, up to 2.5(–5) m high, with erect branches, without a well-developed underground system, branches tomentose, with mostly stellate-porrect trichomes, but also stellate trichomes. **Leaves** mostly 3-partite or rarely with few entire leaves, medium lobe elliptic, 5–10(–18) x 1–2.5(–5.5) cm, and lateral lobes elliptic to oblong, 2–7(–14) x 1–2(–4.5) cm, chartaceous, apex attenuate to long attenuate, base rounded to cordate, margin serrate, with conspicuous teeth, not cartilaginous, ciliate, with simple or stellate trichomes, adaxial surface pilose, except for the densely pubescent primary veins, or rarely glabrescent, with stellate and stellate-porrect trichomes or short (< 0.5 mm) simple trichomes, abaxial surface tomentose, more dense near the base and along the veins, with stellate and stellate porrect trichomes, venation actinodromous; petioles (1–)3–7(–10) cm long, tomentose, with stellate and stellate-porrect trichomes; stipules subulate, entire or 3-lobed, with medium lobe 3–15(–30) mm long, and lateral lobes up to 3.5 mm, pubescent, with stellate, stellate-porrect and simple trichomes. **Thyrse** 15–40 cm long, rachis densely pubescent, with stellate and

stellate-porrect trichomes; basal cymules with up to 10(–20) pistillate flowers, accompanied by 6–8(–10) staminate flowers; distal cymules with 6–8(–10) staminate flowers; bracts triangular to subulate, 2–15(–20) mm long, pubescent, generally more dense at the base, with stellate trichomes, and with (< 0.5 mm) simple trichomes towards the apex; **Staminate flowers** with pedicel up to 5 long, glabrous; calyx pilose, with stellate trichomes. **Pistillate flowers** with pedicels 1.5–3.5 mm, up to 5(–10) mm in fruit, pubescent, with stellate and stellate-porrect trichomes, calyx lobes 5–6, sometimes with one lobe poorly developed and narrower than the others, lobes elliptic to obovate, 1.5–3 mm, up to 6(–7) mm in fruit and 1.5–2 mm wide, tomentose on the external face, with stellate trichomes and glabrescent at the tips, with (< 0.5 mm) simple trichomes, margin entire, not cartilaginous, ciliate, with stellate trichomes, apex acute; ovary 2–2.5 x 2–2.5 mm, glabrous to tomentose, with stellate trichomes or scattered short (< 0.5 mm) simple trichomes. **Fruits** lustrous, 6–8 x 6–8 cm, glabrous or densely pubescent, with stellate trichomes and few short (< 0.5 mm) simple trichomes; seeds tetragonal in cross section, 5–5.5(6.5) x 3.5–4 mm, caruncle 1–1.5 x 1.5–2 mm.

**Nomenclatural notes:**—In the lectotypification of *Astraea comosa* by van Ee (2011), the author choose a collection made by P. Claussen numbered as 1576 and deposited at the general collection of G. However, Müller Argoviensis (1866) cited an unnumbered collection of *P. Claussen* deposited at the Prodrum de Candolle’s collection at G (G-DC). Therefore, the lectotype designated by van Ee (2011) for *A. comosa* is equivocal and therefore corrected here.

In the case of *Croton comosus* var. *minor*, although an unnumbered collection of *J.B.E. Pohl* at B and G is cited as the type specimens by Müller Argoviensis (1866), we found a *J.B.E. Pohl*’s collection from the type locality (“Villa Rica” in the protologue, which corresponds to Ouro Preto municipality in Minas Gerais) numbered as 3911 at W, the herbarium which holds most of Pohl’s collections, usually numbered. Therefore, we add the number found in W specimen and consider this as an isoelectotype for *C. comosus* var. *minor*. The negative of Pohl’s collection from B could not be found in the Berlin Negatives database hold by The Field Museum.

Despite Müller Argoviensis’ (1866) proposal to recognize *Astraea tomentosa* Klotzsch as synonym of his *Croton comosus* var. *minor*, due to the lack of a type specimen for *A. tomentosa* which we could use to confirm its identity, we do not link this name to any of the valid names recognized in this treatment for *A. comosa*. In the case of *C. digitifolius*, although this name lacks a diagnose (and therefore represent a *nomen nudum*), the collections cited by Baillon (1864) fit Müller Argoviensis’ *C. comosus* var. *minor* and, therefore, is linked to this variety in this treatment.

**Etymology and vernacular name:s**—the epithet *comosus* refers to the well-developed bracts of the inflorescence. No vernacular name was found for this species.



**Geographical distribution:**—SOUTHERN AMERICA. *Brazil*: Brazil Southeast (BZL-MG).

*Astraea comosa* is endemic to the Brazilian state of Minas Gerais (Fig. 5), with the great majority of its specimens collected along the Meridional Espinhaço (following the subdivision of the Espinhaço Range by Campos et al. 2016), in central Minas Gerais. Only one specimen, deposited at R (100587!), without collector but numbered as 83 has indication of collection, in São Paulo, but this probably is due to a misplacement of the label. Endemic to the Cerrado domain, this species is found in gallery and 'capão' (mountain top) forests and *canga* or *campos rupestres* (rocky grasslands) vegetation, growing in quartzite-sandstone or iron rich soils and rock outcrops. It is frequently found only above 1,000 meters above sea level, with the lowest register annotated at around 800 meters in the vicinities of Ouro Preto municipality. Although *Astraea comosa* has specific preferences for habitat, it may still be found in these environments even in soils strongly altered by mining.



Figure 5: Geographical distribution of *Astraea comosa*.

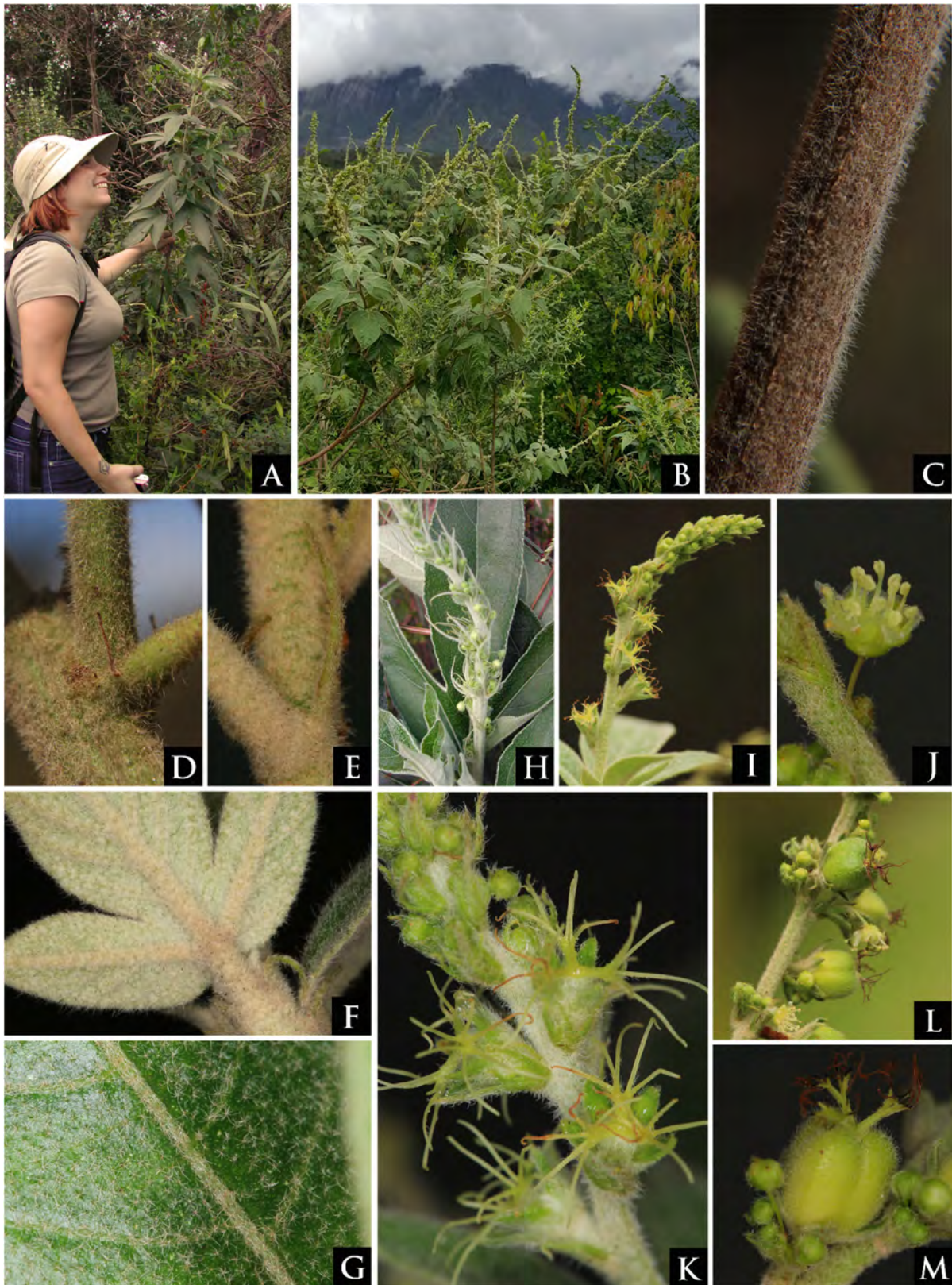
**Phenology:**—Flowering and fruiting is recorded throughout the year and usually at the same time. However, most specimens were collected in the wet season, from January to March.

**Conservation status:**—Despite the large number of known localities, this species is endemic and has an area of occupancy (AOO) < 5,000 km<sup>2</sup> (172,000 km<sup>2</sup>), severely fragmented due to habitat specificity and with continuing decline observed in extent and quality of habitat due to anthropic pressure (mining). Therefore, *Astraea comosa* is here classified as Endangered (B2ab[iii]).

**Taxonomic comments:**—When described by Müller Argoviensis (1866), *Astraea comosa* (as *Croton comosus*) included two varieties: *C. comosus* var. *major* and *C. comosus* var. *minor*. These two varieties are distinguished by the author based on the length of the bracts (surpassing the flowers in *C. comosus* var. *major* and not surpassing the flowers in *C. comosus* var. *minor*) and indumentum of the ovary/fruit (densely tomentose in *C. comosus* var. *major* and glabrescent in *C. comosus* var. *minor*). Furthermore, both varieties were based on materials collected in the southeastern portion of the Meridional Espinhaço (Serra do Caraça for *C. comosus* var. *major* and “Villa Rica” [= Ouro Preto municipality] for *C. comosus* var. *minor*). Van Ee (2011), when transferring *C. comosus* to *Astraea*, did not distinguish these two varieties, a position we agree based on our extensive analysis of herbarium specimens, along with field observation of natural populations from both northern and southern limits in this species’ distribution range.

Although the long bracts and fruit indumentum referred to *Astraea comosa* in Müller Argoviensis’ (1866, 1873) treatments is not a constant characteristic of this species (Fig. 6H-I and 6L-M, respectively), it may be distinguished from other species of *Astraea* by the combination of chartaceous, 3-partite leaves, long inflorescences and pistillate flowers with calyx not strongly accrescent (not surpassing the fruit in length) with ovate lobes. The species may be confused with *A. manihot*, another species found in southern Minas Gerais, which in the meantime differs from *A. comosa* by its usually membranaceous 5-partite leaves (although *A. manihot* may have 3-partite leaves), and long-pedicellate flowers (sessile or subsessile in *A. comosa*) with oblong to linear calyx lobes.

*Astraea comosa* is also similar to *A. praetervisa* by its well-developed indumentum (Fig. 6 D-E), but the later has unique glanduliform stipules (vs subulate in *A. comosa*; Fig. 6D-E) and pistillate flowers with oblong to linear calyx lobes (vs ovate in *A. comosa*). Also, geographically, *A. praetervisa* is currently known only in southern Bahia, in the vicinities of Ilhéus municipality, where it is found in seashore plains vegetation (see Fig. 27).



**Figure 6:** Morphological characters of *Astraea comosa*. **A–B.** habit. **C.** stem. **D–E.** stipules. **F.** abaxial leaf of a leaf. **G.** adaxial surface of a leaf. **H–I.** inflorescence. **J.** staminate flowers. **K.** pistillate flowers. **L–M.** immature fruits. **A** and **H:** population from Serra do Cipó, MG (I. Cordeiro 3026); **B, E, F,** and **G:** population from Catas Altas, MG (O.L.M. Silva 319); **C** and **D:** population from Serra do Cabral, MG (O.L.M. Silva 266); **I, J, K, L** and **M:** population from Serra do Caraça, MG (O.L.M. Silva 318). Photos: **A** and **H:** I. Cordeiro; **B–G** and **I–M:** O.L.M. Silva.

In Müller Argoviensis' (1866, 1873) treatments, *Astraea comosa* was compared to *A. subcomosa* by the similarity in bract length. However, as mentioned for *A. comosa*, *A. subcomosa* also does not always have the



bracts surpassing the flower in length. The differentiation between these two species is mainly geographic: although *A. subcomosa* also occurs along the Espinhaço Range in the central Brazilian Plateau, it is only found in Septentrional Espinhaço and Chapada Diamantina portions (in the concept of Campos et al. 2016). Morphologically, *A. subcomosa* can only be distinguished from *A. comosa* by its predominantly entire (but rarely with few 2–3-partite leaves in a same branch) leaves, while in *A. comosa* the leaves are 3-partite and rarely entire.

This species was identified as *Croton lobatus* by Lima & Pirani (2009) in their treatment of *Croton* for Espinhaço Range. Additional illustrations in Müller Argoviensis (1873).

**Selected specimens examined**—BRAZIL. **Minas Gerais:** Barão de Cocais, Picha do cavalo, Mina Brucutu/CRVD, 19° 53' 08" S, 43° 26' 10.9" W, 31 January 2002, *A.M. Oliveira 18* (BHCB, SPF); Catas Altas, Estrada Catas Altas - Mariana (MG-129), cerca de 3 km após Morro da Água Quente, 881 m, 20° 08' 06.35" S, 43° 24' 23.89" W, 3 December 2016, *O.L.M. Silva 319* (SP); Conceição do Mato Dentro, Estrada Real, 7,5Km depois de Conceição do Mato Dentro sentido BH, 10 March 2014, *M.L.L. Martis 2144* (CEN, HUEFS); Diamantina, Rodovia BR 367, a 16 km N do trevo de Diamantina, rumo a Mendanha, 1200 m, 18° 10' 59" S, 43° 31' 25" W, 13 January 1998, *J.R. Pirani 3961* (SP, SPF, WIS); Gouveia, Fazenda Contagem, 19 July 1980, *J.R. Pirani in CFCR 163* (SP, SPF); Itabira, Cauê, 12 February 1934, *A. Sampaio 7075* (BHCB); Joaquim Felício, Estrada Joaquim Felício - Várzea da Palma, cerca de 20 km de Joaquim Felício, 1132 m, 17° 41' 52.19" S, 44° 15' 40.80" W, 2 April 2016, *O.L.M. Silva 266* (SP); Mariana, Mina Samarco; Norte de Alegria 1 e 6, 1180–1250 m, 20° 09' 17" S, 43° 30' 53" W, 16 October 2009, *S.G. Rezende 3669* (BHCB, BHZB); Nova Era, Presidente Vargas, Pico do Cauê, 30 January 1943, *Mendes-Magalhães 2822* (BHCB); Ouro Preto, Serra de Antônio Pereira. Samarco. Alegria 7., 10 October 2007, *M.C.T.B. Messias 1478* (OUPR, SP); Presidente Kubitschek, Rod. MG-259, 3-5km L da divisa com Datas, 21 November 1997, *G. Hatschbach 67370* (MBM, SP); Rio Acima, Rodovia de Ouro Preto para Belo Horizonte. Campo com afloramentos rochosos, próximo ao Pico do Itabirito, 1230 m, 20° 12' 08" S, 43° 50' 33" W, 12 July 2001, *P. Fiaschi 910* (SP); Santa Bárbara, Serra do Caraça. Trilha na mata de encosta (com *Vanillosmopsis*) em direção ao Campo de Fora, 1350–1500 m, 20° 06' 18" S, 43° 29' 40" W, 22 May 1997, *R. Mello-Silva 1363* (SP, SPF, SPSF, UEC, WIS); Santa Luzia, Serra do Cipó, Va 136 - Est. Conceição, 2 February 1934, *s.col. s.n.* (R 99373); Santana do Riacho, Serra do Cipó, Rodovia Belo Horizonte-Conceição do Mato Dentro Km 117, mata ciliar perturbada do Córrego Três Pontes, junto à trecho desativado do antigo traçado da rodovia, 1270 m, 19° 15' 50.8" S, 43° 32' 48" W, 06 March 2002, *I. Cordeiro 2764* (BHCB, K, SP, SPF, WIS); Serro, São Gonçalo do Rio das Pedras, 1041 m, 18° 24' 43.5" S, 43° 29' 55.8" W, 18 February 2009, *I. Cordeiro 3037* (SP).

**3. *Astraea digitata*** (Müll.Arg.) Silva & Cordeiro (2017: 297). *Croton lobatus* var. *digitatus* Müller Argoviensis (1866: 668). *Croton digitatus* Salzmann ex Schlechtendal (1846: 240), *nom. illeg.* Lectotype (designated by Silva & Cordeiro 2017):—BRAZIL. Bahia: unknown locality, unknown date, *P. Salzmann 492* (G00312450!); remaining syntype:—BRAZIL Bahia: unknown locality, unknown date, *J. Lhotsky s.n.* (G00312449!). Figs. 7–8.

**Perennial subshrubs or shrubs**, phanerophytes, up to 1(–1.5) m high, with erect branches, without a well-developed underground system, branches esparsely pubescent to glabrescent, with simple and/or stellate trichomes. **Leaves** 3(–5)-partite, medium lobe elliptic to wide-elliptic, 5–8(–11) x 2.5–3(–4) cm, and lateral lobes elliptic to oblong, (2–5)4–7(–9.5) x 1.5–2(–3) cm, membranaceous, apex attenuate to long attenuate, base cordate to subcordate, margin serrate, with conspicuous teeth, not cartilaginous, ciliate, with simple trichomes, adaxial surface pubescent, more dense at the base and along the primary veins, simple long (> 1 mm) patent trichomes, especially near the base, abaxial surface densely pubescent, more dense near the base and along the veins, with short (< 0.5 mm) simple trichomes, except for the veins, with long (> 1 mm) patent trichomes, especially, venation actinodromous; petioles (1.5–)4–8.5(–10) cm long, glabrescent to pubescent, more dense near the apex, with simple long (> 1 mm long) or scarce stellate trichomes; stipules subulate, entire or 3-lobed, medium lobe 2–5 mm long and lateral lobe up to 1 mm long, glabrous or with scarce long (> 0.5 mm) simple trichomes. **Thyrse** 15–35 cm long, rachis pilose, with short (< 0.5 mm) simple trichomes; basal cymules with 5–10 pistillate flowers, accompanied by 4–5 staminate flowers; distal cymules with 4–5 staminate flowers; bracts triangular to subulate, 1.5–2.5 mm long, pilose, with (< 0.5 mm) simple trichomes; **Staminate flowers** with pedicel up to 3 long, glabrous or with sparse short (< 0.5 mm) simple trichomes; calyx pilose, generally with 1–2 long (> 0.5 mm) simple trichomes on each lobe. **Pistillate flowers** with pedicels ca. 1 mm, up to 5 mm in fruit, pubescent, with stellate-porrect trichomes, calyx lobes 5–6, sometimes with one lobe poorly developed and narrower than the others, lobes oblong to narrow-obovate, 2–3.5 mm, up to 8 mm in fruit and 1–1.5 mm wide, pilose on the external face, with long (> 1 mm) simple trichomes, margin entire, not cartilaginous, ciliate with long (> 1 mm) simple trichomes, apex acute; ovary 1.5–2 x 1.5–2 mm, glabrous. **Fruits** lustrous, 4.5–5.5 x 4.5–5.5 cm, glabrous; seeds tetragonal in cross section, 3–3.5 x 2.5–2.8 mm, caruncle 0.3–0.5 x 0.8–1 mm.

**Nomenclatural notes:**—Nomenclatural matters of *Astraea digitata* were discussed by Silva & Cordeiro (2017).

**Etymology and vernacular names:**—the epithet *digitatus* is a reference to the leaves of this species, whose lobes are arranged in a pattern similar to the fingers in a hand. No vernacular names were recorded for this species.

**Geographical distribution:**—SOUTHERN AMERICA. *Brazil*: Brazil Northeast (BZE-AL, BZE-BA, BZE-PB, BZE-PE); *Southern South America*: Paraguay (PAR).

*Astraea digitata* is mostly restricted to the Northeastern Brazil (Fig. 8), in the states of Bahia, Alagoas, Pernambuco and Paraíba. There is only one specimen collected in Paraguay by Heircher (P4830246!), which is strongly separated from the remaining populations in northeastern Brazil, raising the question on if this would be a misplaced label. Except for this dubious collection from Paraguay, *Astraea digitata* is endemic to the Atlantic Forest domain, where it is usually found along forest edges, or disturbed sites, such as cocoa plantations or secondary forests, whether in shaded or sunny places. The few field observations available for



**Figure 7:** Line drawing of *Astraea digitata* A. flowering branch, B. detail of indumentum of younger portion of stems, C. detail of stipules, D. abaxial surface of leaf base, E. detail of leaf margin, F. pistillate flower, G. calyx lobe of a pistillate flower – internal face, H. calyx lobe of a pistillate flower – external face, I. gynoecium and floral nectaries (calyx removed), J. staminate cymules with one mature flower, K. immature fruit, L. seed – ventral face. Illustration by Klei Sousa, based on O.L.M. Silva 228 (SP).

this species indicates that it grows in clay or sandy soil. Elevation varies from near the sea level to around 700 meters above sea level in the high montane forest within caatinga ("brejos de altitude") from Pernambuco.



Figure 8: Geographical distribution of *Astraea digitata*.

**Phenology:**—Flowering and fruiting are registered in herbarium specimens for all months, except for April and November, but it is likely that the species may be found in reproductive growing throughout the year.

**Conservation status:**—*Astraea digitata* has an area of occupancy (AOO) of 76,000 km<sup>2</sup>, with population severely fragmented due to non-continuous distribution between Bahia and the other northeastern states. Furthermore, there is a continuing decline in its area and quality of habitat due to the historic anthropic pressure to Atlantic Forest hotspot. Therefore, *A. digitata* is here classified as Endangered, based on its area of occupancy (B2ab[iii]).

**Taxonomic comments:**—*Astraea digitata* is remarkable among the species of *Astraea* by its pistillate flowers with calyx lobes hirsute on the outer surface, with simple, long and patent trichomes (Fig. 7F-H, K). The same trichomes are observed in the calyx of staminate flowers, but usually with only one trichome per lobe (Fig. 7J).

The morphologically closest related species to *A. digitata* is *A. gracilis*, compared in detail with this species by Silva & Cordeiro (2017). Other species that are found in Northeastern Brazil are *A. klotzschii*, *A. paulina*, *A. praetervisa*, *A. subcomosa* and *A. surinamensis*. Among these, *A. paulina* and *A. subcomosa* are not found in the Atlantic Forest domain and *A. subcomosa* may also be distinguished from *A. digitata* by their leaves with stellate trichomes in the indumentum of the abaxial surface (vs. simple trichomes in *A. digitata*). *Astraea digitata* is found in the region of the Ilhéus municipality in southern Bahia, to where *A. praetervisa* is endemic. Both may be found in forests edges but may be distinguished by stipule shape (subulate in *A. digitata* and glanduliform in *A. praetervisa*) and indumentum of stems and leaves (dense indumentum of stellate trichomes in *A. praetervisa* versus sparse indumentum of simple trichomes in *A. digitata*). *Astraea surinamensis*, in turn, may be distinguished from *A. digitata* by its fruits with long simple trichomes, while *A. digitata* fruits are glabrous. Finally, *A. klotzschii* may be distinguished from *A. digitata* by the leaves always 3-partite in *A. digitata*, while in *A. klotzschii* they are predominantly entire or rarely 2–3-partite, subulate stipules (vs. deltoid in *A. klotzschii*), besides indumentum of calyx in pistillate flowers.

**Selected specimens examined:**—BRAZIL. **Alagoas:** Rio Largo, Usina Leão, Mata do Cedro, 09° 47' 83" S, 35° 85' 33" W, 13 May 2009, L.M. Leão 129 (MAC); São Miguel dos Campos, Fazenda São Sebastião - CIMPOR, Área do Furado, 14 August 2007, I.A. Bayma 889 (MAC). **Bahia:** Amélia Rodrigues, Estrada Feira-Salvador. Distante 30-35 Km de Feira de Santana, 23 March 1994, F. França 957 (HUEFS, SP); Camamu, Orojó, 16 June 2003, G. Hatschbach 75396 (ALCB, MBM); Conceição do Almeida, Fazenda Santa Cruz, 6 September 1959, A.L. Costa s.n. (ALCB 2068); Cruz das Almas, unknown locality, 1950, G. Pinto s.n. (MBML 2473, SP 274822); Ilhéus, Mata da Esperança, na primeira parte da trilha, antes de chegar a uma residência, 26 m, 14° 47' 21.58" S, 39° 03' 55.47" W, 8 February 2015, O.L.M. Silva 228 (SP); Salvador, Remanescente de Mata Atlântica da Odebrecht/Coelba, 12° 57' 58" S, 38° 26' 13" W, 19 January 2000, N.G. Jesus s.n. (ALCB 86823, HRB 56593, HUEFS 144763); São Francisco do Conde, Fazenda Engenho Madrugada, 22 July 1991, M.L. Guedes s.n. (ALCB 27934); Una, Along the Rio Maruim between the Reserva Biológica de Una and the Ecoparque de Una, 50 m, 18 September 2004, W.W. Thomas 14137 (CEPEC, NY); Uruçuca, unknown locality, 21 June 1970, T.S. Santos 856 (CEPEC). Unknown locality, unknown date, J. Lhotsky s.n. (G312449). **Paraíba:** Alagoa Nova, Brejo Paraibano. Mata do Uruçu, 521 m, 07° 02' 31" S, 35° 42' 35" W, 12 December 2011, E. Melo 10862 (HUEFS, UFRN). **Pernambuco:** Brejo da Madre de Deus, Fazenda Bituri, 4 February 1995, M. Sales 499 (NY, PEUFR); Caruaru, Brejo dos Cavalos, 10 January 1972, M.B. Ferreira 1544 (HEPH); Moreno, Mata do Engenho Pereira, 17 September 1998, M.F.A. Lucena 669 (PEUFR); Recife, Jardim Botânico, Mata do Curado, 29 February 1994, R. Pereira s.n. (IPA 56771). PARAGUAY. Unknown locality, unknown date, Heircher s.n. (P 4830246).

**4. *Astraea gracilis*** (Müll.Arg.) Silva & Cordeiro (2017: 299). *Croton lobatus* var. *manihot* lusus *gracilis* Müller Argoviensis (1866: 668). *Croton lobatus* var. *gracilis* (Müll.Arg.) Müller Argoviensis (1873: 273). Lectotype (designated by Silva & Cordeiro 2017):—BRAZIL. Rio de Janeiro: 'in pascuis montanis prope Sebastianopolis', unknown date, C.F.P. von Martius s.n. (G312451!, isolectotypes M89080 [photo!], M0089081 [photo!], M0089082 [photo!]); remaining syntypes:—BRAZIL. Rio de Janeiro, unknown date, C.

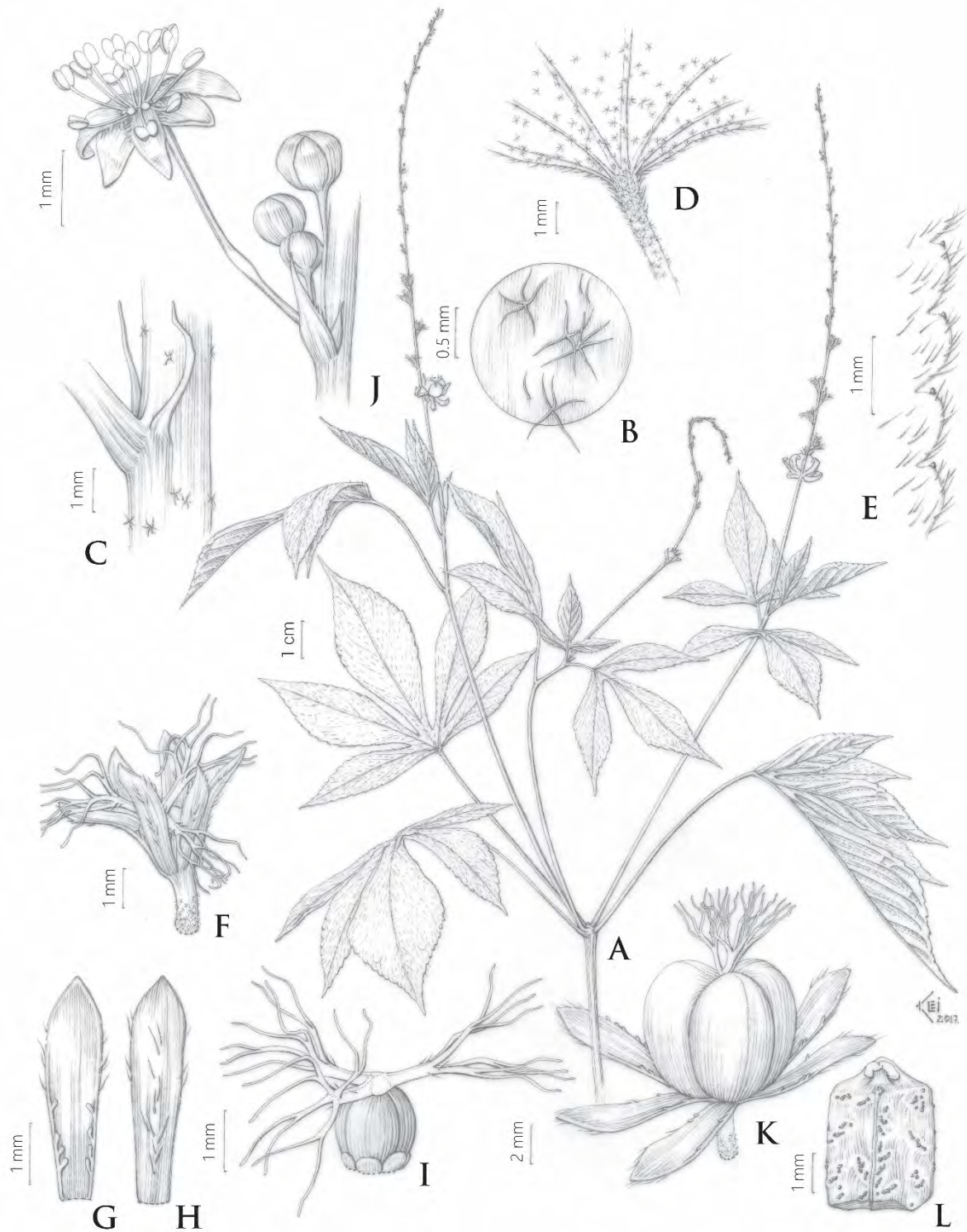
*Gaudichaud-Beaupré* 1129 (G00312452!, P04830274!, P04830315!), *J.B.A. Guillemain* 167 (G00312453!, isosyntypes K001210212!, NY00594296 [photo!], NY00504207 [photo!], P04830281!, P04830282!). Figs. 9–11.

**Perennial subshrubs or shrubs**, phanerophytes, up to 1.5 m high, with erect branches, without a well-developed underground system, branches glabrous or pilose to esparsely pubescent, with simple and/or stellate trichomes. **Leaves** 3(–5)-partite, medium lobe narrow to wide–elliptic, slightly oblanceolate or slightly ovate, 3–8(–11.5) x (1–)1.5–3(–4) cm, and lateral lobes oblong or elliptic, (2.5–)3–7.5 x 1–5 cm, membranaceous, apex attenuate to long attenuate, base rounded, truncate or slightly subcordate or cuneate, margin serrate, with conspicuous teeth, not cartilaginous, ciliate, with simple trichomes, adaxial surface puberulous, puberulent or strigose, more dense at the base and along the primary veins, with mostly long (> 0.5 and < 1 mm) simple trichomes, with stellate and stellate-porrect trichomes restricted to the base, abaxial surface glabrescent to sparsely puberulent, more dense near the base, with short (< 0.5 mm) simple or stellate trichomes, venation actinodromous; petioles (0.5–)2.5–5(–12) cm long, glabrous or pilose, specially at the apex or near the base, with stellate or short (< 0.5 mm) simple trichomes; stipules subulate, entire or 3-lobed, medium lobe up to 3 mm long and lateral lobes up to 1 mm long, glabrous or with few scattered simple or stellate trichomes. **Thyrse** (7–)10–30 cm long, rachis glabrescent to sparsely pubescent, with stellate or short (< 0.5 mm) simple trichomes; basal cymules with 3–10 pistillate flowers, accompanied by 3–4 staminate flowers; distal cymules with 3–4(–5) staminate flowers; bracts triangular to subulate, up to 3 mm mm long, glabrous to glabrescent, with (< 0.5 mm) simple or stellate trichomes; **Staminate flowers** with pedicel up to 5 mm long, glabrous; calyx glabrous. **Pistillate flowers** with pedicels 1–2 mm, up to 7 mm in fruit, glabrous or pubescent, with stellate trichomes, calyx lobes 5–7, sometime with one lobe poorly developed and narrower than the others, lobes obovate to narrow-oblong, 2–4 mm, up to 8(–15) mm in fruit and 1–2 mm wide, sparsely pubescent on the external face, with short (< 0.5 mm) or long (> 0.5 mm and < 1 mm) simple trichomes, margin entire, not cartilaginous, ciliate, with short (< 0.5 mm) simple trichomes, apex acute; ovary 1–1.5 x 1–1.5 mm, glabrous. **Fruits** lustrous, 5–8 x 5–8 cm, glabrous; seeds tetragonal in cross section, 3–5 x 2–4.5 mm, caruncle ca. 0.5 x 1 mm.

**Nomenclatural notes:**—Silva & Cordeiro (2017) when publishing *Astraea gracilis* cited *M.K. Guillemette* 167 as one of the remaining syntypes for this name. However, this is a mistake – the correct collector is *J.B.A. Guillemain*. Also, the barcode cited by Silva & Cordeiro (2017) for *C. Gaudichaud-Beaupré* 1729 is incorrect – the right number is NY885196. Additional notes are presented in Silva & Cordeiro (2017).

**Etymology and vernacular names:**—the epithet *gracilis* refers to the delicate aspect of this species. Vernacular names gathered for this species are: *pé-de-galinha* and *velame-pé-de-galinha* (portuguese).





**Figure 9:** Line drawing of *Astraea gracilis* A. flowering branch, B. detail of indumentum of younger portion of stems, C. detail of stipules, D. abaxial surface of leaf base, E. detail of leaf margin, F. pistillate flower, G. calyx lobe of a pistillate flower – internal face, H. calyx lobe of a pistillate flower – external face, I. gynoecium and floral nectaries (calyx removed), J. staminate cymules with one mature flower, K. immature fruit, L. seed – ventral face. Illustration by Klei Sousa, based on O.L.M. Silva 228 (SP).

**Geographical distribution:**—SOUTHERN AMERICA. *Brazil:* Brazil Northeast (BZE-AL, BZE-BA, BZE-CE, BZE-PE), Brazil Southeast (BZL-ES, BZL-MG, BZL-RJ, BZL-SP), Brazil Western-central (BZC-GO, BZC-MT, BZC-MS); *Northern South America:* French Guiana (FRG); *Southern South America:* Argentina Northwest (AGW-JU, AGW-SA); Paraguay (PAR); *Western South America:* Bolivia (BOL).

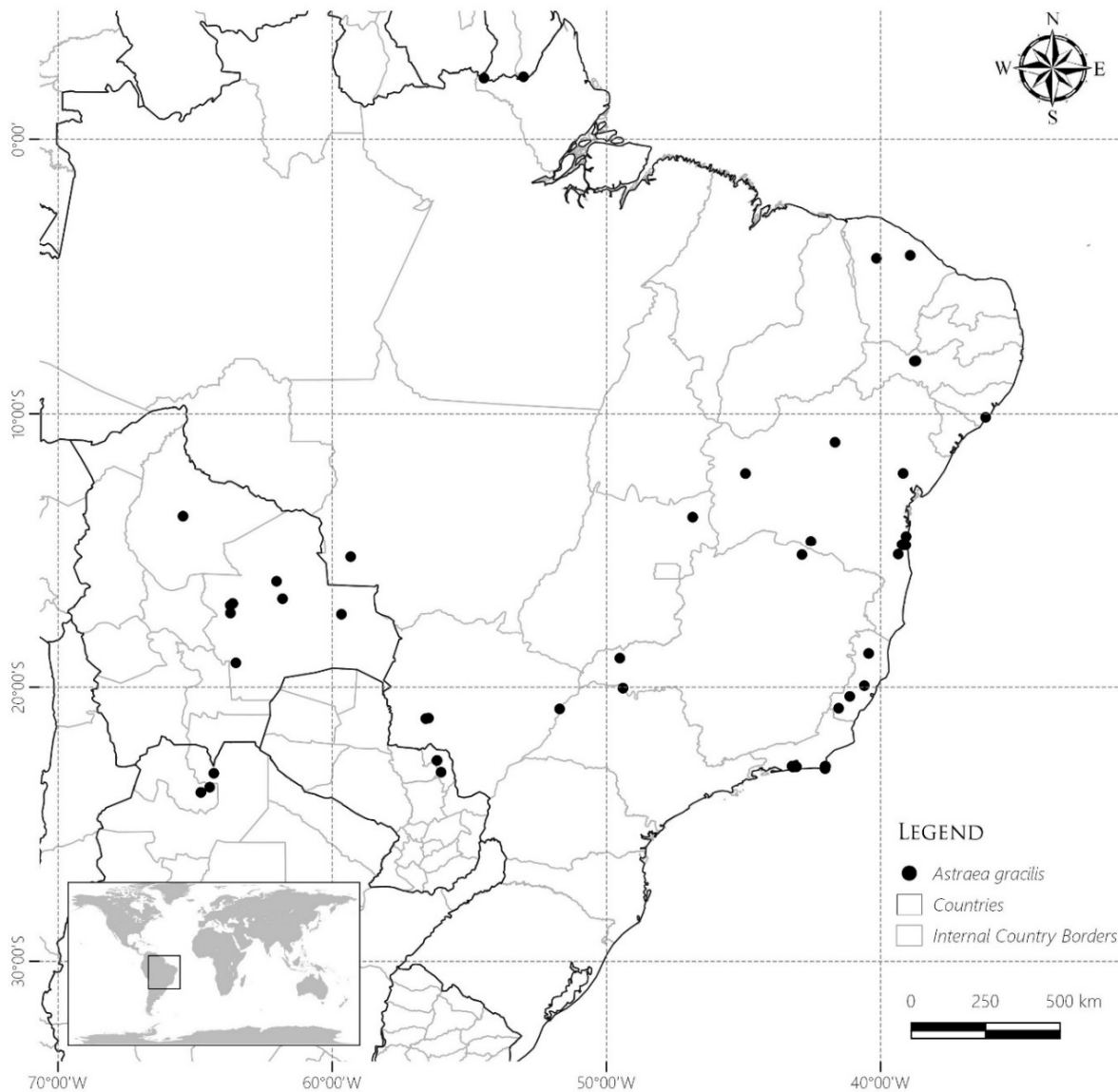


Figure 10: Geographical distribution of *Astraea gracilis*.

Although originally described as endemic to Rio de Janeiro in southeastern Brazil, *Astraea gracilis* is a widely distributed species (Fig. 10), found in northeastern and central Brazil and also in French Guiana, Bolivia, Paraguay and Argentina. Its distribution range follows the seasonally “dry diagonal” vegetation in South America (Prado & Gibbs 1993; Pennington et al. 2004). However, despite its wide distribution, this species presents a sparse pattern, present in many of the seasonally dry vegetation nuclei (Rupununi, Caatingas, Chaco, Misiones and Piedmont) indicated by Pennington *et al.* (2000). This disjunction pattern may be explained by Prado & Gibbs’ (1993) theory of a once extended and continuous seasonal formation during the



Pleistocene. Although found throughout the diagonal of dry vegetation from South America, this species also occurs in humid forests along Atlantic Forest domain. However, within this domain, it is found in dry formations as semideciduous forests, rock outcrops or along edges of secondary vegetation. Elevation varies mostly from near sea level to about 500–700 m above sea level, reaching up to or more than 1,000 m above sea level in some collections along the Espinhaço Range in Central-Eastern Brazil.

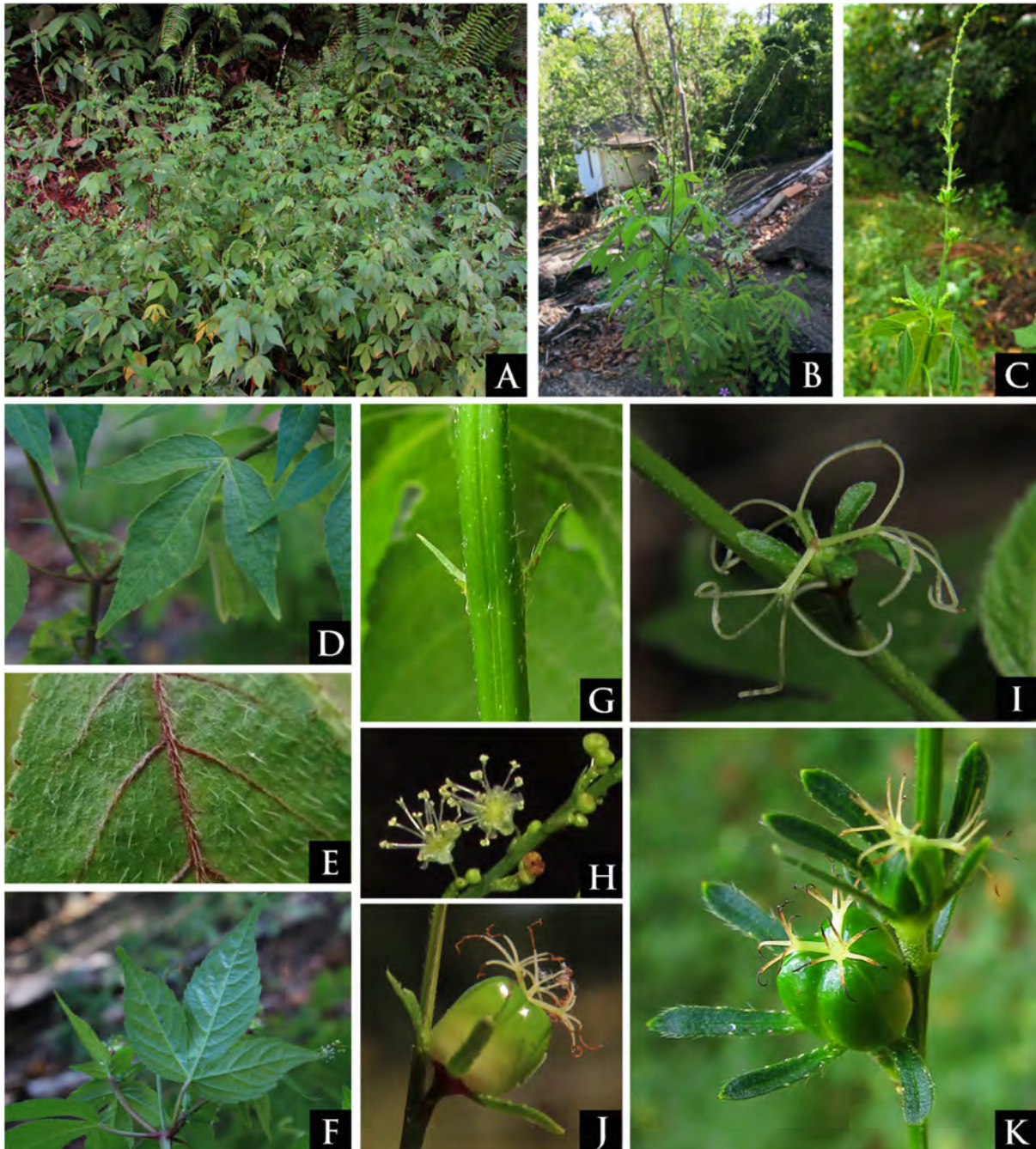
**Phenology:**—Flowering and fruiting were registered throughout the year, and are commonly observed at the same time. During fieldwork we observed small beetles, flies and bees visiting the flowers.

**Conservation status:**—the species has an extent of occurrence (EOO) greater than 2,000 km<sup>2</sup> (6,664,248.91 km<sup>2</sup>), and an area of occupancy (AOO) of 192,000 km<sup>2</sup>, with many known locations. However, these locations are severely fragmented and are subject to continuing decline in area and quality of habitat due to anthropic pressure. Therefore, according to IUCN (2012) guidelines, *Astraea gracilis* is here classified as Near Threatened (NT) once it is likely to qualify for a threatened category in near future, but our present evaluation neither qualify it for Critically Endangered, nor Endangered or Vulnerable.

**Taxonomic comments:**—*Astraea gracilis* is morphologically close and share its distribution range with *A. digitata*, *A. manihot* and *A. paulina*. *Astraea digitata* is found exclusively on Atlantic Forest and may be distinguished from *A. gracilis* by the indumentum of leaves and pistillate flower calyx: abaxial surface of leaves pubescent to densely pubescent, with long simple trichomes (Fig. 7D), and pistillate calyx with long patent simple trichomes on the outer surface (Fig. 7F) in *A. digitata* vs. abaxial surface of leaves glabrous or sparsely pubescent, with short simple trichomes except for the base, with stellate trichomes (Fig. 9D), and pistillate calyx glabrous or with short, appressed simple trichomes (Fig. 9F, 11I, J, K).

*Astraea manihot* is found both on Atlantic Forest and seasonally dry forests within Cerrado phytogeographic domain and may be distinguished from *A. gracilis* by its (3–)5(–7)-partite leaves (vs. 3(–5)-lobed in *A. gracilis*; Fig. 11A, D, F) and long-pedicellate (pedicels > 3 mm long) pistillate flowers (vs. subsessile, with pedicels up to 3 mm long in *A. gracilis*; Fig. 11I). *Astraea paulina*, in turn, is found exclusively within the South American Dry Diagonal, in formations similar to *A. gracilis*, as gallery forest and edges of seasonally dry forests or next to rock outcrops. This species differs from *A. gracilis* by the chartaceous leaves in *A. paulina* vs. membranaceous in *A. gracilis*.

**Selected specimens examined:**—ARGENTINA. **Jujuy:** Ledesma, Ruta 83, entre 5–6 km de la ruta 34, cerca del río San Lorenzo, 11 February 1992, *J.H. Hunziker* 12275 (MO). **Salta:** Orán, El Tubacal, 310 m, 17 February 1943, *T. Meyer* 4508 (F). BOLIVIA. **Beni. José Ballivian:** Espiritu em la zona de influencia del río Yacuma, 200 m, 4 March 1987, *G. Beck* 15024 (MO). **Santa Cruz:** Sara, Río Blanco, entre Boures y Buon Retiro, 20 December 1947, *R. Scolnik* 677 (P, US). **Santa Cruz. Ñuflo de Chávez:** Concepción, C. 5 km E of Concepción on road to San Jorge, 500 m, 2 January 1999, *J.R.I. Wood* 14346 (K[2], USZ); San Antonio de Lomerio, Alrededor del pueblo, 300–500 m, 16° 46' 07" S, 61° 48' 48" W, 4 February 1994, *M. Toledo* 377



**Figure 11:** Morphological characters of *Astraea gracilis*. **A–C.** habit. **D.** adaxial surface of a leaf. **E.** detail of the adaxial surface of a leaf. **F.** abaxial surface of a leaf. **G.** stipules. **H.** staminate flower. **I.** pistillate flower. **J–K.** immature fruits. **A, E and J:** population from Itacaré, BA (O.L.M. Silva 222); **B, D, F, G and J:** population from Nova Venécia, ES (O.L.M. Silva 283); **C, H and K:** population from Ilhéus, BA (O.L.M. Silva 223, 224). Photos: O.L.M. Silva.

(USZ). **Santa Cruz. San José de Velasco:** Concessión Don Mario ubicado a 125 km de San José de Chiquito, 400 m, 17° 20' 00" S, 59° 40' 00" W, 23 February 1997, *F. Mamani 1446* (MA, MBM, USZ). **Santa Cruz. Sara:** Camino a la Laguna Juan Chulo y Brecha petrolera, 250 m, 17° 00' 30" S, 63° 43' 14" W, 6 January 2009, *G.A. Parada 1377* (USZ). Unknown locality, 1921, *Mulford Biological Exploration of the Amazon Basin 1228* (K, NY, US). **BRAZIL. Alagoas:** Coruripe, Mata do Riacho das Pedras, Fazenda Capiatã, 17 October 1999, *R.P. Lyra-Lemos 4384* (MAC). **Bahia:** Anguera, Morro da Fazenda Retiro, próximo à estrada do Feijão, 343 m, 12° 10' 01" S, 39° 11' 01" W, 31 October 2006, *J.S. Novais 24* (HUEFS, SP); Arataca,

Parque Nacional da Serra das Lontras. Na estrada de acesso ao Parque saindo da BR-101, 248 m, 15° 08' 16.48" S, 39° 21' 43.65" W, 6 February 2015, *O.L.M. Silva 225* (SP); Barreiras, Serra do Mimo - Atrás do Motel Emoções, 15 May 2009, *B.T.C. Santos 476* (HUEFS); Ilhéus, Campus da Universidade Estadual de Santa Cruz (UESC), km 16 da Rod. Ilhéus/Itabuna (BR 415), 40 m, 14° 48' 00" S, 39° 10' 00" W, 12 March 1996, *L.A. Mattos-Silva 3386* (CEPEC, HUEFS, HUESC); Itabuna, Centro de Pesquisas do Cacau, CEPLAC, CEPEC, March 1965, *R.P. Belém 534* (CEPEC, NY); Itacaré, Distrito de Serra Grande. Estrada Serra Grande - Uruçuca, próximo a um dos pontos onde a estrada passa pelo Rio Tijupinho, 97 m, 14° 28' 13.76" S, 39° 04' 35.16" W, 4 February 2015, *O.L.M. Silva 222* (SP); Licínio de Almeida, Serra Geral. Mata do Xaxá, 930 m, 14° 39' 06" S, 42° 32' 48" W, 22 January 2013, *F. Hurbath 451* (ALCB, SP); São Gabriel, Fazenda Boa Sorte, 798–800 m, 11° 02' 00" S, 41° 40' 00" W, 2 April 2009, *R.F. Machado 104* (HUEFS, SP). **Ceará:** Pacoti, Serra de Balurita. Sítio B. Inacio de Azevedo, July 1937, *J. Eugênio 759* (RB); Santa Quitéria, Fazenda Itatiaia, 26 April 1984, *A. Fernandes s.n.* (EAC 12469). **Espírito Santo:** Alegre, PCH Santa Fé - Parcela 3, 23 December 2008, *V.C. Manhães 166* (MBML); Nova Venécia, Trilha da Gameleira, após a capela próximo a Estação XV, 178 m, 18° 45' 49.45" S, 40° 26' 29.21" W, 8 April 2016, *O.L.M. Silva 283* (SP); Santa Teresa, Pedra da Onça, 06 January 2000, *V. Demuner 481* (MBML); Venda Nova do Imigrante, Mata Fria, 1100 m, 17 January 1995, *G. Hatschbach 61583* (CEPEC, MBM, U). **Goiás:** Nova Roma, Fazenda Santa Clara (localidade denominada Sucuri ou Pinga), 450 m, 13° 45' 43" S, 46° 51' 31" W, 29 February 2000, *M. Aparecida da Silva 4276* (CEN, IBGE). **Mato Grosso:** Pontes e Lacerda, BR-174, ca 4 km S of Pontes e Lacerda, 25 November 1998, *B. Dubs 2607* (U). **Mato Grosso do Sul:** Bonito, Interior da Gruta do Lago Azul, 21° 08' 31" S, 56° 35' 26" W, 24 February 2000, *G.A. Damasceno-Júnior 1851* (CGMS[2], MBM); Três Lagoas, Em cerrado próximo de Ilha Solteira, 10 September 1981, *H.F. Leitão Filho 12968* (UEC). **Minas Gerais:** Ituiutaba, Fazenda Estância da Ariranha, 535 m, 18° 56' 09.42" S, 49° 30' 50.93" W, 28 December 2010, *A.R. Rezende 222* (HUFU, SP); Monte Azul, Serra do Espinhaço, subida via Montevídiu, 700–1000 m, 14 January 1997, *G. Hatschbach 65703* (G, MBM, SP). **Pernambuco:** Mirandiba, Fazenda Tigre, 572 m, 08° 04.127' S, 38° 43.073' W, 3 May 2008, *K. Pinheiro 623* (UFP). **Rio de Janeiro:** Arraial do Cabo, Estrada de Massambaba, 3 December 1987, *H.M. Ferreira 209* (RB); Cabo Frio, Morro do Gavião, 13 October 1968, *D. Sucre 3926* (R, RB); Niterói, Itaipu, Morro das Andorinhas, parte inicial da trilha, próximo ao afloramento rochoso com vista para Itacoatiara, 19 March 1999, *L.J.S. Pinto 184* (RB); Rio de Janeiro, Maciço da Tijuca, serra da Carioca, morro Mundo Novo, Botafogo, Campus da Universidade Santa Úrsula, 5 June 1992, *J.M.A. Braga 57* (RB, SP). **São Paulo:** Paulo de Faria, Estação Ecológica de Paulo de Faria-Abrangendo uma área de 435,73 ha, 500 m, 17 January 2002, *F. Tomasetto 212* (HRCB, HSJRP, SP). FRENCH GUIANA. Maripasoula, Massif du Mitaraka, Crique Alama "Inselberg" Sommet Cloche, 600 m, 02° 13' 40" N, 54° 28' 10" W, 5 March 2015, *O. Poncy 2864* (P); Tumuc Humac. Frontière Guyana-Brásil. Au pied du Toukouchipann', sur le versant S-E, 450 m, 19 August 1972, *Granville 1300* (P). PARAGUAY. **Amambay:** Cerro Guazú, Circa Cerro Guazú, Amambay, 15 December 1978, *M. Bernardi 19200* (NY, US); Parque Nacional Cerro Cora, 22° 40' 00" S, 56° 05' 00" W, November 1983, *W. Hahn 1728* (DAV, G[2]); In regione cursus superioris fluminis Opa, 15 January 1901–2, *E. Hassler 7989* (G).

5. *Astraea klotzschii* Didrichsen (1857: 137). *Croton klotzschii* (Didr.) Müller Argoviensis (1865: 136). *Croton klotzschii* var *genuinus* Müller Argoviensis (1865: 136), *not val. publ.* Type:—BRAZIL: unknown locality, unknown date, *K. E. v. Mercklin s.n.* (holotype C10022551 [photo!], isotypes LE?, MW?). Figs. 12–13.

*Astraea glandulifera* Klotzsch in Wawra (1866: 31). Lectotype (designated here):—BRAZIL. Pernambuco: unknown locality, 1837, *G. Gardner 1137* (K00186082!, isoelectotypes E [photo!], G!, K00186083!, NY00262913!, P06783105!); remaining syntypes:—BRAZIL. Bahia: unknown locality, unknown date, *J.S. Blanchet 3621 [= 3216]* (G!, isosyntypes F768713 [photo!], MA249988!, P04831422!, W [photo!]); BRAZIL. Bahia: Ilhéus, unknown date, *H. Wawra & K. Maly 342* (W [photo!], isosyntype G!).

*Croton klotzschii* var. *intermedius* f. *minor* Müller Argoviensis (1873: 241) *nom. illeg.* Lectotype (designated here):—BRAZIL. Pernambuco: unknown locality, December 1837, *G. Gardner 1137* (K00186082!, isoelectotypes E [photo!], G[2]!, K00186083!, NY00262913!, P06783105!); remaining syntype:—BRAZIL. Ceará: unknown locality, unknown date, *Kalkman s.n.* (not found).

*Croton klotzschii* var. *intermedius* Müller Argoviensis (1873: 241) *nom. illeg.* *Croton klotzschii* var. *intermedius* f. *major* Müller Argoviensis (1873: 241) *nom. illeg.* Lectotype (designate here):—BRAZIL. Bahia: Ilhéus, unknown date, *H. Wawra & K. Maly 342* (W [photo!], isosyntype G!); remaining syntype:—BRAZIL: unknown locality, unknown date, *L. Riedel 46* (LE?, not found).

*Croton klotzschii* var. *latifolius* Müller Argoviensis (1865: 136) *nom. illeg.* Lectotype (designated here):—BRAZIL: Bahia, unknown locality, unknown date, *C. F. P. Martius s.n.* (M0086087 [photo!], isoelectotypes M0086086 [photo!], M0089105 [photo!], L0234698 [photo!]); remaining syntype:—BRAZIL. Bahia: unknown locality, unknown date, *J. S. Blanchet 3216A* (G00312421!, fragment at A00257948 [photo!]).

*Croton klotzschii* var. *oblongifolius* f. *prunifolius* Müller Argoviensis (1865: 136) *nom. illeg.* Lectotype (designated here)—BRAZIL: unknown locality, unknown date, *F. Sellow s.n.* (G!, isoelectotype W [photo!]); remaining syntype:—BRAZIL: unknown locality, unknown date, *L. Riedel s.n.* (LE?, not found)

*Croton klotzschii* var. *oblongifolius* Müller Argoviensis (1865: 136) *nom. illeg.* *Croton oblongifolius* var. *divaricatus* Müller Argoviensis (1855: 136). *Croton astreatus* Baillon (1864: 341), *nom. nud.* Lectotype (designated here):—BRAZIL: unknown locality, unknown date, *F. Sellow s.n.* (holotype B<sup>+</sup>, lectotype K00186085!, isoelectotypes BR875992 [photo!], G!, K00186084!, P00634925!).

**Perennial shrubs**, phanerophytes, up to 2(–3.5) m high, with erect branches, without a well-developed underground system, branches glabrous or pilose, with simple and/or stellate trichomes. **Leaves** entire or sometimes (2–)3-partite, entire leaves elliptic, oblong or ovate, (1.5–)3–9(–11), x (0.7–)1–4.5(–6), partite leaves with the medium lobe elliptic, oblong or slightly ovate, (4.5–)5–8(–9) x (1–)1.5–3.4(–4) cm, and lateral lobes oblong or elliptic, 3–4 x 0.5–1.5 cm, chartaceous, apex attenuate to long attenuate, base cuneate, obtuse, rounded or subcordate, margin crenate or serrate, with conspicuous teeth, not cartilaginous, ciliate, with simple trichomes, adaxial surface glabrous or pilose near the base and/or along the primary veins, with short (< 0.5 mm) simple trichomes, abaxial surface glabrous or pilose to pubescent, more dense near the base, with mostly short (< 0.5 mm) simple trichomes, generally near the base or along the primary veins, venation camptodromous (when entire) or actinodromous (when partite); petioles (0.5–)1–4.5(–5.5) cm long, glabrous or pilose, especially near the apex and the base, with stellate or short (< 0.5 mm) simple trichomes; stipules deltoid, entire, up to 3 mm long, glabrous or pilose with short (< 0.5 mm) simple or stellate trichomes. **Thyrse** (10–)15–25(–30) cm long, rachis glabrous, pilose or with few scattered short (< 0.5 mm) simple or stellate

trichomes; basal cymules with 3–10 pistillate flowers, accompanied by 3–5(–6) staminate flowers; distal cymules with 3–5(–6) staminate flowers; bracts triangular, up to 2 mm long, glabrous or with few (< 0.5 mm) simple trichomes; **Staminate flowers** with pedicel up to 4(–5) long, glabrous; calyx glabrous. **Pistillate flowers** with pedicels 0.5–2 mm, up to 4(–5) mm in fruit, glabrous to densely pubescent, with stellate trichomes, calyx lobes 5–7, sometimes with one lobe poorly developed and narrower than the others, lobes oblong, elliptic or slightly obovate, 3–5 mm, up to 7(–9) mm in fruit and 0.8–1.5 mm wide, glabrous, pilose or pubescent on the external face, with short (< 0.5 mm) simple trichomes, margin entire, not cartilaginous, ciliate, with short (< 0.5 mm) simple trichomes, apex acute; ovary 1–1.5 x 1–1.5 mm, glabrous or rarely with few short (< 0.5 mm) simple trichomes near the apical portion. **Fruits** lustrous, 5.5–6.5 x 5.5–6.5 cm, glabrous or rarely with few short (< 0.5 mm) simple trichomes; seeds tetragonal in cross section, 4–5 x 2.5–4 mm, caruncle 1–1.5 x 0.5–1 mm.

**Nomenclatural notes:**—As *Croton klotzschii* var. *genuinus* includes the type of *Astraea klotzschii* (by the citation of this name in the protologue) and uses the epithet *genuinus*, should be considered as not validly published (McNeill et al. 2012, Art. 24.3).

Klotzsch in Wawra (1866) indicated *J.S. Blanchet 3621* as one of the syntypes for his *Astraea glandulifera* and Van Ee (2011) already called the possibility of a typographic mistake for *J.S. Blanchet 3216*, a collection indicated as one of the syntypes for *Croton klotzschii* var. *latifolius* by Müller Argoviensis (1865). Indeed, *J.S. Blanchet 3621* was traced as a specimen of *Miconia stenostachya* DC. (Melastomataceae; G317079!).

Among the *nomina nuda* from Klotzsch (1841) three of them are involved with *Astraea klotzschii*: *A. divaricata*, *A. diversifolia* and *A. prunifolia*. Baillon (1858) indicated *A. divaricata* as synonym of his *Croton astraeatus* Baill., but the author also did not provide a diagnosis for his name. In Govaerts et al. (2000), *C. astraeatus* is an accepted name and includes *C. klotzschii* and all its infraspecific taxa. As Govaerts et al. (2000) stands as an important bibliography for Euphorbiaceae, *C. astraeatus* was largely adopted when identifying *A. klotzschii* in herbarium collections, despite being a *nomen nudum*. However, as Baillon cited specimens for his *C. astraeatus*, we can confirm its identity as synonym of *C. klotzschii* var. *oblongifolius* f. *divaricatus*, as mentioned by Müller Argoviensis (1866). Nevertheless, *C. klotzschii* (Didr.) Müll. Arg., along with its infraspecific taxa proposed by Müller Argoviensis (1865, 1866, 1873), are all illegitimate due to later homonymy of *C. klotzschii* Baillon (1864: 346), published one year before the combination by Müller Argoviensis.

**Etymology and vernacular names:**—the epithet *klotzschii* is a reference to Johann Friederich Klotzsch, the german botanist who first recognized *Astraea* as a genus. The epithets adopted for the infraspecific taxa by Müller Argoviensis (1865) mostly represents leaf shape (*latifolius*, *oblongifolius*, *prunifolius*), which are utilized by the author to distinguish them. The epithet *glandulifera*, proposed by Klotzsch, highlights the showy nectaries from pistillate flowers that may be observed in some populations. Vernacular names gathered for



Figure 12: Geographical distribution of *Astraea klotzschii*.

this species are: *cabeça-de-formiga*, *jibão*, *mamona-branca*, *mamona-selvagem*, *mamoninha* and *velame* (portuguese).

**Geographical distribution:**— SOUTHERN AMERICA. *Brazil*: Brazil Northeast (BZE-AL, BZE-BA, BZE-CE, BZE-PB, BZE-PE, BZE-RN, BZE-SE), Brazil Southeast (BZL-ES, BZL-RJ).

*Astraea klotzschii* is a species distributed along the seashore plains (“restinga” vegetation) in the Atlantic coast on northeastern and southeastern Brazil (Fig. 12). In northeastern Brazil, this species’ northernmost occurrence, in Ceará, is an old collection from early 1960s, with no other recent collection ever since. The species only reappears in the frontier between Rio Grande do Norte and Paraíba states. During fieldwork in Rio Grande do Norte, we could not find this species, even in the Natal’s Dunes State Park, one of the largest

sand dunes on Brazilian coast. During fieldwork, we notice that, along the coast of Rio Grande do Norte, the white sandy soils are found only on the southern portion of the state, while most of the dunes in this state have brown sandy soils, usually dominated by *Anacardium occidentale* Linnaeus (1753: 383). Nevertheless, this species is also found in campos rupestres (rocky grasslands), in a disjunction pattern already well-documented for different not related lineages within angiosperms (Alves et al. 2017). *Astraea klotzschii* is found both on open or high forest seashore vegetation, usually on white sandy soils.

However, in the case of forested environments, the species is restricted to forest edges. It is important to notice that in some collections from Sergipe, open seashore vegetation is named in the labels as “cerrado”. This species was also found on severely disturbed environments.

**Phenology:**—Flowering and fruiting is recorded simultaneously and throughout the year, although most specimens were collected during the wet season.

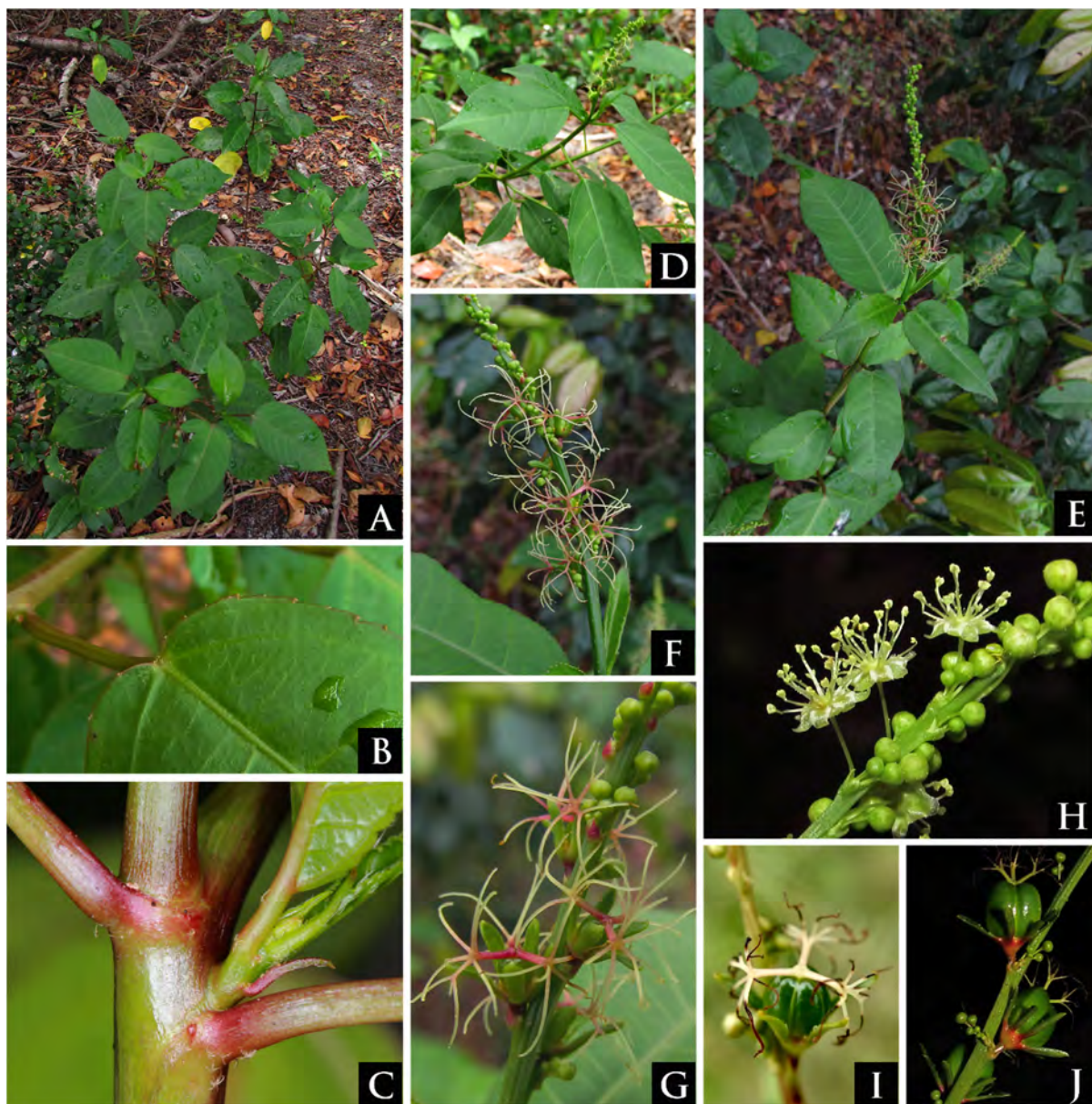
**Conservation status:**—*Astraea klotzschii* is widespread with an area of occupancy (AOO) of 612,000 km<sup>2</sup>, with many known locations. However, the seashore vegetation along the Brazilian coast, where the species is mostly found, are subject to continuing decline in area and quality of habitat due to anthropic pressure. Therefore, according to IUCN (2012) guidelines, *A. klotzschii* is here classified as Near Threatened (NT) once it is likely to qualify for a threatened category in near future, but our present evaluation neither qualify it for Critically Endangered, nor Endangered or Vulnerable.

**Taxonomic comments:**—When transferring *Astraea klotzschii* to *Croton*, Müller Argoviensis (1865) recognized five infraspecific taxa for this taxon, distinguished basically by leaf shape and base. This variation is interpreted in this monograph as phenotypic plasticity, and the same is true for differences regarding indumentum of the external face of the calyx of pistillate flowers and leaves, which may be glabrous, pilose or pubescent, but always with simple trichomes. Therefore, we do not recognize any infraspecific taxon for *A. klotzschii*.

*Astraea klotzschii* is morphologically close to recently proposed *A. macroua*, a species also found in the Brazilian seashore vegetations (“restingas”) from which it may be distinguished by the indumentum of the abaxial surface of leaves composed by stellate trichomes in *A. macroua* (vs. composed by simple trichomes in *A. klotzschii*). Additionally, *A. macroua* is restricted to southeastern Brazil, while *A. klotzschii* expands its distribution range to northeastern Brazil. *Astraea praetervis* is also found in the seashore vegetation of southern Bahia, but the indumentum of leaves, stems and calyx of pistillate flowers are composed by stellate trichomes (vs. simple trichomes in *A. klotzschii*) and *A. praetervis* is unique within the genus by its glanduliform stipules (vs. deltoid in *A. klotzschii*; Fig. 13C). *Astraea surinamensis* may also be found in seashore vegetation, and may be distinguished by the indumentum of young portion of stems (composed by stellate-porrect trichomes bearing a central ray with 3–4 mm long in *A. surinamensis* and glabrous or composed by simple or



stellate short (< 1 mm long) trichomes in *A. klotzschii*; Fig. 13C) and fruit (composed by simple long (3–4 mm long) trichomes in *A. surinamensis* vs. glabrous or with few scattered simple short (< 1 mm long) trichomes in *A. klotzschii*; Fig. 13I-J).



**Figure 13:** Morphological characters of *Astraea klotzschii*. **A.** habit. **B.** Leaf base and adaxial surface. **C.** stipules. **D–E.** branches with inflorescences. **F–G.** pistillate flowers. **H.** staminate flowers. **I–J.** immature fruits. **A, B, D–H:** populations from Mata de São João, BA (O.L.M. Silva 195); **C:** population from Tamandaré, PE (O.L.M. Silva 340); **I:** population from Itacaré, BA (O.L.M. Silva 220); **J:** population from Ilhéus, BA (O.L.M. Silva 215). Photos: O.L.M. Silva.

In the protologue of *Astraea glandulifera* (Wawra 1866) one may find a detailed illustration of this species.

**Selected specimens examined:**—BRAZIL. **Alagoas:** Barra de São Miguel, AL-101, a 1 km do Entrocamento com AL-215, 28 June 1982, *M.N.R. Staviski 442* (MAC, SPF); Maceio, unknown locality, 1838, *G. Gardner 1397* (BM, K[2]); Maragogi, Entre Peroba e Ponta de Mangue, a cerca de 3 km da divisa AL/PE, 31 January 1991, *C.S.S. Barros 49* (MAC); Marechal Deodoro, AL-101, sentido Maceió - Barra de São Miguel, estrada à esquerda, cerca de 1 km antes da rotatória com a AL-215, 0 m,



09° 45' 14.7" S, 35° 50' 47.6" W, 11 July 2017, *O.L.M. Silva 341* (SP); Passo do Camaragipe, Próximo ao Rio Camaragipe, 2 November 2001, *R.P. Lyra-Lemos 5934* (MAC); Piaçabuçu, Marituba, 23 September 1987, *M.N.R. Staviski 1030* (MAC); Pilar, Mata do Lamarão, 18 July 2006, *A.P. Prata 1245* (ASE, MAC). **Bahia:** Alagoinhas, Campus II / UNEB, 12° 10' 68" S, 38° 24' 81" W, 25 January 2001, *L.E. Figueiroa 46* (HUEFS); Alcobaça, Rod. BA 001, trecho Alcobaça/Prado, a 5 km a NW de Alcobaça, 17 September 1978, *S.A. Mori 10598* (CEPEC, DAV, MO, NY, SPF); Barrolândia, Estrada entre Barrolândia e a BA-001, km 21, 16° 01' 37" S, 39° 07' 49" W, 17 July 2006, *J. Paula-Souza 6053* (ESA, SP); Belmonte, Extremo Sul. 3 Km antes de Belmonte, 9 February 2012, *M.L. Guedes 19345* (ALCB); Cairú, Ilha de Boiepeba. Arquipélago do Município de Cairu, APA Tinharé/Boiepeba, 50 m, 13° 37' 10" S, 38° 55' 80" W, 3 January 2007, *A.M.A. Amorim 6768* (CEPEC, NY, SP); Camaçari, Guarajuba, 12° 41' 00" S, 38° 19' 00" W, 18 January 2003, *G.C.A. Silva 2* (ALCB); Canavieiras, unknown locality, 21 February 1970, *J.A. Jesus 563* (CEPEC, IPA); Conceição da Barra, Parque Estadual de Itaúnas, 10 June 2003, *G. Hatschbach 75110* (ALCB, HUFU, MBM); Conceição do Jacuípe, Rio Pojuca, 7 March 2003, *M.V. Moraes 573* (NY); Conde, Cajuerinho, 11° 44' 85" S, 37° 31' 84" W, 4 September 2003, *N.G. Jesus 1788* (ALCB, HRB); Entre Rios, Litoral Norte. Subaúma. No fundo do povoado, 6 m, 12° 14' 19" S, 37° 46' 56" W, 28 January 2011, *F.S. Gomes 852* (ALCB); Esplanada, Fazenda Chapada, caminho para Sítio do Conde, 526 m, 11° 45' 45" S, 37° 51' 16" W, 9 May 2000, *N.G. Jesus 934* (ALCB, CEPEC, HRB, HUESC, SPF); Eunápolis, Saída de Eunápolis à Porto Seguro, 23 September 1968, *J. Almeida 83* (CEPEC, DAV, R, RB); Ilhéus, Distrito de Olivença, bairro Canabrava. Acesso em estrada de terra à direita na rodovia Ilhéus - Olivença, 4 m, 14° 59' 27.10" S, 39° 00' 14.23" W, 9 February 2015, *O.L.M. Silva 229* (SP); Itacaré, 1.2 Km N of the Rio de Contas, Itacaré ferry crossing on road to Maraú, 14° 15' 64" S, 39° 00' 14" W, 5 August 2002, *W.W. Thomas 13081* (CEPEC, NY, RB, SP); Lauro de Freitas, Mata da Pitangueira, Vila do Atlântico, 8 February 1989, *R. Soeiro 43/89* (HRB, HUESC); Lençóis, Trilha Lençóis-Capão, 650 m, 12° 33' 34" S, 41° 24' 66" W, 28 January 1997, *S. Atkins in PCD4594* (ALCB); Maraú, Coastal Zone, ca. 11 km North from turning to Maraú along the road to Campinho, 0 m, 14° 01' 00" S, 38° 55' 00" W, 17 May 1980, *R.M. Harley 22192* (CEPEC, IPA, K, NY, RB, U, UEC, US); Mata de São João, Povoado de Praia do Forte. Estrada lateral (Avenida do Farol) antes de chegar na lagoa Timeantube, 11 m, 12° 34' 35.15" S, 38° 01' 05.37" W, 25 October 2014, *O.L.M. Silva 195* (SP); Mucugê, Chapada Diamantina. Distrito de Guiné. Subida do Beco do Paty, 995 m, 12° 15' 25" S, 38° 55' 54" W, 7 January 2012, *M. Alves 47* (ALCB); Mucuri, Rodovia Mucuri/Nova Viçosa (BA 001), Km 8, 18° 01' 17" S, 39° 30' 34" W, 4 October 2000, *L.A. Mattos-Silva 4153* (ALCB, CEPEC, HRB, HUEFS, HUESC, NY); Nova Viçosa, Rodovia de Mucuri para Nova Viçosa. Fazenda Quixeramobim, 17° 57' 00" S, 39° 28' 00" W, 13 May 2000, *P. Fiaschi 243* (SP, SPF); Palmeiras, Chapada Diamantina. Morrão, 31 August 1996, *A.A. Conceição 180* (SP, SPF); Porto Seguro, Estrada Nossa Senhora da Ajuda a Porto Seguro, a 1,5 km de Nossa Sra. da Ajuda, 16° 14' 00" S, 39° 00' 00" W, 8 February 1993, *J.R. Pirani 2758* (K, NY, SP[2], SPF); Prado, 12Km S de Prado. Estrada para Alcobaça, 7 December 1981, *A.M.V. Carvalho 927* (CEPEC, G, HRB, RB); Salvador, Lagoa do Abaeté, 769 m, 12° 54' 10" S, 38° 22' 44" W, 20 October 2000, *M.M. Silva 503* (HUEFS, SP); Santa Cruz Cabralia, Santo André, caminho para Sapuira, 16° 14' 00" S, 39° 00' 00" W, 19 February 2004, *M.L. Guedes 11105* (ALCB); Santo Antônio, Estrada para Belmonte, 16° 06' 22" S, 38° 57' 43" W, 27 December 2005, *T.S. Nunes 1414* (HUESC, NY); São Sebastião do Passé, Ponto 01, ao lado da Caraíba Metais, 20 October 1998, *A.F.S. Nascimento 190* (ALCB, CEPEC); Simões Filho, Unidade Ecológica de Cotegipe, 18 October 1986, *M.L. Guedes 1192* (ALCB); Una, Comandatuba, ca 6Km na estrada de Comandatuba, para praia de Una, 4 December 1991, *A.M.A. Amorim 496* (CEPEC, DAV, G, MBM, NY, SP, US); Valença, Camino a Guaibim, a 6 km de la rodovia Valença-Nazaré, y 1 km a la izquierda, 100 m, 13° 19' 00" S, 39° 02' 30" W, 14 January 1997, *M.M. Arbo 7173* (CEPEC, DAV, NY, SP). **Ceará:** Fortaleza, Barra do Ceará, 6 July 1960, *A. Fernandes 2007* (R). **Espírito Santo:** Aracruz, Barra do Jacu, 12 February 1992, *O.J. Pereira 2634* (R, SP, VIES); Conceição da Barra, Parque Estadual de Itaúnas, 26 April 2000, *O.J. Pereira 6164* (VIES); Guarapari, Setiba, Parque Estadual Paulo César Vinha, Praia do Setibão,

trilha da beira mar em direção a Lagoa dos Carais (Lagoa da Coca-cola), 0 m, 5 January 2004, *J.M.A. Braga* 7335 (SP); Linhares, Pontal do Ipiranga, 26 October 1995, *O.J. Pereira* 5526 (SP, VIES); São Mateus, Guriri, próximo ao loteamento "Mar Aberto", 29 March 2008, *M.B. Faria* 150 (SP, VIES); Serra, Nova Almeida, Sítio São José, estrada para Putiri, 20.1286° S, 40.3072° W, 18 March 2000, *I.D. Rodrigues* 276 (SP, VIES); Vila Velha, Rodovia do Sol, ca. 22 km após Guarapari. Lagoa de Interlagos. Loteamento Interlagos, 20 m, 20° 28' 03" S, 40° 30' 38" W, 5 March 2001, *P. Fiaschi* 651 (SPF); Vitória, Reserva Ecológica de Camburi, 20° 16' 00" S, 40° 15' 59" W, 2 September 1998, *A.M. Assis* 584 (SP, VIES). **Paráíba:** Cabedelo, Mata da AMEM, 17 March 2000, *A.F. Pontes* 456 (JPB, SP); João Pessoa, Campus UFPB, mata da garagem, 13 April 1995, *A.C.A. Moura* 97 (JPB, PEUFR, SP); Mataraca, Millennium Inorganic Chemicals Mineração LTDA, 06° 29' 37" S, 34° 58' 43" W, 4 October 2007, *P.C. Gadelha Neto* 1851 (HUEFS, JPB, SP). **Pernambuco:** Cabo de Santo Agostinho, Distrito de Ponte dos Carvalhos - PE, Praia do Paiva, 10 August 1998, *A. Sacramento* 454 (PEUFR); Ipojuca, Maracáipe. RPPN Nossa Senhora do Oiteiro de Maracáipe, 12 m, 08° 31' 48" S, 35° 01' 05" W, 13 January 2007, *M. Oliveira* 2641 (IPA, UFP); Jaboatão dos Guararapes, Piedade, unknown date, *C.G. Leal* 58 (RB); Recife, Areias, 24 December 1933, *B. Pickel* 3445 (IPA); Tamandaré, Estrada para a Praia dos Carneiros, trilha em direção ao Rio, atrás da Igreja (Assembleia de Deus), em frente ao Posto Carneiros, 9 m, 08° 42' 50.41" S, 35° 05' 40.23" W, 10 July 2017, *O.L.M. Silva* 340 (SP). **Rio de Janeiro:** Angra dos Reis, Ilha Grande, Reserva Biológica da Praia do Sul, 20 April 1989, *M.V.S. Alves* 210 (R); Cabo Frio, Perinas. Comunidade do Guriri, 29 April 1994, *L. Emygdio* 5643 (R); Carapebus, Primeiro cordão de mata, lado esquerdo sentido contrário à Praia da Capivara, 6 May 1997, *M.C. Oliveira* 487 (R); Casimiro de Abreu, Entre Barra de São João e Rio das Ostras, 21 March 1979, *P.P. Jouvin* 404 (R, RB); Macaé, Próximo ao loteamento Lagoruan; estrada para Petra nova, 22 November 1986, *A. Souza* 1551 (R); Maricá, Restinga de Maricá. Rua Oitenta e Três, esquina com a Rua Trinta e Dois, 22° 57' 34.49" S, 42° 55' 37.72" W, 25 October 2012, *I. Cordeiro* 3384 (SP); Niterói, Parque Estadual da Serra da Tiririca, Pedra de Itacoatiara, Pata do Gato, 1 December 1999, *L.O.F. Sousa* 160 (RB); Rio das Ostras, na Praia Velha, 05 April 1971, *L. Krieger* 10416 (ESA, MBM, RB[2], UB); Rio de Janeiro, Bairro da Barra da Tijuca. Futura instalação do Condomínio Mundo Novo, 4 August 1995, *J.M.A. Braga* 2642 (RB); Saquarema, Ipitangas, 8 March 1989, *A.M.A. Amorim* 87 (RB, SP). **Sergipe:** Areia Branca, Serra de Itabaiana. Trilha para a Serra de Itabaiana, 220 m, 10° 45' 14" S, 37° 20' 35" W, 20 April 2008, *B.S. Amorim* 308 (SP); Estância, Cerca de 19,4 km da BR 101 em direção à Praia do Abais, 28 November 1993, *A.M.A. Amorim* 1517 (CEPEC, NY); Estância, Rodovia para Abais, 11° 16' 35" S, 37° 25' 52" W, 23 October 2012, *D.A. Campos* 192 (ASE); Ilha das Flores, Povado Jenipapo, 10° 27' 44" S, 36° 34' 54" W, 10 October 2014, *M.A. Figueiredo* 56 (ASE); Indiaroba, APA Sul, Povoado Convento, 11,2849° S, 37,2406° W, 22 May 2013, *D.A. Campos* 331 (ASE); Itaporanga d'Ajuda, Fazenda Caju, 11° 11' 10" S, 37° 11' 47" W, 29 November 2012, *D.A. Campos* 227 (ASE); Santa Luzia do Itanhay, RPPN Mata do Castro, 14 August 2012, *L.A. Gomes* 612 (ASE); São Cristóvão, 2 km após a entrada, 3 August 19982, *E. Gomes* 100 (ASE).

**6. *Astraea lobata*** (L.) Klotzsch (1841: 194). *Croton lobatus* Linnaeus (1753: 1005). *Croton lobatus* var. *genuinus* Müller Argoviensis (1866: 669), *not val. publ. Oxydectes lobata* (L.) Kuntze (1891: 612). Lectotype (designated by van Ee 2011):—MEXICO: unknown locality, unknown date, *Herb. Clifford* 445 (BM000647404!). Figs. 14–16.

*Astraea seemannii* Klotzsch in Seeman et al. (1853: 103). *Croton lobatus* var. *seemannii* (Klotzsch) Müller Argoviensis (1866: 669). Neotype (designated here):—COLOMBIA. Isla Gorgona, April 1847, *B. Seemann* 621 (K!).

*Croton lobatus* var. *intermedius* Müller Argoviensis (1866: 669). Lectotype (designated here):—CUBA: unknown locality, 1890–1894, *C. Wright 1961* (G00312437!, isotypes G!, K10085981!, MA608683!, P04831526!).

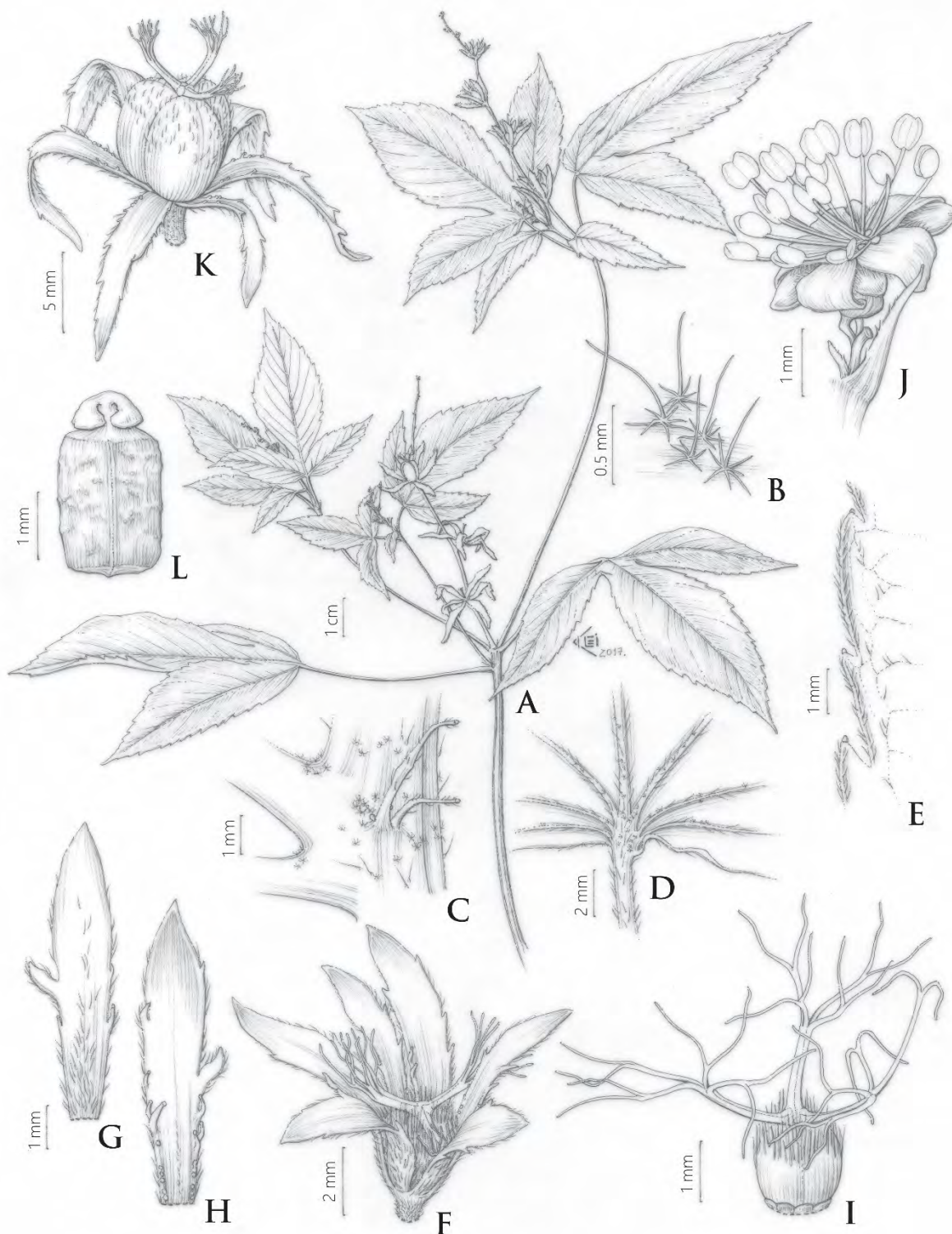
*Croton lobatus* var. *palmatus* Müller Argoviensis (1866: 668). Neotype (designated here):—BRAZIL. Rio Grande do Sul: Porto Alegre, January 1899, *J. Czermak 230* (G! [on 3 sheets]);

*Croton lobatus* var. *sericeus* Müller Argoviensis (1873: 239). Lectotype (designated here):—BRAZIL. Minas Gerais: Lagoa Santa, *J.B.E. Warming 1635* (C10021869 [photo!], isolectotypes C10021868 [photo!], G!).

*Croton mocinoi* Radcliffe-Smith & Govaerts (1997: 188). *Croton trilobatus* Sessé & Mociño (1894: 222), *nom. illeg.* Lectotype (designated here):—MEXICO: ‘in Oppido Apatzingam’, unknown date, *E.M. Sessé y Lacasta 4152* (MA602079!); remaining syntype:—MEXICO: unknown locality, unknown date, *E. M. Sessé y Lacasta 4598* (MA602080!).

*Croton palmatus* Sessé & Mociño (1894: 223). Type:—CUBA: Havana, ‘in subúrbio de Jesus Maria’ (holotype MA? not located).

**Annual or biannual herbs**, phanerophytes, up to 1.5 m high, with erect branches, without a well-developed (xylopodiferous) underground system, branches glabrous or sparsely to densely pubescent, with simple, stellate or stellate-porrect with a distinct central ray (but not surpassing 1 mm long) trichomes. **Leaves** 3–5-partite, occasionally with few entire leaves, medium lobe elliptic to wide-elliptic, ovate or slightly oblanceolate, (1.5–)2–9(–10) x (0.7)–1–4.5(–5) cm, and lateral lobes elliptic, oblong or slightly oblanceolate, (1–)1.5–5(–6.5) x 0.5–3(–3.5) cm, membranaceous, apex attenuate to long attenuate, base rounded, cordate, subcordate, obtuse or slightly truncate, margin serrate, with conspicuous teeth, not cartilaginous, ciliate, with simple or stellate trichomes, adaxial surface glabrous or pilose to esparsely pubescent or pubescent, more dense near the base, with simple short trichomes mixed with stellate or stellate-porrect trichomes (specially near the base and along the primary veins), abaxial surface pilose to sparsely pubescent, more dense near the base, with mostly short (< 0.5 mm) simple trichomes, but also stellate or stellate-porrect bearing a distinct central ray (but not surpassing 1 mm long) trichomes near the base or along the veins, venation actinodromous; petioles (0.5–)1–5(–7) cm long, glabrous or pubescent to densely tomentose, with short (< 0.5 mm), stellate or stellate-porrect trichomes; stipules subulate, entire or lobed, medium lobe up to 8(–10) mm long and lateral lobes diminute or up to 4 mm long, glabrous to sparsely pubescent, with simple and stellate or stellate-porrect bearing a distinct central ray (but not surpassing 1 mm long) trichomes. **Thyrse** 10–15(–20) cm long, rachis pilose to sparsely pubescent, with short (< 0.5 mm) simple, stellate or stellate-porrect trichomes bearing a distinct central ray (but not surpassing 1 mm long); basal cymules with 3–5(–7) pistillate flowers, accompanied by 1–3 staminate flowers; distal cymules with 1–3(–4) staminate flowers; bracts triangular, up to 3 mm long, glabrous or pilose to sparsely pubescent, with short (< 0.5 mm) simple, stellate or stellate-porrect trichomes; **Staminate flowers** with pedicel up to 5 long, glabrous; calyx glabrous. **Pistillate flowers** with pedicels 1–2.5(–3) mm long, up to 5 mm in fruit, glabrous or pilose to densely pubescent, with stellate or stellate-porrect trichomes bearing a distinct central ray (but not surpassing 1 mm long), calyx lobes 5–7(–9), sometime with one or more lobes poorly developed and narrower than the others, lobes elliptic or oblong, 2.5–6(–7) mm



**Figure 14:** Line drawing of *Astraea lobata* **A.** flowering branch, **B.** detail of indumentum of younger portion of stems, **C.** detail of stipules, **D.** abaxial surface of leaf base, **E.** detail of leaf margin, **F.** pistillate flower, **G.** calyx lobe of a pistillate flower – internal face, **H.** calyx lobe of a pistillate flower – external face, **I.** gynoecium and floral nectaries (calyx removed), **J.** staminate cymules with one mature flower, **K.** immature fruit, **L.** seed – ventral face. Illustration by Klei Sousa, based on O.L.M. Silva 120 (SP).

long, up to 15(–20) mm in fruit and 1–2(–2.5) mm wide, glabrous or pilose to pubescent on the external face, with short (< 0.5 mm) simple trichomes or stellate or stellate-porrect trichomes, margin entire or irregularly

serrate, not cartilaginous, ciliate, with short (< 0.5 mm) simple trichomes, apex acute or obtuse; ovary (1–)1.5–2.5 x (1–)1.5–2.5 mm, glabrous or pubescent, sometimes only near the apical portion, with short (< 0.5 mm) simple trichomes. **Fruits** opaque, (4–)6–7(–8) x (4–)6–7(–8) cm, glabrous or pubescent, with short (< 0.5 mm) simple or stellate trichomes, more dense near the apical portion; seeds tetragonal in cross section, (2.5)3–5.5 x 3–4(–4.5) mm, caruncle 0.5–1.5 x 1.5–2 mm.

**Nomenclatural notes:**—Once *Croton lobatus* var. *genuinus* includes the type of *C. lobatus* (by the citation of this name in the protologue) and uses the epithet *genuinus*, it should be considered as not validly published (McNeill et al. 2012, Art. 24.3).

In the protologue of *Astraea seemannii* (Seemann *et al.* 1853), Klotzsch indicated as type an unnumbered collection from “Near Panama” that was not located by van Ee (2011). BM herbarium keeps the main set of B. Seemann’s collections, especially those from the Voyage of H.M.S. Herald. However, we found at K a specimen collected by Seemann, numbered as 621, from Gorgona Island, Colombia, which fits the detailed description of the protologue of *A. seemannii* and is somewhat near Panama. Therefore, this specimen is here designated as the neotype for *A. seemannii*.

The type collection of *Croton lobatus* var. *palmatus* (BRAZIL: “in Brasilia meridionali”, F. Sellow s.n.) at B was destroyed during the Second World War, and no photograph from The Field Museum Berlin Negatives collection was found. Neither did we find a duplicate of this Sellow’s collection at LE. Therefore, we designate J. Czermak 230 as the neotype based on its locality (southern Brazil) and representativeness of the morphological characteristics indicated in the protologue of *C. lobatus* var. *palmatus* by Müller Argoviensis (1866).

*Croton palmatus* Sessé & Mociño is considered as an accepted name in Govaerts et al. (2000), but it clearly represents an *Astraea* and so is included in this treatment as a new synonym. No specimen labeled with this name was found in MA, where most of the collections of these authors are held. Given the plasticity of *A. lobata*, in front of the lack of a specimen their collection at MA, and once the protologue does not present a clear comparison among these species (and therefore it is not sufficient to correctly determine which characters would be diagnosable for this name) we do not designate a neotype for this name. On the other hand, the description presented in the protologue, along with the type locality (“Jesus Maria Havanae”, Cuba), make it possible to consider *C. palmatus* as a synonym of *A. lobata*, since only *A. lobata* is found in Cuba.

*Croton leiocarpus* Bartl. and *Astraea palmata* Klotzsch, have been considered as synonyms of *A. lobata* in its broad delimitation (Govaerts et al. 2000). However, the lack of a type collection and original descriptions with diagnostic features for both names makes it difficult to decide to which species of *Astraea* these names

correspond. Therefore, *C. leiocarpus* and *A. palmata* are included in the *Incertae Sedis* section at the end of this treatment.

**Etymology and vernacular names:**—the epithet *lobata* is undoubtedly a very informative reference made by Linnaeus to the deeply lobed leaves of this species, a unique characteristic among the species of *Croton* known by the time he publishes his *Genera Plantarum*. The same applies to other epithets from some of its synonyms as *palmatus* and *trilobatus*. Other epithets from synonyms related to this species include *seemannii*, described in the resulting observations from the Voyage of the H.M.S. Herald, honoring the naturalist of this expedition, B. Seemann; and *mocinoi*, is in honor to J.M. Moçño, who earlier described the illegitimate (due to posterior homonymy) *Croton trilobatus*.

Vernacular names gathered for this species are: *café-bravo*, *mamoninha* (portuguese), *dominguilla*, *huevo-de-cuche*, *pata-de-Paloma*, *purguita-de-fraille*, *vegiga-de-perro*, *vira-vira*, *yerba-de-la-cucaracha* (spanish) and *lobed-croton* (english).

**Geographical distribution:**— ASIA-TROPICAL. *Malesia*: Philippines (PHI). NORTHERN AMERICA. *Mexico*: Mexico Central (MXC-ME), Mexico Gulf (MXG-VC), Mexico Northeast (MXE-QU, MXE-SL, MXE-TA), Mexico Northwest (MXN-SIL), Mexico Southeast (MXT-CA, MXT-CI, MXT-QR, MXT-TB, MXT-YU), Mexico Southwest (MXS-CL, MXS-GR, MXS-JA, MXS-MI, MXS-NA, MXS-OA); *Southeastern U.S.A.*: Florida (FLA). SOUTHERN AMERICA. *Brazil*: Brazil Northeast (BZE-AM, BZE-MA), Brazil South (BZS-PR, BZS-RS, BZS-SC), Brazil Southeast (BZL-MG, BZL-SP), Brazil West-central (BZC-MT, MZC-MS); *Caribbean*: Bahamas (BAH), Cuba (CUB), Dominican Republic (DOM), Leeward Is. (LEE-BV), Puerto Rico (PUE), Southwest Caribbean (SWC-HC, SWC-NC), Trinidad-Tobago (TRT), Windward Is. (WIN-GR, WIN-SV); *Central America*: Belize (BLZ), Costa Rica (COS), El Salvador (ELS), Guatemala (GUA), Honduras (HON), Nicaragua (NIC), Panama (PAN); *Northern South America*: Venezuela (VEN); *Southern South America*: Argentina Northeast (AGE-CD, AGE-CH, AGE-CN, AGE-ER, AGE-FO, AGE-MI), Argentina Northwest (AGW-CA, AGW-JU, AGW-LR, AGW-SA, AGW-SE, AGW-TU), Paraguay (PAR), Uruguay (URU); *Western South America*: Bolivia (BOL), Colombia (CLM), Peru (PER).

*Astraea lobata* has a wide distribution range, from Mexico to northern Argentina (Fig. 15). Despite its widespread distribution, populations are more concentrated in two main regions: (1) Mexico, Central America and Greater Antilles, and (2) southwestern South America. This species exhibits the trans-NASA amphitropical disjunct pattern of Simpson et al. (2017), also observed for many other angiosperms, and even non-vascular groups. *Astraea lobata* is a weedy species mostly found in disturbed environments, such as anthropic areas or secondary vegetation. However, as a weedy, it also grows on several other sites, as flooded places, edges of dry and humid forests or open vegetations such as cerrado, caatinga and seashore vegetation. Elevation varies from near sea level to around 600 meters above sea level, occasionally reaching more than 1,000 meters above

sea level in Venustiano Carranza (Mexico), Comayagua (Honduras), Valle del Cauca (Colombia) and Lages (Brazil).



Figure 15: Geographical distribution of *Astraea lobata* (only along the American continent).

**Phenology:**—Flowering and fruiting were registered throughout the year, and are commonly observed at the same time.

**Conservation status:**—this is an invasive, widely-distributed species, which has an area of occupancy greater than 2.000 km<sup>2</sup>, with many known locations. *Astraea lobata* is found on disturbed environments and do not suffer with anthropic pressure. Therefore, according to IUCN (2012) guidelines, it qualifies for Least Concern (LC).

**Taxonomic comments:**—*Astraea lobata* had its morphological delimitation revised by Silva et al. (Capítulo III), and under this more refined delimitation six distinct taxa are no longer included as synonym of *A. lobata*: *A. paulina*, *A. digitata*, *A. gracilis*, *A. manihot* (Silva & Cordeiro 2017), *A. surinamensis* and *A. trilobata* (Silva et al. [Capítulo III]). Among the varieties recognized by Müller Argoviensis (1866, 1873), only *C. lobatus* var. *intermedius*, *C. lobatus* var. *palmatius* and *C. lobatus* var. *sericeus* are maintained as synonyms of *A. lobata* due to overlapping of the diagnostic features presented by Müller Argoviensis in their descriptions.

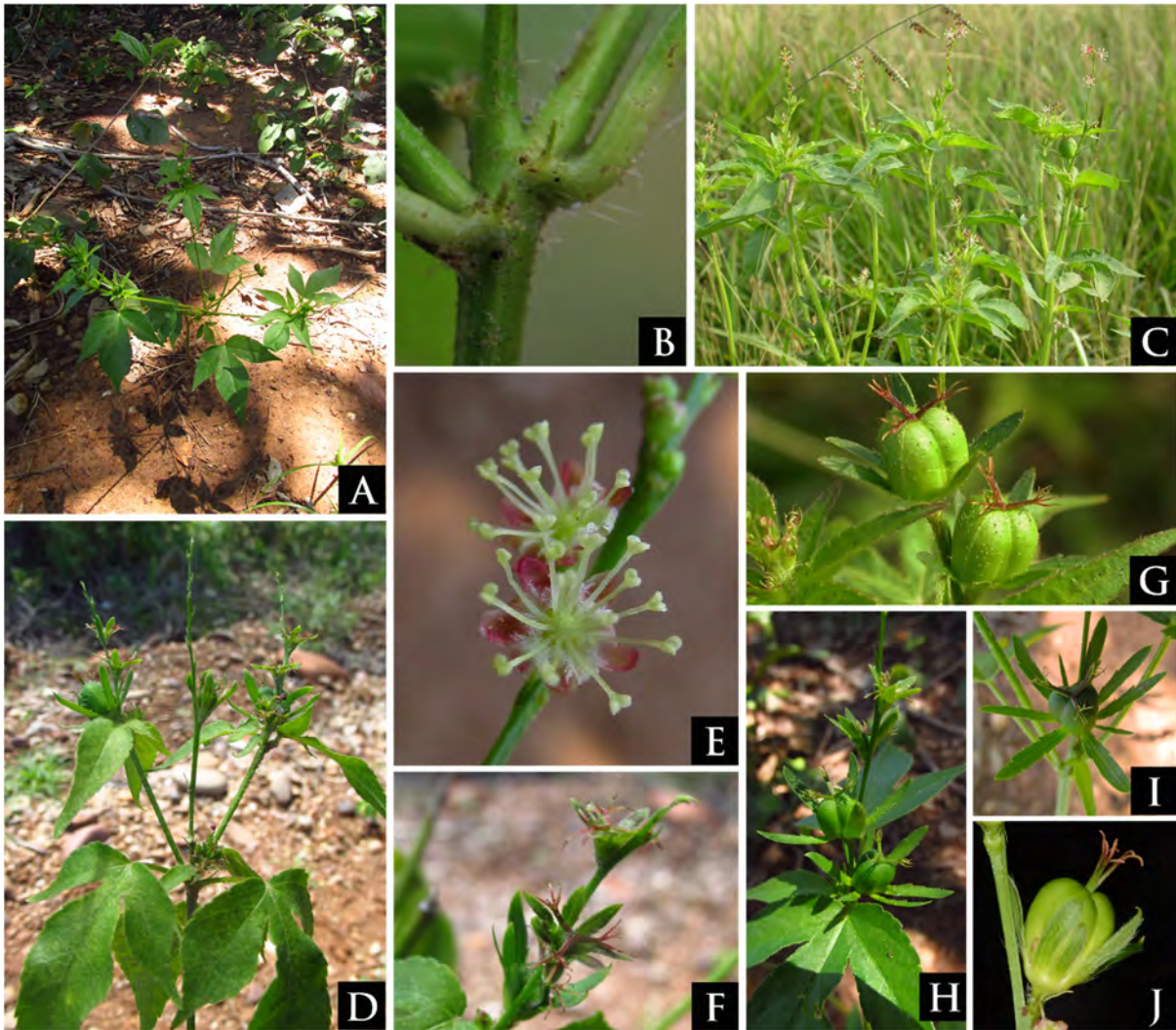
One valuable diagnostic feature of *Astraea lobata* is the pistillate calyx strongly accrescent in fruit, which surpasses the fruit in length (Figs. 14K, 16H-I) once it may easily have more 1 cm long (reaching 2 cm in some cases) a feature observed only in some collections of *A. gracilis* (Fig. 11K). However, in *A. gracilis* the calyx of pistillate flower has entire margin, while in *A. lobata* it is irregularly serrate. On the other hand, specimens of both *A. gracilis* and *A. lobata* may also lack this strongly accrescent calyx in pistillate flowers (Figs. 11J and 16J, respectively). In these cases, differentiation between these species are based on geographical distribution and habitat, with *A. lobata* occurring mostly on Mexico, Central America, part of the Antilles, and southwestern South America (Fig. 15) and in disturbed environments, while *A. gracilis* is found along the diagonal of dry areas of South America and also on eastern Brazil (along Atlantic Forest domain; Fig. 10), in moist or seasonally dry forests and rocky outcrops.

Another diagnostic characteristic of *Astraea lobata* are its opaque fruits (Fig. 16G-J), shared only with *A. cincta* (Fig. 4N-P). This characteristic is difficult to observe in herbarium specimens and relies on live individuals or photographs to be correctly evaluated. However, *A. cincta* is a very distinctive species by features unique within the genus, such as well-developed underground systems (probably xylopodiferous), cartilaginous leaf margin and seeds rounded in cross section.

*Astraea lobata* may be distinguished from other weedy species *A. surinamensis* and *A. trilobata* by its stellate-porrect trichomes bearing a central ray not surpassing 1.5 mm in length (Fig. 14B) and opaque fruits, while in both the central ray is longer than the others, usually surpassing 1.5 mm long and the fruits are lustrous. Also, geographical distribution is indicative of the identity among weedy species since *A. lobata* is mostly found on Mexico, Central America, Greater Antilles and southwestern South America, *A. trilobata* on Africa and northwestern South America (see Fig. 35), and *A. surinamensis* on eastern and northern South America and Lesser Antilles (see Fig. 32).

**Selected specimens examined:**—[ANTILLES] BAHAMAS. **Great Abaco:** Coopers Town, In a fallow field in Fire Road, just south of Coopers Town, 9 July 1974, *D.S. Correll 42772* (FTG, NY). **Nassau:** New Providence, About small nursery on corner of Village Road and Wulff Road, 6 October 1977, *D.S. Correll 49073* (FTG, NY). TRINIDAD AND TOBAGO. **Trinidad:** Couva-Tabaquite-Talparo, Brechin Castle, Fd 105, 31 July 1936, *D. Vesey-Fitzgerald 4500* (BM); Diego Martin, Fort George, 19 April 1974, *O. Kuntze 907* (K, NY); San Fernando, Usine St. Madeleine, 17 July 1926, *W.E. Broadway 6363* (BM, K); San Juan, Las





**Figure 16:** Morphological characters of *Astraea lobata*. **A.** habit. **B.** stipules. **C–D.** branches with inflorescences. **E.** staminate flowers. **F.** pistillate flowers. **G–J.** immature fruits. A, D, F, H and I: population from Aquidauana, MS (O.L.M. Silva 120); B: population from Terrenos, MS (O.L.M. Silva 248); C and G: population from Cuba; J: population from Michoacán, Mexico (C.A. Maya-Lastra 621). Photos: A, B, D–F, H and I: O.L.M. Silva; C and G: B.W. van Ee; J: V.W. Steinmann.

Cuevas to Maracas, 25–150 ft, 22 June 1973, *D. Philcox* 7258 (K, P); Tunapuna-Piarco, 3/4 mile on Lopinot road, 16 July 1973, *D. Philcox* 7465 (K, NY, P). UNITED STATES VIRGIN ISLANDS. **Tortola:** unknown locality, 12 November 1918, *W.C. Fishlock* 247 (K, NY).

[CENTRAL AMERICA] BELIZE. **Cayo:** Belmopan, Beaver Dam Housing Development. North and East of Belmopan and 6 km E of Never Delay Road, just south of Western Highway, 40 m, 15 July 1995, *D.E. Atha* 1143 (BM, MEXU, NY). COSTA RICA. **Alajuela:** Alajuela, Along Costanera highway, ca. 2 km S of Pozón, SW of Orotina, 100 m, 24 April 1988, *M. Grayum* 8562 (MEXU, US). **Guanacaste:** Alajuela, Vicinity of Cascajal (25 km ESSE of Puntarenas), 30–100 m, 6 July 1949, *R.W. Holm* 280 (G); Bagaces, P.N. Palo Verde. Cuenca del Tempisque. Sector Colmenar y laguna Varillal. Borde de laguna Varillal y rio Tempisque, 10° 20' 30" N, 85° 22' 00" W, 28 July 2001, *U. Chavarría* 2199 (MA); Bebedero, unknown locality, 13 June 1930, *A.M. Brenes* 12545 (NY); Cañas, No protegida. Cuenca del Tempisque. Carretera de grava que lleva a Bebedero, entrada ca. De 1 km antes de Cañas centro, 30 m, 10° 21' 09.0410" N, 85° 06' 40.6660" W, 24 May 1999, *A. Rodríguez* 4952 (G); Cantón de Liberia, P.N. Santa Rosa. De Bahía Salinas a Santa Cecília. Estación Santa Rosa, area administrativa, 300 m,

15 July 1992, *R. Espinoza 414* (BM); Vicinity of Palo Verde Biological Station of OTS, immediately south of Cerro Guayacan, ca 2 km N and NE of the Rio Tempisque, with Parque Nacional Palo Verde, 10 m, 18 July 1994, *W.J. Kress 94-4349* (US).

**Puntarenas:** Carretera Nacional 2 at junction with Rio Ceibo, 200 m, 28 February 1984, *Khan 1381* (BM, MEXU). CUBA.

**Cienfuegos:** Cieneguita, unknown locality, 5 February 1896, *R. Combs 6* (K, NY, P); Soledad, Limones, 25 July 1927, *J.G. Jack 6107* (P). **Ciudad de la Habana:** Havana, Vedado. Finca Hicotea. El cobre, December 1947, *Clemente 5750* (NY).

**Guantánamo:** Bayate, unknown locality, 15 June 1919, *E.L. Ekman 9647* (K). **Holguin:** Holguin, Valley of Rio Matamoros, south of Holguin, 15 April 1909, *J.A. Shafer 1367* (NY). **Isla de la Juventud:** Nueva Gerona, unknown locality, May 1904, *A.H. Curtiss s.n.* (NY 138341). **Las Tunas:** Hormiguero, By Hormiguero, 1933, *C. Rutten-Pekelharing 19* (U). **Las Villas:** El Junco region above Siguanea in San Juan Mts, 1–20 July 1950, *R. Howard 206* (K). **Matanzas:** Matanzas, Near Mantanzas, January 1849, *F. Rugel 182* (NY). **Pinar del Rio:** Guanajay, near Guanajay, 9 June 1900, *W. Palmer 783* (NY); Herradura, unknown locality, 30 March 1907, *F.S. Earle 659* (NY); Junto a Sonora, 3–4km al norte, 24 June 1988, *J. Fernández Casas 10808* (MA).

**Sancti Spiritus:** Sur de la Sierra del Escambray; Rio Guaurabo (Rio Negro), caminho de Trinidad al Cubano, 21° 50' 00" S, 79° 50' 00" W, 1 July 1993, *A. Acevedo-Rodriguez 5574* (NY). **Villa Clara:** Santa Clara, Rio San Juan, 24 March 1910, *N.L. Britton 5911* (NY). DOMINICAN REPUBLIC. **Santo Domingo:** Santo Domingo, Along the Avenida just east of Howard Allard's home 1 mi. w. center of city, 0–25 m, 2 December 1945, *H.A. Allard 13774* (NY). EL SALVADOR. **San Miguel:** Norhtwest of Hacienda Potrero Santo, ca 0.1–0.8 km, south side of Lake Olomega, 60 m, 5 February 1942, *J.M. Tucker 911* (US). **Santa Ana:** Metapán, P.N. San Diego–La Barra, alrededores de la poza Cuisizapa, 16 January 2011, *D. Rodríguez 2221* (MO); Sanata Ana, Matorrales a la orilla de la carretera a Metapán, +/- 8 km al N del centro de la Ciudad de Santa Ana (Km 73 de la carretera), Cantón Cutumay Camones, 550 m, 27 July 1995, *J.L. Linares 2950* (MEXU); Texistepeque, Quebrada Honda +/- 1 Km al SO del caserío Guarnequia, 400 m, 30 April 2002, *J.L. Linares 5992* (MEXU). **Sonsonate:** Vicinity of Santa Emilia, 135 m, 22–25 February 1922, *P.C. Standley 22098* (US). GRENADA. Unknown locality, 1853, *I.F. Holton 817* (G, K). GUATEMALA.

**Alta Verapaz:** Cubilhuitz, unknown locality, July 1907, *H. von Tuerckheim 11345* (G, L, NY, US). **El Progreso:** Guastatoya, Jalara, 300 m, 20 January 1908, *W.A. Kellerman 8063* (US). **Izabal:** El Estor, Chichipate, 200 m, 22 August 1998, *M. Véliz 98.6572A* (MEXU); Los Amantes, unknown locality, 9 May 1991, *S.F. Blake 7315* (US); Vicinity of Quiriguá, 75–225 m, 15–31 May 1922, *P.C. Standley 24092* (US). **Peten:** La Libertad, La Libertad and vicinity, August 1933, *M. Aguilar-H. 68* (NY, WIS); Santa Elena, En orillando el camino para La Candelaria, a km 8, 9 June 1970, *R.T. Ortíz 1223* (NY, US). **Zacapa:** Gualan, In the Motagua River, 15 June 1909, *C. Deam 6284* (NY, US); Zacapa, unknown locality, 180 m, January 1908, *W.A. Kellerman 7940* (NY, US). HONDURAS. **Atlántida:** La Ceiba, 1925, *A. van Severén 6* (US); Vicinity of Tela, 0 m, 1927–1928, *P.C. Standley 54785* (US). **Colón:** Trujillo, Hacienda El Tumbador. 27 km SE Trujillo, along Chapagua River, 15 July 1980, *J. Saunders 489* (NY). **Comayagua:** Comayagua, A orillas de la Quebrada Chicúas cerca de El Agua Salada, 1100 m, 21 July 1962, *A. Molina-R. 10991* (NY). **Copan:** Nueva Arcadia, 3 mi SW of Los Tangos along Santa Rosa de Copán–San Pedro Sula highway, 425 m, 15° 06' 25" N, 88° 41' 51" W, 26 June 1994, *G. Davidse 35394* (IEB). **Cortes:** La Lima, unknown locality, 6 July 1964, *J. Dickson 1237* (FTG, USF); San Pedro Sula, at the edge of town, 22 August 1972, *W.G. D'Arcy 6872* (US); between Villa Nueva and Pimenta on way to San Pedro Sula, 200 m, 22 June 1991, *A. Molina-R. 34424* (MEXU, US). **Islas de La Bahia:** Isla de Roatán, unknown locality, 19 April 1967, *A. Molina-R. 20630* (NY, US). **Lempira:** San Andres, Corozal District, July 1933, *P.H. Gentle 4934* (NY). **Ocotepeque:** Nueva Ocotepeque, Along Sinuapa river, vicinity of Nueva Ocotepeque, 26 August 1968, *A. Molina-R. 22164* (NY). **Santa Bárbara:** Ulúa river between Ilima and Gualala, 23 August 1968, *A. Molina-R. 22043* (NY, US). **Yoro:** Coyoles, Aguan River valley, vicinity of Coyoles, 29 June 1938, *T.G. Yunckers 8111* (BM, G, K, NY, US). NICARAGUA. **Atlántico Sur:** Islas del Maíz, Isla del Maíz Grande, 40 m, 20 August 1982, *E. Martínez-S. 1689* (MBM, MEXU). **Chontales:** Hda. Corpus, W of Juigalpa, 100 m, 24 July 1983, *W.D. Stevens 22266* (MEXU). **Grenade:** Isla Zapatera, Ensenada al S de

Hacienda Santa Maria, 22 November 1982, *A. Grijalva 1844* (MEXU, NY). **Managua:** Managua, Vicinity of Managua, unknown date, *A. Garnier 912* (US); Km 24 on Hwy 12 (Carretera vieja a León), 7 km WSW of summit of Sierra de Managua, 200 m, 7 July 1977, *W.D. Stevens 2674* (MEXU). **Matagalpa:** San Isidro, Along Hwy 1 at Km 121, just above and north of flat plains with rice fields, 27 km S of Esteli, 4 km NW of San Isidro, 600 m, 1 September 1983, *M. Nee 27754* (BM, MEXU, NY); SW slopes of Cerro El Pilon and adjacent Laguna Tecomapa, 420–540 m, 20 July 1978, *W.D. Stevens 9444* (MEXU). PANAMA. **Cocle:** 10 miles east Nata at Rio Grande, 4 January 1969, *E.L. Tyson 5271* (FSU). **Panama:** Panamá city, Rio Abajo, December 1921, *B. Heriberto 284* (NY, US). Canal Zone. Vicinity of Rio Cocoli, Road K-9, near bridge over river, 31 May 1959, *W.L. Stern 346* (US).

[NORTH AMERICA] MEXICO. **Campeche:** Calkini, En Calkini, sobre el libramiento de la ciudad, 28 July 1987, *E. Cabrera 14031* (MEXU); Campeche, Crucero de P. Trueba y autopista, Cd de Campeche, 8 m, 90° 31' 38" S, 19N 48' 00" N, 10 August 2003, *C.G. Báez 7866* (MEXU); Carmen, Salida de Nuevo Coahuila rumbo a Justo Sierra, 50 m, 17° 53' 28" N, 90° 46' 46" W, 17 June 1984, *A. Puch 1330* (MEXU); Ciudad del Carmen, Camino a Justo Sierra después del río Candelaria, 8 m, 26 June 1984, *C. Chan 3760* (MEXU); Hopelchén, A 0.26 km al N de Xcan-ha, 165 m, 19° 06' 13" N, 89° 19' 54" W, 24 June 2005, *E. Martínez 37975* (MEXU [2]). **Chiapas:** Acala, Along Río Grijalva, 20 km north of Acala, 550 m, 30 July 1981, *D.E. Breedlove 51886* (MEXU); Catazajá, Poblado de Catazajá, 20 m, 92° 01' 00" S, 17N 43' 15" N, 6 July 1999, *C.G. Báez 6612* (MEXU); Chicoasen, 2 Km al NW de Chicoasen, camino de Soyaló a Chicoasen, 10 August 1998, *E. Martínez-S. 31209* (IEB, MEXU); Escuintla, unknown locality, 13 November 1936, *E. Matuda 953* (K, MEXU, NY); Huehuetán, Cuyo Miapan, 6 March 1985, *E. Ventura-E. 1263* (BM); Huixtla, Piedra Canoa, 8 km al Norte de Huixtla, 0 m, 21 July 1988, *E.V.E. López 5391* (MEXU); La Concordia, 0.4 km al E de Niños Héroes por el camino a Rizo de Oro, Paso de Chalán em uno de los brazos de la presa Belisario Dominguez (La Angostura). Roca caliza, 560 m, 16° 07' 10" N, 92° 35' 28" W, 4 March 2006, *P. Carrillo-Reyes 5157* (IEB, MO); Mazatán, Buenavista, 0 m, 8 May 1986, *E.V.E. López 3608* (MEXU); Ocozocoautla, 20 mi N of Ocozocoautla on road to Mal Paso, 520 m, 16 August 1972, *G.L. Webster 17904* (MEXU); Palenque, 3–5 km north of Palenque along road to Catazaja and Villa Hermosa, 250 m, 28 July 1972, *D.E. Breedlove 26650* (MEXU, NY); Pichucalco, Along F.C. Sureste west of Rancheria Coamapa, 13 September 1944, *C.L. Gilly 153* (MEXU); Tapachula de Córdova y Ordoñez, Cantón Palo Seco, 0 m, 4 July 1985, *E. Ventura 2032* (IEB, MEXU); Tonalá, Moutains near Tonalá, 600–1000 m, 14 August 1895, *E.W. Nelson 2902* (US); Tuxtla Chico, Cantón El Norte, 250 m, 29 May 1985, *E. Ventura 1798* (IEB); Venustiano Carranza, Near Socoltenango, 1170 m, 18 April 1981, *D.E. Breedlove 51010* (MEXU, NY); Villaflores, A 1.2 km al NO de California, 857 m, 16° 15' 59" N, 93° 37' 20" W, 7 July 2004, *E. Martínez-S. 36606* (IEB, MEXU). **Colima:** Colima, unknown locality, July 1894, *E. Palmer 35* (US). **Guerrero:** Ayutla, 2 km adelante de La Union, de Ayutla a Cruz Grande, 220 m, 23 August 1985, *E. Velazquez 733* (MEXU); Eduardo Neri, Ameyaltepec, 1 September 2006, *N. Diego 9719* (IEB); Iguala, Iguala, 750 m, 19 July 1988, *A.A. Juarez 173* (MEXU); La Unión, A 10 km al N de Las Juntas de los Rios, 230 m, 22 July 1985, *J.C.S. Núñez 9643* (MEXU); Tlalchapa, +/- 2 km al NNW de Villa Madero, 530 m, 18° 25' 31" N, 100° 26' 21" W, 2 August 2002, *E. Carranza 6377* (IEB, MEXU); Zirándaro, A 2 km al E de La Calera y 8 km al S de Zirándaro, carr. Zirándaro-Cd. Altamirano, 269 m, 18° 25' 40.3" N, 100° 59' 05.1" W, 18 October 2009, *J.C. Soto-N. 16843* (MEXU). **Jalisco:** La Huerta, Puente de Arroyo Seco, unos 5 km al oeste del Ejido Miguel Hidalgo, 40 m, 15 August 1991, *A. Flores-M. s.n.* (IEB 51084). **Temascaltepec:** Guayabal, 790 m, 22 August 1933, *G.B. Hinton 4568* (BM, K, NY, US). **Michoacán:** Antunez, unknown locality, 8 September 1974, *C. Rodríguez 1358* (US); Apatzingán de la Constitución, 1 mi south of Apatzingan, 365 m, 5 August 1940, *W.C. Leavenworth 494* (NY); Aquila, Santa Cruz de Cachan, 80 m, 28 September 1980, *B. Guerrero-C. 967* (MEXU); Huetamo, Cerca del rancho El Tecolote, aprox. 2.5 km al SO de Huetamo, carr. Huetamo-Comburindio, 318 m, 18° 36' 40.9" N, 100° 55' 27.4" W, 18 October 2009, *J.C. Soto-N.*

16827 (MEXU); Múgica, 6 km NO del entronque de la autopista MEX 37D con la carretera MEX 120, saliendo de Cuatro Caminos, 343 m, 19.0274° N, 102.05635° W, 27 August 2015, C.A. *Maya-L 627* (SP); Nocupétaro, En la desv. a Upácuaro, aprox. a 5 km al O de San Antonio de Las Huertas y a 20 km al NO de Nocupétaro, 815 m, 17 July 2009, J.C. *Soto-N. 16022* (MEXU); Tepalcatepec, Em las afueras de Tepalcatepec, 400 m, 27 July 1988, M. *Cházaro-B. 5607* (IEB, MEXU, WIS); Tiquicheo, En Tiquicheo, 600 m, 27 July 2002, J.C. *Soto-N. 14071* (MEXU); Tuzantla, En Las Juntas. Carr. Zitácuaro-Huetamo, 5 September 1978, J.C.S. *Núñez 930* (MEXU). **Nayarit:** Acaponeta, Planicie pasando Acaponeta, justo antes de entrara a Sinaloa, 50 m, 19 August 2005, M. *Cházaro-B. 8537* (IEB); Bahía de Banderas, A lo largo de la playa, entre Villa Varadero y la desembocadura del río Ameca, 0 m, 11 August 1990, M. *Cházaro-B. 6333* (IEB, MEXU, WIS); Jesús María, Valley of the Rio Jesus Maria near the village of Jesus Maria, 600–700 m, 19 September 1960, C. *Feddema 1286* (MICH). **Oaxaca:** Asunción Ixtaltepec, A 1.4 km en línea recta al SO (192°) de Nizanda, 90 m, 16° 38' 43" N, 95° 00' 53" W, 20 December 1998, E.A. *Pérez-García 1655* (MEXU); Chiltepec, Acahual, 06 June 1965, s.col. 89 (UEC); San Juan Bautista Cuicatlán, Cerro el Cuaché, a 2.2 Km al SE de San José El Chilar, 884 m, 17° 43' 18" N, 96° 57' 21" W, 1 October 2002, C.A. *Cruz-Espinosa 1270* (MEXU); San Lucas Ojitlán, En el poblado Heladio Ramírez, antes Malotal, parcel de Casimiro, 250 m, 16 June 1990, J.I. *Calzada 15402* (MEXU); Santa Maria Chimalapa, Cafetales cerca de Santa Maria, 300 m, 13 August 1984, H. *Hernández-G. 332* (MEXU); Santa María Huatulco, 2 km al norte de la Bahía de Cacaluta, a orillas de una laguna pequeña, 25 m, 15° 44' 08" N, 96° 09' 31" W, 16 July 2003, M. *Elorsa-C. 6978* (IEB, MEXU); Santiago Astata, El Zapotal, 2 km al SE de Barra de la Cruz, 15 m, 15° 50' 25" N, 95° 57' 48" W, 2001 March 5, M. *Elorsa-C. 4348* (IEB, MEXU); Tehuantepec, unknown locality, 28 June 1910, C.R. *Orcutt 5104* (MEXU, NY, WIS); Tuxtepec, Chiltepec and vicinity, 20 m, 1940–1941, G. *Martínez-Calderón 110* (US, MEXU). **Puebla:** Route 130, 2.7 miles south of the Puebla-Veracruz state line, 20 May 1979, N.A. *Harriman 15630* (WIS). **Queretaro:** Jalpan de Serra, Arrededores de Tanchanaquito, 270 m, 17 June 1993, E. *Carranza 4643* (IEB, MEXU). **San Luis Potosí:** Axtla de Terrazas, Arroyo Seco, 10 kms. al noroeste de Picholco, 700 m, 14 February 1982, R.H. *Magaña 7006* (MEXU); San Antonio, unknown locality, 5 September 1978, J.B. *Alcorn 1560* (MEXU); San Luis, Las Palmas, 28 June 1890, C.G. *Pringle 3081* (BM, G, K, MEXU[2], NY[2], P[2], US, WIS). **Sinaloa:** Cosalá, 2 km antes de llegar al pueblo de Cosalá, 150 m, 27 July 1990, R. *Vega-A. 3752* (MEXU); El Rosario, 3 km al N de la población El Rosario, márgen izquierda del río Blauarte, camino a cacalotán, 50 m, 18 September 1994, E.G. *Nolazco 3289* (MEXU); Mazatlán, Entre Villa Unión y Concordia, 50 m, 27 August 1988, R. *Vega 2845* (MEXU); Rosario, unknown locality, 7 July 1897, J.N. *Rose 1556* (US); Villa Union, unknown locality, 1926, J.G. *Ortega 6197* (MEXU, US). **Tabasco:** Balancán de Domínguez, El Arenal, 18 February 1983, S. *Zamudio-R. 700* (IEB, MEXU); Centro, Ranch. dos Montes, km 12, carr. Vsa.-Escárcega, atrás del aeropuerto de Villahermosa, 15 m, 23 July 1988, A.R.A. *Sol 45* (MEXU); Nacajuca, 200 m de la carretera Tucta a Nacajuca, 100 m de Tucta, 7 October 1978, C. *Cowan 1613* (NY); Paraiso, A orilla del camino de terracería que va de Paraiso a Ranchería Moctezuma, a 2 Km dirección Sur de Paraiso, 16 July 1979, *Gonzalez 15* (MEXU); Paraiso, Km 46.7 rumbo de Paraiso a la Barra de Tupilco, 14 June 1979, C. *Cowan 2317* (MEXU, NY); Villahermosa, Isla, 0 m, 11 July 1983, F. *Ventura-A. 20393* (IEB); Villahermosa, Tamulté de la sabana, desviación del km 49 de la carretera de Frontera hacia Villahermosa, 17 April 1980, C. *Cowan 2925* (MEXU). **Tamaulipas:** Ciudad Mante, Plantaciones de arroz el Azteca en los alrededores de Ciudad Mante, 70–80 m, 30 July 1991, J. *Sánchez-Ken 418* (MEXU); Gómez Farías, Ca. 7 km S of Gómez Farías, in cleared ground on edge of quarry, 244 m, 14 July 1982, P.A. *Fryxell 3764* (DAV, NY, US). **Veracruz:** Alto Lucero, Alrededores de Laguna Verde, 100 m, 18 November 1975, *Dorantes 5212* (BM); Boca del Río, Costa de Oro, 0 m, 6 December 1979, F. *Ventura-A. 16660* (IEB, MEXU); Cosamaloapan, Texas, 10 m, 19 April 1969, G. *Martínez-Calderón 1868* (MEXU, US, USF); Coxquihui, En el poblado de Coxquihui, 22 May 1980, M. *Mendoza 27* (MEXU); Dos Ríos, El Aguaje, 150 m, 13 September 1974, F. *Ventura-A. 10537* (MEXU); Emiliano Zapata, Col. Puente Nacional, Ver. Carretera Japala-Veracruz, 250 m, 10 August 1972, J. *Dorantes 1529* (MEXU); Jalcomulco, Al NE de

Jalcomulco por el camino a Apazapan Centro dos poblados, 400 m, 7 August 1984, *G. Castillo-C. 3173* (IEB); Martínez de la Torre, San Carlos, 12 June 1970, *F. Ventura-A. 1293* (NY); Misantla, Santa Cruz de Hidalgo, carretera Misantla-Mtz. De la Torre, 140 m, 26 April 1976, *C. Hernandez-A. 166* (BM); Omealca, A 1 km al Oeste de Cruz Tetela, 300 m, 31 July 1986, *R. Robles-G. 922* (MEXU); Papantla de Olarte, San Pablo, Parcela Geño, 15 m, 24 June 2011, *R.L. López 5* (IEB); Paso de Ovejas, Plan de Manantiales, Alrededores, 40 m, 19 March 1987, *M.G. Zolá-B. 1814* (IEB); Playa de Vacas, unknown locality, 15 m, 31 March 1967, *G. Martínez-Calderón 1340* (MEXU, U); Poza Rica, 1 km N of Poza Rica, 75 m, 20° 33' 00" N, 97° 28' 00" W, 23 June 1980, *B.F. Hansen 7435* (F, USF); Puente Nacional, Tamarindo, 150 m, 9 August 1975, *F. Ventura-A. 11768* (MEXU); San Andrés Tuxtla, Cerro Lazaro Cardenas, Estación de Biología Tropical Los Tuxtlas, 450 m, 16 June 1986, *S.S. Colín 803* (MEXU); Tihuatlan, Quintana Roo, Coba, June-July 1938, *C.L. Lundell 7775* (US); Texistepec, El bajillo, 2 July 1995, *C.H. Ramos 956* (MEXU); Tlapacoyan, Isapa, 250 m, 2 July 1976, *F. Ventura-A. 12897* (MEXU); Tuxpan, Just N of Tuxpan, along the road to Tamiagua on the Gulf coast about 4–8 miles from its intersection with the Tuxpan bypass on hwy 180, 60 m, 13 July 1983, *C.M. Taylor 2079* (MEXU); Ursulo Galván, Loma de San Rafael, 24 November 1971, *F. Ventura-A. 4562* (COL); Veracruz, At the edge of Veracruz, on Mexico 150, 8 April 1975, *D. Seigler 9812* (MEXU, NY); Zacualpan, Rio de Santa Maria, August 1906, *C.A. Purpus 2079* (US). **Yucatan:** Chemax, A 12 km al O de Chemax, sobre la carretera Valladolid-Cancun, 16 July 1985, *E. Cabrera 8883* (MEXU); Mérida, Tekik de Rejil caminho a San Pedro Chimay, 10 m, 19 June 1985, *C. Chan 5428* (MEXU); Pisté, In the village clearing, May-August 1938, *C.L. Lundell 7536* (US); Unknown locality, unknown date, *E.M. Sessé y Lacasta 4598* (MA). UNITED STATES OF AMERICA. **Florida:** Dade, Nixon-Lewis Hammock. Southwest of intersection of SW 217 Ave. & 296 St., 7 June 1998, *K. Bradley 1843* (FTG, NY, USF); Manatee, Under large *Quercus virginiana* along ditch at edge of abandoned citrus grove ca. 3 mile north of 21st Street West and 0.2 mile west of 14th Avenue West, north of Palmetto. Section 10, Township 34S, Range 17E. Uncommon, 11 August 1983, *A.G. Shuey 2569* (USF); Marion, Silva Springs: Silver River State Park, 29° 11.717' N, 82° 01.372" W, 27 August 2006, *J. Hubbard 626* (FLAS); Pinellas, Near path in city park at Maximo Point, St. Petersburg, 13 September 1963, *R.F. Thorne 33888* (USF).

[SOUTH AMERICA] ARGENTINA. **Catamarca:** Ancasti, El Cajón, 18 April 1950, *J. Brizuela 1269* (K, P, US); Capayan, Capayan, 26 April 1947, *B.L. Muller 173* (G); La Paz, El puesto de Pilimon, 26 January 1947, *J. Brizuela 197* (US). **Chaco:** Colonia Benitez, unknown locality, January 1936, *A.G. Schulz 1506* (U); Fontana, unknown locality, March 1937, *T. Meyer 2222* (F, P); Comandante Fernandez, Bajo Hondo Chico, 10 km al Sur de S.Peña, 5 March 1977, *B. Perez 180* (F); General Güemes, Campo Grande, borde del Río Bermejito, 2 March 2000, *R. Fortunato 6532* (MO); Resistencia, Colonia Benítez, 28 December 1941, *A.G. Schulz 1886* (F); Tapenag, Enrique Urien, 28 January 1946, *C.L. Schulz 878* (F). **Córdoba:** Cruz del Eje, Dique Cruz del Eje, 21 February 1950, *A.V. de la Sota 1965* (US); Ischilín, Quilino, 3 April 1944, *C.A. O'Donnell 381* (F, U); Punilla, Sierra Chica. Entre el Puesto del Medio y las Cateras de Ions Allendes, 11 January 1877, *G. Hieronymus 203* (P). **Corrientes:** General Paz, 12 km E de Itá Ibaté, costa río Paraná, 09 April 1972, *L. Mroginski 635* (G[2], MBM, MO, NY, P[2], WIS); Ituzaingó, Ruta 38 y río Aguapey, 7 January 1985, *S.G. Tressens 3005* (F, MO); La Cruz, Boca rios Aguapey y Uruguay, 21 December 1944, *C. Harrola 1783* (NY); San Martín, 6 km SW de La Cruz, sobre río Uruguay, 8 February 1979, *A. Schinini 16826* (MO); San Tomé, Cuay Grande, 21 January 1947, *A.M.R. Huidobro 4213* (G); Santo Tomé, Río Uruguay, Garabi, 30 January 1951, *T.M. Pedersen 998* (US). **Entre Ríos:** Colón, Alrededores de Colón, 28 March 1970, *A. Burkart 27864* (P); Concepcion del Uruguay, unknown locality, April 1877, *P. Lorentz s.n.* (BM, K); Federación, unknown locality February 1949, *R.L. Martinez-Crovetto 4896* (MBM); La Paz, Río Feliciano. Ruta 126, 15 January 1960, *A. Burkart 21250* (MO); Paraná, Cezanos Pinto, 29 November 1946, *A.M.R. Huidobro 3642* (F, U). **Formosa:** Formosa, unknown locality, 1918, *P. Jorgensen 2853* (US); Pilcomayo, unknown locality, 13 January 1949, *I. Morel 6893* (G); Pirané, Las Matacas, 19 December 1945, *J. Morel*

674 (F). **Jujuy:** San Pedro, Camino a Santa Clara, entre el río Grande y el río Lambayen, 5 January 1966, *A.L. Cabrera 17524* (P); Santa Bárbara, Quinta pr. Laguna de la Brea, 23 June 1901, *R.E. Fries 235* (P, US). **La Rioja:** Chilecito, Novegosto, 900 m, 28 December 1928, *S. Venturi 7847* (MA, US). **Misiones:** Cainguás, Tabay, 28 October 1948, *E. Schwindt 950* (NY, US); Candelaria, Loreto, 13 January 1945, *J.E. Montes 922* (NY); General Manuel Belgrano, Andresito (ex Almirante Brawn), 270 m, 14 November 2000, *M.J. Belgrano 2668* (MBM); Guarani, Predio guarani. Aldea aborigen, 03 November 1999, *S.G. Tressens 6491* (MO, SP); Iguazú, Parque Nac. Iguazú, ruta 1010, A° Sto. Domingo, 12 January 1972, *L. Mroginski 356* (P, RB); Montecarlo, Puerto Piray, 27 October 1978, *S.A. Renvoize 3299* (K); Posadas, Prope "La Granja" predium, 30 February 1907, *E.L. Ekman 453* (G); San Ignacio, Mordecarlo, unknown locality, 5 December 1948, *G.J. Schwarz 6775* (G, US); San Javier, unknown locality, 28 December 1946, *Schwarz 3760* (F); Santa Ana, unknown locality, January 1913, *Rodriguez 698* (K, U, US). **Salta:** Chicoana, Rua 9, 4 km al norte de Ampascachi, em el primer vado yendo a Salta, 20 January 1983, *L.J. Noyara 3056* (G); General José San Martín, 4 km S de professor Salvador Mazza, 24 November 1994, *A. Krapovickas 46351* (MBM); Joaquín Víctor Gonzáles, unknown locality, 26 January 1945, *R.M. Aguilar 292* (NY); Metán, Juramento, 4 April 1945, *C.A. O'Donnell 2734* (NY); Orán, Orán-Bado Hondo, 1 April 1951, *A.V. de la Sota 4480* (G); Senda Hachada, 3 Km E de Senda Hachada, río Seco, 2 April 1977, *A. Krapovickas 30822* (MEXU). **Santiago del Estero:** C. Pellegricu, Estancia El Renuste, 500 m, 22 December 1927, *S. Venturi 5737* (US); El Charco, unknown locality, 300 m, 25 February 1930, *S. Venturi 10202* (BM, NY); Choya, De Villa La Punta a Choya, 13 April 1979, *A.D. Rotman 166* (MO). **Tucumán:** Burreyacu, unknown locality, 1 April 1900, *T. Stuckert 9151* (G); Capital, Río Ioli, 450 m, 15 February 1920, *S. Venturi 197a* (US); Cruz Alta, Cacanas, 450 m, 30 December 1925, *R. Schreiter 4607* (U); Monteros, Kilometro 1220, 8 May 1945, *F. Ortiz s.n.* (F 1293363, K); Yerba-Buena, Café, 650 m, 20 January 1919, *S. Venturi 197* (F, US). **BOLIVIA. Beni. Gral. Ballivián:** Yacuma, Estación Biológica del Beni, comunidad Totaizal, 200 m, 66° 37' 00" S, 14° 30' 00" W, 29 June 1995, *J. Balderrama 620* (G, WIS); Rurrenabaque, Rurrenabaque, 26 January 1921, *M. Cardenas 2047* (K, NY). **La Paz. Nor Yungas:** Coripata, unknown locality, 18 April 1894, *M. Bang 2130* (BM, E, F, G[2], K, NY[2], US[2]). **Santa Cruz:** Sara, Yugo em Chacras de Buenavista, 500 m, 8 July 1924, *J. Steinbach 6203* (G, K); **Andrés Ibañez:** Santa Cruz de la Sierra, La Guardia, km 9,5 camino antiguo a Porongo a 8 cuerdas sobre el camino y terreno con vegetación natural, tras casa de I. Linneo, 400 m, 17° 50' 59.6" S, 63° 15' 22.8" W, 28 June 2006, *I. Linneo 613* (USZ); **Chiquitos:** Santiago de Chiquitos, Candelaria, 200 m, 18° 37' 00" S, 58° 58' 00" W, 3 February 1995, *J.R. Abbott 16058* (USZ); **Cordillera:** Basilo, 5.5 km. S of Basilo on road from Santa Cruz to Camiri, 500 m, 18° 03' 45" S, 63° 11' 30" W, 21 January 1994, *M. Nee 44578* (MO, NY, USZ); Bañados del Izozog, Estacia Cachari, 400 m, 13 March 1991, *G. Navarro 362* (MO, USZ); **German Busch:** Puerto Isabel, Baía Mandioré, 90 m, 18° 11' 50.7" S, 57° 30' 39.7" W, 23 November 2010, *F. Bao 8* (CGMS). **Ichilo:** Buena Vista, March 1917, *J. Steinbach 3273* (F); **Ignacio Warmes:** 3 km NNW of La Esperanza and 1.3 km SE of junction with Montero-Okinawa highway, 270 m, 17° 16' 00" S, 63° 03' 00" W, 21 December 1997, *M. Nee 47424* (NY, USZ); **José Miguel de Velasco:** Camino a las Mechitas a 8 km de regreso del aserradero, a la orilla de um arroyo siguiendo el curso hacia abajo, 450 m, 14° 32' 35" S, 61° 29' 52" W, 23 January 1997, *J. Guillen 282* (USZ); **Ñuflo de Chávez:** San Antonio de Lomerio, Estancia San Miguelito, 200 km NE de la ciudad de Santa Cruz; puesto San Miguelito. Em orilla de río San Julián, 260 m, 17° 01' 00" S, 61° 52' 00" W, 31 July 1995, *A. Fuentes 1021* (MO, USZ); **Obispo Santiesteban:** E of la Porfia, 340 m, 17° 03' 20" S, 63° 07' 30" W, 20 February 1994, *M. Nee 45109* (NY, USZ); **Sara:** A 84 km de Santa Cruz, entre Protachuelos y San Juan de Palometilla, 300 m antes del Río Palometilla, 400 m, 17° 23' 12" S, 63° 31' 03" W, 21 June 2004, *R. Riina 1502* (USZ). **BRAZIL. Amazonas:** Beach at Brandos, 25 December 1874, *J.W.H. Traill 728* (K); Lower Amazons, nicolas at Río Jaguari, 21 November 1873, *J.W.H. Traill 727* (K). **Maranhão:** São Mateus do Maranhão, Near Km 150–165 of BR. 135. Appox. 15–30 km N of São Mateus, 03° 46' 00" S, 44° 32' 00" W, 28 September 1980, *D.C. Daly D338* (INPA, NY, US). **Mato Grosso:** Apiacás, Río Juruena, November 2007, *M. Sobral 11126* (BHCB); Poconé, Parque



Nacional do Pantanal, lado leste da sede do Parque, marmenquezal com *Aspilia latissima*, 21 March 2001, *A. Pott 8624* (CGMS); Rondonópolis, Estrada para os ranchos que margeam o Rio Vermelho, sentido São Lourenço de Fátima, na Rota do Peixe, a 1,3 Km do rio, 4,6 Km das plantações de eucalipto da ADM, 16° 27' 16" S, 54° 56' 24" W, 17 December 2008, *L.B. Motta 26* (SPF). **Mato Grosso do Sul:** Aquidauana, Rodovia Campo Grande-Aquidauana, entrada para Ribeirão, 228 m, 20° 26' 53.07" S, 55° 15' 22.98" W, 30 January 2014, *O.L.M. Silva 119* (SP); Batayporã, Rio Baía, Lagoa dos Porcos, 229 m, 22° 41' 55" S, 53° 14' 39" W, 28 November 2012, *C.E.B. Fernandes 197* (HUEM, SP); Corguinho, Pantanal. Margem da Rodovia MS-419. Caixa de empréstimo, 150 m, 19° 13' 53.1" S, 55° 13' 13.24" W, 03 October 2013, *D. Gris 102* (CGMS); Corumbá, Base do cerro do Urucum - 23km S de Corumbá, 22 November 1977, *A.C. Allem 1476* (CEN, R); Ladário, Estrada do Polder, 05 February 1985, *C.A. Conceição 1695* (SP, UB); Miranda, Próximo à Base de Pesquisas da UFMS, 18 December 1990, *U.M. Resende 349* (CGMS, MBM, SP); Naviraí, Córrego do Touro, 23° 03' 55.39" S, 54° 13' 23.81" W, 19 November 2009, *C. Faxina 226* (CGMS, FUEL); Selvíria, Fazenda de Ensino e Pesquisa da Unesp-Campus de Ilha Solteira, 07 February 1991, *O. Tiritam 459* (SP); Taquarussu, Rio Baía, margem esquerda, fazenda 7 Figueiras, 12 November 2011, *M.C. Souza 2546* (HUEM); Terrenos, Cerca de 5 km adentro do acesso à Cachoeirão (à direita na BR-262 no sentido Campo Grande-Aquidauana), próximo a uma antiga estação de trem desativada, 216 m, 20° 26' 10.02" S, 55° 17' 12.6" W, 9 March 2016, *O.L.M. Silva 248* (SP); Três Lagoas, Rodovia CESP, próximo ao início da ponte sobre o Rio Paraná (BR 262), 281 m, 20° 47' 05.21" S, 51° 38' 49.55" W, 31 January 2014, *O.L.M. Silva 121* (SP). **Paraná:** Campo Mourão, Campus da UTFPR - Campo Mourão, 22 January 2010, *M.G. Caxambu 2899* (CGMS, HCF, MBM); Cantagalo, Jacutinga, 8 November 1989, *W.M. Kranz 552* (FUEL); Foz do Iguaçu, Avenida 1, vila A (ITAIPU), 21 February 1980, *A. Botelho s.n.* (MA 380606, MBM 71701); Pinhão, Rio Jordão. Caminho do Salto da Tia Chica, 12 March 1996, *Y.S. Kuniyoshi 5820* (MBM); São Miguel do Iguaçu, Occui. Área a ser inundada pela represa da Itaipu, 25° 32' 00" S, 54° 35' 00" W, 23 March 1982, *A. Custodio Filho 843* (SP). **Rio Grande do Sul:** Campinas, Campinas p. Sta. Rosa, February 1947, *A. Spies s.n.* (PACA 36031); Cerro Largo, Cerro Largo p. São Luiz, January 1943, *P. Buck s.n.* (PACA 11099); Derrubadas, Parque do Turvo, beira do Rio Uruguai, 1 November 1971, *J.C. Lindeman s.n.* (U 1267575); Lagoa dos Quadros, Lagoa dos Quadros p. Torres, 18 January 1951, *B. Rambo s.n.* (PACA 49779); Nonoai, Nonoai p. fl. Uruguay, March 1945, *B. Rambo s.n.* (PACA 28376); Osório, Lagoa dos Quadros, 18 January 1951, *B. Rambo 49779* (US); Porto Alegre, unknown locality, April 1944, *K. Emrich s.n.* (PACA 26838); Santo Antônio das Missões, unknown locality, 28° 34' 35" S, 55° 36' 43" W, 25 February 2010, *E. Melo 7749* (HUEFS, SP); São Borja, unknown locality, 1942, *F. Baglione s.n.* (PACA 2948); São Leopoldo, unknown locality, 1942, *E. Schmidt s.n.* (PACA 47505); São Miguel, São Miguel p. São Luiz, 29 January 1938, *B. Rambo s.n.* (PACA 2896); Tenente Portela, Porto, 3 January 1972, *A. Sehnem 12696* (PACA); Uruguaiana, Estrada para Quaraí, 21 January 1983, *J.R. Pirani 504* (SP). **Santa Catarina:** Concórdia, Volta Grande, próximo ponte ferroviária sobre o Rio Uruguai (M.Ramos), 23 December 1996, *J.A. Jarenkow 3344* (ESA, MBM); Lages, Morro do Pinheiro Seco, 04 February 1963, *R. Reitz 6583* (L, MBM, NY, PACA, RB, US); Mondáí, Floodbanks of Rio Uruguai, 200–300 m, 2 January 1957, *L.B. Smith 9734* (K, NY, R, US). **São Paulo:** Assis, Estação Experimental, região da serraria velha, 15 May 1995, *V.S. Moura 24* (SPSF); Jales, Pastos do Retiro, 17 January 1950, *W. Hoehne s.n.* (R 149074); Mogi Guaçu, Fazenda Campininha, próximo de Pádua Sales. Várzea do rio Mogi Guaçu, 26 October 1956, *M. Kuhlmann 3700* (IAC, NY, RB, SP, US); Rio Grande, unknown date, *Tweedie s.n.* (K 1210214). **COLOMBIA. Atlântico:** Entre Palmar de Varela y Ponedera, hacienda El Paraiso, orillas del rio Magdalena, 10 m, 20–22 December 1950, *A. Dugand 4508* (COL, US). **Bolívar:** Ciénaga de Machado, Sacre, 50 m, 13 July 1973, *J.M. Idrobo 6617* (U, US); Sabana Beltrán y San Pedro, por la carretera, 17 September 1963, *R. Romero-Castañeda 9977* (COL); Santa Catalina, Hacienda El Ceibal, 34 m, 10° 36' 24" S, 74° 17' 42" W, 6 July 2000, *G.M. Rodríguez-M. 204* (COL). **Córdoba:** Montería, Orillas del rio Sinú: hacienda El Covao, 140 m, 28 May 1950, *H. Garcia-Barriga 13419* (COL, NY, US); Entre Cereté y Ciénaga de Oro, hacienda La Hermita (Berástegui),

30 m, 30 May 1950, *H. Garcia-Barriga* 13433 (COL, US). **Cundinamarca:** Bogota, unknown locality, unknown date, *J. Goudot s.n.* (P 4830337). **Huila:** Caguan, Road to Cerro de Neiva, 17 August 1974, *T. Plowman* 4179 (COL). **Magdalena:** Around Rio Frio, between the Ciénaga de Santa Marta and the foothills, 100 m, 22–30 June 1906, *H. Pittier* 1578 (US); Chugo - Rio Minero, unknown date, *J. Goudot s.n.* (P 4830338); Ciénaga, unknown locality, 16 February 1950, *R. Romero-Castañeda* 1971 (COL); El Copey, Palmeras de la Costa, December 1986, *H. Collazos* 148 (COL). **Valle del Cauca:** Cali, Ingenio Meléndez, 1008 m, 8 July 1966, *J.A. Páez-V.* 4 (COL); Palmira, En los alrededores de Palmira, 1000 m, 3 December 1947, *R. Obregón-B. s.n.* (COL 42203); Bordes de la carretera entre Palmira y Cali, 25 April 1963, *L. Figueiras* 8483 (US). PARAGUAY. **Alto Paraná:** Hernandarias, 20Km N de Hernandarias, 10 January 1974, *A. Schinini* 8045 (G). **Alto-Paraguay:** Chaco, unknown locality, 29 July 1910, *K.A.G. Fiebrig* 1273 (G, K); Fuerto Olimpo, Chaco Paraguayo, 12 December 1946, *T. Rojas* 13857 (P); San Pedro, Primavera, 8 March 1955, *A.L. Woolston* 472 (K, US). **Boquerón:** Loma Plata, Isla Poí, 22° 28' 00" S, 59° 40' 00" W, 16 May 1994, *A. Krapovickas* 45498 (MBM, G); Loma Plata, Est. Exp. Isla Poí. 30 Km SE de Loma Plata, 22° 30' 00" S, 60° 00' 00" W, 25 February 1991, *R. Vanni* 2268 (F, G); P.N. Médanos del Chaco, 20° 54' 27" S, 61° 50' 25" W, 23 February 2006, *M. Peña-Chocarro* 2550 (BM). **Cantera:** Colonia Alborada, 225 m, 23 November 1948, *J.E. Montes* 3276 (K). **Central:** Areguá, Quinta Guggiari, 8 January 1976, *P. Arenas* 1310 (NY, MO); Asunción, Base du Cerro Lambaré, 21 October 1875, *B. Balansa* 1700 (BM, G[2], K[2], P[6]); San Lorenzo, Ciudad Universitaria, 25° 21' 00" S, 57° 29' 00" W, 4 February 1987, *S. Ginzburg* 404 (F); Villa Elisa, 8 November 1956, *T.M. Pedersen* 4250 (US). **Chaco:** Cap.[Mayor] Pablo Lagerenza, unknown locality, 250 m, 2 November 1987, *R. Spichiger* RS2789 (G). **Guaira:** Villarica, unknown locality, unknown date, *P. Jorgensen* 4900 (F, NY, US); In regione cursus inferioris fluminis Pilcomayo, April 1906, *T. Rojas* 10 (BM, G, P). **Ñeembucú:** San Fernando, sobre el río Tebicuary, 5 May 1945, *Z. Rojas* 12671 (NY). **Presidente Hayes:** Santa Elisa, Gran Chaco, December 1903, *E. Hassler* 2706 (BM, F, G[4], K, NY, P[3], US); Isla Poí, 24 km N de la ruta Trans-Chaco km 415, 11 December 1992, *A. Krapovickas* 44365 (G); Lolita. 50 Km S del cruce Loma Plata com ruta Trans-Chaco, 27 February 1991, *R. Vanni* 2423 (G). Gran Chaco, unknown locality, 10 January 1903, *A. Prike s.n.* (K); Zwischen Rio Apa und Rio Aquidaban, 1908–09, *K.A.G. Fiebrig* 4281 (G[3], K). PERU. **Cajamarca. San Ignacio:** San Ignacio, Las Juntas de Namball (naciente del Chimchipe por Union de Los Rios Mayos y Chanthis), 750 m, 05° 07' 30" S, 79° 01' 00" W, 13 January 1997, *J. Campos* 3324 (F, MEXU, WIS). **Junin. Chanchamayo:** San Ramón, Outskirts of San Ramón, 11 July 1988, *A. Gentry* 63570 (MO). **San Martín. Huallaga:** Granja Bellavista, 250–260 m, 3 August 1969, *M.S. Chrostowski* 69-152 (WIS). **San Martín:** Tarapoto, Fundo San Isidre, 426 m, 13 February 1976, *A. Sagástegui-A.* 8305 (NY). PHILIPPINES. Unknown locality, unknown date, *L. Neé s.n.* (MA 249996). PUERTO RICO. **Loiza:** Calle Villanueva of Pueblo Indio, ca 1 km N of old bridge by old central, 10–30 m, 13 October 1989, *C.M. Taylor* 9484 (P). **San Juan:** Rio Piedras. Campo Alegre, 22 December 1914, *J.A. Sternson* 2462 (NY). SAINT VINCENT AND THE GRENADINES. **Saint Vicent:** Kingstown, Prés des docks, 20 January 1980, *J. Jérémie* 796 (P). TRINIDAD AND TOBAGO. **Trinidad:** Couva-Tabaquite-Talparo, Plantation between Mile Post 27 Valencia - Toco Road and Savonette Point, 20 May 1975, *D. Philcox* 7767 (K); Tunapuna-Piarco, Valsayn, 5 April 1975, *D. Philcox* 7641 (K). PERU. **San Martin:** Alto Rio Huallaga, 360–900 m, December 1929, *L. Williams* 6682 (F). VENEZUELA. **Apure:** Puerto Paez, unknown locality, 2 May 1946, *I. Velez* 2592 (US). **Barinas:** (vazio), Ticoporo forest reserve, 08° 15' 00" S, 70° 45' 00" W, 03 May 1964, *F.J. Breteler* 3894 (NY, SP, U, WAG[2]). **Bolívar:** Ciudad Bolívar, unknown locality, 35 m, 8 June 1931, *E.G. Holt* 859 (NY); Piar, Los Aceites. Nor-Oeste de EL Manteco, 250 m, July 1978, *F. Delascio-Ch.* 7396 (MO); Sucre, Isla de la gallina, frente a la población de mapire, 20 m, 07° 30' 08" S, 64° 30' 65" W, 18 January 1995, *S. Flores* 53 (NY). **Caracas:** Caracas, Lower Cotiza, near Caracas, 800–1200 m, December 1918, *H. Pittier* 8376 (US). URUGUAY. **Artigas:** San Gregorio, unknown locality, 15 February 1964, *Jones* 3248 (K). **Salto:** Arapey, unknown locality, April 1949, *W.G. Herter* 50729 (MO).

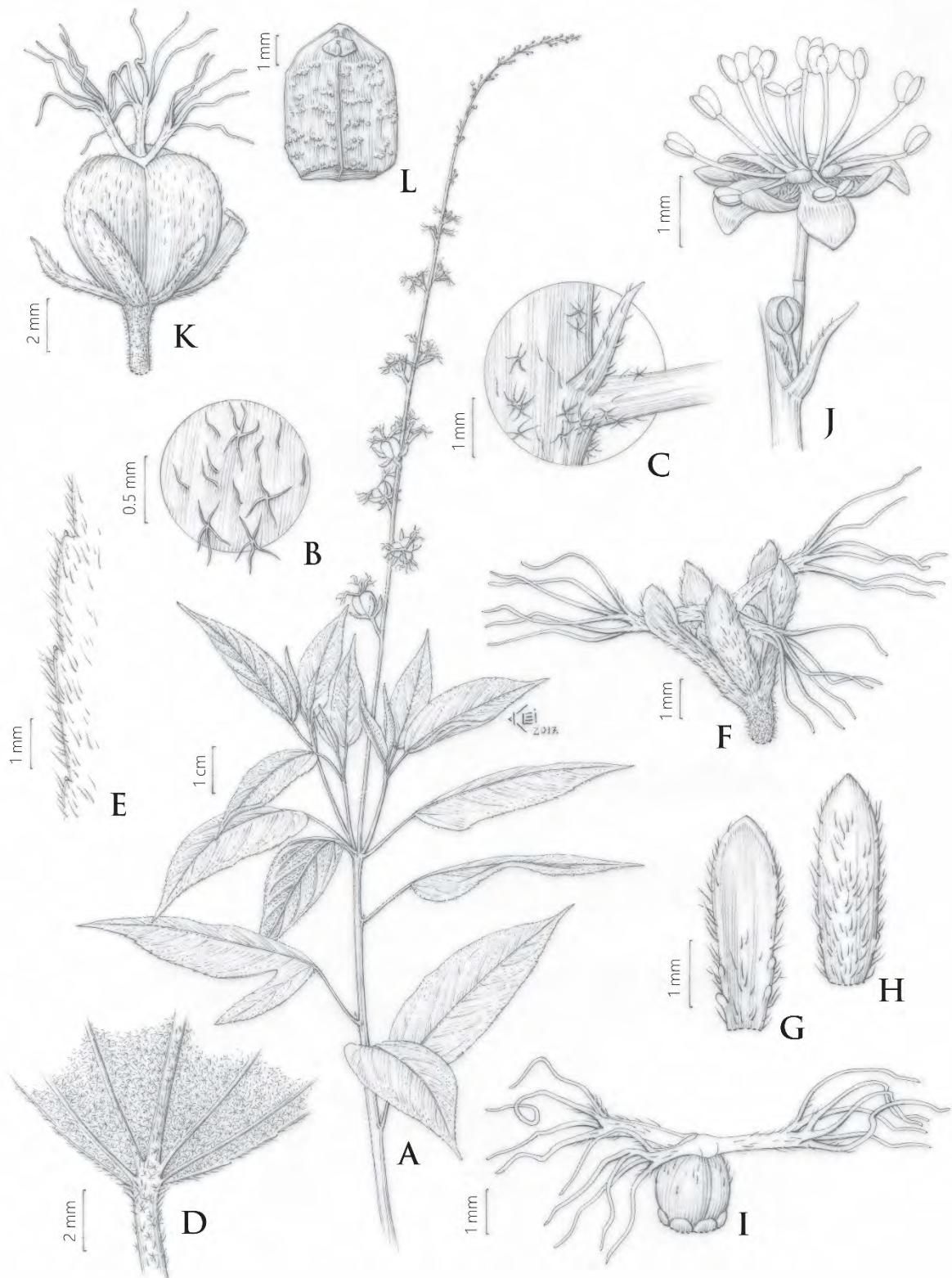


7. *Astraea macrourea* (Colla) Moraes *et al.* (2014: 145). *Croton macroureus* Colla (1836: 110). Lectotype (designated by Moraes *et al.* 2014):—BRAZIL. Rio de Janeiro: Cabo Frio, 1827, *Unknown collector* (Wied-Neuwied?) *s.n.* (TO6460 [photo!], isolectotypes BM001125227!, K00186091!). Figs. 17–19.

**Perennial shrubs**, phanerophytes, up to 1.5 m high, with erect branches, without a well-developed (xylopodiferous) underground system, branches pilose to sparsely pubescent, with stellate trichomes. **Leaves** entire or (2–)3-partite, entire leaves elliptic, oblong or ovate, (2–)3–6.5(–8) x (0.7–)1–2.5(–3) cm, partite leaves with the medium lobe elliptic or oblong, 5–7(–8) x 2–3 cm, and lateral lobes elliptic or oblong, (2–)2.5–4(–5) x 1–2(2.5) cm, chartaceous, apex attenuate to long attenuate, base rounded, obtuse or rarely slightly cuneate, margin serrate, with conspicuous teeth, not cartilaginous, ciliate, with simple or stellate trichomes, adaxial surface pilose to esparsely pubescent, generally more dense at the base and along the margins, with mostly short (< 0.5 mm) simple trichomes, but also stellate or stellate-porrect trichomes near the base or along the primary veins, abaxial surface pubescent to densely pubescent, more dense near the base and along the veins, with stellate or stellate-porrect trichomes, venation camptodromous (when entire) or actinodromous (when partite); petioles (0.5–)1.5–2.5(–3) cm long, pilose, more dense near the apex and the base, with stellate trichomes; stipules subulate, entire, up to 3 mm long, pilose to sparsely pubescent, with stellate or short (< 0.5 mm) simple trichomes. **Thyrse** (15–)20–30 cm long, rachis pilose to sparsely pubescent, with mostly short (< 0.5 mm) simple or stellate trichomes; basal cymules with 5–15 pistillate flowers, accompanied by 3–6(–7) staminate flowers; distal cymules with 3–6(–7) staminate flowers; bracts triangular to subulate, up to 2(–3) mm long, pilose or sparsely pubescent, with short (< 0.5 mm) simple or stellate trichomes; **Staminate flowers** with pedicel up to 3(–5) long, glabrous; calyx glabrous. **Pistillate flowers** with pedicels 1–2(–2.5) mm long, reaching up to 4(–5) mm in fruit, pubescent, with stellate trichomes, calyx lobes 5–6, sometimes with one lobe poorly developed and narrower than the others, lobes oblong to slightly obovate, 2–3 mm, reaching up to 5(–6) mm in fruit and 0.8–1.5 mm wide, sparsely to densely pubescent on external face, with short (< 0.5 mm) simple trichomes, margin entire, not cartilaginous, ciliate, with short (< 0.5 mm) simple trichomes, apex acute; ovary 1–1.5 x 1–1.5 mm, sparsely pubescent or pubescent, with short (< 0.5 mm) simple trichomes. **Fruits** lustrous, 5.5–6.5 x 5.5–6.5 cm, glabrous or pilose, with short (< 0.5 mm) simple trichomes; seeds tetragonal in cross section, 3–4 x 5–6 mm, caruncle ca. 0.5 x 1.5 mm.

**Etymology and vernacular names:**— the epithet *macrourea*, from Greek (makros [μακρος] = large, and oura [ουρά] = tail), means long tail. Therefore, when describing *Croton macroureus*, Colla (1836) was probably referring to the long inflorescence of this species. The only vernacular name found for this species is *mamona-branca* (portuguese), but as it is usually misidentified as *Astraea klotzschii* the same vernacular names of the later may apply to *A. macrourea*.

**Geographical distribution:**—SOUTHERN AMERICA. *Brazil*: Brazil Southeast (BZL-ES, BZL-RJ).



**Figure 17:** Line drawing of *Astraea macroua* **A.** flowering branch, **B.** detail of indumentum of younger portion of stems, **C.** detail of stipules, **D.** abaxial surface of leaf base, **E.** detail of leaf margin, **F.** pistillate flower, **G.** calyx lobe of a pistillate flower – internal face, **H.** calyx lobe of a pistillate flower – external face, **I.** gynoecium and floral nectaries (calyx removed), **J.** staminate cymules with one mature flower, **K.** immature fruit, **L.** seed – ventral face. Illustration by Klei Sousa, based on O.L.M. Silva 137 (SP).

*Astraea macroua* is endemic to the states of Rio de Janeiro e Espírito Santo, in southeastern Brazil (Fig. 18). This species grows in seashore vegetation, on white sandy soils, usually on sunny places.

**Phenology:**— Although there are not collections for every month, specimens with flowers and fruits are recorded for every season. Therefore, flowering and fruiting may occur throughout the year and simultaneously, as it is observed in the majority species of the genus.

**Conservation status:**—*Astraea macroua* has an area of occupancy (AOO) of 24,000 km<sup>2</sup> and is known for less than 10 localities. Also, there is a continuous declining of area extent and/or quality of the habitat where this species is found due anthropic pressure on seashore vegetation along Brazilian coastal region resulting from advance urban growth. Therefore, this species qualifies for Vulnerable (B2ab[iii]).

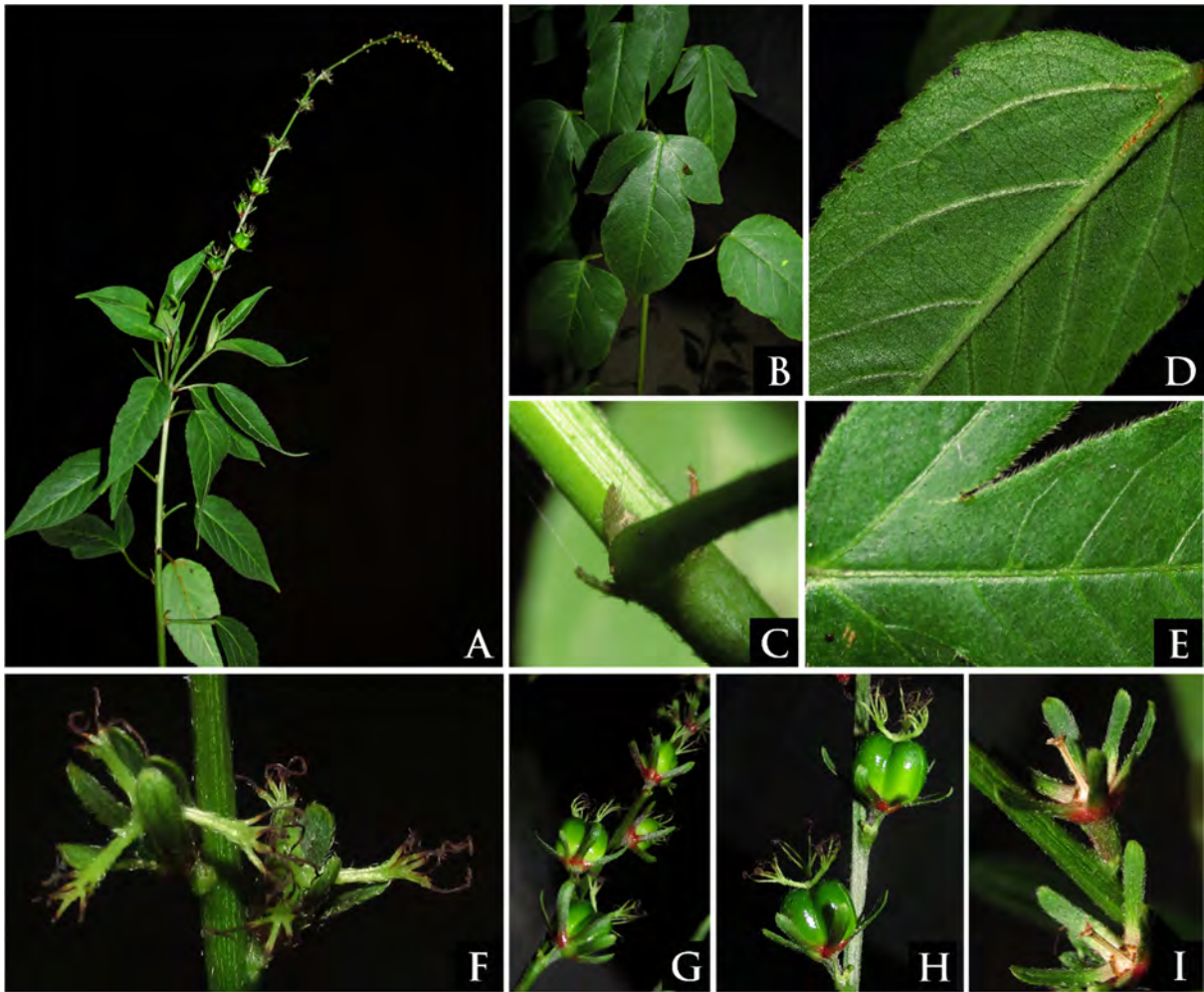


Figure 18: Geographical distribution of *Astraea macroua*.

**Taxonomic comments:**—Moraes *et al.* (2014) found a forgotten name, *Croton macrouus*, described by Colla in 1836. Moraes *et al.* (2014) recognized *Astraea macroua* as an earlier name for the well-known *A. klotzschii*,

described in 1857 by Didrichsen. However, the examination of the type collections of both taxa revealed differences in the abaxial surface of leaves (denser and composed by stellate trichomes in *A. macroua* (Figs. 17D and 19D) vs glabrous or composed by simple trichomes, usually sparser, in *A. klotzschii*) and therefore we recognized these as distinct taxa within *Astraea*. Besides morphological differences *A. klotzschii* is widely distributed along seashore plains from northeastern to southeastern Brazil, while *A. macroua* is only found in southeastern Brazil.

The indumentum of abaxial surface of leaves composed by stellate trichomes (Figs. 17D and 19D), allied to the presence of both entire and (2–)3-partite leaves (Figs. 17A and 19B), put *Astraea macroua* morphologically closer to *A. subcomosa*. However the latter is restricted to rocky grasslands (*campos rupestres*) from northern Minas Gerais and Chapada Diamantina on central Bahia (Fig. 30), while *A. macroua* is found only on seashore vegetation from the states of Rio de Janeiro and Espírito Santo (Fig. 18). Also, *A. macroua* has pubescent young portion of branches (vs tomentose in *A. subcomosa*) and the adaxial surface of leaves has mostly simple trichomes (vs. stellate trichomes in *A. subcomosa*).



**Figure 19:** Morphological characters of *Astraea macroua*. **A.** branch with inflorescence. **B.** branch with heterophyllous leaves. **C.** stipules. **D.** abaxial surface of a leaf. **E.** adaxial surface of a leaf. **F.** pistillate flowers. **G–H.** immature fruits. **I.** fruit after dehiscence with persistent collumela. A–I: population from Linhares, ES (O.L.M. Silva 137). Photos: O.L.M. Silva.

Another species found in seashore vegetation with a well-developed indumentum composed mostly by stellate trichomes is *Astraea praetervisa*. This species may be distinguished from *A. macroura* by its unique glanduliform stipules (vs subulate in *A. macroura*; Figs. 17C and 19C) and is endemic to southern Bahia. *Astraea surinamensis* is also found in seashore vegetation, but, due to its weedy nature, usually in disturbed places and may be distinguished from *A. macroura* by its herbaceous habit, and young portions of stems and petioles with stellate-porrect trichomes bearing a central ray much longer than the lateral rays, not present in *A. macroura*.

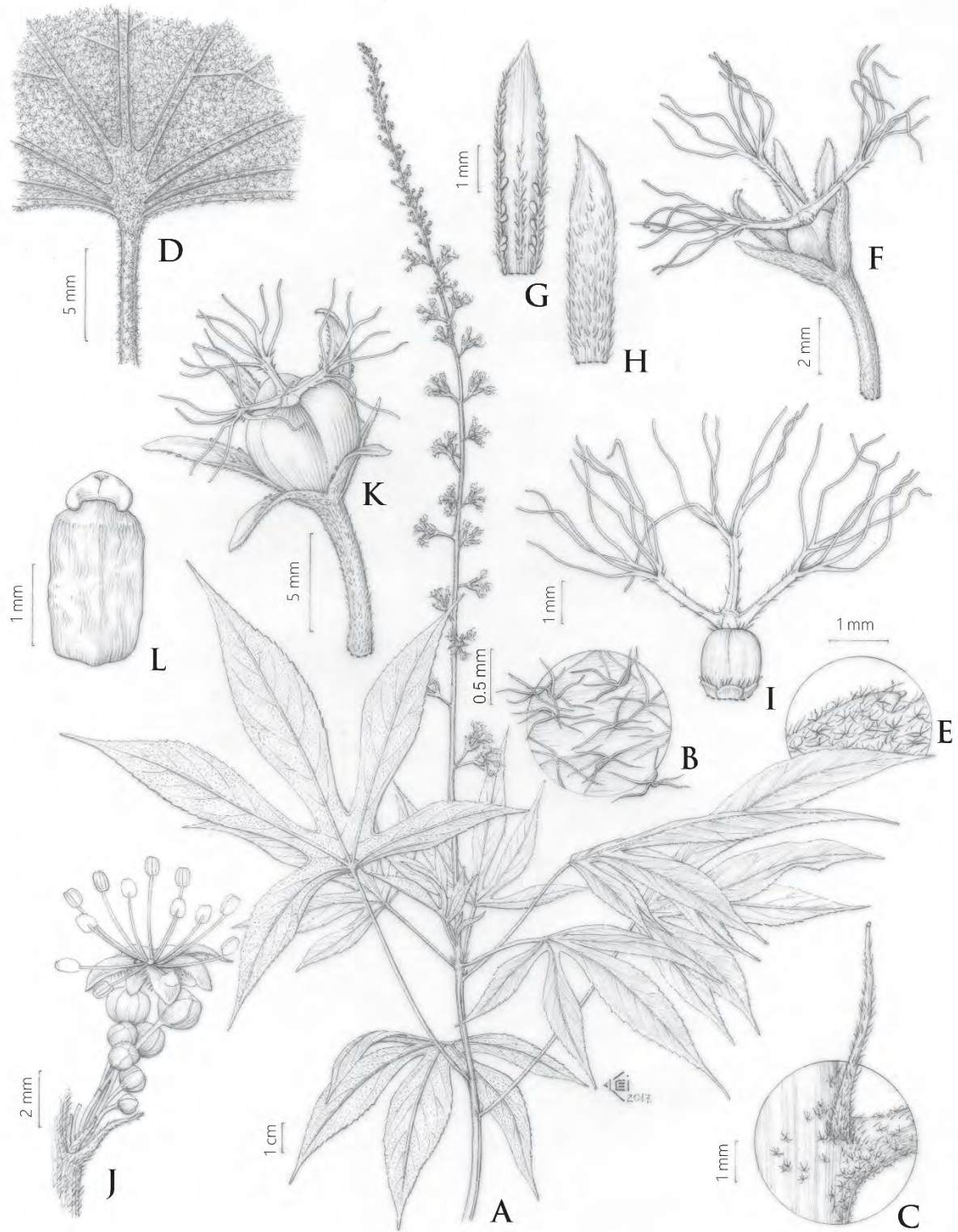
**Selected specimens examined:**—BRAZIL. **Espírito Santo:** Anchieta, APA da Tartaruga, 20.8058° S, 40.6456° W, 8 August 2009, J.M.L. Gomes 3356 (VIES); Domingos Martins, Parque Estadual da Pedra Azul. Trilha das Piscinas, 13 July 2005, L. Kollman 8041 (MBML, SP); Linhares, Reserva Natural da Companhia Vale do Rio Doce. Ao final da estrada Jureiana Vermelha, nas margens do Rio Barra Seca, 10 m, 19° 05' 13.82" S, 39° 53' 05.25" W, 11 June 2014, O.L.M. Silva 137 (SP); Vitória, unknown locality, 26 November 1991, M.L.L. Martins 137 (SP, VIES). **Rio de Janeiro:** Maricá, Barra de Maricá, 5 March 1985, V.L.G. Klein 220 (RB); Rio de Janeiro, Estrada do Autódromo, a 150 m da Lagoa Marapendi, 2 October 1972, J.A. Jesus 2076 (RB).

**8. *Astraea manihot*** (Müll.Arg.) Silva & Cordeiro (2017: 299). *Croton lobatus* var. *manihot* Müller Argoviensis (1866: 668). *Croton manihot* (Klotzsch) Baillon (1864: 361), *nom. nud.* Lectotype (designated by Silva & Cordeiro 2017):—BRAZIL. Minas Gerais: Caldas, 1846, J.F. Widgren 364 (S17-36789 [photo!], islectotypes BR583842 [photo!], BR583843 [photo!], BR583844 [photo!], S17-36787 [photo!]); remaining syntypes:—BRAZIL: unknown locality, unknown date, F. Sellow s.n. (BR00583982 [photo!], isosyntypes K01210198!, P00634915!, TUB009126 [photo!]). Fig. 20–22.

*Astraea jatropa* (Müll.Arg.) van Ee (2011: 17). *Croton jatropa* Müller Argoviensis (1866: 667). *Oxydectes jatropa* (Müll.Arg.) Kuntze (1891: 612). Lectotype (designated by van Ee 2011):—BRAZIL. Minas Gerais: Estrella, 1844, H.A. Weddell 778 (G-DC00312457!, islectotypes P00634932!, P00634933!, P00634934!); remaining syntypes:—BRAZIL: unknown locality, unknown date, F. Sellow s.n. (syntypes K00186086!, B† [photo F-BN5123!]). **syn.nov.**

**Perennial shrubs**, phanerophytes, up to 2.5(–5) m high, with erect branches, without a well-developed (xylopodiferous) underground system, branches glabrous or pilose to densely pubescent, with stellate trichomes. **Leaves** (3–)5-partite, medium lobe elliptic to obovate, 5–12 x 1–3 cm, and lateral lobes elliptic to oblong or narrow-oblong 2–10(–11) x 0.5–2.5 cm, membranaceous or chartaceous, apex attenuate to long attenuate, base obtuse to truncate, margin serrate, with conspicuous teeth, not cartilaginous, ciliate, with simple or stellate trichomes, adaxial surface pilose to sparsely pubescent, generally more dense at the base and along the margins, with mostly short (< 0.5 mm) simple trichomes, with stellate and stellate-porrect trichomes restricted to the base or along the margins, abaxial surface glabrescent to pubescent, rarely densely pubescent, more dense near the base, with mostly stellate trichomes, or with, scarce stellate-porrect trichomes





**Figure 20:** Line drawing of *Astraea manihot* **A.** flowering branch, **B.** detail of indumentum of younger portion of stems, **C.** detail of stipules, **D.** abaxial surface of leaf base, **E.** detail of leaf margin, **F.** pistillate flower, **G.** calyx lobe of a pistillate flower – internal face, **H.** calyx lobe of a pistillate flower – external face, **I.** gynoecium and floral nectaries (calyx removed), **J.** staminate cymules with one mature flower, **K.** immature fruit, **L.** seed – ventral face. Illustration by Klei Sousa, based on O.L.M. Silva 237 (SP).

and short (< 0.5 mm) simple trichomes along the veins and near the base, venation actinodromous; petioles (1–)4–10(–12) cm long, glabrescent to pubescent, generally more dense near the apex and the base, with stellate trichomes; stipules subulate, entire or 3–5-lobed, with medium lobe 3–10 mm long, and lateral lobes diminute (up to 0.5 mm), pilose, with mostly short (<0.5 mm) simple trichomes. **Thyrse** 25–60 cm long, rachis glabrescent to pubescent, with stellate, stellate-porrect and short (< 0.5 mm) simple trichomes; basal cymules with 10–15 pistillate flowers, accompanied by 6–8(–10) staminate flowers; distal cymules with 6–8(–10) staminate flowers; bracts triangular to subulate, 2–5 mm long, pilose, with (< 0.5 mm) simple trichomes; **Staminate flowers** with pedicel up to 5(–6) long, glabrous; calyx glabrous. **Pistillate flowers** with pedicels 3–5 mm, up to 6–7(–9) mm in fruit, glabrescent to pubescent, with stellate and short (< 0.5 mm) simple trichomes, calyx lobes 5–7, sometime with one lobe poorly developed and narrower than the others, lobes obovate to narrow-obovate, 1.5–3, up to 7 mm in fruit and 0.8–1.5 mm wide, sparsely to densely pubescent on the external face, with short (< 0.5 mm) simple trichomes, margin entire or sometimes slightly serrate towards the apex, not cartilaginous, ciliate, with short (< 0.5 mm) simple trichomes, apex acute; ovary 1.5–2 x 1.5–2 mm, glabrous or with few short (< 0.5 mm) simple trichomes near the apical portion. **Fruits** lustrous, 6–8 x 6–8 cm, glabrous or with few sparse short (< 0.5 mm) simple trichomes near the apical portion; seeds tetragonal in cross section, 4.5–5 x 3.5–4 mm, caruncle 0.8–1,2 x 1–1.5 mm.

**Nomenclatural notes:**—Nomenclatural matters of *Astraea manihot* were discussed by Silva & Cordeiro (2017) when proposing the combination of *Croton lobatus* var. *manihot* into *Astraea*. *Croton manihot* (Klotzsch) Baill. is here linked to *A. manihot*, despite the lack of a diagnosis which makes it a *nomen nudum*, once the collections cited by Baillon (1864) fit Müller Argoviensis' *C. lobatus* var. *manihot*.

**Etymology and vernacular names:**—the epithet *manihot*, as well as *jatropha*, as references to *Manihot* Mill. and *Jatropha* L., well known genera within Euphorbiaceae by their lobed or partite leaves. No vernacular names were found for this species.

**Distribution and ecology:**—SOUTHERN AMERICA. *Brazil*: Brazil South (BZS-PR, BZS-SC), Brazil Southeast (BZL-MG, BZL-RJ, BZL-SP).

*Astraea manihot* is found in southern Brazil, in the states of Minas Gerais, Espírito Santo, Rio de Janeiro, São Paulo, Paraná and Santa Catarina (Fig. 21). However, most of the specimens were collected in Minas Gerais and São Paulo. This species is found along seasonally dry forests from southern Minas Gerais and eastern São Paulo and Paraná, but also in humid montane forests in southern Minas Gerais, gallery forests within cerrado and rocky grassland ("*campos rupestres*") vegetation, and also disturbed environment, such as secondary forest, or even *Eucalyptus* plantations.



Figure 21: Geographical distribution of *Astraea manihot*.

**Phenology:**—Flowering and fruiting were recorded throughout the year, simultaneously, with most of specimens collected during the moist season (from December to March).

**Conservation status:**—*Astraea manihot* has an area of occupancy of 288,000 km<sup>2</sup> and has many known populations. However, localities where it occurs are constantly subordinate to anthropic pressure, which is especially strong in southeastern Brazil. Therefore, following IUCN (2012) guidelines, here we treat *A. manihot* as Nearly Threatened once it is likely to qualify for a threatened category in near future, but our present evaluation neither qualify it for Critically Endangered, nor Endangered or Vulnerable.

**Taxonomic comments:**—this species is peculiar within *Astraea* by its distinctive pedicellate pistillate flowers (Figs. 20F, 22N–O) and staminate cymules with 6–8(–10) flowers (Fig. 20J, 22M, O). However, it is commonly misidentified as *A. paulina* amongst specimens from São Paulo, or *A. comosa* in the case of specimens from

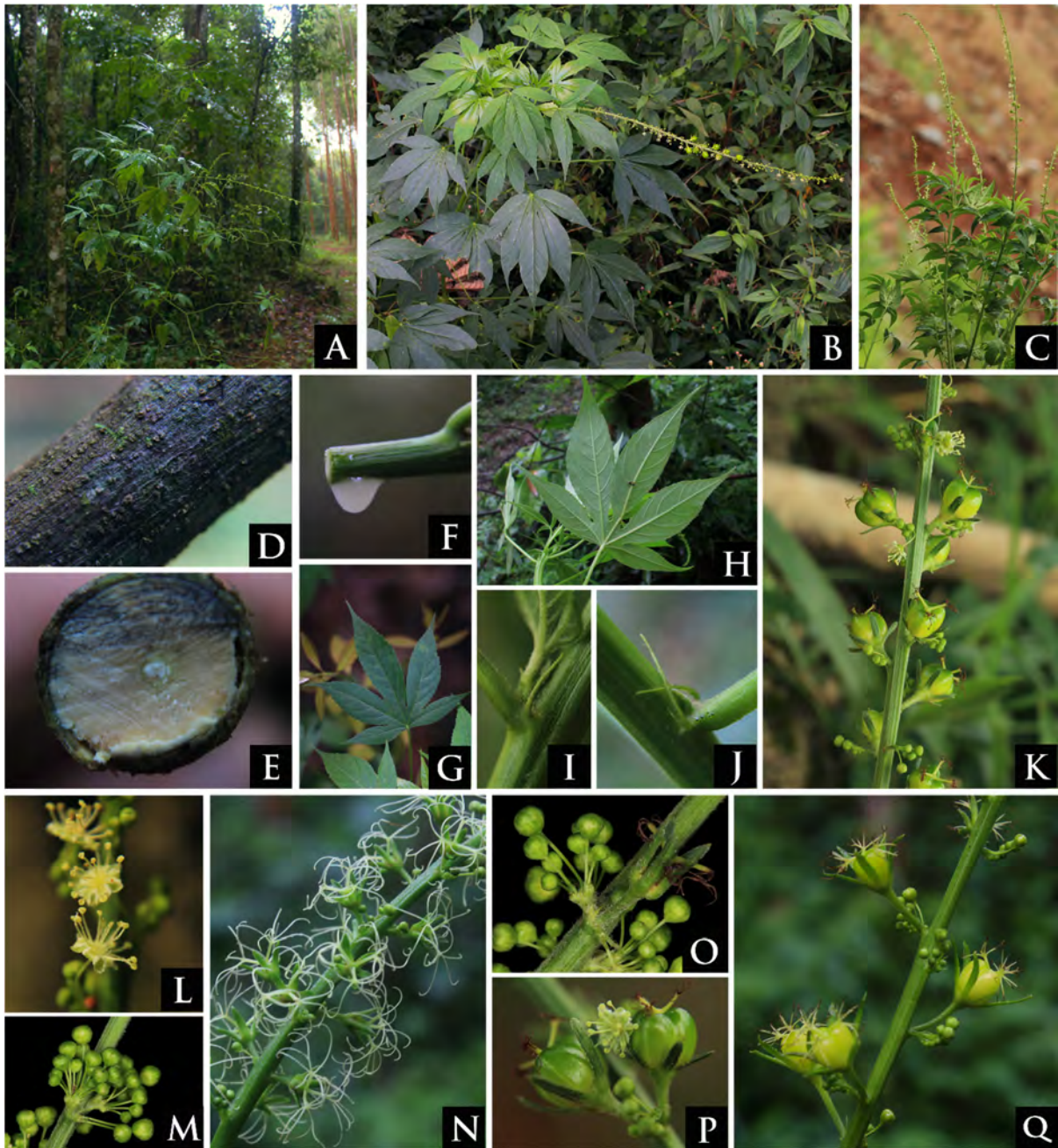


Minas Gerais. *Astraea manihot* is distinguished from *A. paulina* by the length of the pedicels of pistillate flowers (3–5 mm vs. 0.5–2 mm in *A. paulina*), number of pistillate flowers per cymule (6–8[–10] in *A. manihot* vs. 2–5 in *A. paulina*) and usually 5-partite leaves since *A. paulina* has usually 3-partite leaves. But it is not uncommon to observe individuals of *A. manihot* with 3-partite leaves, while rare states in *A. paulina* are entire or 2- or 5-partite. Besides length of pistillate flower pedicel and number of staminate flowers per cymule, indumentum of young portion of branches may help distinguishing *A. manihot* (pilose to densely pubescent) from *A. comosa* (tomentose). Besides, *A. comosa* has usually thicker leaves (with a consistency between chartaceous and coriaceous).

Contrarily to *Astraea manihot*, *A. jatropa* (as *Croton jatropa*) was considered a species distinct from *C. lobatus* by Müller Argoviensis (1866), although the author compared it with *C. lobatus* var. *manihot*. *Astraea jatropa* was described by Müller Argoviensis as having predominantly 3-partite leaves (rarely 5-partite), versus predominantly 5-partite and rarely 3-partite in *C. lobatus* var. *manihot*, but the diagnostic characteristic would be the short petiolate leaves of *A. jatropa* (4–10 times shorter than the leaf blade) against the long petiolate leaves of *A. manihot* (almost the same length or longer than the leaf blade). However, this differentiation does not hold in our morphological analysis, based on approximately 250 specimens, but is clear when comparing type specimens seen by Müller Argoviensis. Also, Müller Argoviensis indicates that pistillate flowers do not have a distinctive pedicel (i.e., shortly pedicellate or subsessile), but we could observe flowers with pedicels with up to 3 mm long in one of the syntypes of *A. jatropa* (H.A. Weddell 778, at P00634933!), while other types specimens do not show this distinctive pedicel due to the early development stage of the pistillate flowers, whose styles are not yet spread.

Both earliest names for *Astraea jatropa* and *A. manihot* were described in the same work (Müller Argoviensis 1866) and therefore none of them has priority. Therefore, although *Croton jatropa* was early combined in *Astraea* by van Ee (2011), in this work we prefer to use the name *A. manihot*, which was more recently transferred to *Astraea* (Silva & Cordeiro 2017), once we consider its type specimens and protologue more suitable, since they reflect the predominantly 5-partite leaves and pistillate flowers with a distinctively long-pedicel when mature.

**Selected specimens examined:**—BRAZIL. **Minas Gerais:** Antônio Carlos, Instituto Missionário, 07 January 1972, L. Krieger 11446 (MBM, RB, SP); Barão de Cocais, unknown locality, 10 April 1990, M. Brandão 17221 (PAMG); Belo Horizonte, Serra do Curral, 28 December 1989, M. Brandão 17247 (PAMG); Belo Vale, Serra da Moeda, 12 July 2002, P.L. Viana 704 (BHCB); Brumadinho, Inhotim, 870 m, 20° 08' 21" S, 44° 14' 13" W, 22 January 2008, J.G. Oliveira 106 (BHCB, RB); Caeté, Serra da Piedade, km 1–5 on road to top of Serra, 1200–1700 m, 19° 55' 00" S, 43° 45' 00" W, 02 February 1982, L.R. Landrum 4282 (MBM); Caiana, Serra da Caiana, 21 December 1989, C. Medeiros s.n. (SP 245742); Caldas, unknown locality, unknown date, A.F. Regnell 247 (BR[3], K, P, R, US[2]); Cambuquira, Matta da Empresa, 25 December 1935, H.L. Mello-Barreto 5062 (BHCB); Cantagalo, unknown locality, unknown date, A. Peckott 100 (BR); Carandaí, Pedra do Sino Hotel Fazenda, BR 040 km 6:



**Figure 22:** Morphological characters of *Astraea manihot*. A–C. habit. D. detail of the external surface of stem. E. stem in cross-section. F. latex exuding from branch. G. adaxial surface of a leaf. H. abaxial surface of a leaf. I–J. stipules. K. inflorescence. L–M. staminate flowers. N–O. pistillate flowers. P–Q. immature fruits. A, B, D–J, N and Q: populations from Poços de Caldas, MG (O.L.M. Silva 237); C, K, L, and P: population from Arujá, SP (O.L.M. Silva 236); M and O: population from Ouro Branco, MG (O.L.M. Silva 322). Photos: O.L.M. Silva.

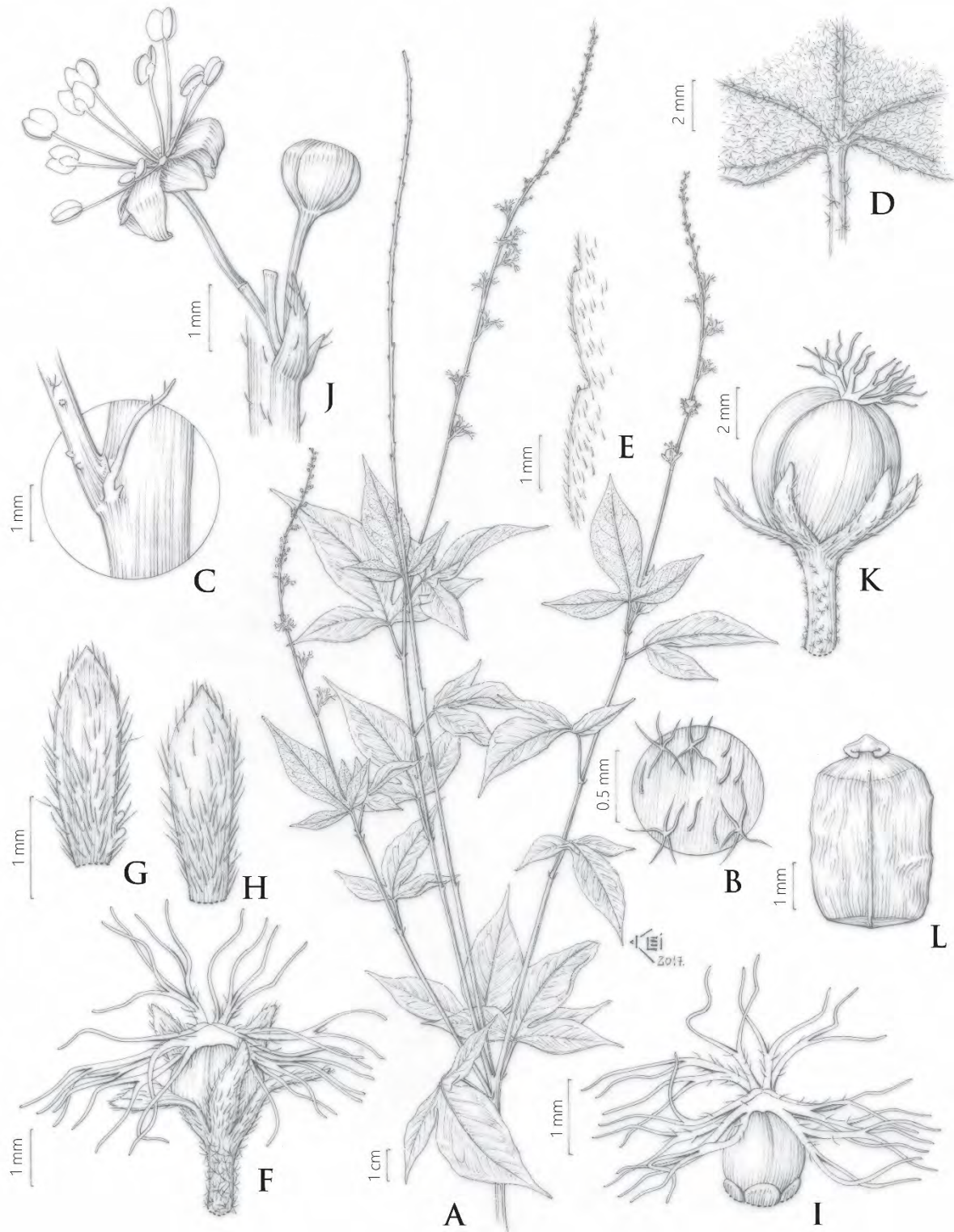
Trilha da Matinha, 1000–1200 m, 1 October 2005, *N.F.O. Mota 379* (BHCB); Caxambu, unknown locality, 21,9772° S, 44,9325° W, 3 May 2004, *H. Lorenzi 4819* (IAC); Congonhas do Norte, Serra Talhada. Fazenda Vereda do Cambota, alto da Serra do João Camilo, 6,8 km sudoeste da estrada Congonhas do Norte-Gouveia, entrada a 3,7 km noroeste de Congonhas do Norte, 18° 48' 39" S, 43° 45' 09" W, 19 January 2004, *R. Riina 1321* (SPF); Coronel Pacheco, Estação Experimental de Café, 10 November 1940, *E.P. Heringer 420* (RB, SP); Coronel Xavier Chaves, Estrada Lagoa Dourada - São João Del Rei (BR-383), cerca de 9,5 km após Lagoa Dourada, 1107 m, 20° 58' 43.30" S, 44° 07' 49.93" W, 3 December 2016, *O.L.M. Silva 323* (SP); Diamantina, Caminho para Costa Sena ca. 3 km antes do acesso à vila, 12 February 1998, *P.T. Sano 849* (SPF, WIS); Itabira, unknown locality, 1816–21, *A.F.C.P. Saint-Hilaire 2489* (P); Juíz de Fora, unknown locality, October 1969, *L. Krieger 7522* (ESA,

MBM); Lagoa Dourada, BR-383, 17 December 2012, *M. Sobral 15266* (ESA, SP); Madre de Deus de Minas, unknown locality, August 1896, *C. Rabelo 1615* (R); Marliéria, Parque Estadual do Rio Doce, 21 February 1995, *L.V. Costa s.n.* (BHCB 29496, MBM 256233); Matozinhos, Fazenda Cauaia - Lapa do Santo, 678 m, 19° 28' 58.4" S, 44° 01' 05" W, 23 October 2006, *J.C.F. Melo-Junior 563* (BHCB, SPF); Nazareno, Estrada para Represa do Camargo, 20 April 1986, *A. Souza 1465* (R); Ouro Branco, Estrada Ouro Preto - Ouro Branco (MG-129), cerca de 7,5 km antes de Ouro Branco, 1074 m, 20° 29' 51.31" S, 43° 37' 08.96" W, 3 December 2016, *O.L.M. Silva 322* (SP); Ouro Preto, Santo Antônio do Leite, 16 December 1982, *J.R. Pirani 321* (CEN, MAC, SP, SPF); Passa Quatro, Espigão do Retiro na Estação Florestal da Mantiqueira, October 1948, *J. Vidal s.n.* (R 158262); Poços de Caldas, Fazenda Chiqueirão, fragmento de mata preservado pelo Sr. Ernesto na beira da Rodovia Poços de Caldas - Águas da Prata, próximo ao trevo da Fazenda Chiqueirão, 1253 m, 21° 48' 29.26" S, 46° 39' 25.43" W, 14 January 2016, *O.L.M. Silva 237* (SP); Rio Acima, Rio do Peixe Bacia do Córrego Fazenda Velha, 825–1050 m, 20° 09' 23" S, 43° 49' 37" W, 25 March 2010, *S.G. Rezende 4107* (BHCB); Rio Preto, Serra do Funil, 11 September 2004, *C.N. Matozinhos 68* (CESJ, R); Sabará, Caieira - Cachoeira do Cambo, 13 February 1981, *J. Badini s.n.* (OUPR 4509); Santa Luzia, Fazenda da Chicaca, 20 November 1945, *V. Assis 92* (SP); Santana do Paraíso, unknown locality, 236 m, 19°24.40' S, 42°31.43' W, 23 December 2011, *M. Sobral 14570* (RB, SP); São João del-Rei, unknown locality, 1887, *W. Belle 153* (R); São João Nepomuceno, Serra dos Núcleos, 20 February 2003, *A.S.M. Valente 290* (ESA, MBM, SPF); Sapucaí-Mirim, Acampamento Nosso Recanto NR2, trilha da mata, 22° 50' 16" S, 45° 46' 52" W, 03 January 2003, *M.C.E. Amaral 04/2003* (UEC, WIS); Tiradentes, unknown locality, 8 November 1952, *A.P. Duarte 3767* (RB); Vespasiano, unknown locality, November 1915, *F.C. Hoehne 6522* (R); Viçosa, Agricultural college grounds. Hill south of College, 30 December 1929, *Y. Mexia 4187* (BM, F, G, K, P, US). **Paraná:** Antonina, Rio Faisqueira, Ilha dos Ratos Brancos, 06 August 1958, *G. Hatschbach 4984* (MBM, US); Balsa Nova, unknown locality, 12 October 1999, *A. Dunaiki Jr. 1388* (MBM); Bocaiúva do Sul, Tunas (ex Pedra Preta), 24 February 1958, *G. Hatschbach 4403* (MBM[2], PACA, US); Campina Grande do Sul, Estrada Quatro Barras a Campo Grande, 14 December 1961, *G. Hatschbach 8648* (MBM, UFP); Campo Largo, Caverna do Pinheirinho, 13 October 1996, *G. Tiepolo 550* (MBM); Cerro Azul, Estrela, 22 July 1970, *G. Hatschbach 24516* (K, MBM[2], NY, US); Itaperuçu, Rio Açungui, Jacaré, 07 December 1995, *J. Cordeiro 1258* (BHCB, MBM, MEXU, UB); Rio Branco do Sul, Coloninha, 31 December 2001, *A. Dunaiki Jr. 1775* (MBM). **Rio de Janeiro:** Rio de Janeiro, Fazenda da Rocinha, February 1937, *C.V. Freire 752* (R). **Santa Catarina:** Rio d'Oeste, Sumidor, 15 March 2011, *A. Korte 3876* (RB). **São Paulo:** Alumínio, unknown locality, 680 m, 3 December 1998, *A.M.G.A. Tozzi 313* (SP, UEC); Arujá, Próximo ao trevo do Rodoanel, no Jardim Emília, 808 m, 23° 25' 04.04" S, 46° 21' 44.76" W, 20 September 2015, *O.L.M. Silva 236* (SP); Campo Limpo Paulista, Estância Figueira Branca, 6 August 1977, *H. Makino s.n.* (SP 146648, UEC 4658, UEC 111065); Capão Bonito, Estação Experimental, 7 Km ao sul de Capão Bonito, 18 October 1966, *J.R. Mattos 13935* (SP); Franco da Rocha, Parque Estadual do Juquery. Caminho para trilha do Ovo da Pata, 797 m, 23° 21' 29.11" S, 46° 41' 58.97" W, 12 June 2015, *O.L.M. Silva 233* (SP); Guaratinguetá, unknown locality, unknown date, *C.F.P. von Martius s.n.* (M 233649); Jundiá, unknown locality, 04 April 1915, *A.C. Brade 7337* (SP); Pirassununga, unknown locality, 20 August 1997, *B.G. Fina 57* (HRCB); Santo Antonio do Pinhal, Início do Roteiro Turístico das Flores, na subida cerca de 100 m antes do início do trecho em estrada de terra, 1074 m, 22° 49' 19.69" S, 45° 40' 00.56" W, 11 January 2017, *O.L.M. Silva 328* (SP); São José dos Campos, unknown locality, 23 March 1909, *A. Loefgren 263* (RB); São Paulo, Eucaliptal no Condomínio Quintas da Cidade, 758 m, 23° 26' 85" S, 47° 38' 22" W, 5 October 2012, *R.J. Almeida-Scabbia 713* (SP). Unknown locality, unknown date, *F. Sellow s.n.* (BR00583982, K1210198, P00634915, TUB009126).

9. *Astraea paulina* Didrichsen (1857: 138). *Croton lobatus* var. *paulinus* (Didr.) Müller Argoviensis (1866: 667). *Croton paulinus* (Didr.) Müller Argoviensis (1873: 236). *Oxydectes paulina* (Didr.) Kuntze (1891: 613). Type:—BRAZIL. São Paulo: Itu, February 1834, *N. T. Lund s.n.* (holotype C, isotype G00312455!). Figs. 23–25.
- Astraea comantha* (S.Moore) Caruzo in Caruzo *et al.* (2014: 127). *Croton comanthus* Moore (1895: 460). Lectotype (designated here):—BRAZIL. Mato Grosso: between Santa Cruz and Villa Maria, December 1891, *S.L. Moore 1022* (BM000947396!, isotypes B+ [photo F5075! and NY5075!], G!, K00574176!, NY00246531 [photo!], P00634927!, R000006534!), *syn.nov.*
- Astraea douradensis* (Steyerm.) Caruzo in Caruzo *et al.* (2014: 217). *Croton douradensis* Steyermark (1958: 4). Type:—BRAZIL. Goiás: in gallery forest along stream 17 km east of Formoso, region of the southern Serra Dourada, at 48° 40' W, 13° 40' S", 19 May 1956, *E.Y. Dawson 14973* (holotype R000104976!, isotypes F60066 [photo!], RSA0002661 [photo!]).
- Astraea gardneri* (Müll.Arg.) Caruzo in Caruzo *et al.* (2014: 217). *Croton gardneri* Müller Argoviensis (1865: 135). *Croton gardneri* var. *cordatus* Müller Argoviensis (1865: 135). *Oxydectes gardneri* (Müll.Arg.) Kuntze (1891: 611). Lectotype (designated by Caruzo *et al.* 2014):—BRAZIL. Ceará: Serra do Araripe, September 1838, *G. Gardner 1839* (K00186088!, isolectotypes B+ (photo F5101!, G5101!, NY5101! and NY10796!), BM [on 2 sheets!], F875666 [photo!], G-DC00312463!, G00434481!, G!, K00186087!, L234368 [photo!], NY00246541 [photo!], NY00246542 [photo!], P00634930!, P00634931!, S-R-10516 [photo!], US00109563 [photo!], W [on 2 sheets {photo!}], *syn.nov.*

**Perennial shrubs**, phanerophytes, up to 2 m high, with erect branches, without a well-developed (xylopodiferous) underground system, branches pilose to pubescent, with mostly stellate trichomes, sometimes also with few short simple or stellate-porrect trichomes. **Leaves** entire or (2–)3(–5)-partite, entire leaves ovate, (2–)2.5–8(–13) x 1–4(–6) cm, partite leaves with medium lobe elliptic, oblong or ovate, (2–)3–8(–15) x (0.5–)2–4.5(–5.5) cm, and lateral lobes elliptic or oblong, (0.5–)2–6(–10) x (0.3–)0.5–3(–4.5) cm, chartaceous, apex attenuate to long attenuate, base rounded, cordate, subcordate, truncate or obtuse, margin crenate or serrate, with conspicuous teeth, not cartilaginous, ciliate, with simple or stellate trichomes, adaxial surface pilose, pubescent or with only a few scattered trichomes, more dense at the base and along the veins, with short (< 0.5 mm) simple or stellate trichomes, abaxial surface sparsely to densely pubescent or tomentose, more dense near the base and along the veins, with mostly stellate, sometimes with few scattered stellate-porrect, or short (< 0.5 mm) simple trichomes, venation camptodromous (when entire) or actinodromous (when partite); petioles (0.2)–0.5–7(–10) cm long, pilose to densely pubescent, more dense near the apex and the base, with short (< 0.5 mm) simple or stellate and scattered stellate-porrect trichomes; stipules subulate, entire or 3(–5)-lobed, subulate, medium lobe up to 3(–5) mm long and lateral lobes up to 1 mm long, pilose or pubescent, with stellate or short (< 0.5 mm) simple trichomes. **Thyrse** 8–20(–35) cm long, rachis pilose to pubescent, with mostly stellate trichomes, but also with scattered short (< 0.5 mm) simple trichomes; basal cymules with 3–10(–15) pistillate flowers, accompanied by 2–5 staminate flowers; distal cymules with 2–5 staminate flowers; bracts triangular to subulate, up to 2 mm long, glabrous to pubescent, generally more dense at the base, with





**Figure 23:** Line drawing of *Astraea paulina* A. flowering branch, B. detail of indumentum of younger portion of stems, C. detail of stipules, D. abaxial surface of leaf base, E. detail of leaf margin, F. pistillate flower, G. calyx lobe of a pistillate flower – internal face, H. calyx lobe of a pistillate flower – external face, I. gynoeceum and floral nectaries (calyx removed), J. staminate cymules with one mature flower, K. immature fruit, L. seed – ventral face. Illustration by Klei Sousa, based on O.L.M. Silva 214 (SP).

stellate and (< 0.5 mm) simple trichomes; **Staminate flowers** with pedicel up to 3(–5) long, glabrous; calyx glabrous or pilose, with 1–2 short (< 0.5 mm) simple trichomes on each lobe. **Pistillate flowers** with pedicels 0.5–2 mm, up to 6 mm in fruit, pubescent or tomentose, with stellate and stellate-porrect trichomes, calyx lobes 5–6, sometimes with one lobe poorly developed and narrower than the others, lobes oblong, elliptic or slightly ovate or obovate, 2–4 mm, up to 6 mm in fruit and 1–1.5 mm wide, pilose, pubescent or tomentose on the external face, with stellate, stellate-porrect or short (< 0.5 mm) simple trichomes, margin entire, not cartilaginous, ciliate with short (< 0.5 mm) simple or stellate trichomes, apex acute; ovary 1–1.5 x 1–1.5 mm, glabrous, pilose or pubescent, with short (< 0.5 mm) simple or stellate trichomes. **Fruits** lustrous, 5–5.5(–6) x 5–5.5(–6) cm, glabrous to pilose, with short (< 0.5 mm) simple or stellate trichomes; seeds tetragonal in cross section, 4–5 x 2.5–3 mm, caruncle ca. 0.5 x 1.5 mm.

**Nomenclatural notes:**—*Astraea comantha*, *A. douradensis* and *A. gardneri* had their lectotypes designated when transferred to *Astraea* by Caruzo et al. (2014). However, in the case of *A. comantha*, Caruzo et al. (2014) called the specimen at BM as holotype, although no herbarium is mentioned in the protologue of *Croton comanthus* (Moore 1895). Following the International Code of Nomenclature for algae, fungi and plants (McNeill et al. 2012) and Prado et al. (2015), this cannot be considered an inadvertent lectotypification as this was published after 1 January 2001 (Art. 9.19). Therefore, the lectotype for this name is here designated, and a specimen found in G is added to the list of isolectotypes. We also added more isolectotypes found in G and W for *A. gardneri*.

**Etymology and vernacular names:**—the epithet *paulina* is a reference to the type locality (São Paulo, southeastern Brazil). Among its synonyms, *douradensis* is a reference to the type locality, Serra Dourada, at the limits of the states of Bahia, Goiás and Tocantins in central Brazil; *gardneri* is in honor to G. Gardner, a British botanist and explorer who made important collections in Brazil; and, finally, *comantha*, is a junction of *coma* (a reference to the dense trichomes of a structure) and *anthos* (flower), which may be interpreted as a reference to the dense indumentum of pistillate calyx. The only vernacular name found for this species is *mamoninha* (Portuguese).

**Geographical distribution:**—SOUTHERN AMERICA. *Brazil*: Brazil North (BZN-PA, BZN-TO), Brazil Northeast (BZE-AL, BZE-BA, BZE-CE, BZE-MA, BZE-PE), Brazil Southeast (BZL-MG, BZL-SP), Brazil West-central (BZC-DF, BZC-GO, BZC-MT); *Southern South America*: Paraguay (PAR); *Western South America*: Bolivia (BOL).

*Astraea paulina* is widespread in Brazil, reaching also eastern Bolivia and Paraguay (Fig. 24). In Bolivia, it is only known in the Chiquitania region, while in Paraguay there is one single specimen collected by E. Hassler by the end of the 19<sup>th</sup> century in Maracajú Range. In Brazil, it is not recorded only in southern region, but there are very few occurrences in the northern region, while most specimens are from Goiás and Bahia. This species is mostly found along cerrado domain and seasonally dry tropical forests, where it grows mainly in forest



Figure 24: Geographical distribution of *Astraea paulina*.

edges, gallery forests and rocky grasslands (*campos rupestres*). Elevation varies from around 300 to 1000 meters above sea level, reaching around 100 meters above sea level in Pará and Goiás, and up to 1,500 meters above sea level in the rocky grasslands from Espinhaço Range in Bahia.

**Phenology:**— Flowering and fruiting were recorded throughout the year, usually at the same time.

**Conservation status:**—the species has an area of occupancy of 608,000 km<sup>2</sup>, with many known locations. However, these locations are subject to continuing decline in area and quality of habitat due to anthropic pressure. Therefore, according to IUCN (2012) guidelines, *Astraea paulina* is here classified as Near Threatened (NT) once it is likely to qualify for a threatened category in near future, but our present evaluation neither qualify it for Critically Endangered, nor Endangered or Vulnerable.



**Taxonomic comments:**— In this work we recognize *Astraea paulina* as a distinct species rather than a synonym of *A. lobata* as proposed by Caruzo & Cordeiro (2007). Both species are somewhat plastic in characters such as type of trichomes and indumentum of several structures but may distinguished mainly by habit (shrubby in *A. paulina* [Fig. 25A] vs. herbaceous in *A. lobata* [Fig. 16A]) and fruits (lustrous in *A. paulina* [Fig. 25R–T] and opaque in *A. lobata* [Fig. 16G–J]). Also, while *A. paulina* is widely distributed along the diagonal of dry areas of South America, occurring in habitats such as rocky grasslands (*campos rupestres*), seasonally dry forests or gallery forests along Cerrado domain (Fig. 24), *A. lobata* is found from Mexico to southern Brazil, but more commonly on western South America (see Fig. 15) and is a weedy species, occurring mainly on disturbed areas.

In this work we recognized *Astraea comantha*, *A. douradensis* and *A. gardneri* as synonyms of *A. paulina*. In the case of *A. douradensis*, the unique morphological features of this species were identified as malformations resultant of infestation by phytoplasmas (Silva et al. 2017; see also “Infestation by phytoplasma” subsection within Taxonomy section of this work). *Astraea gardneri* is mainly distinguished, according to Müller Argoviensis (1873), by the relative length of petioles and leaves (3–4 times shorter than leaf blade in *A. gardneri* and almost equal or, in young branches, shorter than leaf blade in *A. paulina*) and leaf margin (strongly crenate in *A. gardneri* and inconspicuously denticulate in *A. paulina*). Also, examination of type collections of these species, demonstrate that *A. gardneri* have both entire and (2–)3-partite, while *A. paulina* have predominantly 3-partite leaves. However, the analysis of more than 750 herbarium specimens, allied to fieldwork in Brazil and Bolivia, revealed much overlapping in these features. Specimens from southern Ceará, the type locality of *A. gardneri*, were found with only 3-partite leaves (as *B.M.T. Walter 6581*), while individuals of *A. paulina* from central Brazil may present only entire (U.G. Fernandes 247), both entire and partite (U.G. Fernandes 246) or only partite (U.G. Fernandes 248) leaves within a same population. Regarding leaf margin, *A. paulina* may present crenate to strongly serrate margin and therefore also overlaps with *A. gardneri*. Specimens analyzes in this work also showed variation in petiole length that could not support the distinction between these two species.

Moore (1895) distinguished *Astraea comantha* (as *Croton comanthus*), from *A. gardneri* by petiole length, number of stamens, size of calyx lobes in pistillate flowers and style ramification. As mentioned above, petiole length is variable within *A. paulina* and therefore does not represent a useful character to recognize species. Number of stamens varies from 11 to 15 in *Astraea* (see Morphology section), but as this variation is usually observed within species, we do not treat a discrete variation as the one presented by Moore (1895) as strong enough to sustain *A. comantha* as a different species. The same applies to style ramification, since 6-fid are within the variation range observed within some species in *Astraea* (4–8-fid styles) as in *A. paulina*, and calyx lobes length in pistillate flowers, with the length in *A. comantha* overlapping with *A. paulina*.

*Astraea paulina* may be misidentified with many other *Astraea* due to its wide distribution range and lack of a unique feature that could distinguish it from all other species. The shrubby habit, allied to the occurrence

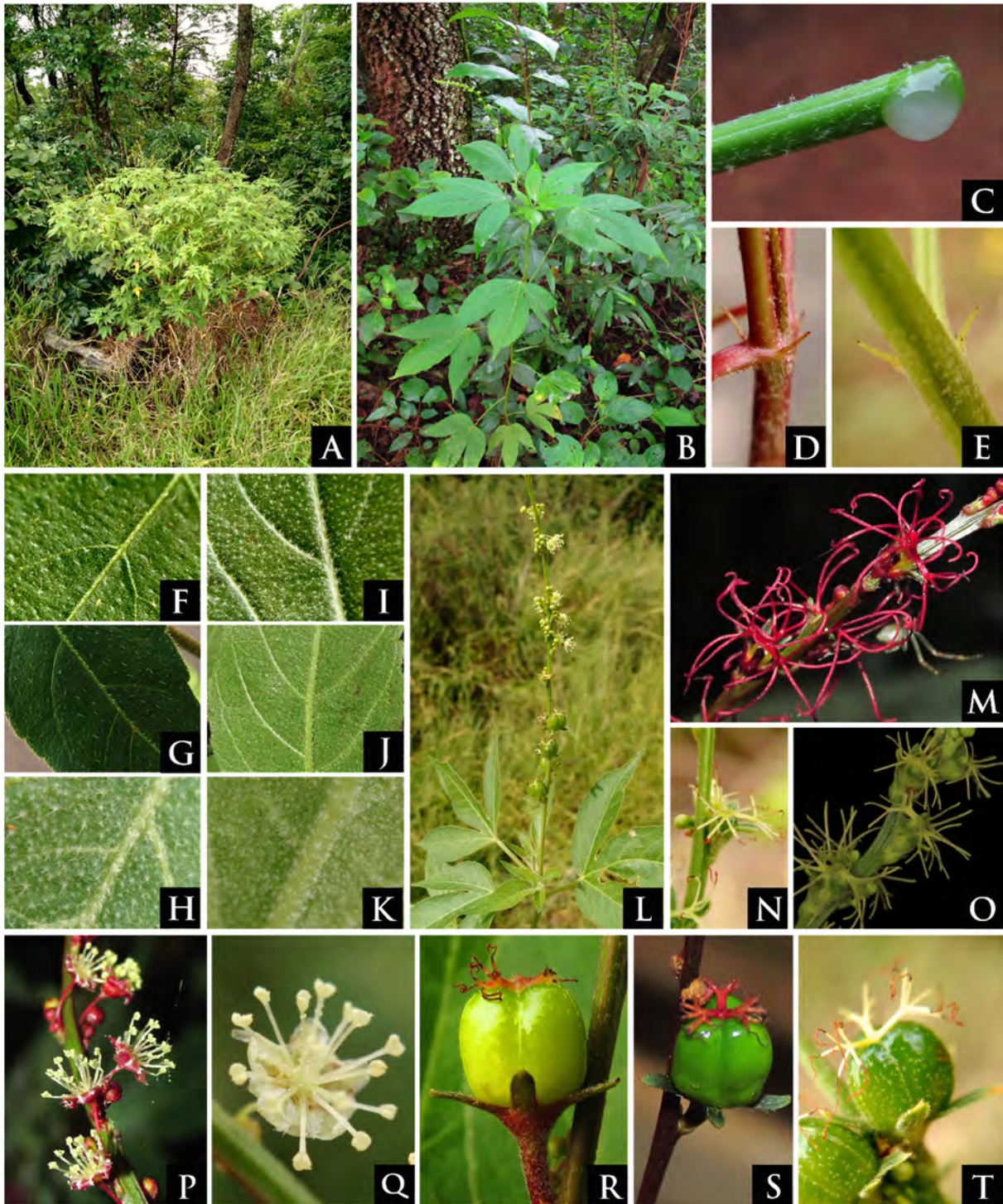
in other habitats rather than disturbed environments distinguish *A. paulina* from *A. lobata*, *A. surinamensis* and *A. trilobata*.

Among the shrubby species of *Astraea*, *A. paulina* may be distinguished from *A. manihot* by its entire or (2–)3-partite leaves and sessile or subsessile flowers (vs. [3–]5-partite leaves and long-pedicellate [3–5 mm long] pistillate flowers in *A. manihot*), and from *A. comosa* and *A. subcomosa* by its pubescent young portion of branches (vs. tomentose in *A. comosa* and *A. subcomosa*). The unique indumentum of pistillate calyx of *A. digitata* formed by long (> 1 mm) simple trichomes distinguishes it from *A. paulina* (with short [< 0.5 mm long] simple trichomes).

*Astraea paulina* may be distinguished from *A. klotzschii* and *A. macrourea* by the habitat, once the latter two are mostly restricted to seashore vegetation, where *A. paulina* is not found. However, *A. klotzschii* is also found in rocky grasslands of central Bahia and may be distinguished from *A. paulina* by its mostly entire leaves with abaxial surface bearing simple or no trichomes (vs. mostly 3-partite leaves with stellate trichomes on the abaxial surface in *A. paulina*). *Astraea praetervisa* is also restricted to seashore vegetation of southern Bahia, and also may be distinguished from *A. paulina* by its unique glanduliform stipules (vs. subulate in *A. paulina*).

*Astraea gracilis* is morphologically the closest species to *A. paulina*. The differentiation between these species is supported by leaf consistency (chartaceous in *A. paulina* vs. membranaceous in *A. gracilis*) and habitat: *A. gracilis* is mostly found in the Atlantic Forest domain (in moist forest edges and rocky outcrops), while *A. paulina* in Cerrado (in gallery forests or rocky grasslands). Also, calyx length of pistillate flowers may be useful (not surpassing 6 mm long in *A. paulina* and sometimes surpassing 10 mm in fruit in *A. gracilis*). However, both species are also found in seasonally dry forests, and, in this scenario, they may be distinguished by indumentum of abaxial surface of leaves (composed by mostly simple trichomes in *A. gracilis* [except for the stellate trichomes near the base] and by mostly stellate trichomes in *A. paulina*).

**Selected specimens examined:**—BOLIVIA. **Santa Cruz. Chiquitos:** Santiago de Chiquitos, 2 km SW of Santiago de Chiquitos, 650 m, 18° 21' 00" S, 59° 38' 00" W, 22 November 1989, *M. Nee 37844* (F, K, MEXU, NY, U, US, WIS). BRAZIL. **Alagoas:** Chã Preta, Serra Lisa, 16 October 2010, *Chagas-Mota 9033* (MAC); Quebrangulo, Reserva Biológica Federal da Pedra Talhada, 570 m, 9,254676° S, 36,404983° W, 28 April 2014, *L. Nusbaumer 3980* (G, JPB). **Bahia:** Abaíra, Estrada Catolés-Inúbia, 13 km de Catolés, 1080 m, 10 March 1992, *B.L. Stannard H51838* (HUEFS, K, NY, SP, SPF); Água Quente, Pico das Almas. Vertente oeste. Entre Paramirim das Crioulas e a face NNW do pico, 1140 m, 13° 31' 00" S, 42° 00' 00" W, 16 December 1988, *R.M. Harley 27194* (CEPEC, K, NY, SP, SPF); Andaraí, Slope with large sandstone rocks above R. Paraguaçu, 400 m, 12° 50' 00" S, 41° 19' 00" W, 24 January 1980, *R.M. Harley 20545* (CEPEC, K); Bonito, Estrada Bonito-Utinga, ca. 5km da cidade, 11 November 1998, *D.S. Carneiro 62* (CEPEC, HUEFS, SP); Itaberaba, ARIE Serra do Orobó. Serra da Gameleira, 540–600 m, 12° 23' 16" S, 40° 32' 13" W, 21 September 2005, *D. Cardoso 801* (HUEFS, NY, SP); Itaeté, Chapadinha, 12° 33' 01" S, 41° 23' 33" W, 21 February 2004, *R. Funch 148* (HUEFS); Jacobina, Antera do Bairro dos Índios, 840 m, 11° 12' 42" S, 40° 30' 22" W, 5 September 1999, *E. Melo 2963* (HUEFS, HUESC); Lençóis, Arredores da cidade, próximo à Academia de



**Figure 25:** Morphological characters of *Astraea paulina*. **A–B.** habit. **C.** latex exsudating from branch. **D–E.** stipules. **F–H.** detail of the indumentum of adaxial surface. **I–K.** detail of the indumentum of abaxial surface. **L.** inflorescence. **M–O.** pistillate flowers. **P–Q.** staminate flowers. **R–T.** immature fruits. A, E, H, K, L, N, Q, T; population from Santiago de Chiquitos, Bolivia; B, C, R: population from Alto Paraíso de Goiás, GO (O.L.M. Silva 112, 113); D, F–G, I–J : population from Botucatu, SP (O.L.M. Silva 213); M, P, S : population from Mucugê, BA (O.L.M. Silva 185); O: population from Colinas do Sul, GO (O.L.M. Silva 335). Photos: O.L.M. Silva

Saúde, 375 m, 12° 33' 40.22" S, 41° 23' 36.36" W, 25 August 2014, O.L.M. Silva 184 (SP); Miguel Calmon, Serra das Sete Passagens, Parque Estadual das Setes Passagens, próximo à sede do parque, Vale das pedras, 820 m, 11° 24' 27" S, 40° 33' 16" W, 5 April 2001, H.P. Bautista 3029 (CEPEC, HRB, HUEFS); Mirangaba, A 3 Km de Mirangaba, 10° 40' 00" S, 40° 37'

00" W, 1 September 1981, *L.M.C. Gonçalves 167* (CEPEC, HRB, RB); Morro do Chapéu, Estrada do Feijão, 28 November 1980, *A. Furlan in CFCR 273* (K, SP, SPF); Mucugê, Entrada da cidade, margem da rodovia ao lado direito, 992 m, 13° 00' 11.60" S, 41° 22' 01.78" W, 26 August 2014, *O.L.M. Silva 188* (SP); Nova Redenção, Peruco, Beira do Rio Paraguaçu, 330 m, 12° 46' 17" S, 41° 09' 58" W, 2 March 2003, *L.R. Senna 157* (HUEFS); Palmeiras, Serras dos Lençóis. Lower slopes of Morro do Pai Inácio, ca. 14.5 km. N.W. of Lençóis, just N. of the main Seabra-Itaberaba road, 700–1000 m, 12° 27' 00" S, 41° 28' 00" W, 27 May 1980, *R.M. Harley 22723* (CEPEC, K, NY, RB, U); Piatã, Cerrado na base do Morro de Três Morros, 1400 m, 13° 02' 00" S, 41° 53' 00" W, 19 January 2006, *A.A. Conceição 1679* (HUEFS, SP); Pindobaçu, Serra da Paciência, 1000 m, 10° 56' 36" S, 40° 24' 28" W, 10 April 2001, *T. Ribeiro 209* (ALCB, CEPEC, HRB, HUEFS, HUESC); Ribeirão do Largo, Ca. 23 km na estrada Itambé/Encruzilhada, 870 m, 15° 19' 39" S, 40° 45' 05" W, 14 August 2001, *A.M.V. Carvalho 6905* (ALCB, CEPEC, HRB, HUEFS, HUESC, NY, SP); Rio de Contas, Pico das Almas, NW do campo do Queiroz. Vertente leste. Campo e mata ao NW do Campo do Queiroz, 1500–1550 m, 13° 31' 00" S, 41° 58' 00" W, 26 November 1988, *R.M. Harley 26625* (CEPEC, F, K, MBM, NY, SP, SPF); Rio do Pires, Beira do Riacho da Forquilha, 1500 m, 13° 54' 00" S, 42° 29' 00" W, 24 July 1993, *W. Ganey 1943* (HUEFS, K, NY, SP); Rui Barbosa, Serra do Orobó, 814 m, 12° 18' 47" S, 40° 29' 01" W, 18 December 2004, *L.P. Queiroz 9926* (HUEFS, SP); Seabra, unknown locality, 4 December 1980, *N.L. Menezes in CFCR 384* (SPF, WIS); Senhor do Bonfim, Monte Santo (Alto do Cruzeiro), 903 m, 10° 31' 02" S, 40° 14' 55" W, 28 October 2005, *S.F. Conceição 302* (CEPEC, ESA, HUEFS); Umburanas, Serra do Curral Feio (localmente referida como Serra da Empreitada), entrando para W a cerca de 20 km S de Delfino na estrada para Umburanas, 1000–1200 m, 10° 22' 00" S, 41° 19' 00" W, 9 April 1999, *L.P. Queiroz 5179* (HUEFS, SP); Utinga, Remnants of mata seca 17 km S of Bonito, 850 m, 12° 06' 00" S, 41° 15' 00" W, 19 November 1986, *G.L. Webster 25769* (DAV). **Ceará:** Araripe, Cairiri, unknown date, *F.F. Allemão s.n.* (R 100549); Barbalha, Baixa do Cão. Floresta Nacional do Araripe, 947 m, 07° 18' 40" S, 39° 18' 15" W, 19 January 2012, *C.G. Crepaldi 20* (PEUFR); Crato, Estrada para o Granjeiro (club). Sítio Caiana. Arredores da cidade de Crato. Chapada do Araripe, 780 m, 07° 16' 30" S, 39° 26' 37" W, 21 January 2014, *B.M.T. Walter 6581* (CEN, EAC, RB, UB); Guaraciaba do Norte, Serra da Ibiapaba, Recanto São Benedito, 7 January 1942, *P. Bezerra s.n.* (EAC 478). **Distrito Federal:** Brasília, Fazenda Sucupira, 1100 m, 15° 52' 00" S, 48° 00' 00" W, 4 September 2000, *E.S.G. Guarino 399* (CEN, SP). **Goiás:** Alexania, Margem esquerda do rio Corumbá (próximo à ponte). Acesso secundário à Abadiânia, 820 m, 16° 12' 20" S, 48° 27' 07" W, 20 February 2003, *G. Pereira-Silva 7263* (CEN); Alto Paraíso de Goiás, Trilha para o Vale da Lua (Chapada dos Veadeiros), um pouco antes de chegar no estacionamento, 958 m, 14° 10' 53.94" S, 47° 47' 25.45" W, 26 January 2014, *O.L.M. Silva 112* (SP); Anápolis, Estrada de Goiânia a Anápolis, km 12, 26 November 1976, *G.J. Shepherd 3571* (MBM, NY, UEC); Cabeceiras, Serra do Rio Preto. 25 km E of Cabeceiras, ca. 4 km E of Minas gerais border, 19 November 1965, *H.S. Irwin 10535* (NY, R, UB); Cavalcante, RPPN Serra do Tombador, trilha da cachoeira, 776 m, 13° 38' 03" S, 47° 50' 34" W, 14 April 2013, *E. Barboza 3623* (MBM); Cocalzinho, Parque Estadual dos Pirineus. Área de cerrado perto do portal da Fazenda Capitão do Mato, em direção do morro, 1280 m, 15° 48' 40" S, 48° 48' 54" W, 10 December 2005, *P.G. Delprete 9402* (NY); Colinas do Sul, Estrada para a RPPN Cachoeira das Pedras Bonitas (Tingó), cerca de 2 km após a saída da GO-132, 467 m, 14° 11' 51.33" S, 48° 04' 28.45" W, 8 February 2017, *O.L.M. Silva 335* (CEN, SP, SPF); Corumbá de Goiás, Serra dos Pirineus. Ca. 12 km S of Corumbá de Goiás, 1000 m, 30 November 1965, *H.S. Irwin 10837* (F, G, P, R, SP, U, UB); Formoso, Serra do Morcego. Ca. 35 km. NE of Formosa. Córrego Estrema, 800 m, 22 April 1966, *H.S. Irwin 15281* (K, NY, R, UB); Goiânia, Campus da UFG. Bosque St. Hil., 6 March 1999, *J.A. Rizzo 10065* (UFG); Goianira, Margem esquerda da estrada que demanda a fazenda Louzandira, 16 May 1970, *J.A. Rizzo 5139* (UFG); Minaçu, Em frente ao viveiro antigo da UHE Serra da Mesa (5 Km da entrada N do canteiro de obras), 500 m, 9 December 1991, *B.M.T. Walter 868* (CEN, SP); Mossâmedes, Encostas da Serra Dourada. Estrada a Reserva Ecológica de Serra Dourada, 4 km da rodovia Goiás-Mossâmedes (GO 164), 785 m, 16° 05' 44" S, 50° 11' 07" W,

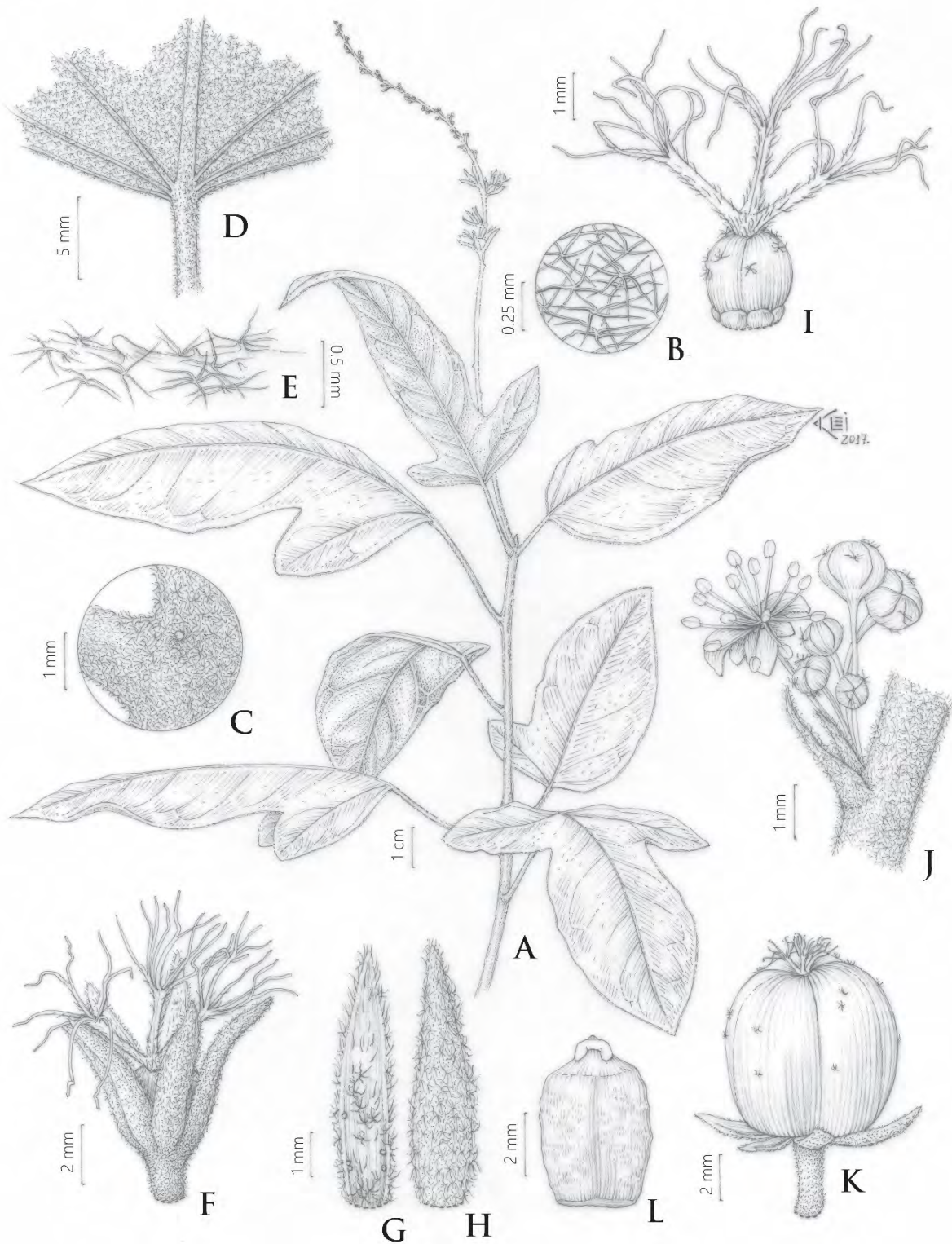
29 November 2003, *R. Mello-Silva 2235* (RB, SPF); Niquelândia, córrego afluente da margem esquerda do rio Acaba Saco; próximo ao encontro deste com o rio Maranhão, 440 m, 4 August 1992, *B.M.T. Walter 1824* (CEN, RB, SP); Pirenópolis, Serra dos Pireneus; 19,5 km do trevo de Anápolis e Goiânia em direção ao Parque. Mata descendo à esquerda na bifurcação após a antenna, 1200 m, 15° 47' 37" S, 48° 50' 13" W, 18 January 2005, *J. Paula-Souza 4255* (ESA, FUEL, RB, UB); Teresina de Goiás, Chapada dos Veadeiros. 7 km by road S of Terezina, 17 March 1973, *W.R. Anderson 7315* (F, K, UB, US); Uruaçu, Córrego Macaco. Ao Norte da cidade de Uruaçu (na direção do Rio Maranhão) para (Jeriaçu); Agral Dalur, 450 m, 9 February 1996, *B.M.T. Walter 3201* (CEN, R). **Maranhão:** Anajatuba, unknown locality, 26 January 1976, *B.G.S. Ribeiro s.n.* (HRB 12821); Carolina, Parque Nacional das Chapadas das Mesas, Complexo Turístico de Pedra Caída, próximo à cachoeira do Capelão, 7° 19' 65" S, 47° 26' 52" W, 24 March 2016, *O. Monteiro PA-MA-080* (MG). **Mato Grosso:** Chapada dos Guimarães, 5 km E of town of Chapada dos Guimarães on road to EMBRATAL, 720 m, 24 October 1973, *G.T. Prance 19369* (INPA, U); Nobres, Arredores do Lago Azul. Cerca de 42 km ENE (em linha reta) de Nobres, 14° 35' 00" S, 56° 12' 00" W, 24 May 1997, *V.C. Souza 17129* (ESA, SP); Novo Mundo, Parque Estadual Cristalino. Serra do Rochedo, limite sul do parque, acesso pela Fazenda AJJ, 435 m, 09° 41' 06.11" S, 55° 26' 32.4" W, 2 February 2008, *D. Sasaki 2144* (K, NY, SPF); Vila Bela da Santíssima Trindade, Fazenda Jatuarã, Rio Verde, 16 April 2012, *O.S. Ribas 8684* (MBM); 240 km N of Xavantina on Xavantina-São Felix road, 7 May 1968, *J.A. Ratter 1324* (E, K, NY, P, UB). **Minas Gerais:** Araxá, Barreiro, 10 February 1995, *A. Macedo 3158* (US); Barbacena, Entre Barbacena e Sitio, Unknown date, *A.F.M. Glaziou 11510* (P); Delfinópolis, Serra da Canastra, Trilha do Macaco, 924 m, 20° 25' 19" S, 46° 32' 46" W, 19 February 2011, *J.H. Kinoshita 11-198* (UEC); Paracatú, Ca 10 km S.E. of Paracatú, 675 m, 7 February 1970, *H.S. Irwin 26240* (E, MEXU, NY, RB, UB); São Sebastião do Paraíso, unknown locality, unknown date, *F.S.C. Teodoro 650* (RB); Uberlândia, Reservatório de Miranda, ca. de 20 km do centro de Uberlândia, 18 November 2004, *A.P.M. Santos 320* (ESA, HUFU, SP, SPF); Estrada Belo Horizonte-Uberaba km 758, 30 January 1981, *I. Cordeiro in CFCR 663* (R, SPF). **Pernambuco:** Bonito, Reserva Municipal de Bonito. Trilha da Mata, 1100 m, 21 May 1996, *L.F. Silva 229* (PEUFR); Brejão, Fazenda do Inst. Brasileiro do Café, 6 September 1986, *V.C. Andrade s.n.* (PEUFR 21949); Brejo da Madre de Deus, Fazenda Bituri. Trilha no interior da mata, 636 m, 08° 09' 00" S, 36° 22' 15" W, 28 March 1996, *M.B. Costa e Silva 312* (K, PEUFR); Garanhuns, Nascente do Rio, 07° 59' 39" S, 39° 34' 07" W, 6 November 2010, *M. Oliveira 5402* (IPA); Pesqueira, Serra do Ororobá, Fazenda São Francisco, 1082 m, 28 September 1995, *M. Correia 381* (UFP); Vicência, Eng. Jundiá, 30 July 1968, *D.A. Lima 68-5404* (IPA). **São Paulo:** Analândia, Parque Rawitscher. Fazenda Pedra Vermelha. Trilha da Cachoeira, 840 m, 22° 05' 48" S, 47° 45' 44" W, 23 May 2013, *D.O. Dinato 271* (HRCB); Botucatu, Caminho para a Igreja Santo Antonio no Distrito Rubião Júnior. Curva antes da subida final, logo após o portão, margem esquerda, 908 m, 22° 53' 36.70" S, 48° 29' 18.81" W, 30 January 2015, *O.L.M. Silva 213* (SP); Campinas, Instituto Agrônomo de Campinas (IAC). Mata da Fazenda Santa Elisa, 31 March 2004, *M.B.R. Caruzo 55* (IAC, SP, WIS); Corumbataí, Rodovia Washington Luiz, 22° 14' 52.8" S, 47° 43' 01.4" W, 20 September 1993, *K.D. Barreto 1462* (SP); Guaratinguetá, Fragmento 34 (TAV), 549 m, 22,77179° S, 45,22958° W, 15 April 2013, *V.C. Souza 35738* (ESA); Itirapina, Estação Experimental de Itirapina, February 1978, *E. Giannotti 8379* (UEC); Itú, Sur les bordes du Tietê, 10 November 1897, *A. Russel 129* (SP); Mogi Guaçu, Fazenda Campininha, 7 km NNW de Padua Sales, 17 November 1960, *J.R. Mattos 8512* (NY, SP, US); São Sebastião, Ilha de Alcatrazes, encosta voltada para o Porto dos Faroleiros, 11 December 1990, *L. Rossi 1073* (SP); Votorantim, Serra de São Francisco, Represa de Itupararanga, 6 March 1984, *V.F. Ferreira 3303* (R). **Tocantins:** Darcinópolis, Bacia do Araguaia, Sub-bacia: Ribeirão Corda, (A-15, área 1, pto 457), 287 m, 06° 38' 04" S, 47° 57' 31" W, 19 May 2010, *F.C.A. Oliveira 2325* (IBGE, SP); Goiatins, KAPEY - União das Aldeias Krahò. Próximo à casa de visitantes, 08° 27' 36" S, 47° 40' 38" W, 28 March 2002, *A.A. Santos 1023* (CEN); Mateiros, APA do Jalapão, Cachoeira da Velha, 314 m, 10° 16' 08.6" S, 46° 52' 50.7" W, 31 July 2010, *M.G. Caxambu 3126* (HCF); Ilha de Bananal, Santa Isabel, direção norte, "Prainha", 17 September 1960, *A.G.*



*Andrade 525* (R); **Pará:** Almeirim, Monte Dourado, Bloco Bananal, área 43, 15 May 1986, *M.J. Pires 1013* (INPA); Itaituba, Estrada Santarém-Cuiabá, BR 163, km 794, Serra do Cachimbo, Base Aérea, margem do rio Braço-Norte, afluente do Curuá, 09° 22' 00" S, 54° 54' 00" W, 26 April 1983, *I.L. Amaral 956* (K, NY, R, RB, UB, US); Marabá, Serra Norte (Carajás), N<sup>3</sup>, 17 March 1985, *R.S. Secco 480* (RB); Novo Progresso, Área da Aeronáutica (Campo do Provas Brigadeiro Veloso), serra do Cachimbo, margem do rio Braço Norte, próximo da usina antiga, 445 m, 09° 21' 45" S, 54° 54' 56" W, 3 August 2015, *L. Rossi 2503* (SP); Santarem, Serra Diamantina, 14 December 1966, *P. Cavalcante 1750* (MG); Serra de Piracana, 25 April 1909, *Pessoal do Museu 10384* (MG); Tucuruí, Approx. 25 km S of Tucuruí, just off old BR 422 at junction with old railroad bed, 03° 58' 00" S, 49° 38' 00" W, 30 October 1981, *D.C. Daly 1066* (HRB, INPA, NY, US). PARAGUAY. Unknwon locality, unknown date, *E. Hassler 5068* (BM, G, K, NY, P).

10. *Astraea praetervis* (Müll.Arg.) Berry in Berry *et al.* (2005: 1532). *Croton praetervis* Müller Argoviensis (1873: 234). *Oxydectes praetervis* (Müll.Arg.) Kuntze (1891: 613). Lectotype (designated here):—BRAZIL. Bahia: partie méridionale de la prov. de Bahia, 1840, *J.S. Blanchet 3155* (G434637 [on 2 sheets!], isoelectotypes F768716 [photo!], G!); remaining syntype:—BRAZIL. Bahia: partie méridionale de la prov. de Bahia, 1840, *J.S. Blanchet 3155A* (G00312462!, isosyntypes: B<sup>+</sup> [photo F!], G00434636!, P04830058!). Figs. 26–28.

**Perennial shrubs**, phanerophytes, up to 2 m high, with erect branches, without a well-developed (xylopodiferous) underground system, branches tomentose, with stellate trichomes. **Leaves** entire or 2–3-partite, entire leaves elliptic, oblong or widely-ovate, 6.5–10 x 2.5–5 cm, partite leaves with the medium lobe elliptic, (6.5–)9–15(–18) x (2.5–)4–6.5(–7.5) cm, and lateral lobes elliptic, (4–)5–12 x (2–)4–4.5(–6) cm, chartaceous, apex attenuate to long attenuate, base truncate to cordate on both entire and lobed leaves, margin serrate, with inconspicuous teeth, not cartilaginous, ciliate, with stellate trichomes, adaxial surface pilose, except for the densely pubescent primary veins, with stellate and stellate-porrect trichomes, abaxial surface tomentose, more dense near the base and along the veins, with stellate and stellate porrect trichomes, venation actinodromous; petioles (2–)4–10(–13) cm long, tomentose, with stellate and scattered stellate-porrect trichomes; stipules glanduliform, entire, diminute (up to 0.5 mm), glabrous. **Thyrse** 20–35(–55) cm long, rachis tomentose, with stellate trichomes; basal cymules with 5–10 pistillate flowers, accompanied by 4–5(–6) staminate flowers; distal cymules with 4–5(–6) staminate flowers; bracts triangular to subulate, 2–3 mm long, densely pubescent, with stellate trichomes; **Staminate flowers** with pedicel up to 3 long, glabrous; calyx pilose, with 1–2 stellate trichomes on each lobe. **Pistillate flowers** with pedicels 1–2 mm, up to 3 mm in fruit, tomentose, with stellate and stellate-porrect trichomes, calyx lobes 5–7, sometimes with one or two lobes poorly developed and smaller than the others, lobes narrow-oblong (to linear in fruit), 5–7 mm, up to 12 mm in fruit) and 1–1.5 mm wide, tomentose on the external face, with stellate trichomes, margin entire, not cartilaginous, ciliate, with stellate trichomes, apex acute; ovary 1.5–2 x 1.5–2 mm, pilose, with stellate trichomes.



**Figure 26:** Line drawing of *Astraea praetervisa* A. flowering branch, B. detail of indumentum of younger portion of stems, C. detail of stipules, D. abaxial surface of leaf base, E. detail of leaf margin, F. pistillate flower, G. calyx lobe of a pistillate flower – internal face, H. calyx lobe of a pistillate flower – external face, I. gynoeceum and floral nectaries (calyx removed), J. staminate cymules with one mature flower, K. immature fruit, L. seed – ventral face. Illustration by Klei Sousa, based on A-E S.C. *Santa'Anna 1123* (RB); F-J, L W. *Thomas 9709* (SP); and K A.M. *Carvalho 2005* (MBM).



**Fruits** lustrous, 8–10 x 8–10 cm, glabrous to glabrescent, with scarce stellate trichomes; seeds tetragonal in cross section, 5–5.5 x 3–4 mm, caruncle ca. 0.5 × 1.5 mm.

**Nomenclatural notes:**—Both syntypes of *Astraea praetervis* (*J.S. Blanchet 3155* and *3155A*) represent well the species, but *J.S. Blanchet 3155* was chosen for lectotypification since one of its duplicates, deposited at F, is the richest in reproductive structures. We elected the specimen at G as the lectotype because it is most likely to be the one analyzed by Müller Argoviensis when describing *Croton praetervis* in the treatment for Flora Brasiliensis (Müller Argoviensis 1873).

**Etymology and vernacular names:**—The epithet *praetervis* comes from Latin “*praeter*” (beyond) and “*visus*” (seen), and may be related to its type collections (*J.S. Blanchet 3155* and *3155A*), which were first linked to *Croton gardneri* var. *lanceolatus* in 1865 (including *J.B.E Pohl 3416* and *J.S. Blanchet 3155* and *3155A* as types), and later split into *C. subcomosus* (*J.B.E Pohl 3416*) and *C. praetervis* (*J.S. Blanchet 3155* and *3155A*). No vernacular name is recorded for this species.

**Geographical distribution:**—SOUTHERN AMERICA. *Brazil*: Brazil Northeast (BZE-BA).

*Astraea praetervis* is a micro-endemic species, found only in the region of Ilhéus municipality, in southern Bahia (Fig. 27). It is a very rare species, known for only seven collections. This species grows in seashore forests, in sandy soils, near the sea level.

**Phenology:**—The few specimens available were collected in October and February, and perhaps flowering and fruiting of this species may be restricted to the wet season.

**Conservation status:**—*Astraea praetervis* has an area of occupancy (AOO) of 12,000 km<sup>2</sup>, but its extent of occurrence (EOO) is only 57,93 km<sup>2</sup> and is only known for the region of the municipality of Ilhéus, in southern Bahia. Also, there is a strong and continuous declining of area extent and/or quality of the habitat where this species is found due anthropic pressure on seashore vegetation along Brazilian coastal region resulting from advance urban growth. Therefore, this species qualifies for Critically Endangered (B1ab[iii]).

**Taxonomic comments:**—*Astraea praetervis* is remarkable due to its glanduliform stipules (Fig. 26C) since all other species of the genus have deltoid to subulate stipule. However, *A. praetervis* may be misidentified as *A. comosa*, with which shares the well-developed indumentum with stellate trichomes. *Astraea comosa*, however, may be distinguished from *A. praetervis* by its ovate pistillate calyx lobes that are oblong to linear in *A. praetervis* (Figs. 26F–H and 28D–E).

Among the species found in coastal southern Bahia, *Astraea praetervis* may be distinguished from *A. surinamensis* by many features, such its mostly glabrous fruits, young portion of stems with stellate-porrect



Figure 27: Geographical distribution of *Astraea praetervis*.

trichomes bearing a central ray with less than 1 mm long (equal or slightly longer than the lateral rays; Fig. 26B) and calyx of pistillate flowers with stellate trichomes (Fig. 26F, H) on the outer surface (vs fruits pilose to pubescent, with long erect trichomes, young portion of stems with stellate-porrect trichomes bearing a central ray with 5 mm long or more and calyx of pistillate flowers with simple trichomes on the outer surface in *A. surinamensis*). The stellate trichomes of pistillate calyx also distinguishes *A. praetervis* from *A. digitata* and *A. gracilis*, which have simple trichomes on the calyx. *Astraea klotzschii* is also found in the seashore vegetation of southern Bahia, but collections of this species from this region may be distinguished from *A. praetervis* by its glabrous or pubescent calyx with simple trichomes, except for the ciliate margin.

**Selected specimens examined:**—BRAZIL. Bahia: Ilhéus, Estrada vicinal de Olivença a Buerarema, 6 km de Olivença, 12 February 1994, J.R. Pirani 2938 (K, MO, SP, SPF, WIS); *ibidem*, Km 35 na estrada Ilhéus/Serra Grande, 22 October 1983, A.M.V. Carvalho 2005 (ALCB, G[2], HUEFS, MBM); *ibidem*, Road from Olivença to Serra das Trempes, 6 km from Olivença,



**Figure 28:** Morphological characters of *Astraea praetervisa*. **A–B.** habit. **C.** leaves. **D.** pistillate flowers. **E.** immature and young fruits. A–E: population from Ilhéus, BA (S.C. Sant'Ana 1123). Photos: P.E. Berry.

14° 59' 00" S, 39° 03' 00" W, 3 February 1993, *W.W. Thomas* 9709 (CEPEC, DAV, MBM, NY, R, SP); *ibidem*, Rod. a 6,0 km de Olivença na estrada para Vila Brasil, 70 m, 14° 58' 39" S, 39° 02' 08" W, 19 February 2004, S.C. *Sant'Ana* 1123 (CEPEC, MICH, NY, RB[2]).

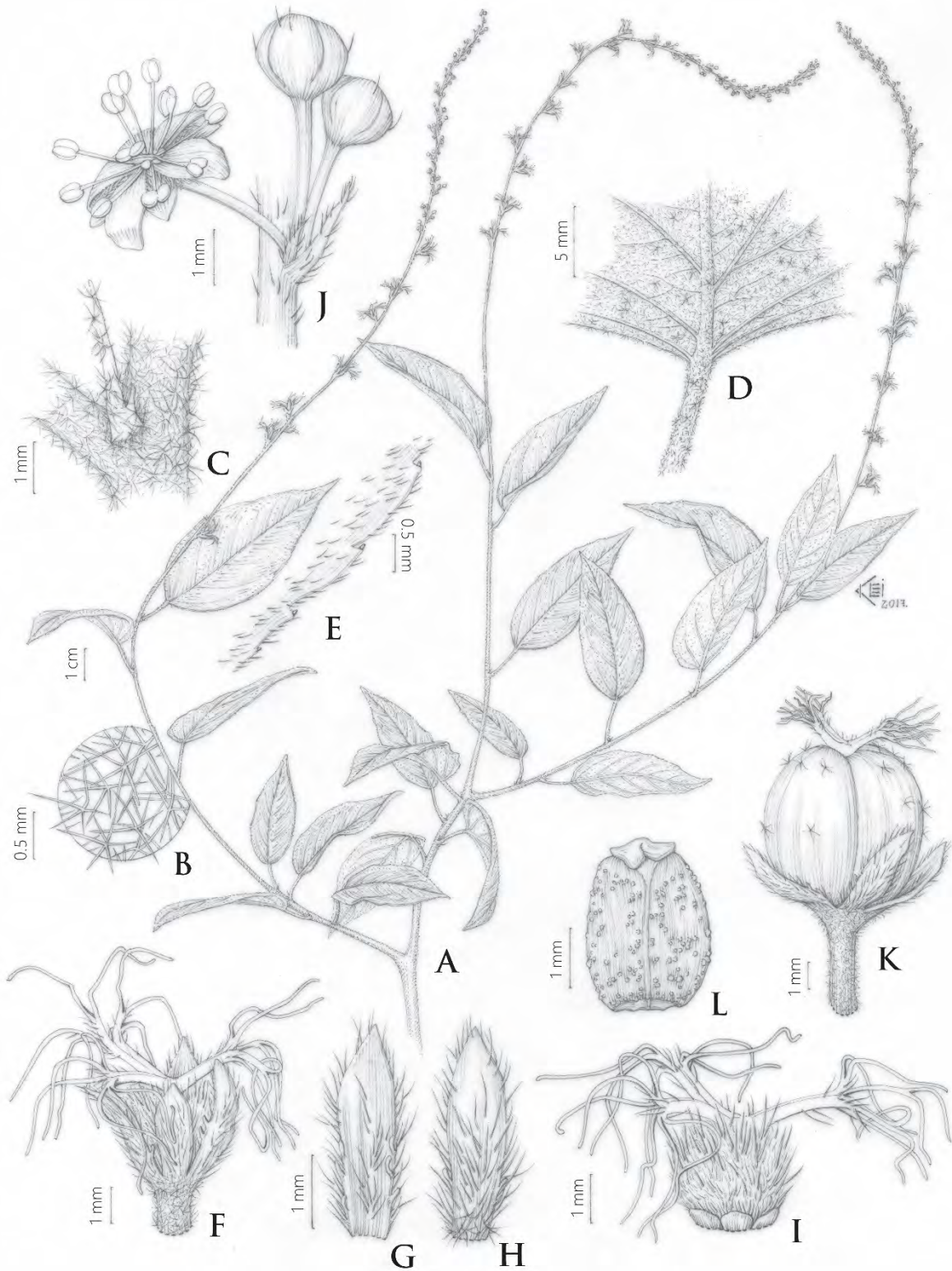
11. *Astraea subcomosa* (Müll.Arg.) Caruzo in Caruzo *et al.* (2014: 127). *Croton subcomosus* Müller Argoviensis (1873: 234). *Croton gardneri* var. *lanceolatus* Müller Argoviensis (1865: 135). *Oxydectes subcomosa* (Müll.Arg.) Kuntze (1891: 613). Lectotype (designated by Caruzo *et al.* [2014]):—BRAZIL. Minas Gerais: prope

José Gonzambres [= José Gonçalves], *J.B.E. Pohl 3416* (G00434679!, isolectotypes B† [photo F!], F771814 [fragment; photo!], W [on 2 sheets!]). Figs. 29–30.

**Perennial shrubs**, phanerophytes, up to 2 m high, with erect branches, without a well-developed (xylopodiferous) underground system, branches tomentose, with stellate and stellate-porrect trichomes. **Leaves** mostly entire or rarely with few 2–3-partite, entire leaves ovate, oblong or elliptic, (3–)5–10(–14.5) × 2–4.5 cm, partite leaves with the medium lobe elliptic, 4.5–11.5 × 2.5–5 cm, and lateral lobes elliptic to oblong, 5.5–6 × 1–2 cm, chartaceous, apex attenuate to long attenuate, base obtuse to rounded, lobed leaves sometimes cordate, margin serrate, with conspicuous teeth, not cartilaginous, ciliate, with simple or stellate trichomes, adaxial surface pilose, except for the densely pubescent primary veins, with stellate and stellate-porrect trichomes and few scattered short (< 0.5 mm) simple trichomes, abaxial surface tomentose, more dense near the base and along the veins, with stellate and stellate porrect trichomes, venation actinodromous; petioles 0.5–2(–5) cm long, pubescent to tomentose, with stellate and stellate-porrect trichomes; stipules entire, subulate, up to 3 mm long, sparsely pubescent to pilose, with stellate and short (< 0.5 mm) simple trichomes. **Thyrse** 20–45 cm long, rachis pubescent, generally more sparse at the base, with stellate trichomes; basal cymules with 6–13(–18) pistillate flowers, accompanied by 4–5(–6) staminate flowers; distal cymules with 4–5(–6) staminate flowers; bracts triangular to subulate, 2–3 mm long, pubescent, generally more dense at the base, with stellate trichomes, and with (< 0.5 mm) simple trichomes towards the apex; **Staminate flowers** with pedicel up to 3 long, glabrous; calyx glabrous, or with 1–2 short (< 0.5 mm) simple trichomes on each lobe. **Pistillate flowers** with pedicels 1–2 mm, up to 4(–9) mm in fruit, pubescent, with stellate and stellate-porrect trichomes, calyx lobes 5–7, sometimes with one lobe poorly developed and narrower than the others, lobes elliptic to obovate, 3–3.5 mm, up to 6(–8) mm in fruit and 1–1.5 mm wide, pubescent on the external face, with stellate, stellate-porrect and short (< 0.5 mm) simple trichomes, margin entire, not cartilaginous, ciliate, with short (< 0.5 mm) simple trichomes, apex acute; ovary 1.5–2 × 1.5–2 mm, glabrous to pubescent, more dense near the apical portion, with short (< 0.5 mm) simple and stellate trichomes. **Fruits** lustrous, 6–6.5(–8) × 6–6.5(–8) cm, sparsely pubescent, with stellate and/or few scattered short (< 0.5 mm) simple trichomes, more dense near the apical portion; seeds tetragonal in cross section, 4.5–5(5.5) × 3–3.5(–4) mm, caruncle ca. 0.5(–1) × 1(–2) mm.

**Nomenclatural notes:**—No specific herbarium is cited for the type specimen in the protologue of *Croton subcomosus* (Müller Argoviensis 1873) and, although Caruzo et al. (2014) cited the lectotype of *Astraea subcomosa* as a specimen from the De Candolle's herbarium at G, no collection of this species was found in this specific set. Instead, the barcode cited by these authors (434679) corresponds to a specimen in the general collection at G and therefore is emended in this treatment.





**Figure 29:** Line drawing of *Astraea subcomosa* **A.** flowering branch, **B.** detail of indumentum of younger portion of stems, **C.** detail of stipules, **D.** abaxial surface of leaf base, **E.** detail of leaf margin, **F.** pistillate flower, **G.** calyx lobe of a pistillate flower – internal face, **H.** calyx lobe of a pistillate flower – external face, **I.** gynoecium and floral nectaries (calyx removed), **J.** staminate cymules with one mature flower, **K.** immature fruit, **L.** seed – ventral face. Illustration by Klei Sousa, based on *R. Mello-Silva 2703* (SP).

**Etymology and vernacular names:**—The epithet *subcomosa* is probably a reference made by Müller Argoviensis comparing this species to *Astraea comosa*, indicating that it would have bracts slightly shorter than what is observed in *A. comosa*. No vernacular names were recorded for this species.

**Geographical distribution:**—SOUTHERN AMERICA. *Brazil*: Brazil Northeast (BZE-BA), Brazil Southeast (BZL-MG).

*Astraea subcomosa* is found along the northern portion of the Espinhaço Range (Fig. 30), mainly in northern Minas Gerais (Septentrional Espinhaço) and central Bahia (Chapada Diamantina). This species grows in campos rupestres and also in gallery or seasonally dry forests, within or nearby campos rupestres. Elevations generally are higher than 1,000 meters above sea level, but *Astraea subcomosa* is also found in elevations between 700–800 meters above sea level, as in Grão Mogol municipality in northern Minas Gerais.

**Phenology:**—Flowering and fruiting are recorded from October to May. Considering the high efforts for floristic works and floras in Chapada Diamantina National Park and Grão Mogol State Park, this species seems to not tolerate the winter's drier season from June to September.

**Conservation status:**—*Astraea subcomosa* has an area of occupancy (AOO) of 72,000 km<sup>2</sup>, with more than 10 known locations. Despite the protection inside protected areas for a considerable part of these localities, as in National and State Parks, campos rupestres are still subject to continuing decline in area and quality of habitat due to anthropic pressure. Therefore, according to IUCN (2012) guidelines, we classify *A. subcomosa* as Near Threatened (NT) once it is likely to qualify for a threatened category in near future, but our present evaluation neither qualify it for Critically Endangered, nor Endangered or Vulnerable.

**Taxonomic comments:**—*Astraea subcomosa* is morphologically more closely related to *A. comosa*, *A. macroura* and *A. paulina*, and may be distinguished of them by its tomentose indumentum on younger portions of branches, predominantly entire leaves and geographical distribution (for more detail see taxonomic comments on *A. comosa*, *A. macroura* and *A. paulina*). This species was treated as *Croton lobatus* in Cordeiro (2004).

**Selected specimens examined:**—BRAZIL. **Bahia**: Abaíra, Caminho Catolés-Cristais. Mata dos Frios, 1800 m, 13° 20' 00" S, 41° 53' 00" W, 25 May 1992, *W. Ganey 375* (HUEFS, NY, SP, SPF); Mucugê, Guiné, Serra do Esbarrancado, 1300 m, 29 June 2002, *A.A. Conceição 1069* (SP, SPF); Rio de Contas, Arapiranga. Alto da serra na trilha para o rio Água Suja. Campo limpo brejoso, 1090 m, 13° 25' 59" S, 41° 47' 27" W, 1 February 2003, *L.R. Lima 261* (SP, SPF). **Minas Gerais**: Botumirim, Serra da Canastra. São Domingos. Encostas do ribeirão São Domingos, em trilha para o alto da serra, 1109 m, 16° 51' 26" S, 43° 01' 36" W, 20 December 2004, *R. Mello-Silva 2703* (RB, SP[2], SPF); Caparaó, Estrada Caparaó para Pedra Menina, 10 March 2010, *J. Cordeiro 3599* (ESA, MBM); Capelinha, unknown locality, 31 January 1947, *D. Romariz 104* (RB); Grão Mogol, Próximo da saída na estrada para Francisco Sá, 1000 m, 7 January 1986, *I. Cordeiro in CFCR 9020* (SP, SPF, WIS); Itacambira, Chapada de Itacambira, c. 10 km de Itacambira na estrada para Montes Claros, 1210 m, 17° 02' 20" S, 43° 20' 39" W, 16 February 2003, *F. França 4489* (HUEFS, SP); Novo Cruzeiro, Fazenda Araras, 754 m, 17° 36' 47.6" S, 41° 57' 49.3" W, 2 October 2004,



Figure 30: Geographical distribution of *Astraea subcomosa*.

*J.R. Stehmann 3559* (BHCB, SP); Serranópolis de Minas, Parque Estadual Serra Nova, Talhado, 812 m, 15° 48' 56" S, 42° 48' 00" W, 26 April 2013, *E. Barboza 3808* (MBM).

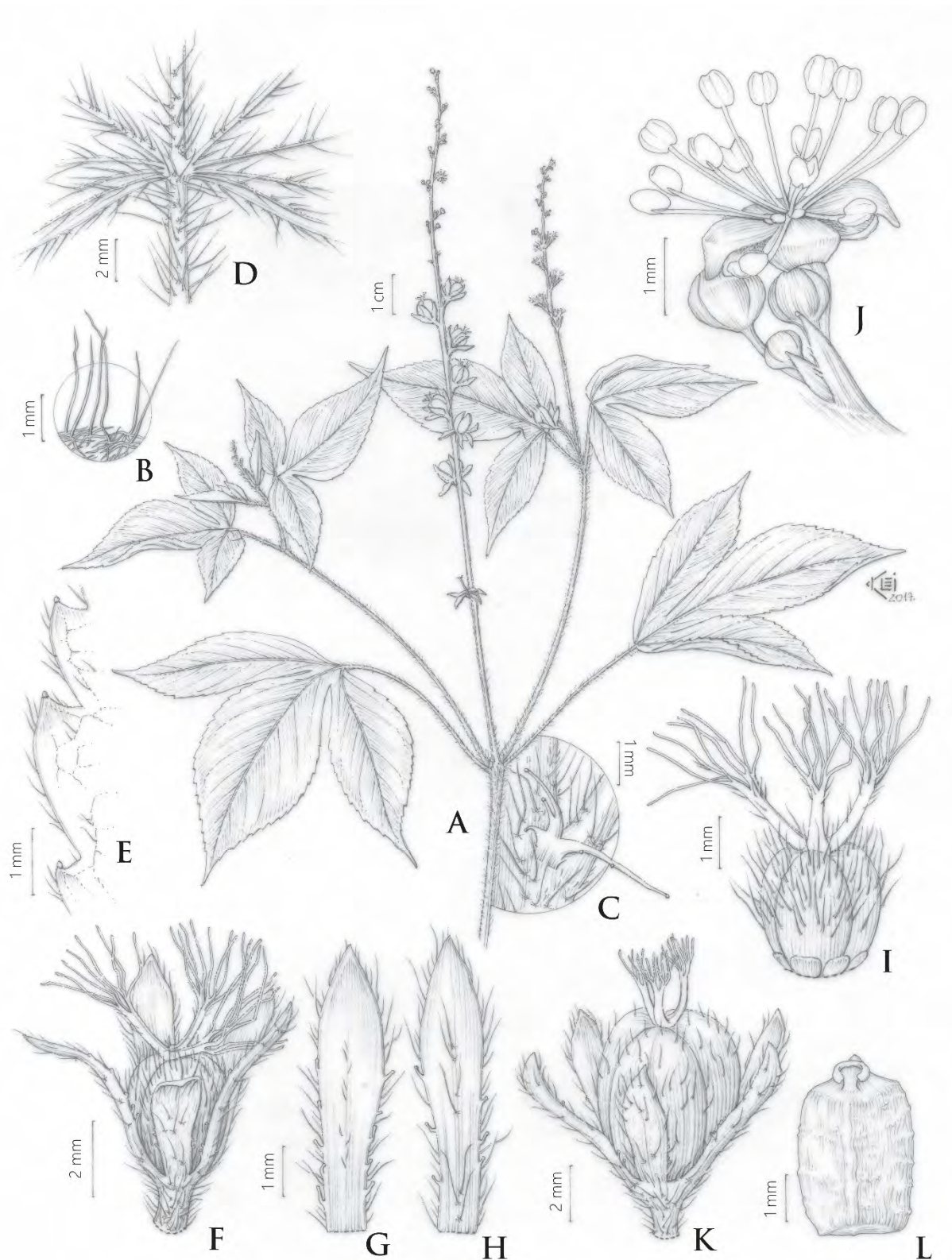
12. *Astraea surinamensis* (Miq.) Silva & Cordeiro (Capítulo III). *Cnidoscolus surinamensis* Miquel (1845: 749). Lectotype (designated here):—SURINAME, unknown locality, unknown date, *A. Kappler 1573* (U0001887 [photo!], isolectotypes GI, P04831490!TUB9125 [photo!], TUB009125 [photo!]). Figs. 31–33a–j.

*Croton trilobatus* Willdenow in Linnaeus *et al.* (1805: 556), *nom. illeg.* Lectotype (designated here):—GUINE. Unknown locality, unknown date, *C.L. Willdenow* (B-W 17099-01 [photo!], isolectotypes B-W17099-02 [photo!], B-W17099-03 [photo!], B-W17099-04 [photo!], B-W17099-05 [photo!],



**Annual or biannual herbs**, phanerophytes, up to 1.5 m high, with erect branches, without a well-developed (xylopodiferous) underground system, branches sparsely to densely pubescent, with stellate-porrect trichomes bearing a central ray much longer than the lateral rays (with up to 3–4 mm long), sometimes also with simple, long (> 1.5 mm) trichomes. **Leaves** 3(–5)-partite, medium lobe elliptic to wide-elliptic, (1.5–)2–9(–10) x (0.7)–1–4.5(–5) cm, and lateral lobes elliptic or oblong, (1–)1.5–5(–6.5) x 0.5–3(–3.5) cm, membranaceous, apex attenuate to long attenuate, base rounded, cordate, subcordate, truncate, obtuse or cuneate, margin serrate, with conspicuous teeth, not cartilaginous, ciliate with simple trichomes, adaxial surface glabrescent to pilose, more dense near the base and along the proximal portion of the primary veins, with mostly with long (> 1 mm) simple trichomes, but also with some stellate or stellate-porrect trichomes bearing a central ray much longer than the lateral rays (with up to 3 mm), specially near the base or along the primary veins, abaxial surface pilose, more dense near the base, with mostly long (> 1 mm) or short (< 0.5 mm) simple trichomes, but also with stellate or stellate-porrect trichomes bearing a central ray much longer than the lateral rays (with up to 3–4 mm long) especially near the base or along the veins, venation actinodromous; petioles (0.5–)1–5(–7) cm long, pilose to densely pubescent, with simple, long (> 3 mm long) trichomes or stellate-porrect trichomes bearing a central ray much longer than the lateral rays (with up to 3–4 mm long); stipules subulate, entire or 3(–5)-lobed, medium lobe 3–8(–10) mm long, and lateral lobes up to 3 mm long, pilose to pubescent, with long (> 1 mm) simple or stellate-porrect bearing a central ray much longer than the lateral rays (with up to 3–4 mm) trichomes. **Thyrse** 8–15(–20) cm long, rachis pilose to sparsely pubescent, with stellate-porrect trichomes bearing a central ray much longer than the lateral rays (with up to 3–4 mm long); basal cymules with 3–8 pistillate flowers, accompanied by 1–3 staminate flowers; distal cymules with 1–3 staminate flowers; bracts triangular to subulate, up to 2 mm long, glabrous or pilose to pubescent, with short (< 0.5 mm) simple trichomes; **Staminate flowers** with pedicel up to 5 long, glabrous; calyx glabrous. **Pistillate flowers** with pedicels 2–3 mm, reaching up to 5 mm in fruit, pubescent, with stellate-porrect trichomes bearing a central ray much longer than the lateral rays (with up to 3–4 mm long), calyx lobes 5–6, sometimes with one lobe poorly developed and narrower than the others, lobes elliptic or oblong, 2–3, reaching up to 6–7 mm long in fruit and 1–2 mm wide, pilose on the external face, with long (> 1 mm) simple trichomes, margin entire, not cartilaginous, ciliate, with short (< 0.5 mm) or long (> 1 mm) simple trichomes, apex acute; ovary 1.5–2.5 x 1.5–2.5 mm, pubescent to densely pubescent, with simple elongated, rarely mixed with few stellate-porrect trichomes bearing a central ray much longer than the lateral rays (with 3–4 mm long). **Fruits** lustrous, 4–5(–6) x 4–5(–6) cm, pilose to sparsely pubescent, with long (> 1 mm) simple trichomes, rarely mixed with few stellate-porrect trichomes bearing a central ray much longer than the lateral rays (with up to 3 mm long); seeds tetragonal in cross section, (3.5–)4–5 x 2.5–3 mm, caruncle ca. 0.5 x 1.5 mm.

**Nomenclatural notes:**—*Croton trilobatus* Willd. is here included as synonym of *Astrae surinamensis* as its identity was confirmed through high resolution images available from B. However, *C. trilobatus* is an illegitimate



**Figure 31:** Line drawing of *Astraea surinamensis* A. flowering branch, B. detail of indumentum of younger portion of stems, C. detail of stipules, D. abaxial surface of leaf base, E. detail of leaf margin, F. pistillate flower, G. calyx lobe of a pistillate flower – internal face, H. calyx lobe of a pistillate flower – external face, I. gynoeceum and floral nectaries (calyx removed), J. staminate cymules with one mature flower, K. immature fruit, L. seed – ventral face. Illustration by Klei Sousa, based on O.L.M. Silva 117 (SP).

name for later homonymy (*C. trilobatus* Forssk., from 1775), and therefore *Cnidoscolus surinamensis* was the name chosen to serve as the basionym for this species.

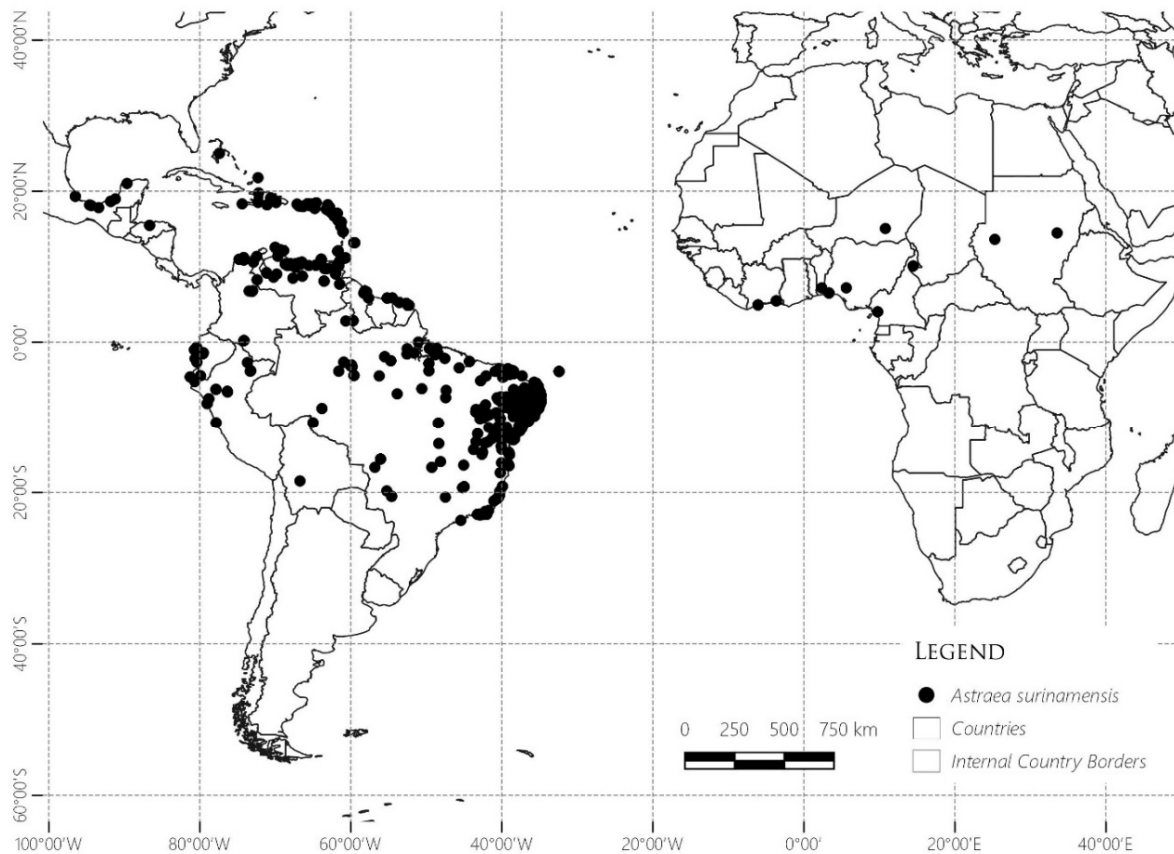
**Etymology and vernacular names:**—the epithet *surinamensis* is a reference to the type locality, Suriname, of this species. The basionym of this species was described by Miquel as a *Cnidoscolus* possibly due to the spiny appearance of its trichomes in young portion of stems. However, the author highlighted that this would be a very strange *Cnidoscolus* due to the strong differences between flowers in *Croton* and *Cnidoscolus*.

Many vernacular names were gathered for this species: *assovio-de-macaco*, *cabeça-de-formiga*, *café-bravo*, *velame*, *mandioquinha*, *cunhão-de-velho*, *erva-de-rola*, *mato-de-raposa*, *mozambé*, *pé-de-galinha*, *pilão-de-purga*, *pião-rana*, *picão*, *pimentinha-de-rolinha* (portuguese), *lilac-bush* (english), *eru* and *papaya-kihua* (unknown african dialects).

**Geographical distribution:**—AFRICA. *Northeast Tropical Africa*: Sudan (SUD); *West Tropical Africa*: Benin (BEN), Ivory Coast (IVO), Niger (NGR), Nigeria (NGA); *West-Central Tropical Africa*: Cameroon (CMN). ASIA-TROPICAL. *Indian Subcontinent*: Bangladesh (BAN); NORTHERN AMERICA. *Mexico*: Mexico Gulf (MXG-VC), Mexico Southeast (MXT-CA, MXT-TB, MXT-YU). PACIFIC. *Southwestern Pacific*: New Caledonia (NWC). SOUTHERN AMERICA. *Brazil*: Brazil North (BZN-AP, BZN-AM, BZN-PA, BZN-RO, BZN-TO), Brazil Northeast (BZE-AL, BZE-BA, BZE-CE, BZE-MA, BZE-PB, BZE-PE, BZE-PI, BZE-RN, BZE-SE, BZE-FN), Brazil Southeast (BZL-ES, BZL-MG, BZL-RJ, BZL-SP), Brazil West-central (BZC-DF, BZC-GO, BZC-MT, MZC-MS); *Caribbean*: Aruba (ARU), Bahamas (BAH), Dominican Republic (DOM), Haiti (HAI-HA), Leeward Is. (LEE-AG, LEE-AB, LEE-BV, LEE-GU, LEE-MO, LEE-NL, LEE-SK, LEE-SM, LEE-VI), Netherlands Antilles (NLA-BO, NLA-CU), Puerto Rico (PUE), Trinidad-Tobago (TRT), Turks-Caicos Is. (TCI), Venezuelan Antilles (VNA), Windward Is. (WIN-BA, WIN-DO, WIN-GR, WIN-MA); *Central America*: Honduras (HON); *Northern South America*: French Guiana (FRG), Guyana (GUY), Suriname (SUR), Venezuela (VEN); *Western South America*: Bolivia (BOL), Colombia (CLM), Ecuador (ECU), Peru (PER).

*Astraea surinamensis* is primarily found in the Americas, but there are few records along tropical Africa (Fig. 32). It is widely distributed in Americas, although most specimens were collected in eastern Brazil (especially in the northeastern region), northern South America and Lesser Antilles. *Astraea surinamensis* is a ruderal species, usually found in disturbed sites as roadsides or waste places. However, this species may also be found in seashore vegetation, caatinga, seasonally dry forests, savannas, white sand ecosystems within Amazonia domain (*campinaranas*), among other formations. It grows on different soils types, such as sandy, flooded, clay, swampy or rocky (including rock outcrops). Elevation varies from near sea level to around 850 meters above sea level, but in some cases reaches more than 1,000 meters above sea level along the Espinhaço Range in Bahia or the savannas from western-central Brazil.

**Phenology:**—Flowering and fruiting is recorded throughout the year, usually at the same time.



**Figure 32:** Geographical distribution of *Astraea surinamensis*. Cultivated specimens and occurrence in Asian continent are omitted.

**Conservation status:**— this is an invasive, widely-distributed species, which has an extremely wide extent of occurrence (EOO), with many known locations and found on disturbed environments, expanding its distribution range with anthropic activities. Therefore, according to IUCN (2012) guidelines, it qualifies for Least Concern (LC).

**Taxonomic comments:**—*Astraea surinamensis* may be distinguished from most of the species of *Astraea* found in the Neotropical region by its stellate-porrect trichomes bearing a central ray much longer than the lateral rays, which are easily observed in younger portions of branches and petioles (Figs. 31B, D and 33B–C). These trichomes give the appearance of a hirsute indumentum composed by simple trichomes (Fig. 33B), and the stellate nature of these trichomes can be confirmed only under a stereoscope.

The only other species which has this same type of trichomes is *Astraea trilobata*. To distinguish *A. surinamensis* from *A. trilobata* one should look at indumentum of the adaxial surface of leaves (with stellate trichomes in *A. trilobata* vs. simple in *A. surinamensis*), the external face of calyx lobes in pistillate flowers (with simple trichomes in *A. surinamensis* vs. stellate or stellate-porrect trichomes in *A. trilobata*) and fruits (with mostly simple trichomes in *A. surinamensis* vs. with stellate or stellate-porrect trichomes in *A. trilobata*).

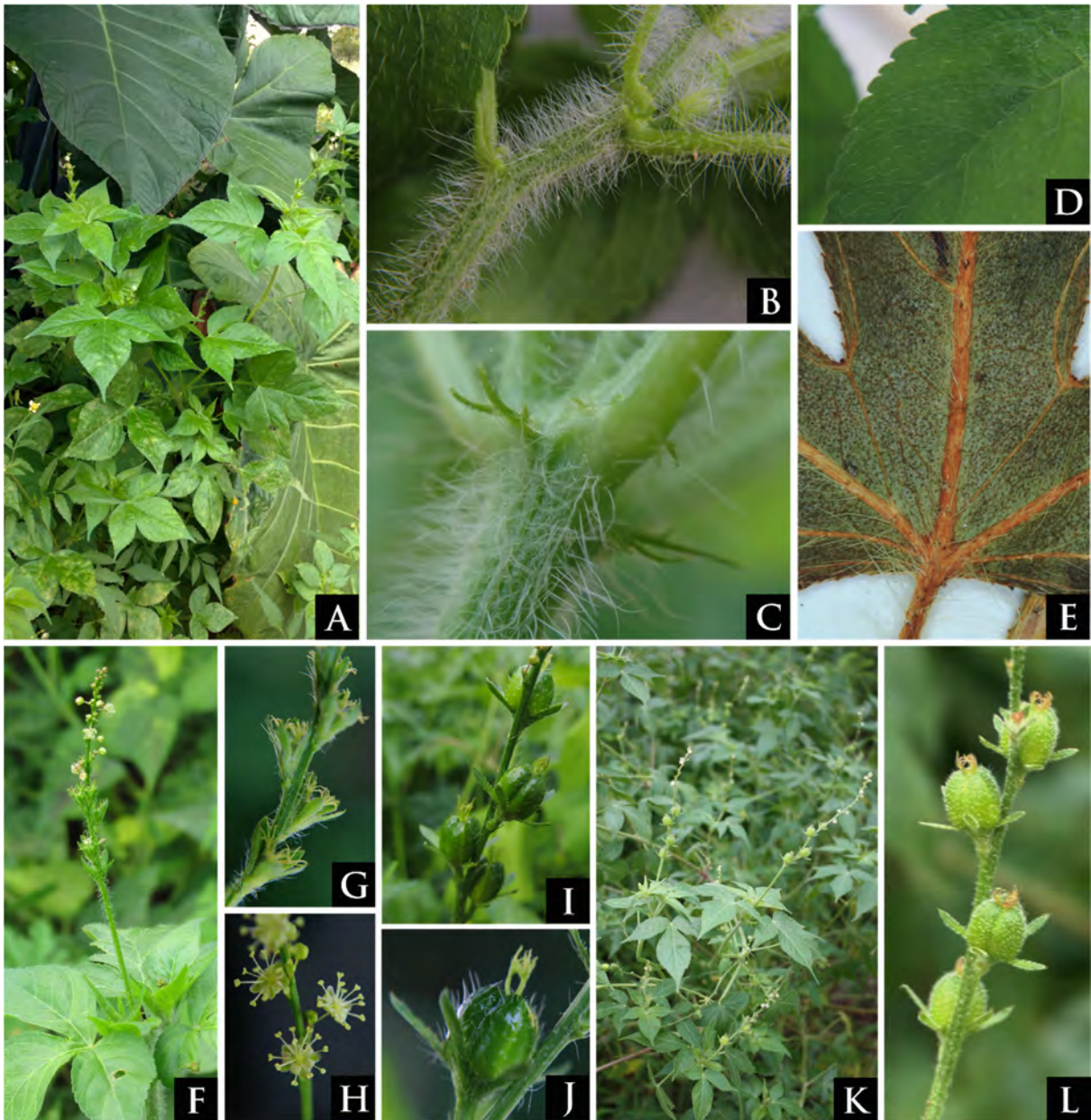
Additionally, *A. surinamensis* is mostly found in Neotropics, while the majority of specimens of *A. trilobata* were collected in Africa (see Figs. 32 and 35, respectively).

Most floras and taxonomic works in Brazil have identified this species as *Astraea lobata* (or *Croton lobatus*), such as in Caruzo & Cordeiro (2007), Wanderley et al. 2012 and Déda et al. (2013), due to the poorly defined morphological delimitation of *A. lobata*. *Astraea surinamensis* may be distinguished from *A. lobata*, besides the characteristics cited above, by its lustrous fruits (opaque in *A. lobata*) and geographical distribution of these species may also aid in the correct identification of them (see Silva et al. [Capítulo III]).

**Selected specimens examined**—[AFRICA] BENIN. Zagnanado, July 1902, *L. Esteve 130* (BM). CAMEROON. Douala. Près Plaos de la Poste centrale, 16 April 1976, *R. Letouzey 14593* (K, P); Hosséré Boboyo, à l'ouest de Kaele, 1000 m, 3 September 1964, *E. Bounougou 90* (P). CÔTE D'IVOIRE. **Bas-Sassandra:** Sassandra, 5 km N of Sassandra, 50 m, 19 December 1958, *A.J.M. Leeuwenberg 2264* (K, P, U, WAG). **Lagunes:** Alépé, Right bank Lower Comoé R, 12 May 1962, *A.J.M. Leeuwenberg 4160* (K, P, U, WAG). NIGER. **Zinder:** Gouré, unknown locality, 28 August 1964, *P. Fabrégues 778* (P); Gafata, Gromits de Gafata, 8 September 1966, *P. Fabrégues 2380* (P). NIGERIA. **Lagos:** unknown locality, April 1883, *Moloney s.n.* (K). **Ondo:** Owo, Banks of River Ogbesse near Akinjare below confluence with Asisenwen stream, 2 April 1943, *A.P.D. Jones s.n.* (K). SUDAN. **Al Jazirah:** Abu Haraz, unknown locality, August 1873, *T. Pfund 129* (K). Darfur, unknown locality, unknown date, *s.col.* 23 (P).

[ANTILLES] ANGUILLA. The Valley, 5 January 1959, *G.R. Proctor 18636* (BM). ANTIGUA AND BARBUDA. **Antigua:** In the central (tuff) & S.W. (volcanic) areas, 2 August 1937, *H.E. Box 946* (BM, NY). **Redonda:** unknown locality, 18 July 1938, *H.E. Box 1689* (BM). ARUBA. **Cudawecha:** unknown locality, 18 February 1999, *A.S.J. van Proosdij 709* (K, NY, U). **Noord:** Lagos area, 17 January 1986, *R.A. Howard 20338* (NY). BAHAMAS. **Nassau:** New Providence, About small nursery on corner of Village Road and Wulff Road, 6 October 1977, *D.S. Correll 49069* (FTG, NY). BARBADOS. **Saint James:** Oyster Bay, June 1981, *J.M. Mullin 12* (BM). **Saint John:** Bath Beach, 0 m, January 1940, *E.G.B. Goodwip 267* (BM). BONAIRE, SAINT EUSTATIUS AND SABA. **Bonaire:** Fontein, 1909–10, *I. Boldingh 6475G* (U). **Saba:** The Bottom. In village by Wesleyan Holiness Church, 450 m, 17° 38' 00" S, 63° 15' 00" W, 7 March 2007, *S.A. Mori 26820* (NY). **Saint Eustatius:** Southeast corner of island, Botanical Garden Trail from Miriam C. Schmidt Botanical Garden to junction with The Around The Mountain Trail, 100 m, 17° 28' 28" N, 62° 57' 15" W, 31 January 2008, *B.M. Boom 11121* (NY). CURAÇAO. Shalome, 24 September 1952, *A.L. Stoffers 12* (K, U). DOMINICA. **Saint Mark Parish:** Sulphur springs and vicinity, Soufriere, 15 March 1993, *S.R. Hill 24814* (NY, USF). **Saint Paul Parish:** Roadsides at Sag Toyota dealership, Canefield, southeast of airport, 30 July 1992, *S.R. Hill 24043* (USF). **Saint Peter:** Above Bioche, 4 April 1987, *C. Whitefoord 5718* (BM). DOMINICAN REPUBLIC. **Barahona:** Near west end of Barahona on north side of Route 44; a little west of the Hotel Caribe, 5 m, 18° 12' 08.8" N, 71° 05' 14.6" W, 6 June 2006, *J.R. Abbott 20947* (FLAS). **La Vega:** Jabaracoa, unknown locality, October 1962, *B. Augusto 324* (NY). **Santo Domingo:** Santo Domingo, Sector residencial Los Restauradores, detras del edificio de CEDOPEX. Avs. Luperón y 27 de Febrero, 30–50 m, 18° 28' 00" S, 69° 57' 00" W, 22 March 1990, *T. Zaroni 44159* (NY). GRENADA. **Saint George:** unknown locality, 26 October 1904, *W.E. Broadway s.n.* (G, NY 1384372). GUADELOUPE. Bailey, 15 April 1936, *L. Rodriguez 4658* (P); Basse Terre, unknown date, *P. Duss 2460* (NY). HAITI. **Nord:** Ducroix, near Cap-Hatien, 3 May 1988, *H. Chandler 23* (USF). **Ouest:** Péitionville, Vicinity of Péitionville, 350 m, 15 June 1920, *E.C. Leonard 4886* (NY); Port-au-Prince, Masef. de la Lelle, Port au Prince, Marlistants, 17 October 1926, *E.L. Ekman 7106* (K, NY). **Sud:** Tiburon, Massif. de La Hotte: en la orilla del Riviére de Tiburón, al norte del poblado de Tiburón, 0–5 m, 18° 22' 00" S, 74° 24' 00" W, 26 January 1985, *T. Zaroni 33287* (NY). MARTINIQUE. Fort de





**Figure 33:** Morphological characters of *Astraea surinamensis* and *Astraea trilobata*. **A–J.** *Astraea surinamensis*. **A.** habit. **B.** young portion of a branch. **C.** stipules. **D.** adaxial surface of a leaf. **E.** abaxial surface of a leaf. **F.** inflorescence. **G.** pistillate flowers. **H.** staminate flowers. **I–J.** fruits. **K–L.** *Astraea trilobata*. **K.** habit. **L.** fruits. A–C, G–H and J: population from Corguinho, MS (O.L.M. Silva 247); D, F and I: population from Campo Grande, MS (O.L.M. Silva 117); E: populations from Ilhéus, BA (O.L.M. Silva 218); K–L: population from Cotonou, Benin. Photos: A–J: O.L.M. Silva; K–L: Dressler *et al.* (2014).

France, Fort de France, July 1904, *M. Mouret 103* (P). MONTSERRAT. **Plymouth:** Story Crach south of Plymouth, 22 January 1907, *J.A. Shafer 141* (NY); Fox's bay area, 19 April 1979, *R.A. Howard 19027* (NY). PUERTO RICO. **Alta Verapaz:** Ile de Bieques ou Vieques, 1864, *R. Grosourdy s.n.* (P 4831502). **Añasco:** Rt 401. 2.6 km S of Rt 115, 1–3 m, 18° 17' 00" S, 67° 11' 00" W, 1 November 1994, *D.E. Atha 691* (MEXU, NY). **Ceiba:** Roosevelt Roads Naval Reservation: Barrio Quebrada Seca. Wetland area just E. of Río Daguao, 0.4 km. NW. of reservoir, 1–2 m, 20 March 1996, *G.R. Proctor 50613* (FTG). **Fajardo:** Cabezas de San Juan, 4 April 1995, *A. Liogier 269* (NY). **Luquillo:** Hedgerow and W. Luquillo, 25 March 1971, *D. Burch 3439* (NY, USF). **Ponce:** Just W of Ponce at the construction site of the new prison, 10 July 1988, *C.M. Taylor 8181* (NY). **Salinas:** Camp Santiago. National Guard Training Area; Kilo sector; by road bordering Río Nigua, 90 m, 18° 02' 33" N, 66° 14' 45" W, 10 May 2013, *A. Acevedo-Rodríguez 15403* (US). **San Lorenzo:** Along rte 7740 ca. 0.5 km from rte 181, 200–300 m, 9 May 1986,

*C.M. Taylor 7598* (NY). **Veja Baja:** Near Laguna Tortugero. Along Rte. 387 near the entrance to Haciendas del Tortugero, 18° 27' 45,3" S, 66° 25' 19,6" W, 17 October 2005, *B.W. van Ee 549* (WIS). **Vieques Island:** Bo. Mosquitos, 29 March 1939, *J.I. Otero 628* (NY). **Yauco:** Bo. Frailes. Sector Monte Lejos. Further up the rd: Monte Frailes along an unnumbered paved road that may be a new extension of Road 365, ca. 100–200 m from its junction with two other roads, one of which goes east, 600 m, 18° 07' 30" S, 66° 55' 20" W, 17 September 2000, *G.J. Breckon 6353* (NY). SAINT BARTHÉLEMY. **Gustavia:** unknown locality, 24 June 1938, *A. Questel 188* (NY, P). **Public:** unknown locality, 2 July 1938, *A. Questel 412* (NY). **Saint Jean:** unknown locality, unknown date, *A. Questel 579* (NY); Chemin de la montagne du Colombier, 11 December 1977, *H. Stehle 77/119* (P). SAINT KITTS AND NEVIS. **Saint Kitts:** Roadside near Basse-Terre, 8 September 1901, *N.L. Britton 226* (K, NY); East side of island, along hillsides between Mansion and Tabernacle, 28 September 1982, *R.P. Saulea 7770* (USF). TRINIDAD AND TOBAGO. **Tobago:** Eastern Tobago, Mount Saint Georg, 19 June 1981, *Y.S. Baksh 466* (NY); Western Tobago, Bacolet, 6 October 1937, *N.Y. Sandwith 1633* (K, NY). **Trinidad:** Cedros, Between Bonassec and Green Hill, 11 July 1973, *D. Philcox 7443* (K, P); Puerto de España, Woodbrook, 23 October 1932, *W.E. Broadway 9040* (BM, G, K); Saint Patrick Parish, unknown locality, 19 July 1989, *R.D. Worthington 18192* (L); Siparia, Icacos, at St. Quiton, 20 November 1931, *W.E. Broadway 7832* (BM, G); Vicinity of Brighton, 12 April 1921, *N.L. Britton 2911* (NY). TURKS AND CAICOS ISLANDS. **Wheeland Settlement:** Providenciales, Nicky Turner's farm, Kew Town, 16 m, 21.780629° N, 72.27281° W, 26 May 2013, *M.A. Vincent 16537* (FTG). UNITED STATES VIRGIN ISLANDS. **Guana Island:** Guana Island Club, near Grenada House, 68 m, 22 April 1987, *G.R. Proctor 43436* (NY). **Saint Croix:** Ca. 1 km S of Fredericksted along the road that runs nexto to the coast, 0 m, 22 September 2001, *V.W. Steinmann 2024* (IEB, NY, WIS). **Saint John:** Reef bay Quarter; Fish Bay near mouth of Fish Bay Gut, 2 m, 10 January 1991, *A. Acevedo-Rodriguez 3874* (NY). **Saint Thomas:** Walter Island, 8 November 1969, *R.O. Woodbury WI-50* (NY). **Tortola:** Road Town streets, 0 m, 13 February 1965, *W.G. D'Arcy 34A* (BM).

[ASIA] BANGLADESH. Chittagong, unknown locality, 2 June 1967, *N. Khan 1* (K). NEW CALEDONIA. **Ouaco:** Ouakina, 18 April 1981, *H.S. McKee 38986* (BR, L, P). Bords de la Taim, base altitude, 9 November 1984, *Schmid 5374* (P).

[CENTRAL AMERICA] HONDURAS. **Yoro:** Olanchito, +/- 15 km al SO de Olanchito, 200 m, 15° 28' 49" N, 86° 39' 07" W, 9 September 2003, *J.L. Linares 7090* (MEXU).

[NORTH AMERICA] MEXICO. **Campeche:** Champotón, A orilla del estero, a la altura del puente Sabancuy, 18° 58' 58" N, 91° 11' 03" W, 15 June 1995, *P. Zamora-C. 4513* (MEXU); Ciudad del Carmen, Cerca de la Estación del Carmen, del ICMYL, UNAM, aprox. 9 Km al E de Cd. del Carmen, sobre la carr. a Campeche, 23 November 1987, *E. Cabrera 14811* (MEXU); Isla del Carmen, Em los alrededores de la Ciudad del Carmen, sobre Avenida Camarón, 21 September 1987, *E. Cabrera-C. 14548* (IEB, MEXU). **Tabasco:** Ciudad del Carmen, Aproximadamente 17 km al NE de d. del Carmen, sobre la carretera a Campotón. En la Isla del Carmen, 29 November 1987, *E. Cabrera 15087* (MEXU); Huimanguillo, En 5 presidentes, área situada entre Villa Benito Juárez y Sánchez Magallanes (porción norte), 0–100 m, 12 June 1996, *R.A. Novelo 1575* (MEXU). **Veracruz:** Coatzacoalpos, A 1.8 km del Hotel de solteros de la refinería de PEMEX, camino a Pajaritos, 23 m, 18° 06' 27" N, 94° 22' 54" W, 15 June 2003, *C.H. Ramos-A. 2610* (MEXU); Pajapan, Barrilas. Laguna Ostión, 0–3 m, 28 March 1980, *L. Gutiérrez 207* (MEXU); Puente Nacional, Chichicastle, 50 m, 7 March 1979, *F. Ventura-A. 15851* (MEXU). **Yucatan:** Mérida, Alrededores del Jardín Botánico Regional del CICY, región noroeste de la Ciudad de Mérida, cerca de Cordemex, 8–10 m, 21° 01' 42" N, 89° 38' 17" W, 10 October 1998, *G. Carnevali 5243* (MEXU).



[SOUTH AMERICA] BRAZIL. **Alagoas:** Batalha, Margem do Rio Traipu, 09° 45' 08" S, 37° 03' 42" W, 22 February 2009, *R.P. Lyra-Lemos 11933* (MAC); Boca da Mata, Serra da Naceia, 24 April 2005, *R.P. Lyra-Lemos 8640* (MAC); Ibateguara, Usina Serra Grande, 08° 57' 00" S, 36° 04' 80" W, 8 February 2006, *T. Leão 125* (UFP); Jaramataia, Serra das Mães, Margem do Rio Traipu, 22 February 2009, *R.P. Lyra-Lemos 11843* (MAC); Joaquim Gomes, Fazenda Três Barras, 03 December 1980, *C.R. Campêlo 1351* (UEC); Maceió, Lagoa de Anta, Praia de Jatiúca, 09° 55' 00" S, 36° 02' 30" W, 18 November 1977, *G.L. Esteves 555* (MAC); Marechal Deodoro, AL 101- Sul, 4 August 2005, *R.P. Lyra-Lemos 8616* (MAC); Novo Lino, Fazenda Criança, 22 September 1981, *C.R. Campêlo s.n.* (EAC 10648); Olho D'Água do Casado, unknown locality, 09° 30' 24" S, 37° 49' 56" W, 27 September 1999, *D. Moura 771* (SP, UFP); Piaçabuçu, Próximo à fazenda Tatu, 17 March 1983, *R.F.A. Rocha 507* (MAC); Piranhas, Próximo a sementeira da CHESF, 09° 36' 38.8" S, 37° 46' 09.2" W, 30 August 2001, *L.M. Cordeiro 461* (PEUFR); Roteiro, unknown locality, 26 April 2008, *G.B. Araujo 358* (MAC); Santana do Ipanema, Serra da Camonga, 24 July 2008, *Chagas-Mota 873* (MAC); São José da Lage, Usina Serra Grande. Próximo à sede, 20 February 2002, *M. Oliveira 769* (IPA, UFP); São Luís do Quitunde, RPPN Garabu, Usina Santo Antônio, 10 January 2009, *P.B.A. Silva 13* (MAC); São Miguel dos Campos, Área urbana da cidade às margens do rio São Miguel, 12 April 1999, *I.A. Bayma 206* (MAC); Viçosa, Fazenda Aniceto, 30 March 2008, *Chagas-Mota 361* (MAC). **Amapá:** Macapá, unknown locality, 9 April 1985, *B.V. Rabelo 3255* (NY). **Amazonas:** Anori, Estrada Anori-Anamá, 27 November 1975, *D. Coelho 683* (INPA); Borba, On the Rio Madeira. Campinarana 5 km east of town, 03° 23' 00" S, 59° 35' 00" W, 25 June 1983, *C. Todzia 2250* (F, INPA, K, NY, RB, UB, US); Careiro da Várzea, Ilha do Careiro, 25 November 1985, *Junk 1052* (INPA); Manaus, Área just NE of INPA, estrada do Aleixo. km 3. NE Manaus, U/Alt m, U/C, 26 July 1974, *A. Lasseign P21183* (INPA, MEXU, NY, R); Novo Airão, Proximidades do porto de passageiros de Novo Airão, 6 April 2015, *M.F. Devecchi 431* (SP, SPF); Rio Tocantins, margem esquerda, montante da U.H.T., 1/2h de barco, acima dos canteiros da obra, 7 December 1979, *M.F.F. Silva 116* (INPA). **Bahia:** Abaíra, Catolés. Serra do Barbudo, 13° 17' 00" S, 41° 50' 00" W, 29 April 2006, *M.L. Guedes 12243* (ALCB); Abaré, Beira do Rio São Francisco, 321 m, 08° 43' 46" S, 39° 04' 35" W, 1 November 2009, *E. Melo 7055* (HUEFS, SP); Anadaraí, Rio Paraguassú, ao longo da rodovia para Mucugê, 370 m, 12° 50' 67" S, 41° 19' 16" W, 19 October 1997, *M. Alves in EBNN 1144* (UFP); Baixa Grande, Fazenda Olhos d'Água. Ca. 10km de Utinga em direção a Morro do Chapéu, 400 m, 12° 00' 00" S, 40° 16' 00" W, 21 July 2006, *J. Paula-Souza 6346* (ESA); Bom Jesus da Lapa, Médio São Francisco. Garagem do Hotel Teófilo Otoni, 13° 15' 23" S, 43° 25' 11" W, 29 April 2003, *N. Roque 709* (ALCB, CEPEC); Cachoeira, Vale dos Rios Paraguaçu e Jacuípe. Estação da EMBRASA. Na margem do rio Paraguaçu, June 1980, *Grupo Pedra do Cavalo 115* (ALCB, CEPEC, HRB, HUEFS, IPA, NY, RB); Camaçari, unknown locality, 23° 42' 00" S, 39° 07' 00" W, 18 October 1996, *D.S. Carneiro 7* (HUEFS, UB); Carinhanha, Rod. BR-101, Fazenda Tamanduá, 26km N de Carinhanha, 17 May 2000, *G. Hatschbach 71273* (MBM); Casa Nova, Ca. 5 km N de Pau a Pique na estrada para a BR (Casa Nova - Remanso), 515 m, 09° 34' 55" S, 41° 38' 09" W, 9 February 2004, *L.P. Queiroz 9121* (HUEFS, SP); Castro Alves, Estrada para Castro Alves, 182 m, 12° 36' 35" S, 39° 31' 00" W, 9 March 2008, *S.F. Conceição 577* (HUEFS, SP); Conde, Fazendinha, 20 June 2003, *G. Hatschbach 75573* (CEPEC, G, HRCB, MBM); Cruz das Almas, Recôncavo Sul. Povoado Sapucaia. Ca. 6 km do centro da cidade, estrada da Escola de Agronomia da UFBA, 12° 40' 00" S, 39° 06' 00" W, 17 November 2000, *A.A.C. Rodrigues 2* (ALCB); Entre Rios, Fazendo Rio do Negro, ca. 15 km southeast of Entre Rios, 12° 01' 00" S, 38° 02' 00" W, 7 April 2009, *A.V. Popovkin 547* (HUEFS, SP); Glória, Povoado de Brejo do Burge, 1 July 1995, *F.P. Bandeira 167* (HUEFS, MBM, UB); Iaçu, Morro da Garrafa, 312 m, 12° 45' 48" S, 39° 51' 00" W, 22 February 1997, *E. Melo 2063* (HUEFS, MBM, SP); Ibotirama, Arredores da cidade, na saída para Bom Jesus da Lapa, 12,1955° S, 43,2123° W, 11 October 2007, *J. Paula-Souza 9349* (SP, SPF); Ilhéus, Ramal à esquerda na estrada Ilhéus - Itacaré, 0 m, 14° 41' 32.64" S, 39° 04' 18.66" W, 3 February 2015, *O.L.M. Silva 217* (SP); Itaberaba, Fazenda Itaberaba. Morro de Itaberaba. Sítio com pinturas, 285 m, 12° 30' 06" S, 40° 05' 00" W, 5 June 2005, *E. Melo 3906* (CEPEC, HUEFS, SP); Itagi, Fazenda

Palestina, 14° 16' 37" S, 40° 01' 18" W, 24 August 2011, *R.S. Souza 6* (UFP); Itaparica, Ilha do Medo, 9 March 1989, *E. Queiroz s.n.* (HRB 30896, RB 482298); Itatim, Afloramento rochoso na BR-116, lado direito (sentido Itatim - Milagres), pouco antes do posto Uirapuru, 210 m, 12° 41' 12.31" S, 39° 41' 02.82" W, 21 August 2014, *O.L.M. Silva 147* (SP); Jacobina, Piemonte da Diamantina. Bananeiras, caminho para a Cachoeira do Brito, 645 m, 11° 09' 46" S, 40° 29' 50" W, 20 April 2009, *M.L. Guedes 14704* (ALCB); Jaguarari, Encosta da Crista, na fazenda Umburanas, 620 m, 10° 06' 10" S, 40° 13' 46" W, 13 April 2006, *R.F. Souza-Silva 156* (CEPEC, HUEFS); Jandaíra, Mangue Seco, 2 April 1988, *M.C. Ferreira 165* (HRB, RB); Jequié, Rod. BR 330, trecho Jequié/ Ipiáú, 4 km a L de Jequié, 600 m, 13° 52' 00" S, 40° 03' 00" W, 14 July 1979, *S.A. Mori 12197* (CEPEC, NY, RB, US); João Dourado, Piemonte da Diamantina. Ponto 07, 363 m, 11° 19' 51" S, 41° 44' 14" W, 10 April 2013, *M.L. Guedes 20655* (ALCB); Juazeiro, Baixo Médio São Francisco. Caminho para a cidade de Juazeiro, 09° 24' 00" S, 40° 30' 00" W, 13 June 2009, *M.L. Guedes 16281* (ALCB); Lauro de Freitas, Jockey Clube, 6 March 1989, *R. Soeiro 38/89* (HRB); Licínio de Almeida, Serra Gera. Faz. Xaxá, antes da Faz. Tabuleiro, 1022 m, 14° 38' 47" S, 42° 33' 16" W, 21 February 2014, *F. Hurbath 620* (ALCB); Mata de São João, Terreiro de candomblé Unzó Min Kizangirá. Loteamento açuzinho, rua Direta, Açu da Torre, 12° 31' 00" S, 38° 17' 00" W, 12 January 2004, *L.P. Vieira 53* (ALCB); Medeiros-Neto, Estrada de terra (BA-126), BA-290/BA-284, 110 m, 17° 19' 00" S, 39° 58' 00" W, 25 January 2008, *J.A. Lombardi 7145* (HRCB, SP); Milagres, Estrada para laçu, 4 November 2010, *E. Barbosa 2745* (MBM); Morro do Chapéu, Estrada para a Serra, no caminho para a Gruta dos Brejões, 11° 55' 00" S, 41° 15' 00" W, 6 December 2009, *R.F. Machado 487* (HUEFS); Paramirim, Estrada para a torre de TV, 660 m, 13° 27' 08" S, 42° 12' 55" W, 30 January 2008, *J.L. Ferreira 279* (HUEFS, SP); Paulo Afonso, unknown locality, 10 July 2005, *D.V. Braga s.n.* (IPA 73896); Pilão Arcado, Brejo do Morro, 420 m, 10° 07' 10" S, 42° 53' 35" W, 19 March 2006, *D.S. Carneiro-Torres 626* (FUEL, HRCB, HUEFS); Porto Seguro, Paquetá, 25 June 1962, *A.P. Duarte 6849* (RB); Riachão do Jacuípe, unknown locality, 11° 48' 10" S, 39° 20' 13" W, 28 December 2011, *F. França 6178* (HUEFS); Salvador, Área de Pituagú (UCSal), 12° 57' 06" S, 38° 25' 12" W, 18 February 1992, *L. Paraguassú 11/92* (ALCB, HRB); Santa Brígida, BR 116, 480 m, 09° 41' 48" S, 38° 13' 54" W, 23 August 2005, *D.S. Carneiro-Torres 493* (HUEFS); Santa Cruz Cabrália, Estação Ecológica Pau Brasil, 14 km NW of Porto Seguro, 80–100 m, 16.23 ° S, 39.15 ° W, 23 July 1984, *G.L. Webster 25028* (CEPEC); Santa Luz, unknown locality, 7 July 1976, *A. Rocha s.n.* (IAC 23271); Santa Terezinha, Ca. 6 Km NE do entrocamento da BR 116, com a BA 046 (para laçu e Itaberaba), ao lado da BR 116, 12° 47' 00" S, 39° 47' 00" W, 2 June 1993, *L.P. Queiroz 3187* (CEN, CEPEC, HUEFS, K, MBM); Sapeaçu, Comunidade de Água Branca, zona rural do município, 13 October 2010, *M.L. Maia 1* (HUEFS); Sento Sé, Serra da Ingrata, 400 m, 09° 44' 26" S, 41° 58' 23" W, 27 February 2008, *C. Correia 416* (HUEFS); Simões Filho, Área do Empreendimento da BELOV, Mapele, 12° 46' 27" S, 38° 26' 45" W, 20 May 2002, *L.J. Alves 430* (ALCB, CEPEC); Urandi, Serra Geral, caminho pra o Rio Raízes. Ponto 01, 709 m, 14° 55' 55" S, 42° 39' 03" W, 4 August 2009, *M.L. Guedes 15764* (ALCB, HUEFS, MBM); Wagner, Chapada Diamantina, Entrada para Wagner, Ponto 03, U/Alt m, 12° 28' 12" S, 41° 05' 54" W, 11 March 2016, *M.L. Guedes 24296* (UFRN). **Ceará:** Aracati, Fazenda Belém, 82 m, 2 June 2014, *M.I.B. Loiola 2284* (EAC); Barbalha, Sítio Santa Cruz. Área externa à FLONA Araripe, propriedade particular, 640 m, 07° 18' 40" S, 39° 18' 15" W, 17 August 2011, *C.G. Crepaldi 1* (PEUFR); Crato, Clube Recreativo Granjeiro; entrada do Clube, 30 August 1998, *M.I.B. Loiola 491* (PEUFR); Fortaleza, Campo da E.A.C., 11 March 1940, *P. Bezerra s.n.* (EAC 150, UFP 50121); Horizonte, Barra, próximo a sede (casa), 04° 07' 03" S, 38° 21' 54" W, 3 April 2004, *A.V. Vieira s.n.* (EAC 33763); Meruoca, Serra da Meruoca, Sítio Santo Antônio, 9 March 1981, *A. Fernandes s.n.* (EAC 9921); Pacajus, EMBRAPA, 30 April 2004, *Gislane s.n.* (EAC 33903); Pacatuba, Serra da Aratanha, Sítio Pitaguari, 1 October 1979, *P. Martins s.n.* (EAC6980, IBGE10910); Pacoti, Serra de Baturité, Cafezal de Boa Vista, 21 December 1972, *I.D. Gemtchújnicov s.n.* (BOTU 12282); Pentecoste, Fazenda Experimental Vale do Curu, 19 April 2012, *M.I.B. Loiola 1457* (EAC); Santa Quitéria, 13,8 km SW (em linha reta) da sede da fazenda Itatiaia, 04° 36' 55.11" S, 39° 54' 32.48" W, 28 April 2012, *J. Paula-Souza 11065* (SPF); São Gonçalo do Amarante, Dunas do Pecém, próximo ao

porto, 13 June 2004, *A.V. Vieira s.n.* (EAC 34236); Sobral, Fazenda Crioulo- ANPC, 10 April 1996, *Coll. Illeg. s.n.* (UFP 59907); Ubajara, Planalto Cafundó-Entrada, Planalto da Ibiapaba - PARNA, 22 January 1999, *A. Fernandes s.n.* (EAC 27895). **Distrito Federal:** Brasília, Às margens da rodovia BR-060 (Anápolis-Brasília), um pouco antes da estrada para Samambaia, 1131 m, 15° 54' 09" S, 48° 07' 33.9" W, 19 January 2012, *M.B.R. Caruzo 155* (SP). **Espírito Santo:** Anchieta, unknown locality, 18 November 1987, *J.M.L. Gomes 259* (PAMG, SP, VIES); Aracruz, Estação de Biologia Marinha Mello Leitão, 18 July 1973, *D.S.D. Araujo 299* (R, RB); Guarapari, Praia de Setiba, lado sul, em costão rochoso na praia (também observada ao longo das calçadas e em meio à vegetação do Morro do Cruzeiro), 5 m, 20° 38' 01.96" S, 40° 26' 31.54" W, 8 June 2014, *O.L.M. Silva 132* (SP); Linhares, Reserva Natural da CVRD. Estrada MME, área do café, 6 November 1996, *D.A. Folli 2834* (CVRD, SP); Piúma, Entre Piúma e Itapemirim, 50 m, 09 September 1977, *G.J. Shepherd 5889* (UEC); Presidente Kennedy, unknown locality, 06 February 1988, *J.M.L. Gomes 485* (SP, VIES); Vitória, Campus da UFES - Goiabeiras, 20° 16' 36" S, 40° 18' 15" W, 12 May 1997, *E.S.S. Alves 18* (SP, VIES). **Goiás:** Goiânia, Rua 01, esq. 7, Qd-11, Lt-10. Vila Nossa Sra. Aparecida, 709 m, 16° 39' 41.8" S, 49° 16' 59.04" W, 27 January 2014, *O.L.M. Silva 115* (SP); Minaçu, Perto da Represa de Cana Brava, 30 May 1987, *J.G. Silva s.n.* (R). **Maranhão:** Carolina, Parque Nacional das Chapadas das Mesas, zona urbana, Rua Elias Barros, em frente ao n° 1175, 7° 19' 65" S, 47° 26' 52" W, 24 March 2016, *O. Monteiro PA-MA-074* (MG); Governador Newton Bello, BR 315, Km 209, perto de Rosilândia, Monção - Maranhão, 17 February 1979, *A. Fernandes s.n.* (EAC 5563); Porto Franco, BR010, km 146, Posto de gasolina na saída da cidade, 17 May 2011, *I. Cordeiro 3266A* (SP); São Luís, Área da Vale, 28 April 1998, *R.S. Secco 888* (NY, SP). **Mato Grosso:** Cuiabá, Jardim Leblon, 29 October 2005, *J.R. Oliveira s.n.* (HCF 35792, UB); Poconé, About 50 km. south of Poconé, 12 September 1992, *M. Schessl 120992-1-2* (SP). **Mato Grosso do Sul:** Campo Grande, UFMS, próximo ao cerradinho da universidade, logo após atravessar a ponte de acesso ao cerradinho, 20° 30' 21.14" S, 54° 36' 53.88" W, 29 January 2014, *O.L.M. Silva 117* (SP); Corguinho, Instituto Quinta do Sol, próximo à sede, 19° 46' 30.01" S, 55° 14' 39.51" W, 9 March 2016, *O.L.M. Silva 247* (SP). **Minas Gerais:** Martinho Campos, unknown locality, 9 February 1999, *J.F. Macedo 4194* (PAMG); Pompeu, unknown locality, 12 April 1999, *J.F. Macedo 3360* (PAMG); Salto da Divisa, Fazenda Santana, 150 m, 16° 03' 41.5" S, 40° 03' 23.5" W, 4 March 2004, *J.A. Lombardi 5821* (BHCB); São Romão, Porto São Romão, Rio São Francisco, 27 July 1939, *P.T. Mendes s.n.* (IAC 4966). **Pará :** Abaetetuba, Vila de Beja, 01° 37' 08" S, 48° 48' 45" W, 16 March 2002, *A.S.L. Silva 3558* (SP, SPF); Almeirim, Monte Dourado, Pacanari, área 47, centro, 13 May 1986, *M.J. Pires 961* (MG); Altamira, Rio Iriri, margem direta do rio Iriri próximo à "Pedra do Ó", 5 September 1986, *R.T.P. Vasconcelos 215* (MG); Aurora do Pará, unknown locality, 27 June 2013, *C.A.S. Silva 212* (MG); Baião, South of village, ruderal, along road, 2 June 1978, *N.B.M. Brantjes 706409* (BOTU, SP, U, UEC); Belém, unknown locality, January 1963, *J.M. Pires 8117* (NY, P, R, UB); Gurupá, Comunidade de Carrazedo, 25 December 2016, *L.C.B. Lobato 4530* (MG); Ilha de Marajó, R. Camari, September 1902, *U.C.R. Miranda 3178* (MG); Itaituba, São Luíz do Tapajós, às margens do Rio Tapajós, trecho onde se localiza a frente da vila, 23 November 1999, *R. Lisboa 6780* (MG); Marabá, Serra dos Carajás, Serra Norte, Clareira N-1, 18 April 1970, *P. Cavalcante 2642* (F); Obidos, In vicinibus Obidos, December 1849, *R. Spruce s.n.* (K 1210173, TCD 4971); Salvaterra, Vila do Caldeirão, 26 October 1999, *L.M. Carreira 1903* (MG); Santarém, Belterra, Porto Novo. Estrada para o acampamento, 5 December 1978, *M.G.A. Lobo 159* (NY); Região do Rio Jari, Monte Dourado, 1 October 1968, *N.T. Silva 1074* (NY). **Paraíba:** Alagoinha, unknown locality, January 1940, *J. Deslandes s.n.* (IAC 6065, SP 48842); Areia, Engenho Cepilho, 16 March 1975, *V.P. Barbosa 169* (RB); Baía da Traição, Aldeia São Miguel, unknown locality, 17 May 2008, *R. Lima 2321* (JPB); Cabedelo, Camboinha, Chácara Bargas, 3 March 1969, *L. Xavier s.n.* (JPB 2093, PEUFR 36493, SP 476557); Cuité, Campus da UFCG, ao lado do bloco H, 3 April 2010, *K. Randau 268* (IPA); Ingá, Itacoatiara, microrregião do Piemonte da Borborema, October 1993, *M.F. Agra 2147* (JPB); Itaporanga, Serra Água Branca, 07–10 January 1994, *M.F. Agra 2479* (JPB); João Pessoa, Jacarapé, Mangabeira, EMEPA, 27 March 1984, *O.T. Moura 185* (JPB, SP); Mataraca, Millennium Inorganic

Chemicals Mineração LTDA. Mata da Mineradora, 06° 29' 37" S, 34° 58' 43" W, 29 January 2008, *I.B. Lima 877* (JPB, SP); São Bento, unknown locality, 148 m, 06° 28' 39.7" S, 37° 27' 04.5" W, 22 February 2014, *F.G. Silva 52* (PEUFR); São José da Mata, Sítio Bosque, estrada para Patos, BR-230, 07° 10' 47" S, 36° 00' 05" W, 29 August 1998, *M.I.B. Loiola 473* (PEUFR); São José dos Cordeiros, RPPN Fazenda Almas, Manga do Cardoso, 07° 26' 77" S, 36° 54' 58" W, 11 May 2007, *I.B. Lima 687* (JPB); Sousa, Vale dos Dinossauros, 10 July 2004, *P.C. Gadelha Neto 1192* (JPB, SP); Sumé, Sítio Olho D'Água, 07° 39' 58.7" S, 36° 32' 39.3" W, 22 May 2007, *M.F.A. Lucena 1742* (UFP). **Pernambuco:** Alagoinha, Rock outcrop ca. 700 m southwest of the Fazenda Morros., 750 m, 08° 26' 865" S, 36° 46.762' W, 25 September 1999, *L. Krause 172* (PEUFR); Araripina, BR 316, estrada para Ouricuri, km 46-limite de municípios Araripina/Trindade, 6 November 1986, *V.C. Lima 478* (IPA, MEXU); Arcoverde, Serra das Varas. Mata do Jacú, no entorno do açude, na barragem, 29 March 2006, *M.B. Costa e Silva 2143* (HUEFS, IPA); Barreiros, unknown locality, 28 March 1988, *R. Pereira 219* (IPA); Betânia, Floresta. RPPN Mauricio Dantas. Interior da área, 08° 17' 22.7" S, 38° 12' 22" W, 24 February 2003, *K.C. Costa 410* (PEUFR); Bezerros, Distrito de Sapucarana. Serra da Camarutuba, inselbergue Pedra Antônio Bezerra, U/Alt m, U/C, 9 April 2005, *P. Gomes 36* (UFP); Brejo da Madre de Deus, Serra da Prata, 700 m, 08° 09' 18" S, 36° 21' 42" W, 11 June 1998, *M.F.A. Lucena 543* (WIS); Buíque, Vale do Catimbau, 23 March 2010, *L.O. Costa-Filho 16* (UFP); Buíque, Cigano, entrada logo em frente ao posto, na cidade de Buíque, 7 May 2003, *A. Laurênio 2031* (PEUFR); Cabo de Santo Agostinho, Entre praia do Xeréu de Itapoama, 21 April 1998, *M.V. Alves in EBNN 1567* (RB, SP); Cabrobó, Mãe Rosa. Eixo Norte - Projeto de Integração do rio São Francisco, 320 m, UTM 0449569 9057301, 19 July 2007, *M. Oliveira 2978* (UFP); Camarajibe, Chã de Cruz, 11 August 1998, *M.F.A. Lucena 617* (PEUFR); Carnaíba, Fazenda Cacimba Velha, 8 May 2008, *C. Ferreira 83893* (IPA); Carpina, Mata do Engenho Trapuá - Usina Petribú, 10 August 1998, *M.F.A. Lucena 605* (PEUFR); Caruaru, Próximo à borda da mata do IPA, 535 m, 08° 14' 18" S, 35° 55' 20" W, 23 May 2011, *A.C.O. Silva 55* (PEUFR); Catende, Zona da Mata Pernambucana. "Pedra do Trevo", 307 m, 05° 41' 13.2" S, 35° 43' 13" W, 22 April 2009, *M. Sobral-Leite 647* (IPA, RB, UFP); Fernando de Noronha, Próximo ao armazem de cereais, 21 October 2004, *A.M. Miranda 4507* (IPA, RB, UB, UFRN); Floresta, Serra Negra, 29 May 1971, *E.P. Heringer 974* (IPA, PEUFR, RB); Goiana, RPPN Fazenda Tabatinga, 07° 36' 22" S, 34° 49' 14" W, 27 January 2010, *D. Cavalcanti 119* (JPB); Ibimirim, unknown locality, 6 February 2000, *L.M.C. Maia s.n.* (IPA 58714); Igarassu, Fragmento Chave, 07° 48' 30" S, 34° 58' 49" W, 18 December 2009, *E. Pessoa 225* (JPB, UFP); Ilha de Itamaracá, Canal de Santa Cruz, 4 May 1998, *M.F.A. Lucena 457* (PEUFR); Ipojuca, Mata de Penderama. Trilha principal de acesso a mata, 11 May 1998, *M.F.A. Lucena 470* (PEUFR); Jaboatão dos Guararapes, Barra da Jangada. Próximo a Ilha do Amor, 16 April 1998, *M.V. Alves in EBNN 1560* (SP); Lagoa dos Gatos, RPPN Pedra Danta: Estrada de acesso à sede RPPN, 21 November 2011, *J.L. Viana 329* (JPB); Limoeiro, Margem da PE-90, próximo a entrada da cidade, 12 May 1998, *M.F.A. Lucena 478* (PEUFR); Mirandiba, Barra da Cachoeira, 470 m, 08° 06.511' S, 38° 46.967' W, 1 May 2008, *K. Pinheiro 522* (UFP); Nazaré da Mata, Engenho Alcaparra, 5 November 1997, *M.F.A. Lucena 349* (PEUFR); Olinda, Nas proximidades de Horta de Plantas Medicinais do Córrego do Genipapo (Terra Prometida), 2 October 1996, *A. Cardoso s.n.* (IPA 45906); Ouricuri, Fazenda Barrinha, May 1984, *G.C. Lima 44* (IPA, UFRN); Parnamirim, Km 27,8 da estrada Parnamirim/Petrolina, 18 May 1984, *F. Araújo 50* (IPA, PEUFR, UFP); Paulista, Janga, 500 na praia no Canal do Tururu, 26 February 1995, *M.B. Costa 291* (IPA); Petrolândia, Apolônio Sales, 08° 58' 03" S, 38° 15' 46" W, 8 March 2014, *M. Pommeranz 8* (IPA); Petrolina, Área do CPTSA/EMBRAPA, próximo a estrada de acesso a cidade, 23 February 1999, *M.V. Alves in EBNN 1511* (SP); Recife, Mata de Dois Irmãos, 7 August 1999, *I.M. Paiva-Júnior 35* (PEUFR); São Bento do Una, Estação Experimental do IPA, margens do Rio Uma, Parcela L, subparcela 1, 17 June 1968, *O.H. Bonilla 10* (IPA); São Caetano, unknown locality, 25 February 1994, *S.I. Silva 678* (PEUFR); Serra Talhada, Estação Experimental do IPA, Área 37, 9 May 2008, *C. Ferreira 83845* (IPA); Tamandaré, Loteamento Estrela do Mar. Próximo ao sítio Porto do Tijolo, 16 May 1999, *M.F.A. Lucena 755* (PEUFR); Taquaritinga do Norte, unknown locality, 18 April 1997, *A. Laurênio 473* (PEUFR);

Venturosa, Parque Municipal Pedra Furada, 1 July 2007, *P. Gomes 395* (UFP). **Piauí:** Boqueirão do Piauí, Serra Boqueirão, 6 July 1912, *P. von Luetzelburg 1601* (RB); Caldeirão Grande do Piauí, unknown locality, July 1913, *P. von Luetzelburg 413* (NY); Caracol, Entrada do Parque, estrada à direita da guarita, 710 m, 09° 12' 47" S, 43° 27' 58" W, 26 February 2011, *E. Melo 9218* (HUEFS, SP); São João do Piauí, Saída para Nova Santa Rita, 329 m, 08° 17' 00" S, 42° 10' 32" W, 7 February 2007, *D.S. Carneiro-Torres 804* (HUEFS); São Raimundo Nonato, Serra Vermelha, 3 February 1986, *L. Emperaire s.n.* (RB 343901); Teresina, EMBRAPA - Cultivo de Sorgo, 29 April 1998, *N.M.S. Mendes s.n.* (HUEFS 130402). **Rio de Janeiro:** Cabo Frio, Sítio Guriri - Però, 21 July 2003, *G.S.Z. Resende 192* (RB, SP); Casimiro de Abreu, Próximo à Lagoa de Juturnaíba, 8 November 1984, *A. Souza s.n.* (R 161059); Macaé, Cacajuba, próximo à lagoa, 22 November 1986, *A. Souza s.n.* (R 161128); Maricá, Itaipuaçu, 7 April 1977, *B. Larcher 14745* (MBM, RB, SP); Niterói, Bairro de Jurujuba, Forte Imbuí, 27 March 2006, *L.J.S. Pinto 841* (RB); Rio de Janeiro, Campos. Campus da HENF, 13 November 1999, *V. Maia 142* (R); São Gonçalo, Paraíso, Universidade do Estado do Rio de Janeiro, Faculdade de Formação de Professores, Rua Francisco Portela, n° 794, 7 May 2001, *H.P. Moreira 27* (RB); Saquarema, Jacarepaguá, 29 May 1946, *H.L. Mello-Barreto s.n.* (BHC 80504). **Rio Grande do Norte:** Canguaretama, Barra de Chunhau, 6 December 1984, *A. Dantas 198* (IPA); Coronel João Pessoa, Platô da Serra São José, 70 m, 7 May 1984, *J.S. Assis 365* (ALCB, HRB, IPA, K, MBM, NY, RB); Equador, Área para Instalação do Complexo Eólico Santapape, 663 m, 06° 55' 10" S, 36° 43' 25" W, 12 August 2015, *V.F. Sousa 8* (UFRN); Florânia, Serra da Garganta, 165 m, 06° 06' 24" S, 36° 53' 43" W, 27 February 2011, *A.C.P. Oliveira 1276* (UFRN); Jucurutu, RPPN Stoessel de Britto, 2 February 2008, *A.A. Roque 432* (JPB, UFRN); Macaíba, BR 304, próximo ao km 285, estrada Mossoró - Natal, RN, 10 March 1979, *A. Nunes s.n.* (EAC 5691); Natal, Campus Central da UFRN, ao lado do anatômico, 53 m, 05° 50' 55.6" S, 35° 12' 11.6" W, 1 October 2004, *R. Melo-Soares 5* (EAC, UFRN); Parnamirim, EMPARN - Mata do Jiqui, 28 November 2007, *A.C.P. Oliveira 768* (UFRN); Riachuelo, Near Riachuelo, 60km W from Natal, along the Rt. BR-304, 28 August 1987, *S. Tsugaru 1260* (NY); Rio do Fogo, unknown locality, 05° 24' 00" S, 35° 27' 36" W, 16 September 2014, *A.F. Silva 120A* (UFRN); São Miguel do Gostoso, Novo Horizonte, 05° 16' 79" S, 35° 44' 44" W, 14 May 2007, *G.B.C. Paterno 152* (UFP, UFRN); São Vicente, Serra de Santana, 382–512 m, 06° 11' 33" S, 36° 42' 05" W, 16 August 2009, *J.L.C. Lima 233* (UFRN); Serra Caiada, Serra Caiada. Trilha para a vertente Sul, próximo ao final da trilha, no paredão de escalada, 165 m, 06° 05' 39.03" S, 35° 43' 16.03" W, 8 July 2017, *O.L.M. Silva 338* (SP); Serra Negra do Norte, Estação Ecológica do Seridó, 06° 34' 32" S, 37° 15' 56" W, 15 April 2006, *R.T. Queiroz 695* (HUEFS, JPB, UFRN). **Rondônia:** Nova Mamoré, Entre Guajara Mirim e Nova Mamoré, 15 July 2011, *N.C. Bigio 316* (MG); Porto Velho, Prope Urbi, 26 September 1962, *A.P. Duarte 7085* (RB). **Roraima:** Boa Vista, Sede do INPA, 3 June 2003, *R.I. Barbosa 47* (INPA). **São Paulo:** Caraguatubá, Bairro Balneário dos Golfinhos, 21 February 2018, *U.G. Fernandes 483* (SP); Restinga, Estrada Batatis-Franca (SP 334), km 373, ca 22 km de Franca, 680 m, 8 January 1996, *V.C. Souza 9753* (ESA). **Sergipe:** Aracaju, unknown locality, 9 October 2005, *C. Koczicki 510* (MBM); Brejo Grande, Povoado Brejão dos Negros, 10° 27' 58" S, 36° 29' 07" W, 18 September 2015, *M.A.M. Figueiredo 56* (ASE); Canindé de São Francisco, Fazenda Poço Verde, 23 March 2000, *R.A. Silva 1408* (SP, UFP); Maruim, Fundo do Posto Flecha, na margem do Rio Sergipe, no entorno da Caverna de Pedra Branca, 10° 46' 18" S, 37° 07' 53" W, 10 June 2015, *J.A. Santana-Júnior 170* (ASE); Porto da Folha, Povoado Lagoa Grande, Fazenda São Pedro, lado esquerdo da estrada principal em direção ao Assentamento São Judas Tadeu. Próximo à trilha principal do fragmento, 10 May 2011, *D.G. Oliveira 184* (ASE); Riachão do Dantas, Fazenda Salubre, 3 September 1981, *E. Carneiro 32* (ASE); Salgado, Sítio Boa Vista, 5 August 1982, *G. Viana 596* (ASE); Santa Luiz do Itanh, unknown locality, 11° 24' 24" S, 37° 25' 53" W, 27 March 2013, *M.C.V. Farias 390* (ASE). **Tocantins:** Porto Nacional, Perimetro urbano, 25 March 1993, *E.R. Santos 141* (R, SPF, UB); Pords du Rio Tocantins, 1844, *M.A. Weddell 2433* (P). **COLOMBIA. Atlântico:** Barranquilla, unknown locality 1927, *Elias 101* (US). **Guajira:** Cipanao. Finca de Nemesio Montiel, 29 November 1953, *R. Romero-Castañeda 4446* (COL). **Magdalena:** Ciénaga, unknown locality, 17

February 1950, *R. Romero-Castañeda 1980* (COL); Santa Marta, unknown locality, 152 m, December 1898, *H.H. Smith 1476* (BM, E, F, G, K, L, NY, P, U, US, WIS). **Norte de Santander:** La Esmeralda, Vicinity of La Esmeralda, 750 m, 19 March 1927, *E.P. Killip 20939* (NY, US). **Santander:** Inspección de Policía de Pesacadero, sobre el margen derecho del Río Chicamocha, a 100 m de este, 630 m, 06° 49' 05.9" N, 72° 59' 54.3" W, 28 July 1997, *S. Albesiano ALB171* (COL); Intendencia La Guajira: Serranía La Macuira, 500 m, 13 April 1964, *C. Saravia-T. 3632* (COL, US). ECUADOR. **Guayas:** Playas, unknown locality, 19 February 1939, *E. Asplund 5037* (US). **Los Ríos:** Río Palenque Science Center. Km. 56 Rd. Quevedo - Sto Domingo, 30 November 1978, *C.H. Dodson 7317* (MO). **Manabí:** Bahía de Ceraquez, 20 km por la carretera a Chone, 00° 38' 00" S, 80° 25' 00" W, 4 June 1989, *C. Céron 6716* (G, MO, NY); Manta, Dunes E of the town, 4 April 1955, *E. Asplund 15929* (NY, R). **Santa Elena:** La Libertad, 7 March 1941, *H.K. Svenson 11294* (NY, US). FRENCH GUIANA. Cayenne, Est de Cayenne sur rochers de Montravail, 8 April 1982, *G. Cremers 7731* (P); Îles du Salut, Île Royale, 22 February 1985, *G. Cremers 8511* (NY, P); Kourou, Bord de chemin de la savane aux env. de Kourou, May-June 1969, *J. Petitbon 2* (P). GUYANA. **Berbice:** Berbice, Rosiqasi, 1926, *Geison 171* (K, NY, RB). **Demerara-Mahaica:** Georgetown, Golden Grove, November 1905, *A.W. Bartlett s.n.* (K, NY); Mahaica, On coast 20 miles east of Georgetown, 15 November 1919, *A.S. Hitchcock 16774* (NY). **Upper Takutu - Upper Essequibo:** Dadanawa, Rupununi. Foot of Mount Shiriri, 02° 53' 00" N, 59° 43' 00" W, 17 June 1995, *M.J. Jansen-Jacobs 4122* (K, MO, NY, SP); Ogle Estate, E.C. Demerara, 2 m, 7 July 1974, *G. Lee 43* (K). PERU. **Amazonas. Chachapoyas:** Chachapoyas, Balsas, entre Huancabamba y Pusac., 1000 m, 14 April 1982, *I. Sánchez-Vega 2792* (F[2], MO). **La Libertad. Gran Chimú:** Cascas, Alrededores de Puente Ochape, 650 m, 5 May 1994, *A. Sagástegui-A. 15226* (F, MO, NY). **La Libertad. Trujillo:** Trujillo, El Cartigo, 45 m, 17 April 1969, *A. Sagástegui-A. 7196* (F). **Lima:** Panamericana Norte, Río Fortaleza, 25 July 1954, *W. Rauh P1654* (U). **Loreto. Maynas:** Iquitos, Bluff on Río Amazonas, 19 August 1968, *S. McDaniel 10869* (NY, RB); Quistococha, Quistococha, 100 m, 26 December 1973, *F. Ayala 388* (MO); Between Quistococha and Pto Almendras, 03° 46' 00" S, 74° 17' 00" W, 4 May 1987, *W.D. MacRae 100* (F). **Piura:** Negritos, 1928, *O. Haught 36* (G). **Piura. Paitá:** Talara, unknown locality, 10 November 1925, *O. Haught 41* (F, NY, US). **San Martín. San Martín:** Tarapoto, Along Río Cumbaza, 350 m, 06° 29' 00" S, 76° 24' 00" W, 7 November 1980, *T.B. Croat 51139* (F, MO); Granja El Porvenir near Juan Guerra, 260 m, 22 September 1970, *M.S. Chrostowski 100* (WIS). **Tumbes:** Region El Tutumo, 500 m, 22 March 1947, *O. Velarde-N. 428* (US). SURINAME. **Marowijine:** Wia-Wia Res., 250 m ZO van kamp 3 km O van Motkreek, 12 March 1969, *J.T. Sterringa 12446* (WAG); Paramaribo, Paramaribo Gardens, *F.A. Stockdale 8848* (K). VENEZUELA. **Anzoátegui:** Guanta, unknown locality, 1909–10, *I. Boldingh 4125* (U); Puerto La Cruz y Bahía de Mochima, 5 July 1965, *L. Aristeguieta 5565* (COL, L, NY, US). **Aragua:** Maracay, Alrededores de la Facultad de Agronomía, 18 May 1966, *L. Cardenas 17* (F). Tovar, Colonia Tovar, 1854, *A. Fendler 1223* (K, NY). **Barinas:** Barinas, A weed of cultivation, January 1949, *L. Croizat s.n.* (F 1497071). **Bolívar:** Ciudad Bolívar, Ciudad Bolívar and vicinity, on the Orinoco, in the dry season, 3 March 1921, *L.H. Bailey s.n.* (WIS 323776); Southeast of Cerro Pichacho, N. of Las Nieves, 45 kms. N of Tumeremo. Altiplanicies de Nuria, 100–300 m, 1 February 1961, *J.A. Steyermark 88925* (COL, F, NY). **Carabobo:** San Esteban, unknown locality, 1893, *A. Mocquerys s.n.* (COL 150706, NY, P 4830328, US 3022861); Valencia, Vicinity of Valencia, 400–800 m, 22 June 1920, *H. Pittier 8893* (US). **Caracas:** Caracas, Jardín Botánico, 16 March 1950, *L. Aristeguieta 83* (NY). **Delta Amacuro:** Tucupita, Camino entre Tucupita y Los Güires, 50 m, 17 April 1973, *G. Agostini 1614* (INPA, K, L, NY). **Falcón:** Coro, F4. 15 km SE de Coro, arriba de Siburúa, 100 m, 21 April 1978, *R. Wingfield 5346* (U). **Guárico:** San Juan de Los Morros, Near Morro, 400 m, 3 January 1939, *A.H.G. Alston 6079* (BM, NY, US); Ca 39 km south-southwest of Calabozo on Hato Masaguaral, < 100 m, 23 May 1983, *R. Rondeau 241a* (MO, US). **Mérida:** La Guaira, Curucuti, above La Guaira, 30 September 1921, *H. Pittier 9857* (US). **Miranda:** Nueva Esparta, Island of Margarita, 16 July 1901, *O.O. Miller 120* (BM, F, K, NY, P); Pedro Gual, Club Bosquemar, entre Cúpira y Boca de Uchire, September 1997, *A. Fernández-Christian 11573* (WIS); Santa Lucía, unknown locality, 150–200 m, 6–8 March 1943, *E.P. Killip 37059* (US).

**Monagas:** Jusepin, West of Jusepin, Rio Huarapiche, 30 April 1979, *D. Seigler 11157* (MEXU); Maturín, North side of Maturín, 40 m, 4 August 1979, *M. Nee 17154* (F). **Portuguesa:** Guanare, Mesa de Cavanás, Rio Guanare, 7 May 1985, *G. Aymard 3565* (NY). **Sucre:** Cumaná, Bordonos, unknown date, *A. Bonpland 455* (P); Cumanacoa, unknown locality, 1893, *A. Mocquerys 730* (COL, K, NY, P[2], U); El Cocollar de Curuaná, 2 January 1941, *H. Pittier 14684* (US); Em margens de la carretera Cumaná-Cumanacoa, 7 May 1982, *M. Ponce 951* (F). **Vargas:** Entre Osma y Todasana, 150 m, October 1997, *A. Fernández 11916* (WIS). **Yaracuy:** Miranda, Selvas pluviales del Guatopo, 400–600 m, 22 November 1956, *A.L. Bernardi s.n.* (NY); Iboa, 450 m, 3 January 1929, *H. Pittier 13083* (F, G, NY, US). **Zulia:** Bobures, unknown locality, June 1917, *A. Jahn 1319* (US); Quebrada Chiquéra, 29 July 1891, *B. Eggers 13475* (US).

13. *Astraea trilobata* (Forssk.) Silva & Cordeiro (Capítulo III). *Croton trilobatus* Forsskal (1775: 163). Neotype (designated here):—YEMEN: ‘Hille, Gebel Bura’, 400 m, 5 January 1889, *G. Schweinfurth 237* (G!, isoneotype P05478221!). Figs. 33k–l–35.

*Croton courtetii* Beille in Chevalier (1908: 71). Lectotype (designated here):—CHAD. ‘Fort Archmabault’, September 1903, *A. Chevalier 10542* (P04786558!, isolectotypes K!, P04786560!, P04786559!); remaining syntypes:—CENTRAL AFRICAN REPUBLIC. ‘Dendela, dans les terrains cultivés autour des villages’, 26 March 1899, *A. Chevalier 631* (syntype P00540369!); MALI. ‘Sikasso, terrains cultivés’, 21 April 1899, *A. Chevalier 750* (syntype P04786588!); CHAD. ‘Moyenne Tomi: Krébedjé’, 15 December 1902, *A. Chevalier 5749* (syntype P04786568!); CHAD. ‘Ndellé’, 15–20 December 1902, *A. Chevalier 6842* (syntype P04786566!); CHAD. ‘Ndellé’, 23–27 February 1903, *A. Chavalier 7657* (syntype P04786565!); CHAD. ‘Région du lac Iro; Koulfé’, 25–30 June 1903, *A. Chevalier 9200* (syntype P04786564!); CHAD. ‘sud du Baguirmi: Corbol’, 16–22 July 1903, *A. Chevalier 9288* (syntype P04786563!).

*Croton decorsei* Beille in Chevalier (1908: 72). Lectotype (designated here):—CENTRAL AFRICAN REPUBLIC. ‘Région du lac Iro: Souka’, 1 July 1903, *A. Chevalier 9026* (P00540355!, isolectotypes P00540356!); remaining syntypes:—Bas-Chari. Baguirmi: Tchecna, 10–15.VIII.1903, *A. Chevalier 9522* (sintipo P04786561!).

*Croton lobatus* var. *riparius* f. *crispus* Müller Argoviensis (1866: 669). Type:—SENEGAMBIA: unknown locality, 15 March 1829, *G.S. Perrottet 739* (holotype G00312439!).

*Croton perrottetianus* Baillon (1860: 67). Lectotype (designated here):—SENEGAL: ‘in locis siccis circa Joal’, 1824(5), *G.S. Perrotet 190* (P05477674!, isolectotypes G00312447!).

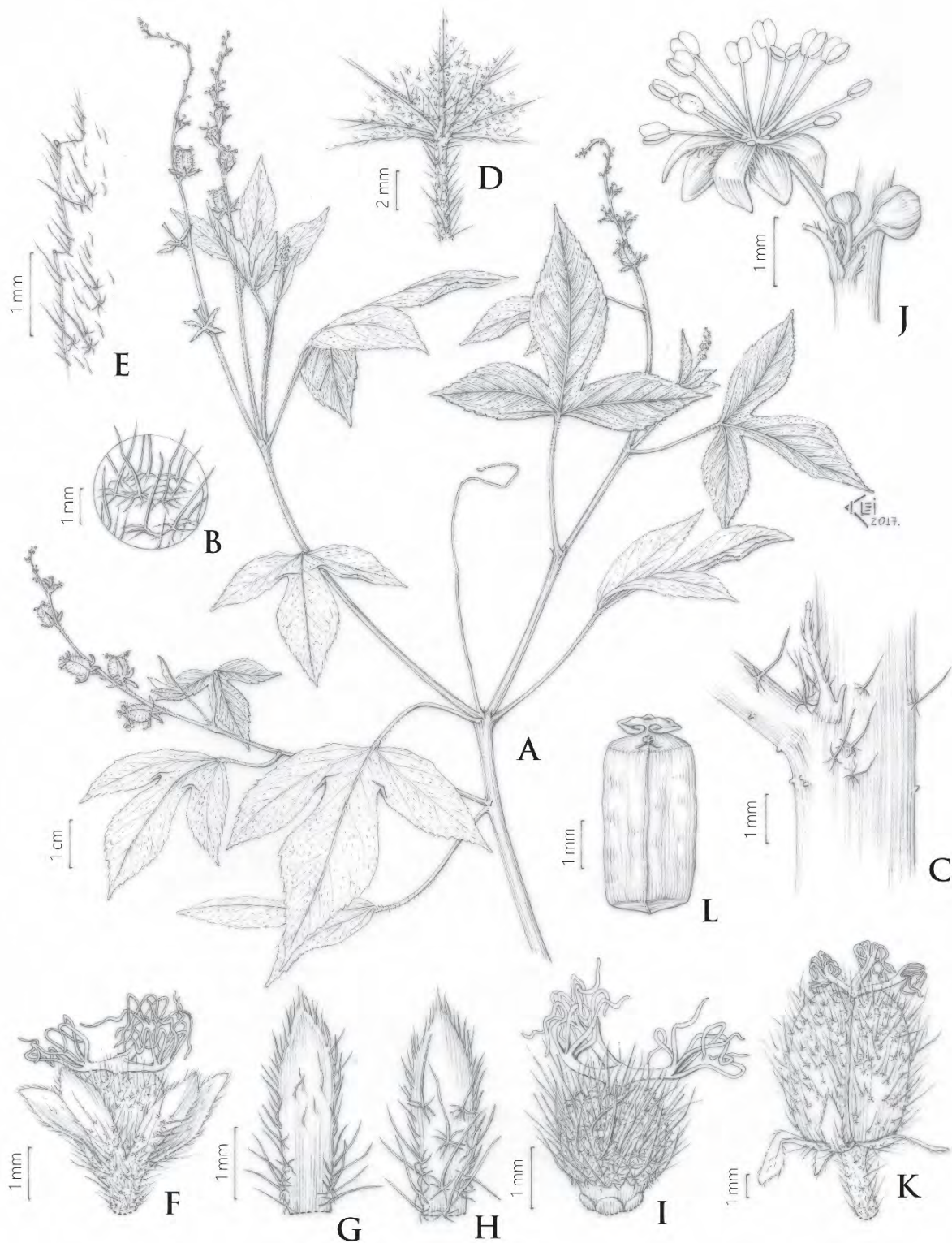
*Croton riparius* Kunth in Humboldt et al. (1817: 90). *Croton lobatus* var. *riparius* (Kunth) Müller Argoviensis (1866: 668). Lectotype (designated here):—PERU: ‘crescit in apricis calidis prope pagum Chamaya’, unknown date, *F.W.H.A. von Humboldt 3654* (P00669896!); remaining syntypes:—PERU: ‘Tomependa’, unknown date, *F.W.H.A. von Humboldt s.n.* (P? – not located); PERU: ‘in ripa fluminis Amazonum, Prov. Jaen de Bracamoros’, unknown date, alt. 200 hex, *F.W.H.A. von Humboldt* (P? – not located).

**Annual or biannual herbs**, phanerophytes, up to 1.5 m high, with erect branches, without a well-developed (xylopodiferous) underground system, branches sparsely to densely pubescent, with stellata-porrect trichomes, bearing a central ray much longer than the lateral rays (with up to 2(–3) mm long), sometimes also



with stellate trichomes. **Leaves** 3(–5)-partite, medium lobe elliptic to wide-elliptic, (3–)4–7(–7.5) x (0.5–)1–3(–3.5) cm, and lateral lobes elliptic or oblong, (1–)1.5–4(–6) x (0.5–)1–2.5(–3) cm, membranaceous, apex attenuate to long attenuate, base rounded, cordate, subcordate, truncate, obtuse or cuneate, margin serrate, with conspicuous teeth, not cartilaginous, ciliate, with simple and stellate or stellate-porrect trichomes, adaxial surface pilose or pubescent, more dense near the base and along the proximal portion of the primary veins, with mostly stellate trichomes, but also with some stellate-porrect trichomes bearing a central ray much longer than the lateral rays (with up to 2(–3) mm long) or intermixed with short (< 0.5 mm) simple trichomes, abaxial surface esparsley to densely pubescent or tomentose, more dense near the base, with stellate or stellate-porrect trichomes bearing a central ray much longer than the lateral rays (with up to 2[–3] mm long), especially near the base or along the veins, venation actinodromous; petioles (0.5–)1–5(–7) cm long, pilose to densely pubescent, with stellate or stellate-porrect trichomes bearing a central ray with much longer than the lateral rays (with up to 2[–3] mm long); stipules subulate, entire or 3(–5)-lobed, medium lobe subulate, 3–8(–10) mm long, and lateral lobes up to 3 mm long), pilose to pubescent, with stellate or stellate-porrect bearing a central ray much longer than the lateral rays (with up to 2[–3] mm) trichomes. **Thyrse** 8–15(–20) cm long, rachis pilose to pubescent, with stellate-porrect trichomes bearing a central ray much longer than the lateral rays (with up to 2 mm long); basal cymules with 3–8 pistillate flowers, accompanied by 1–3 staminate flowers; distal cymules with 1–3 staminate flowers; bracts triangular to subulate, up to 2 mm long, glabrous or pilose to pubescent, with stellate trichomes; **Staminate flowers** with pedicel up to 5 long, glabrous or with sparse stellate or stellate porrect trichomes; calyx glabrous. **Pistillate flowers** with pedicels 2–3 mm, reaching up to 5 mm in fruit, pubescent to densely pubescent, with stellate or stellate-porrect trichomes bearing a central ray much longer than the lateral rays (with up to 2[–3] mm long), calyx lobes 5–6, sometimes with one lobe poorly developed and narrower than the other, lobes elliptic or oblong, (1.5–)3–4, reaching up to 5–7 mm in fruit and 1–2 mm wide, pilose to pubescent on the external face, with stellate or stellate-porrect trichomes bearing a central ray longer than the lateral rays (with up to 2 mm long), margin entire, not cartilaginous, ciliate, with short (< 0.5 mm) simple trichomes, apex acute; ovary 1.5–2.5 x 1.5–2.5 mm, pilose, pubescent or tomentose, with stellate and stellate-porrect trichomes bearing a central ray much longer than the lateral rays (with up to 2[–3] mm long). **Fruits** lustrous, 5–7 x 5–7 cm, pubescent to densely pubescent, with stellate or stellate-porrect trichomes bearing a central ray much longer than the lateral rays (with up to 2[–3] mm long); seeds tetrangular in cross section, 3.5–4(–4.5) x 2–2.5(–3) mm, caruncle ca. 0.5 x 1.5 mm.

**Nomenclatural notes:**—Despite the efforts of Christensen (1922) and Hepper & Friis (1994), the type collection of *Croton trilobatus* Forssk. could not be located at C or any other herbarium where Forsskål’s collections could be deposited. However, Hepper & Fries (1994) refer that the Forsskål’s specimen was collected in 1763, in Wadi Surdud (“Srd= Uadi Surdûd”), Yemen, which corresponds to the Sumara Pass (15°10’N, 42°52’E) in the list of localities these authors presented. Within this background, we designated *G. Schweinfurth 237* as the neotype once this fits the type locality (Yemen) and Schweinfurth’s collections in Yemen were carried out in the memory



**Figure 34:** Line drawing of *Astraea trilobata* **A.** flowering branch, **B.** detail of indumentum of younger portion of stems, **C.** detail of stipules, **D.** abaxial surface of leaf base, **E.** detail of leaf margin, **F.** pistillate flower, **G.** calyx lobe of a pistillate flower – internal face, **H.** calyx lobe of a pistillate flower – external face, **I.** gynoecium and floral nectaries (calyx removed), **J.** staminate cymules with one mature flower, **K.** immature fruit, **L.** seed – ventral face. Illustration by Klei Sousa, based on *L. Holm-Nielsen 2086* (NY).

of Pehr Forsskål and they represent very well the diagnostic characters of this species. Another Schweinfurth's

collection (# 940) also fits the specification above mentioned, but *G. Schweinfurth 237* is deposited in two

herbaria (G and P, instead of just in P in the case of the one numbered as 940) and for this reason was preferred when designating the neotype.

Baillon (1860) cited, as type of *Croton perrottetianus*, an unnumbered specimen collected by G.S. Perrottet in 1825 in Senegal. The author also indicated that this would be a specimen from De Lessert's herbarium. We could not locate any collection fitting all this characteristics at P, but found only one Perrottet's specimen from De Lessert's herbarium, the one numbered as 190. This specimen fits the type locality (Senegal), but was collected in 1824 instead of in 1825 as the protologue indicates. We interpret this as a typo and, therefore, designate G.S. Perrottet 190 as the lectotype of *C. perrottetianus*.

For *Croton riparius* we designated as lectotype the only syntype we found in P, where specimens collected by Humboldt most likely would be held, while for *C. courtetii* and *C. decorsei*, with many syntypes, lectotypes were chosen according to availability of duplicates on different herbaria and/or better conditions of the material regarding presence of as much structures possible.

**Etymology and vernacular names:**—the epithet *trilobata*, as in *lobata*, *palmata* and other names in *Astraea*, is another reference to the lobed leaves of this species. As this species is mainly found in Africa, most of the vernacular names gathered for this species are in African dialects: *abu-thalát*, *alaotouin*, *allahaton*, *allohaton*, *balasa-natudi*, *eru*, *gkwe-one*, *gomakfrin*, *holikonu* and *mataiya*.

**Geographical distribution:**—AFRICA. *Northeast Tropical Africa*: Chad (CHA), Eritrea (ERI), Ethiopia (ETH), Sudan (SUD); *West Tropical Africa*: Benin (BEN), Burkina (BKN), Gambia (GAM), Ghana (GHA), Guinea (GUI), Guinea-Bissau (GNB), Ivory Coast (IVO), Mali (MLI), Mauritania (MTN), Niger (NGR), Nigeria (NGA), Senegal (SEN), Sierra Leone (SIE), Togo (TOG); *West-Central Tropical Africa*: Cameroon (CMN), Central African Republic (CAF), Gulf of Guinea Is. (GGI-BI). ASIA-TEMPERATE. *Arabian Peninsula*: Yemen (YEM-SY); SOUTHERN AMERICA. *Caribbean*: Jamaica (JAM), Windward Is. (WIN-SV); *Northern South America*: Venezuela (VEN); *Southern South America*: Chile (CL); *Western South America*: Colombia (CLM), Ecuador (ECU), Peru (PER).

*Astraea trilobata* is disjunctly distributed between Americas and Africa (Fig. 35). In America, however, it is mostly found in northwestern South America (in Ecuador and Peru), with few specimens from Colombia, Chile, Venezuela and Antilles. The massive majority of specimens are from Tropical Africa, specially from western Africa, and reaching the Arabian Peninsula in Yemen. This species usually grows in disturbed places as anthropic areas and secondary vegetation, but is also found in sandy or rocky soils in savannas, seashore vegetation and sandy dunes, seasonally dry forests, gallery forests and flooded areas. Elevation mostly varies from near sea level to around 600 meters above sea level, reaching up to 1,300-1,400 meters above sea level in Wadi Dabab (Yemen) and Vodni (Nigeria).

**Phenology:**—Flowering and fruiting were recorded throughout the year, usually at the same time. Since no population of this species could be observed in the field, there is no data about visitors and putative pollinators.

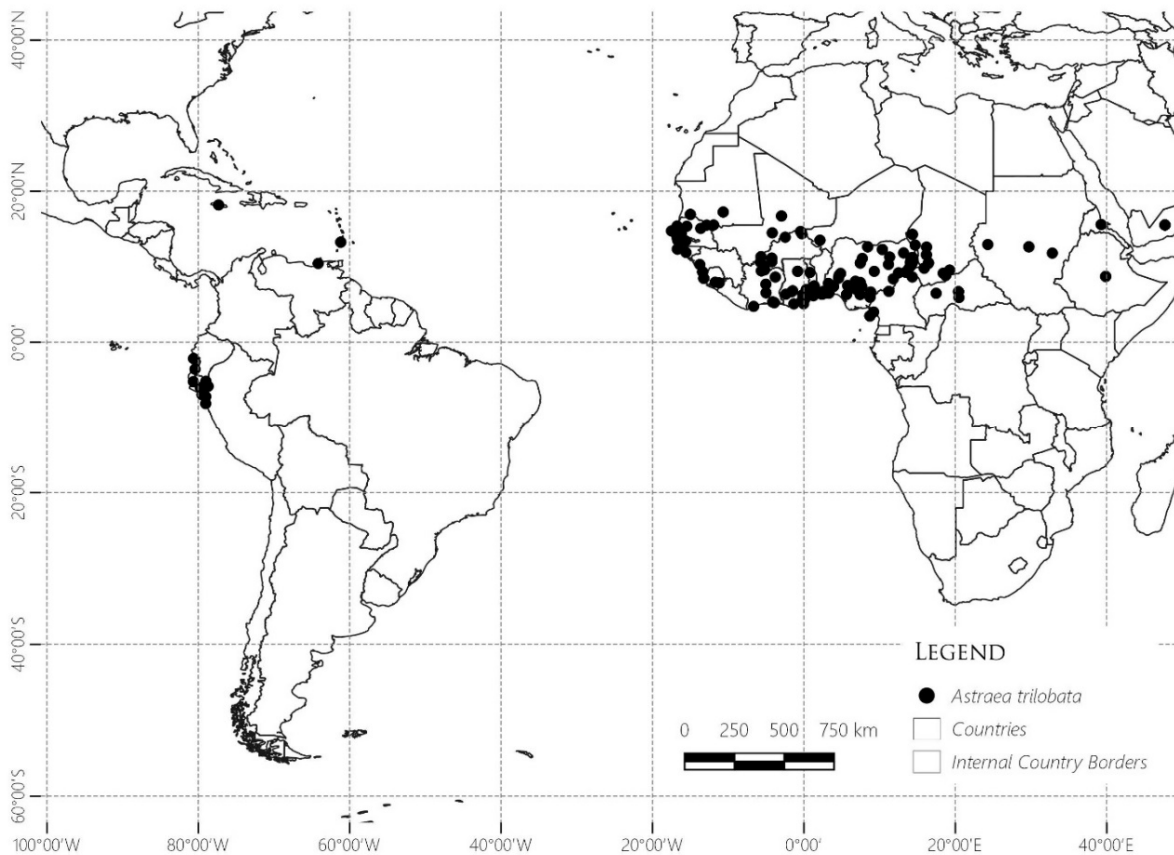


Figure 35: Geographical distribution of *Astraea trilobata*.

**Conservation status**—this is an invasive, widely distributed species, which has a wide extent of occurrence (EOO), with many known locations. As *Astraea surinamensis*, it is found on disturbed environments, apparently expanding its distribution range with anthropic activities. Therefore, according to IUCN (2012) guidelines, it qualifies for Least Concern (LC).

**Taxonomic comments**—*Astraea trilobata* is morphologically more closely related to *A. surinamensis* and may be distinguished from the later by type of trichomes on adaxial surface of leaves, external face of pistillate calyx lobes (Fig. 34H) and fruits (34K). Also, geographical distribution may help in the correct identification of *A. trilobata* (see comments in *A. surinamensis* and Silva et al. [Capítulo III]). This species is mostly found in western Tropical Africa and therefore most of *A. lobata* (or *Croton lobatus*) listed in floras and taxonomic works in this area refers to *A. trilobata*.

**Selected specimens examined:**—[AFRICA] BENIN. **Atlantico:** Djéregbé, unknown locality, 12 October 1971, A.P.M. van der Zon 13 (WAG). **Atlantique:** Abomey-Calavi, Ouèdo jachère, 14 October 2000, A. Akoegninou 3863 (WAG). **Mono:** Lokossa, Lokossa, 06° 38.35' N, 01° 43.02' E E, 14 September 2011, A.M. Towns 549 (WAG). **Ouémé:** Adjohoun, Adjohon, dans un

jardin familial, 11 December 1970, *A.P.M. van der Zon 279* (WAG); Azaourissè, 1 December 1970, *A.P.M. van der Zon 267* (WAG); Porto-Novo, Dahomey, 16 July 1967, *C.L.M. van Eijnatten 2163* (WAG). Cotonou, Sur le sable, pries de la La Lagune, 12 January 1910, *A.J.B. Chevalier 22689* (P); Hovetu, Nouvelle Friche, 2 March 1998, *A. Akoegninou 1354* (WAG). BURKINA FASO. **Oudalan:** Menegou, Village Menegou, 250 m, 21 September 1996, *J.E. Madsen 5758* (HNBU, K). Bobo-Dioulasso, Near Bobo-Dioulasso, 7 October 1967, *C. Geerling 1171* (WAG); **Hte Volta:** Bidi, 4 October 1977, *B. Toutain 1788* (P); Oursi, 16 November 1976, *B. Toutain 1755* (P); Sideradougou, Station Jachère, 897 m, 3 November 1977, *B. Toutain 2218* (P). CAMEROON. **Diamaré:** Maroua, Road to Airport, unknown date, *H.C.D. de Wit 524* (WAG). **North:** Bila, About 8 km E of Pitowa, near the village of Bila, 200 m, December 1964, *W.J.J.O. de Wilde 4954* (WAG[3]); Garoua, Garoua Ecole de Faune, 3 May 1974, *C. Geerling 4645* (WAG); Marshes along the Mayo Kebi, in the Benoue River floodplain, 12 August 1983, *D. Thomas 2415* (K, P); Guider, unknown locality, June 1939, *H. Jacques-Felix 3803* (P); Mora, unknown locality, 1 November 1943, *A. Vaillant 1446* (P); Sanguéré, unknown locality, 24 November 1984, *G. Rippstein 233* (P); About 25 km NNW of Maroua, along road to Mokolo, 450 m, 3 September 1964, *W.J.J.O. de Wilde 3001* (P, WAG); Colline de l'aiguille Messengel près Moutouroua (45 km SSO de Maroua), 28 July 1964, *R. Letouzey 6496* (K, P, WAG); Moran - Wazam, Kassor Gueruevec (mofu), July 1945, *A. Vaillant 376* (P); NE of Magdémé, Km 18 of Mora-Waza road, 324 m, 23 January 1966, *A.J.M. Leeuwenberg 7495* (P, WAG); S.W. Province, Mabeta-Moliwe forest (proposed Reserve). E of Limbe. Mabeta-Limbe road between TC and TD, 50 m, 9 July 1992, *M. Cheek 3526* (K, WAG). CENTRAL AFRICAN REPUBLIC. **Ouaka:** 15 Km NO Bambari, June 1927, *R.P. Tisserant 1825* (P). **Ouham:** Bossangoa, Sudanian wooded savannah with gallery forest with *Uapaca togoensis*, *Hymenocardia acida*, *Detarium microcarpum*, *Daniellia oliveri*, 600 m, 1981–83, *J.M. Fay 5023* (K); Dendela, 26 March 1899, *A.J.B. Chevalier 631* (P); Territoire du Chari: Chari central; rég. Du Iro. Souka, 1 July 1903, *A.J.B. Chevalier 9026* (K, P). CHAD. **Baguirmi:** Sud du Baguirmi: Corbol, 16–22 July 1903, *A.J.B. Chevalier 9288* (P). **Barh Köh:** Sarh, Fort Archambault, September 1903, *A.J.B. Chevalier 10542* (K, P). **Chari:** Lac Iro, Region du Lac Iro; Koulfé, 28–30 June 1903, *A.J.B. Chevalier 9200* (P); Ndellé, Dor. Banda, 15–20 December 1902, *A.J.B. Chevalier 6842* (P). **Hadjer-Lamis:** Rochers de Hadjer el Hamis, 410 m, 14 December 1964, *J. Léonard 3564* (K, P). **Haut-Oubangui:** Moyenne Tomi. Krébedjé, 10 October 1902, *A.J.B. Chevalier 5749* (P). **Mayo-Kebbi Ouest:** Mayo-Boneye, Koyom, 30 November 1969, *G. Fotius 1875 bis* (G). **Moyen-Chari:** Moussafoyo, Ferme de Moussafoyo, 21 November 1964, *J. Audru 1804* (P); Ba Ili, Ferme du Ba Ili, 27 June 1964, *J. Audru 85* (P); Mindera, unknown locality, 27 November 1968, *G. Fotius 1205* (P). CÔTE D'IVOIRE. **Abidjan:** Abidjan, Along Agnéby R., 5 km on road Dabou to Abidjan, 20 June 1979, *A.P.M. de Kruif 187* (WAG); Adiopodoumé, unknown locality, 05° 20' 00" S, 04° 08' 00" W, 29 November 1974, *J. Koning 4937* (G, MA, WAG). **Bas-Sassandra:** San Pedro, unknown locality, 9 February 1900, *s.col. 35* (P). **Lagos:** Tomoudi, Triangle aride de Toumodi. Boka de Titrékro, 21 January 1951, *G. Roberty 13953* (G). **Savanas:** Ferkessedougou, unknown locality, November 1930, *Aubreville 2584* (P); Korhogo, Féléguékaha, 10 June 1984, *P. Poilecot 760CI* (G). **Vallée du Bandama:** Bouaké, Bordes du Nzi, NE de Bouaké, 18 January 1947, *G. Roberty 1912* (G). **Zanzan:** Kakpin, Near Kakpin, 18 April 1968, *C. Geerling 2547* (WAG). Ouangolodougou, 10 km W of Poste de Lingba, along road from Comoé to Ferkessedougou, 9 March 1968, *C. Geerling 2173* (WAG). Reserva de LAMTO, 85 m, 29 May 1986, *D. Béguin 85* (G). EQUATORIAL GUINEA. **Bioko (Fernando Po):** Santa Isabel, 1902, *J.T. Swarbrick 2904* (K). ERITREA. Sciotel, Abida. Falde dello Zedamba, June 1870, *O. Beccari 102* (K); Mt. Kibo pris Saati, unknown date, *G. Schweinfurth 539* (G[2]); Saati, 1891, *G. Schweinfurth 19* (G). ETHIOPIA. Poelleb, unknown locality, 915 m, 25 August 1854, *G.H.W. Schimper 2311* (BM); Abessiniens Halal, August 1972, *J.M. Hildebrandt 610* (BM); Ad pedes montium pr. Goelleb., 23 August 1854, *G.H.W. Schimper 2140* (B); In montibus pr. Mawerr, Alt. 3000–4000, 18 August 1854, *G.H.W. Schimper 2215* (G[2], K[2]). GAMBIA. Bakau, Mile 7, 11 December 1979, *P.J. Terry 2379* (K); Genieri, Upper swamp Crish Old Rd WC, 11 April 1949, *R.H. Fox 134* (K). GHANA. **Accra:** Accra, Achimots College Compound, October 1951, *J.K. Morton 6024* (K); Achimota,

(vazio), November 1937, *J.E. Andoh 4468* (K, P); Prampram, unknown locality, November 1951, *J.K. Morton 6161* (K); Tema, Tema Harbour, 20 March 1954, *J.K. Morton A120* (K). **Ashanti:** unknown locality, unknown date, *H.A. Cummins s.n.* (K). **Northern region:** East Gonja district, Salaga, 10 March 1889, *G.A. Krause s.n.* (E); Tamale, Pong Tamale, 5 July 1932, *T.L. Williams 833* (K). **Volta:** Kpando, unknown locality, 4 June 1974, *W.F. Rodenburg 79* (L, WAG). Elmina, Ashantu, 27 November 1889, *W.H. Brown 99* (US); Kumasi, Ayigyce, June 1973, *F.S. Cudje 629* (WAG); 3 miles before Lumbaga, December 1951, *J.K. Morton 6232* (K); Bomase [Bomasi Tenya], 10 April 1930, *A.S. Thomas D181* (K). GUINEA. Unknown locality, unknown date, *P. Thonning s.n.* (C 10003679). GUINEA-BISSAU. **Bissau:** Antula, unknown locality, 12 October 1949, *E. Sousa 2550* (K). **Cacheu:** São Domingos, Tabanca Varela, Bairro Bile, 11° 56' 08.4" S, 14° 56' 51.7" W, 18 October 1995, *M. Adelia-Diniz 1079* (MA). MALI. **Mopti:** Mopti, Somadougou-Diallo road. At the foot of Bandiagara cliffs, 320 m, 4 October 2007, *R. Dembélé ML-437* (K). **Sikasso:** Kadiolo, Woroni. Chutes de Woroni, 354 m, 11 July 2009, *L. Sanou ML-637* (K); Sikasso, Longorola. Env. 10 km au Nord-Est de Sikasso, 1 October 1996, *A. Raynal-Roques 23917* (P). **Tombouctou:** Tombouctou, unknown locality, 1909, *M.R. Chudeau s.n.* (P 4786585). MAURITANIA. **Gorgol:** Maghana, unknown locality, 19 November 1986, *C. Marc 198* (P). **Guidimaka:** Tektaka, Falaise de l'Assaba, 212 m, 15° 32' 00" N, 11° 56' 31" W, 11 September 2008, *J.-N. Labat 4019* (P). **Hodh el Gharbi:** Tamchakett, N plateau, El Haguer, près Tamchakett, 27 August 1934, *T. Monad 2058* (P). **Trarza:** R'Kiz, unknown locality, 31 August 1934, *T. Monad 2118* (P). NIGER. **Niamey:** Niamey, Yantala-bas, bord du fleuve, 3 November 1974, *P. Lavie 710* (P). Guidinsouni, unknown locality, 1 August 1964, *P. Fabrégues 627* (P); Zamale Station, 3 May 1936, *G. Roberty 1345* (P). NIGERIA. **Adamawa:** Vogel Peak Area. R. Kirimi (=Jiri) valley, Ganglani village, 6 miles east of confluence of R. Kirimi and R. Kam, 360 m, 22 November 1957, *F.N. Hepper 1435* (K, P). **Bauchi:** Katagum, unknown locality, May 1908, *J.M. Dalziel 211* (K). **Bornu:** Fika, Fika, 17 October 1949, *M. Daggash s.n.* (K); Maiduguri, Border of Lake Alo, SE of Maiduguri, 18 July 1982, *E. Denys 669* (WAG). **Cross River:** Ikom, Just East of A. o E.T.C. atives (?), 5 May 1946, *C.F.A. Onochie s.n.* (K). **Edo:** Benin, Left bank of R. Osse at Iguoriakki Ferry, 29 January 1948, *J.P.M. Brenan 8929* (BM, K, P). **Jigawa:** Kazaure, Kafa Mariya Kainchi, October 1979, *R.E. Sharland 834* (K). **Kabba:** Ankpa, Acharane village, 3 February 1958, *J.C. Okafor s.n.* (K, P 5477696); Ukwo-KotonKarfe, 1/2 mile to Niger River, 24 February 1968, *B.O. Daramola s.n.* (K). **Kaduna:** Zaria, Anara F.R. Kan Gimi, 30 November 1946, *R.M.J. Keay s.n.* (K). **Kogi:** Lokoja, unknown locality, 18 September 1908, *A.C. Parsins 40* (K); Nupe, unknown locality, 1906–7, *C.C. Yates s.n.* (BM). **Kwara:** Igala, Ankpa-Ogodo bush, 9 May 1973, *Olorunfemi s.n.* (K); Ilorin, Ilorin Catering Rest House Farmland, 17 September 1971, *P. Wit 367* (K, WAG); Jebba, Nigerdal, 10–20km van Jebba, April 1960, *A. Kamphorst 76* (WAG). **Lagos:** Remartis weed near village, unknown date, *H. Millen 142* (K). **North Eastern:** Gombe, Daddin Kowa. Bank of river Gongola, 2 May 1972, *P. Wit 1652* (K, P, WAG). **Ogoja:** Near Yake village. Bank of river Ahkaliki-Ogoja road, 21 February 1973, *Latilo s.n.* (K, WAG). **Ondo:** Ikare, Ipe-Ikun road, 18 August 1973, *B.O. Daramola BG430* (WAG); Isua, Sosen village, 5 March 1973, *Olorunfemi s.n.* (K, WAG[2]); Oka, Near Iba-Ipe dispensary, 1 May 1979, *B.O. Daramola 135* (K). **Onitsha:** Udi, Enugu, 5 October 1942, *A.P.D. Jones s.n.* (K). **Oyo:** Ibadan, Forestry Hill. Behind Forest Head Office, Ibadan, 30 September 1046, *S. Tamajong s.n.* (K, P). **Yola:** Vango Malaby Hills, 18 May 1909, *J.M. Dalziel 158* (K). **Zaria:** Kaduna, 1 1/2 miles E of Kaduna, 7 July 1965, *J.A.D. Jackson 331* (WAG). Lemme, unknown locality, 790 m, 7 May 1921, *H.V. Lely 134* (K); Tapa, Inselberg near Tapa, 21 April 1958, *D.J. Hambler 432* (K); Vodni, unknown locality, 1400 m, 13 July 1921, *H.V. Lely 429* (K). SENEGAL. **Dakar:** Ngor, Route de la pointe des Almadies, 25 August 1960, *J. Raynal 6258* (P). **Fatick:** Delta du Saloum National Park, 0–40 m, 6–25 September 1991, *A.M. Lykke 445* (K). **Matam:** Namari, unknown locality, 11 July 1934, *J. Trochain 3787* (P). **Thies:** Diourbel [Diourmel], Kaolak. Ravin des Voleurs, 1950–51, *R.P. Berhaut 412 bis* (P); M'Boro[Mbour], unknown locality, 28 August 1934, *J. Trochain 4234* (P); Pir-Goureye, Forêt de Pir-Goureye, 29 October 1930, *J. Trochain 1593* (P); Tivaouane, Diogo. Grande Cote Operations Project N of Dakar = 5 miles from sea, 31 m, 15° 20' 23.7" N, 16° 45' 48.6" W, 27 September 2013, *F.F. Merklinger 2013-9-87* (K). **Ziguinchor:** Oussoye, Basse-Casamance, Abéné,

7 August 1998, *C. Vanden-Berghen 10339* (WAG); Oussoye department, Kabrousse arrondissement. On bord de la ronte, 17 September 1981, *C. Vanden-Berghen 4555* (MBM). SIERRA LEONE. **Meridional:** Bo, unknown locality, 19 January 1914, *N.W. Thomas 7424* (K). **Oriental:** Kenema, unknown locality, 16 November 1926, *F.C. Deighton 440* (K). **Western Area:** Freetown, East of Hastings near Robungba, 21 August 1958, *F.A. Melville 184* (K, P). SUDAN. **Dafur Occidental:** Jebel Marra, unknown locality, 1 August 1964, *G.E. Wickens 2058* (K). **Kurdufan:** unknown locality, 1837–38, *T. Kotschy 85* (BM, G, HBG, K, L, P, TUB, US, W, WAG). **Upper Nile:** Reuk. 902 Ngyok, SSE of Renk, 22 December 1947, *A.C. Hoyle 928* (BM). Bahé á Baudrajaie Dourparadjé, 6 May 1902, *A.J.B. Chevalier 148* (P); Cercle de Gao. Brousse au bord du Niger. Gao rens le montagne Noire, 5 October 1935, *M. Wailly 4835* (P); Palmeraire de Hombori. Subdivision de Douentza. Cercle de Mofti, 25 December 1936, *M. Wailly 5306* (P). TOGO. **Kara:** Bassar, N von Bassar, 18 km W von Kabou, 25 April 1978, *M. Hakki 495* (K). **Maritime:** Lomé, Cacaveli: Felder in der Umgebung des Pflanzenschutz-Instituts, 1 September 1976, *H. Ern 132* (K, P). **Plateaux:** Klouto, Südostseite des Mt. Agou, na der Strasse zum Pic Baumann, 350–450 m, 11 September 1973, *P. Hiepko 159* (K, P); Kpalimé, unknown locality, April 1963, *W. Schwabe s.n.* (B); Ogou, unknown locality, June 1987, *K. Akpagana 1685* (TOGO); Baga, unknown locality, 28 May 1987, *A. Koumantega 333* (TOGO).

[ANTILLES] JAMAICA. Unknown locality, July 1817, *s.col. s.n.* (BM). SAINT VINCENT AND THE GRENADINES. **Saint Vicent:** unknown locality, September 1889, *H.H. Smith 703* (K, NY).

[SOUTH AMERICA] CHILE. Unknown locality, unknown date, *Dombey 917* (P). COLOMBIA. Unknown locality, 1842, *Coll. Illeg. s.n.* (K). ECUADOR. **Santa Elena:** Beach ridges and road side along the Pacific Ocean, between Santa Elena and San Pablo, 02° 10' 00" S, 80° 50' 00" W, 17 March 1973, *L. Holm-Nielsen 2086* (F, NY, MO); Between Santa Elena and Punta Blanca, 22 March 1973, *L. Holm-Nielsen 2393* (NY); Low mountains NE of Chanduy, 19 March 1973, *L. Holm-Nielsen 2169* (NY); Pacifica coast 400 m E of Punta Carnero, 17 March 1973, *L. Holm-Nielsen 2064* (NY). PERU. **Cajamarca:** Pucará, 900 m, 15 April 1950, *F. Woytkowski 5685* (G, US). **Cajamarca. San Ignacio:** San Ignacio, Puerto Huaquillo y Casa Quemada, 600–800 m, 29 January 1996, *J. Campos 2278* (MO). **San Miguel:** Entre Quindén y Platanar (carretera hacia el pueblo de Unión Agua Blanca), 650–1100 m, 6 October 2001, *E. Rodriguez 2418* (F). **La Libertad. Trujillo:** Trujillo, Jardines del Cementerio, 60 m, 15 January 1967, *E. Sánchez-V. 6289* (US). **Lambayeque:** Olmos, unknown locality, 400 m, 4 May 1957, *H. Ellenberg 1245* (U). **Lambayeque. Chiclayo:** Cayalti, At the foot of Cerro Prieto, about 10 miles east of Cape Paviña, 300 m, 1928, *O. Haught F-36* (F). **Piura:** unknown locality, 1909, *A. Weberbauer 5945* (F). **Tumbes:** Tumbes, unknown locality, 50 m, 7 May 1957, *H. Ellenberg 1288* (U); Between Piura and Ñomala, 100–250 m, March 1912, *A. Weberbauer 5948* (US). VENEZUELA. **Sucre:** Cumaná, Bordones, unknown date, *A. Bonpland s.n.* (P 4830335). YEMEN. Agra. Hodjela, 28 January 1889, *G. Schweinfurth 904* (G); Hadjeilah: wadi Hawayat, 700 m, 3 May 1887, *A. Defflers 191* (P); Hille, Gebel Bura, 400 m, 5 January 1889, *G. Schweinfurth 237* (G, P); Jibal Raymah. Road from Al Jabin to Suq Ar Ribat, 1100 m, 22 March 1984, *A.G. Miller 5379* (E); Msil: Wadi Hidjan, 1000 m, 6 May 1887, *A. Defflers 227* (P); Wadi Dabab. 12 km SW of Taiz on At Turbah road, 1300 m, 15 March 1981, *A.G. Miller 3059* (E).



## Incertae sedis

***Astraea palmata*** Klotzsch (1841: 194). nom.nud.

*Astraea palmata* was included as synonym of *Croton lobatus* var. *palmatus* by Müller Argoviensis (1866, 1873), but as no type material, nor diagnosis, is available for any of Klotzsch's name in the original description of *Astraea* we cannot confirm the identity of this name and, therefore, do not link it to any of the currently recognized species of *Astraea*.

***Astraea tomentosa*** Klotzsch (1841: 194), nom. nud.

*Astraea tomentosa* was included as synonym of *Croton comosus* var. *minor* by Müller Argoviensis (1866, 1873), but as no type material, nor diagnosis, is available for any of Klotzsch's name in the original description of *Astraea* we cannot confirm the identity of this name and, therefore, do not link it to any of the currently recognized species of *Astraea*.

***Astraea divaricata*** Klotzsch (1841: 194), nom. nud.

*Astraea divaricata* was included as synonym of *Croton klotzschii* var. *oblongifolius* f. *divaricatus* by Müller Argoviensis (1865, 1866, 1873), but as no type material, nor diagnosis, is available for any of Klotzsch's name in the original description of *Astraea* we cannot confirm the identity of this name and, therefore, do not link it to any of the currently recognized species of *Astraea*.

***Astraea diversifolia*** Klotzsch (1841: 194), nom. nud.

*Astraea diversifolia* was included as synonym of *Croton klotzschii* var. *genuinus* by Müller Argoviensis (1866, 1873), but as no type material, nor diagnosis, is available for any of Klotzsch's name in the original description of *Astraea* we cannot confirm the identity of this name and, therefore, do not link it to any of the currently recognized species of *Astraea*.

***Astraea prunifolia*** Klotzsch (1841: 194), nom. nud.

*Astraea prunifolius* was included as synonym of *Croton klotzschii* var. *oblongifolius* f. *prunifolius* by Müller Argoviensis (1866, 1873), but as no type material, nor diagnosis, is available for any of Klotzsch's name in the original description of *Astraea* we cannot confirm the identity of this name and, therefore, do not link it to any of the currently recognized species of *Astraea*.

***Astraea manihot*** Klotzsch (1841: 194), nom. nud.

*Astraea manihot* was included as synonym of *Croton lobatus* var. *manihot* by Müller Argoviensis (1866, 1873), but as no type material, nor diagnosis, is available for any of Klotzsch's name in the original description

of *Astraea* we cannot confirm the identity of this name and, therefore, do not link it to any of the currently recognized species of *Astraea*.

***Astraea jatropha*** Klotzsch (1841: 194), *nom. nud.*

*Astraea jatropha* was included as synonym of *Croton jatropha* by Müller Argoviensis (1866, 1873), but as no type material, nor diagnosis, is available for any of Klotzsch's name in the original description of *Astraea* we cannot confirm the identity of this name and, therefore, do not link it to any of the currently recognized species of *Astraea*.

***Croton leiocarpus*** Bartling (1855: 3).

This name was published in the Göttingen's seed index. However, no type material could be found at GOET (Marc Appelhans, curator, pers. com.). This name was indicated as synonym of *Croton lobatus* var. *seemanii* by Müller Argoviensis (1866), which is maintained under *Astraea lobata* in this treatment. With no original material available and considering that the description available in the protologue is not sufficient to exactly determine its identity, we do not link this name to any species of *Astraea* in our treatment.

***Schradera scandens*** Willdenow (1797: 1).

*Schradera scandens* is one of the earliest names among the ones involved with *Astraea*. This name was indicated as synonym of *Croton trilobatus* Willd., which we synonymized under *Astraea surinamensis*, but with no original material available and considering that the description available in the protologue is not sufficient to exactly determine its identity, we do not link this name to any species of *Astraea* in our treatment.

## ACKNOWLEDGEMENTS

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## APPENDIX I: NUMERICAL LIST OF TAXA AND LIST OF COLLECTIONS EXAMINED

## Numerical list of taxa

1. *Astraea cincta* (Müll.Arg.) Caruzo & Cordeiro
2. *Astraea comosa* (Müll.Arg.) B.W. van Ee
3. *Astraea digitata* (Müll.Arg.) O.L.M. Silva & Cordeiro
4. *Astraea gracilis* (Müll.Arg.) O.L.M. Silva & Cordeiro
5. *Astraea klotzschii* Didr.
6. *Astraea lobata* (L.) Klotzsch
7. *Astraea macroura* (Colla) P.R.L. Moraes, DeSmedt & Guglielmone
8. *Astraea manihot* (Müll.Arg.) O.L.M. Silva & Cordeiro
9. *Astraea paulina* Didr.
10. *Astraea praetervisa* (Müll.Arg.) P.E. Berry
11. *Astraea subcomosa* (Müll.Arg.) Caruzo
12. *Astraea surinamensis* (Miq.) O.L.M. Silva & Cordeiro
13. *Astraea trilobata* (Forssk.) O.L.M. Silva & Cordeiro

## Collections examined

Collections examined are arranged in alphabetical order by collector's surname, followed by collector number and species number in parentheses. For those collections in which the collector is unknown or unilegible we adopted "s.col." and these collections are presented by the end of the list. "s.n." stands for without number, and herbarium catalogue number are provided in these cases, when available.

A.R.B. 12 (6); Abbott, J.R. 16058 (6), 20947 (12); Abonba, A. P 4786589 (13); Acevedo, P. 645 (12); Acevedo-Rodriguez, A. 1955 (12), 2352 (12), 3103 (12), 3874 (12), 5382 (12), 5574 (6), 15403 (12); Adams, C.D. 3337 (13); Adanson, M. 25A (13); Adelia-Diniz, M. 1079 (13); Adorno, H. 61 (5); Agostini, G. 1614 (12); Agra, M.F. 2019 (12), 2147 (12), 2479 (12), 2532 (12), 2540 (12); Aguilar, R.M. 292 (6); Aguilar-H., M. 68 (6); Akoegninou, A. 1354 (13), 3863 (13); Akpagana, K. 1685 (13); Albesiano, S. ALB1351 (12); ALB171 (12); Albuquerque, J.M. 48 (12), INPA 143085 (12), INPA 143086 (12); Albuquerque, N.A. 34 (9); Alcorn, J.B. 1560 (6); Allard, H.A. 13774 (6); Allem, A.C. 627 (9), 628 (9), 1233 (6), 1354 (6), 1369 (6), 1476 (6); Allemão, F.F. 1362 (12), 7363 (9), R 100549 (9); Almeda, F. 8896 (2); Almeida, E.B. 375 (5), 399 (5); Almeida, J. 83 (5), 1437 (5), 1444 (5); Almeida-Scabbia, R.J. 713 (8); Alonso, A.M. 133 (9), 252 (9), 322 (9), R1248-1 (9); Alston, A.H.G. 6019 (12); Alunos de Botânica III ALCB 67204, CEPEC 107635 (9); Alves, E.S.S. 18 (12); Alves, L.J. 71 (5), 430 (12); Alves, M. 47 (5), EBNN 1144 (12); Alves, M.V. EBNN 1467 (12), EBNN 1511 (12), EBNN 1554 (12), EBNN 1560 (12), EBNN 1567 (12); Alves, M.V.S. 159 (5), 210 (5), 251 (5), 343 (5), 1160 (12), R 172434 (5); Alves, R.J.V. R 217134 (2); Alves, T.M.A. 18 (2); Alves-Araújo, A. 224 (12), 401 (12); Amado, E.F. RB 527758 (4); Amaral, C. 23 (5); Amaral, I.L. 956 (9); Amaral, M.C.E. 04/2003 (8), CFSC 7884 (2); Amaral-Júnior, A. 2052 (9), 2075 (9); Amorim, A.M.A. 87 (5), 496 (5), 1517 (5), 3484 (5), 6768 (5), 7798 (5); Amorim, B.S. 176 (5), 308 (5); Amorim, E. ALCB 21290 (5); Anderson, W.R. 7315 (9), 8846 (2), 11653 (5), 35194 (2), 36079 (2), 10169 (9), 10313 (9), 8953 (2); Andoh, J.E. 4468 (13); Andrade, A.G. 525 (9), 1551 (12); Andrade, N.M. 175 (5); Andrade, V.C. PEUFR 21949 (9), PEUFR 34331 (9);



Andreata, R.H.P. 58 (5); Aparecida da Silva, M. 2368 (9), 4276 (4), 6755 (9); Araújo, A.A.M. 4 (12); Araújo, A.C. 994 (6); Araujo, D.S.D. 66 (7), 299 (12); Araújo, F. 50 (12); Araújo, G. 69 (5); Araujo, G.B. 358 (12); Araújo, I. 7 (12); Araújo, T. 14 (5); Arbo, M.M. 5064 (2), 5281 (2), 5809 (9), 7172 (5), 7173 (5); Archer, W.A. 7668 (12); Arenas, P. 1310 (6); Aristeguieta, L. 83 (12), 5565 (12); Arnaldo 2046 (12); Arnoldo, M. 331 (12), 499 (12), 733 (12), 1724 (12); Arnoldo-Broeders, M. 3646 (12); Arouck-Ferreira, J.D.C. 364 (9); Arruda, W.S. 35 (6); Arthur, F. EAC 39434 (12); Asplund, E. 5037 (12), 15929 (12); Assis, A.M. 584 (5); Assis, J.S. 365 (12); Assis, M.C. 294 (9); Assis, V. 92 (8); Ataíde, M. 99 (12); Atala, F. 74 (5), 82 (5), 87 (5); Atha, D.E. 691 (12), 1143 (6); Atkins, S. PCD4594 (5); Atwater, W.G. 781 (6); Aubreville 2584 (13); Audru, J. 29 (13), 85 (13), 1804 (13), 3997 (13), 4003 (13); Audry, P. B7 (13), E4 (13); Augusto, B. 324 (12); Avery, G.N. 1743 (6); Ayala, F. 388 (12); Aymard, G. 3565 (12); Azevedo, N.G. 4 (12).

Bacelar, T.G. 55 (4); Badini, J. OUPR 4509 (8), OUPR 6083 (2), OUPR 6087 (2), OUPR 6089 (2), OUPR 6110 (2), OUPR 6111 (2); Báez, C.G. 6612 (6), 7449 (6), 7866 (6); Baglione, F. PACA 2948 (6); Bailey, L.H. WIS 323776 (12); Baker 528 (6); Baker, J.G. 9204 (12); Baksh, Y.S. 466 (12); Balansa, B. 1700 (6), 1705 (6); Balderrama, J. 620 (6); Bambey, C.R.A. 668 (13); Bandeira, F.P. 167 (12); Bang, M. 2130 (6); Bao, F. 8 (6); Barbosa, E. 2745 (12); Barbosa, M. 113 (12); Barbosa, R.I. 47 (12); Barbosa, V.P. 169 (12); Barboza, E. 3623 (9), 3676 (9), 3808 (11); Barreto, K.D. 1462 (9); Barreto, M. ALCB 6456 (8); Barros, A.A.M. 518 (8), 927 (5); Barros, C.S.S. 49 (5); Barros, F. 1349 (2); Barter, C. 1158 (13); Bartlett, A.W. K, NY (12); Batalha, M.A. 3109 (1); Baumgratz, J.F. 139 (5); Bautista, H.P. 481 (5), 535 (5), 3029 (9); Bayma, I.A. 62 (5), 185 (5), 206 (12), 889 (3), MAC 61886 (5); Beauvois, P. G 312445, G[3] (13); Beccari, O. 102 (13); Beck, G. 8180 (6), 15024 (4); Béguin, D. 85 (13); Behar, L. 19 (5), 540 (5); Bélanger, C.P. 269 (12); Belchior, V. 1 (8); Belém, R.P. 291 (5), 534 (4), 2062 (5); Belgrano, M.J. 2668 (6); Belle, W. 153 (8); Bello R 100906 (5); Bena, P. 215 (12), 358 (12), 1603 (12), P 4831552 (12); Benko-Iseppon, A.M. 1791 (9); Berg, C.C. BG 512 (9); Berhaut, R.P. 412 bis (13); Bernardi, A.L. NY (12); Bernardi, M. 19200 (4); Bernoulli, K.G. 2489 (6); Bezerra, G.J. 62 (12), 63 (12); Bezerra, P. EAC 150, UFP 50121 (12), EAC 478 (9); Bianchetti, L.B. 1182 (9), 1206 (9); Bicudo, L.R.H. 1 (9); Bigio, N.C. 316 (12); Billiet, F. 4520 (12); Binuyo, A. K, WAG (13); Blake, S.F. 7315 (6); Blanchet, J.S. 92 (3), 167 (3), 422 (3), 1071 (5), 3155 (10), 3216 (5), 3654 (9), 3155A (10), 3216A (5), BM (12), F 521057 (3), G (3), (5), (12), G 312461 (10), SP 8505 (12); Boege, W. 830 (6); Boldingh, I. 1276 (12), 4125 (12), 4685 (12), 1839B (12), 1843B (12), 6475G (12), 74B (12), 964B (12); Bonilla, O.H. 10 (12); Bonpland, A. 450 (12), 455 (12), P 4830335 (13); Boom, B.M. 11121 (12); Bordas, E. 4186 (6); Botelho, A. MA 380606, MBM 71701 (6); Botta, S.M. P 5478220 (13); Bounougou, E. 90 (12), 112 (13); Box, H.E. 946 (12), 1689 (12); Boyle, B. 6618 (6); Brace, L.J.K. 41 (6), 353 (6); Brade, A.C. 11216 (4), 14147 (5), 7336 (8), 7337 (8); Bradley, K. 1596 (6), 1843 (6); Braga, D.V. IPA 73896 (12); Braga, J.M.A. 57 (4), 2642 (5), 4266 (9), 7335 (5); Braga, L.M. 1 (9); Braga, P.I.S. 2384 (5); Brandão, M. 11366 (2), 17221 (8), 17247 (8); Brantjes, N.B.M. 706409 (12); Breckon, G.J. 2345 (6), 6353 (12); Bredemeyer, F. W (12); Breedlove, D.E. 26650 (6), 51010 (6), 51886 (6); Brenan, J.P.M. 8929 (13); Brenes, A.M. 12545 (6); Breteler, F.J. 3894 (6); Brito, J.C. 23 (9), 96 (9); Britton, N.L. 120 (6), 226 (12), 783 (6), 2911 (12), 3006 (12), 5911 (6); Brizuela, J. 197 (6), 942 (6), 1269 (6), 1325 (6); Broadway, W.E. 5164 (12), 6363 (6), 7832 (12), 9040 (12), G[2], NY 1384372 (12); Broun, A.F. 5 (13); Brown, W.H. 99 (13); Brunel, J.-F. 609 (13), 674 (13), 3891 (13), 5396 (13), 7273 (13), 7484 (13), 10529 (13); Buchtien, O. 640 (6), 1200 (6); Buck, P. PACA 11099 (6); Burch, D. 1320 (12), 3216 (12), 3439 (12), 6609 (12); Burchell, W.J. 1015 (4), 2855 (4), 7882 (8), 9021 (12), 9606 (12); Burkart, A. 21250 (6), 21256 (6), 23385 (6), 27864 (6); Burton, R. 118 (12).

C.M.M. 18 (4); Caballero-Marmori, G. CTES 166098 (1); Cabrera, A.L. 17254 (6); Cabrera, E. 8883 (6), 14031 (6), 14745 (6), 14811 (12), 15087 (12); Cabrera-C., E. 14548 (12); Caldeira, F.M. 17 (8); Calderon, G.M. 1340 (6); Calzada, J.I. 15402 (6); Campêlo, C.R. 1351 (12), EAC 10648 (12); Campos, D.A. 192 (5), 227 (5), 331 (5); Campos, J. 2278 (13), 3324 (6); Cano, O. 88

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Daggash, M. K (13); Daly, D.C. 1738 (9), 2159 (9), 1066 (9); D338 (6); Dalziel, J.M. 158 (13), 211 (13), 212 (13), 1177 (13), 1363 (12), BM (13); Damasceno-Júnior, G.A. 1851 (4); Damazio, L. 220 (2), 1779 (2); Dantas, A. 198 (12); Daramola, B.O. 135 (13), BG430 (13), K (13); D'Arcy, W.G. 4705 (12), 6872 (6), 13391 (12), 34A (12); Davey, J.T. 8 (13); Davidse, G. 35394 (6), 35502 (12); Davis, P.H. 60385 (12); Dawody, T.B. 30 (13), 147 (13); Dawson, E.Y. 14973 (9); De Kruif, A.P.M. 187 (13); De la Sagra, R. 103 (6), G (6), P 4831523 (6), P 4831524 (6); De la Sota, A.V. 1965 (6), 4480 (6); De Lessert, J.P.B. G (6), NY-BN (2); De Signaup, R. G (12); De Wilde, P.A.W.J. 64a (12), L 2202964 (12); De Wilde, W.J.J.O. 3001 (13), 4954 (13); De Wit, H.C.D. 524 (13); Deam, C. 6284 (9); Debeaux, O. 163 (13), 339 (13), P 4831545 (12); Deflers, A. 191 (13), 227 (13), 230 (13); Deginani, N.B. 1592 (6);

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F.C.C. 181 (6); Fabrégues, P. 627 (13), 778 (12), 2380 (12); Fabris, H.A. 5044 (4); Falcão, J.I.A. 780 (12); Faria, J.E.Q. 955 (2), 1028 (9); Faria, M.B. 150 (5); Farias, M.C.V. 390 (12); Faxina, C. 226 (6); Fay, J.M. 5023 (13); Feddema, C. 1286 (6); Felix, L.P. 11278 (12); Fendler, A. 686 (6), 1223 (12); Fernandes, A. 2007 (5), EAC 12469 (4), EAC 14808 (9), EAC 27895 (12), EAC 5563 (12), EAC 9921 (12); Fernandes, C.E.B. 197 (6); Fernandes, C.H.M. 97 (12), 106 (12); Fernandes, U.G. 246 (9), 247 (9), 248 (9), 483 (12); Fernández Casas, J. 6048 (4), 10808 (6); Fernández, A. 11916 (12); Fernández-Christian, A. 11573 (12); Ferrari, G. 134 (12); Ferraz RB 77752 (3); Ferreira P 4830306 (12); Ferreira, A.G. 32 (1); Ferreira, C. 83838 (12), 83845 (12), 83893 (12), 83905 (12); Ferreira, C.D.M. 121 (5); Ferreira, H.M. 141 (5), 209 (4), 255 (4); Ferreira, J.L. 279 (12); Ferreira, M.B. 1544 (3); Ferreira, M.C. 165 (12), 639 (5); Ferreira, M.S.G. 250 (12); Ferreira, P. 67-29 (5); Ferreira, V.F. 3303 (9); Ferreira-Júnior, W.S. 40 (12); Feuillet, C. 2184 (12); Fevereiro, V.P.B. M153 (12); Fiaschi, P. 243 (5), 651 (5), 873 (2), 910 (2), 1103 (5); Fiebrig, K.A.G. 1273 (6), 4281 (6), 4446 (4), 4564 (4), 4586 (6); Figueiras, L. 8483 (9); Figueiredo, M.A. 56 (5); Figueiredo, M.A.M. 56 (12); Figueiroa, L.E. 46 (5); Filardi, F.L.R. 824 (5); Fina, B.G. 57 (8); Fishlock, W.C. 247 (6); Flaster, B. 37 (5); Flint, E. US 1229360 (BC) (6); Flores, S. 53 (6); Flores, T.B. 1742 (5); Flores-M., A. IEB 51084 (6); Folli, D.A. 1974 (7), 2683 (5), 2834 (12), 3208 (5), 3335 (7), 5974 (7); Fonseca, M.L. 1362 (9), 1698 (9); Fontella, H. 1382 (5); Fontella, J.P. 231 (5); Fontenelli, G. 10 (5); Forsström, J.E. S 13-19979 (12); Fortunato, R. 6532 (6); Forzza, R.C. 2831 (5), 5346 (5); Fosberg, F.R. 55367 (12); Fotius, G. 1205 (13), 3259 (12), 1875 bis (13), P 5477588 (13); Fournet, A. 4181 (12); Fox, R.H. 134 (13); França, F. 957 (3), 4489 (11), 4556 (2), 6178 (12); Frazão, A. RB (4); Freire, A.S. 506 (5), 550 (5), R 99790 (4); Freire, C.V. 752 (8); Freire-Fierros, A. 1688 (9), CFCR 12700 (11); Freitas-Filho, F. 54 (12); Fries, R.E. 235 (6), 1436 (4); Fróes, R.L. 20226 (9); Fryxell, P.A. 3764 (6); Fuentes, A. 1021 (6); Funch, R. 148 (9), FCD5 (9); Furlan, A. CFCR 273 (9), CFCR 396 (9), CFCR 7640 (9).

Gadelha Neto, P.C. 275 (12), 1192 (12), 1292 (12), 1828 (12), 1851 (5); Gajardo, I.S.M. 08-2001 (2); Ganev, W. 60 (11), 375 (11), 1943 (9); Garcia, E.A.P. 1874 (6); Garcia, L.M. 731 (6), 811 (6); Garcia-Barriga, H. 13419 (6), 13433 (6); Gardner, G. 230 (4), 1131 (12), 1137 (5), 1397 (5), 1839 (9); G (5), NY-BN (9), P 4830276 (4); Garnier, A. 912 (6); Gaston, A. 2311 (13); Gaudichaud-

Beaupré, C. 56 (3), 969 (8), 1129 (4), 1729 (4), P 4830311 (3); Gaumer, G.F. 760 (6); Gchriger, W. 120 (12); Geerling, C. 39 (13), 1171 (13), 1470 (13), 2173 (13), 2547 (13), 4645 (13); Geison 171 (12); Gemtchújnicov, I.D. BOTU 12234 (12), BOTU 12282 (12), BOTU 12283 (12), BOTU 17036 (12), BOTU 9826 (9); Gentle, P.H. 4934 (6); Gentry, A. 63570 (6), 71409 (6); Giannotti, E. 8379 (9); Giaretta, A.O. 93 (5); Gillis, W.T. 8358 (6); Gilly, C.L. 153 (6); Ginzburg, S. 404 (6), 652 (4), 653 (4); Giorni, V.T. BHCB 163858 (2); Gislane EAC 33903 (12); Giulietti, A.M. 2239 (11), CFCR 13833 (2), CFCR 1424 (9), CFCR 2496 (2), CFSC 6406 (2); Giulietti, N. 707-68 (9); Glaziou, A.F.M. 686 (4), 9588 (4), 11509 (12), 11510 (9), 13200 (4), 14246 (12), 15390 (2), 15402 (11), 19827 (2); Glocker, E.F. 58 (3), BM (3); Godoy, S.A.P. CFSC 10834 (2); Goldenberg, R. 1044 (5), 1415 (5); Gomes, E. 74 (12), 100 (5); Gomes, F.S. 852 (5); Gomes, J.M.L. 59 (12), 148 (12), 259 (12), 485 (12), 3356 (7); Gomes, L.A. 612 (5); Gomes, P. 36 (12), 395 (12); Gomes, S.M. 751 (8); Gonçalves, D. 6 (5); Gonçalves, L.M.C. 167 (9); Gontijo, F.D. 608 (8); Gonzaga, D.R. 569 (2); Gonzalez 15 (6); González, J. 3939 (6); Goodwip, E.G.B. 267 (12); Goudon G (6); Goudot, J. P 4830337 (6), P 4830338 (6); Gouin, F.M.G. 18 (6); Graham K 1210210 (4); Grandi, T.S.M. 15 (9), 22 (8), 338 (9); Granville 1300 (4); Grayum, M. 8562 (6); Grijalva, A. 1844 (6); Gris, D. 102 (6); Groenendijk, E. 87 (12); Grosourdy, R. P 4830325 (12), P 4831502 (12), P 4831521 (6); Grupo Pedra do Cavalo 115 (12), 284 (12), 1065 (12); Guarino, E.S.G. 399 (9); Guedes, M.L. 1093 (9), 1192 (5), 1556 (9), 1804 (9), 2015 (9), 3170 (5), 4071 (5), 4713 (5), 4878 (5), 6036 (5), 6533 (5), 7426 (9), 8199 (5), 8212 (5), 9605 (5), 9615 (5), 9974 (5), 10818 (5), 11105 (5), 11485 (12), 12243 (12), 14704 (12), 15138 (5), 15764 (12), 16281 (12), 19023 (4), 19345 (5), 19610 (5), 20240 (5), 20655 (12), 20913 (12), 21145 (5), 23230 (5), 23895 (9), 24296 (12), 24737 (12), ALCB 15832 (5), ALCB 27521, MBM 249968 (5), ALCB 27934 (3), PCD 595 (9), PCD 597 (9); Guerrero-C., B. 967 (6); Guillemin, J.B.A. 167 (4); Guillen, J. 282 (6); Guimarães, E.F. 175 (5); Guimarães, J. 203 (1); Gusmão, E.F. 38 (12); Gutierrez, J. 81999 (6); Gutiérrez, L. 207 (12).

Hage, J.L. 455 (4), 917 (4), 929 (4), 1118 (3), 1986 (4), 2138 (4); Hageroup, O. 542 (13); Hahn, W. 1728 (4); Hakki, M. 495 (13); Hall, D.W. 1276 (12); Hambler, D.J. 432 (13); Hans, D. 124 (5); Hansen, B.F. 7435 (6); Harley, R.M. 11502 (9), 17215 (5), 17592 (5), 18293 (5), 20545 (9), 20581 (9), 20640 (9), 22192 (5), 22442 (9), 22681 (9), 22723 (9), 24417 (9), 25109 (11), 25311 (9), 26231 (9), 26625 (9), 27194 (9), 27295 (11); Harriman, N.A. 15630 (6); Harrison, S.G. 882 (12); Harrola, C. 1783 (6); Harter K (13); Hassler, E. 2706 (6), 4386 (1), 5010 (1), 5068 (9), 7989 (4), 9509 (1); Hatschbach, G. 4403 (8), 4984 (8), 8648 (8), 12959 (1), 15918 (1), 24516 (8), 34401 (8), 39689 (9), 42375 (9), 42733 (8), 44730 (2), 47053 (5), 48011 (9), 52613 (1), 53490 (5), 56805 (9), 61583 (4), 63096 (5), 63333 (5), 65703 (4), 67370 (2), 70033 (9), 71273 (12), 75110 (5), 75307 (5), 75396 (3), 75573 (12); Haight, O. 36 (12), 41 (12), 6463 (12), F-36 (13); Hauthal, R. 14 (1); Hayes, S. 712 (6); Hayes, T.R. 588 (13); Heircher P 4830246 (3); Heleodoro, N.M. 124 (12); Heller, A.A. 1007 (12), 4607 (12); Hensold, N. CFCR 2930 (2), CFSC 7734 (2); Hepper, F.N. 1435 (13); Heriberto, B. 284 (6); Heringer, E.P. 420 (8), 974 (12), 1689 (9), 3093 (9), 3830 (9), 3996 (9), 6853 (9), 13838 (9), 10184 (9), 3435a (3); Hernandez-A., C. 166 (6); Hernández-G., H. 332 (6); Herndon, A. 2249 (6); Herter, W.G. 50729 (6); Heudelot 465 (13), P 5477684 (13); Hiepko, P. 159 (13); Hieronymus, G. 203 (6), 276 (6); Hildebrandt, J.M. 610 (13); Hill, S.R. 24043 (12), 24814 (12); Hinton, G.B. 3577 (6), 4568 (6), 5508 (6); Hitchcock, A.S. 16774 (12); Hoehne, F.C. 2695 (6), 2697 (6), 6522 (8), SP 1521 (8), SP 35784 (1), SP 4877 (2); Hoehne, W. 5545 (12), 5578 (5), 5517 (12), 5771 (5), R 149074 (6), R 149075 (8); Hoff, M. 5103 (12), 5491 (12); Holm, R.W. 280 (6); Holm-Nielsen, L. 2064 (13), 2086 (13), 2169 (13), 2393 (13); Holt, E.G. 1 (12), 120 (12), 859 (6); Holton, I.F. 817 (6), 851 (12); Hooker, W.J. K (6); Hostman L 2202942 (12); Houle 167 (4); Hourst, M. P 4786584 (13); Howard, R. 206 (6); Howard, R.A. 5150 (6), 19027 (12), 20338 (12); Hoyle, A.C. 928 (13); Hubbard, J. 626 (6); Huidobro, A.M.R. 3471 (6), 3583 (6), 3642 (6), 4213 (6); Humboldt, F.W.H.A. 411 (12), 3654 (13), P 669895 (6); Hunziker, J.H. 12275 (4); Hurbath, F. 451 (4), 531 (12), 620 (12), 666 (9).

Idrobo, J.M. 6617 (6); Irwin, H.S. 2124 (8), 6038 (9), 7313 (1), 7527 (1), 8490 (9), 9142 (9), 10535 (9), 10837 (9), 10932 (9), 11876 (9), 15281 (9), 15591 (9), 19093 (9), 19780 (8), 22603 (2), 22877 (2), 26240 (9), 27517 (2), 28057 (2), 28289 (8), 28983 (2), 30286 (8), 30289 (8), 34038 (9), 20520a (2), Isler 224 (6).

Jack, J.G. 6107 (6); Jackson, J.A.D. 331 (13), WAG 1798128 (13); Jacquemont, V.V. P 4831449 (12), P 4831451 (12); Jacques-Felix, H. 3803 (13); Jahn, A. 1319 (12); Janieson, M. E (4); Jansen-Jacobs, M.J. 4122 (12); Jarenkow, J.A. 3344 (6); Jenman, G.S. 152 (12); Jérémie, J. 181 (12), 796 (6); Jesus, J.A. 335 (4), 385 (5), 485 (5), 498 (5), 563 (5), 1558 (7), 2016 (7); Jesus, N.G. 862 (12), 934 (5), 1788 (5), 1828 (5), ALCB 86823, HRB 56593, HUEFS 144763 (3); Jimenez, J. 827 (12); Jiménez, S.M.C. UFP 6794 (12); Jones 3248 (6); Jones, A.P.D. K (12), (13); Jongkind, C.C.H. 1353 (13); Jorgensen, P. 2853 (6), 4900 (6); Jouvin, P.P. 404 (5); Juarez, A.A. 173 (6); Jung, S.L. 32 (8), 33 (8), 34 (8), 35 (8), 36 (8); Junior, J.H.C. 5 (12); Junk 1052 (12); Jussieu, A.H.L. 16370 (2), +A (12), K (4).

Kamphorst, A. 76 (13), 230 (13); Kappler, A. 1573 (12); Karsten, H. 1 (12), BM (12); Kawall, S.L. SP 468426, SPF 70593 (9); Keay, R.M.J. K (13); Kegel, H.A.H. 115 (12); Kellerman, W.A. 7940 (6), 8063 (6); Kennedy, H. 865 (7), 998 (4); Kerr, J.G. E, K (6); Khan 1381 (6); Khan, N. 1 (12); Killip, E.P. 20939 (12), 37059 (12), 30305 (12); Kinoshita, J.H. 00/246 (2), 11-198 (9), 11-259 (9); Kirkbride, J.H. 3339 (9); Kitson, A.E. BM (13); Klein, V.L.G. 220 (7), 2779 (9), 3021 (9), 3387 (9); Koch, R.G. 4886 (6); Koczicki, C. 510 (12); Kollman, L. 8041 (7), 9128 (5), 12090 (5), 6605 (5); Koning, J. 674 (13), 4937 (13); Korte, A. 3876 (8); Korthal L 2209248 (12); Kotschy, T. 21 (13), 44 (13), 85 (13), L 2202983 (13); Koumantega, A. 333 (13); Kranz, W.M. 552 (6); Krapovickas, A. 23200 (5), 23946 (6), 30822 (6), 44365 (6), 45498 (6), 45759 (1), 46351 (6); Krause, G.A. E (13), K (13); Krause, L. 172 (12); Krebs NY 1384387 (12); Kress, W.J. 94-4349 (6); Krieger, L. 7522 (8), 10416 (5), 11446 (8); Kuhlmann, J.G. 736 (6), VIC 1492 (8), VIC 2331 (8); Kuhlmann, M. 3700 (6), SP 36675 (8); Kuniyoshi, Y.S. 5820 (6); Kuntze, O. 907 (6), NY (6), NY 1384362 (12).

Labat, J.-N. 4019 (13); Labaux L 2202934 (13); Laca-Buendia 1178 (8), 1199 (8); Lamand, A. 20 (9); Lamarck, J.B.A.P.M. 181 (12), P (13); Landrum, L.R. 4282 (8); Lanna-Sobrinho, J.P. 488 (5); Larcher, B. 14745 (12); Lasseign, A. P21183 (12); Latilo K, WAG (13); Laurênio, A. 473 (12), 1012 (5), 2031 (12); Lavie, P. 710 (13); Le Testu, G. 155 (13); Leal, C.G. 58 (5), RB 62098 (12); Leão, L.M. 129 (3); Leão, T. 125 (12); Leavenworth, W.C. 494 (6), 1364 (6); Lécard, T. 64 (13), 186 (13); Ledin, R.B. 50 (6), 390 (6); Lee, G. 43 (12); Leeuwenberg, A.J.M. 2264 (12), 4160 (12), 7495 (13); Lehmann 68 (4); Leitão Filho, H.F. 1576 (8), 12968 (4), 9565 (2); Lely, H.V. 134 (13), 429 (13); Léman P 5478219 (13); Lemée, A.M.V. P 4831477 (12); Lemos, J.P. BHCB 68544 (2); Lems, K. NY 504546 (5); Leonard, E.C. 2775 (12), 4886 (12), 15818 (12); Léonard, J. 3564 (13); Leprieur, F.M.R. P 5477679 (13); Lequillou P 4831494 (12); Letouzey, R. 6496 (13), 14593 (12); Lévy, P. 245 (6), P 4831505 (6); Lewis, G.P. 890 (9), CFCR 7149 (9), CFCR 7299 (9); Lhostky, J. G 312449 (3); Liebmann P 4831461 (6); Liene 3561 (5), 3680 (5); Lima, A. PEUFR 1413 (12), PEUFR 1414 (12); Lima, A.F.S. UEC 183691 (5); Lima, D.A. 98 (5), 49-298 (5), 50-508 (5), 51-824 (2), 68-5404 (9), 81-8978 (9), 81-9017 (9); Lima, G.C. 44 (12); Lima, H.C. 6530 (5), 6543 (5); Lima, I.B. 681 (12), 877 (12); Lima, J.L.C. 233 (12), 294 (12); Lima, L. IPA 46915 (12), IPA 46916 (12); Lima, L.R. 133 (2), 147 (2), 173 (9), 236 (2), 261 (11), 367 (8), 478 (9); Lima, R. 2321 (12); Lima, T.E. 28 (6); Lima, V.C. 478 (12); Linares, J.L. 2950 (6), 5091 (6), 5992 (6), 7090 (12); Lindeman, J.C. 41 (5), 4531 (1), U 1267575 (6); Linneo, I. 613 (6); Liogier, A. 269 (12), 17380 (12); Liogier, A.H. 20314 (6); Lira, O.C. 63-67 (5); Lira, S.S. 355 (5), 356 (5), 431 (5), 496 (5), 528 (5), 562 (5); Lira-Neto, J.A. 288 (4); Lisboa, P. 1365 (9); Lisboa, R. 6780 (12); Lisowski, S. D-36 (13); Lobão, A.Q. 2 (5), 12 (5), 36 (5), 46 (5), 48 (5), 56 (5); Lobato, L.C.B. 4530 (12); Lobo, M.G.A. 159 (12); Lockhart, D. 87 (6), BM (6); Loefgren, A. 263 (8), 1521 (9); Loiola, M.I.B. 473 (12), 491 (12), 1422 (12), 1457 (12), 2284 (12); Lombardi, J.A. 5821 (12), 7145 (12), 8870 (5), 8912 (4); Longa, C.M. 12 (5); López, E.V.E. 1380 (6), 1798 (6), 3608 (6), 5391 (6); López, R.L. 5 (6);

Lorentz, P. BM, K[2] (6), K (6); Lorentz, P.G. 276 (6); Lorenzi, H. 4819 (8); Loureiro, D.M. 465 (9); Lowe, J. 3970 (12); Lucena, M.F.A. 141 (9), 327 (12), 349 (12), 436 (12), 457 (12), 470 (12), 478 (12), 492 (12), 543 (12), 599 (9), 603 (9), 605 (12), 617 (12), 669 (3), 755 (12), 1550 (5), 1742 (12); Luceño, M EBBN 478 (9); Luederwaldt, H. SP 13819 (8); Lund, N.T. G 312455 (9); Lundell, C.L. 7536 (6), 7775 (6); Lutz, A. 7 (5), 21 (4), 27 (4), 39 (4), 468 (5), 1094 (5); Lutz, B. 588 (5), 1373 (5); Lykke, A.M. 445 (13); Lyra, R.P. 364 (5), 778 (5), 959 (5); Lyra-Lemos, R.P. 4195 (5), 4215 (5), 4384 (4), 4429 (5), 4508 (5), 4648 (5), 5467 (5), 5489 (5), 5934 (5), 8017 (5), 8616 (12), 8640 (12), 8902 (12), 11843 (12), 11933 (12).

**M**acedo, A. 2692 (1), 3158 (9), 3997 (12), RB 95606 (12); Macedo, J.F. 3000 (12), 3360 (12), 4194 (12), BHCB 28236 (8); Machado, A. 67 (4), RB 71308 (4); Machado, O. RB 71311 (5); Machado, R.F. 104 (4), 487 (12); MacRae, W.D. 100 (12); Madrigal-Sánchez, X. 4745 (6); Madsen, J.E. 5758 (13); Magaña, M.A. 1595 (6); Magaña, R.H. 7006 (6); Magnago, L.F.S. 1195 (5); Maguire, B. 22933a (12); Mahoux, P.G. P 4831455 (13); Maia, L.M.C. IPA 58714 (12); Maia, M.L. 1 (12); Maia, V. 142 (12), 143 (12), 144 (12); Major, J. 42 (12); Makino, H. MG 159114, SP 146648, UEC 4658, UEC 111065 (8); Mamani, F. 1446 (4); Mangabeira, M.O. 1829 (12); Manhães, V.C. 166 (4); Mann 405 (13); Mantone, L. 558 (5); Marc, C. 198 (13); Marlene, F.M. EAC 13606 (12); Marquete, R. 4434 (9); Martin, R. 466 (9); Martinelli, G. 83 (5), 5306 (9), 5311 (9), 17928 (12), 18323 (11); Martínez, E. 37975 (6); Martínez-Calderón, G. 110 (6), 1340 (6), 1868 (6); Martínez-Crovetto, R.L. 4814 (6), 4896 (6); Martinez-S., E. 31209 (6), 36606 (6); Martínez-S., E. 1689 (6); Martins, D. ALCB 55227 (9), ALCB 55228 (9); Martins, M.L.L. 137 (7); Martins, P. DAV 116782, EAC 8104 (9), EAC6980, IBGE10910 (12); Martis, M.L.L. 2144 (2); Martius & Regnell G (8); Martius, C.F.P. von BR 13312718 (12), BR 13312732 (12), E[2] (5), G 312451 (4), K[photo] (2), K[photo], L 2203125 (5), M 233650 (3), M 233649 (8), M 233651 (3), M 86086 (5), M 86087 (5), M 89080 (4), M 89081 (4), M 89082 (4), M 89105 (5); Mass, L. 23 (12); Mata, M. 2262 (9); Mata, M.F. EAC 17195 (12); Matias, M.C. JPB 2964, SP 476558 (12); Matos, D.S. 8 (6); Matos, E.N. 701 (5); Matozinhos, C.N. 9 (8), 68 (8); Mattos, J.R. 10772 (12), 13935 (8), 8512 (9); Mattos-Silva, L.A. 797 (5), 831 (5), 3337 (4), 3386 (4), 3795 (5), 3925 (5), 4153 (5), 4187 (5), 4584 (5); Matuda, E. 953 (6); Maya-L, C.A. 621 (6), 622 (6); McDaniel, S. 10869 (12), 13851 (12); McKee, H.S. 38986 (12); McVaugh, R. IEB 128572, MEXU 823253 (6); Medeiros, C. SP 245742 (8); Medeiros, D. 11 (5), 279 (2); Meikle, R.D. 1186 (13); Mello-Barreto, H.L. 664 (8), 2613 (2), 2614 (2), 2677 (8), 2678 (8), 2679 (8), 2680 (8), 5062 (8), 10480 (8), 13011 (5), 63291 (8), 10479 (8), BHCB 80504 (12); Mello-Filho, L.E. 3052 (5); Mello-Silva, R. 689 (11), 1363 (2), 2235 (9), 2703 (11), CFR 7206 (9), CFR 7949 (2); Melo, E. 624 (9), 1542 (12), 2063 (12), 2963 (9), 3906 (12), 7055 (12), 7749 (6), 9218 (12), 10862 (3), PCD 1214 (9), PCD 1285 (9), PCD 1356 (9); Melo-Junior, J.C.F. 563 (8); Melo-Soares, R. 5 (12), 16 (12); Melville, F.A. 184 (13); Menager, L.P. P 4786573 (13), P 4786574 (13); Mendes, K. 346 (5); Mendes, M.S. 1159 (8); Mendes, N.M.S. HUEFS 130402 (12); Mendes, P.T. IAC 4966 (12); Mendes-Magalhães 2822 (2), 2823 (2); Mendonça, R.C. 2975 (9); Mendoza, M. 27 (6); Menezes, N.L. CFR 384 (9); Merckling, K.E. v. s.n. (5); Merello, M. 1575 (13); Merckling, F.F. 2013-9-87 (13); Messias, M.C.T.B. 1478 (2); Mexia, Y. 4187 (8); Meyer, T. 2222 (6), 4508 (4), 4509 (6); Miers, J. US 1421166 (3); Mikan, J.C. 10 (5), 11 (4); Milanezi, M.A. SP 465117, VIES 523 (12); Milla, A.P. 217 (9); Millen, H. 36 (12), 142 (13); Miller, A.G. 3059 (13), 5379 (13); Miller, O.O. 120 (12); Miquel K[2] (12); Miranda, A.M. 1104 (9), 2652 (9), 3160 (9), 4507 (12), 6218 (5); Miranda, E. 483 (2); Miranda, U.C.R. 3178 (12); Mocquerys, A. 730 (12), COL 150706, NY, P 4830328, US 3022861 (12); Moiser, B. 51 (13), 55 (13), 129 (13), K (13); Molina, J.A. 279 (12); Molina-R., A. 10991 (6), 14344 (6), 20630 (6), 22043 (6), 22164 (6), 34424 (6); Moll, L.B. BR 13312862 (12); Moloney K (12); Monad, T. 2058 (13), 2118 (13), 2058 ter (13), 2118 bis (13), 2118 ter (13); Montalvo, E. 24A (7); Monteiro, C.H. 41 (9); Monteiro, O. PA-MA-074 (12), PA-MA-080 (9); Monteiro, R.F. 642 (9); Montes, J.E. 922 (6), 1429 (6), 3276 (6); Moore, S. 1022 (9); Moquin, M. 1836 (13); Moraes, M.V. 573 (5); Moraes, P.L.R. 2787 (9), 2983 (9); Moreira, H.P. 27 (12), 43 (12); Morel, I. 437 (6), 4373 (6), 5216 (6), 5533 (6), 6743 (6), 6893 (6), 7041 (6); Morel, J. 674 (6); Mori, S.A. 10411 (4), 10468 (5), 10579 (5), 10598 (5), 10988 (4), 12197 (12), 12966 (9), 13540 (9), 13641 (5), 14055 (5),

14259 (9), 25938 (12), 26820 (12); Morong, T. 939 (6); Morton SL 320 (13); Morton, J.F. FTG 39513 (12); Morton, J.K. 6024 (13), 6161 (13), 6232 (13), A120 (13); Moruz, C.V.A. 104 (9); Mosén, H. 1628 (9); Mosnier, M. 2329 (13); Mostacedo, B. 3306 (6); Mosteiro São Bento 36 (12); Mota, N.F.O. 167 (8), 379 (8); Mota, R.C. 107 (2), 502 (2), 1946 (2), 3194 (2), 3308 (2); Motta, L.B. 26 (6); Moura, A.C.A. 97 (5), 98 (5); Moura, D. 1102 (12), 771 (12); Moura, L.M. 48 (9); Moura, L.S. 138 (8); Moura, O.T. 185 (12), 432 (5); Moura, R. 112 (5); Moura, V.S. 24 (6); Mouret, M. 103 (12); Mroginski, L. 297 (6), 356 (6), 635 (6); Mukherjee F 2005276 (12); Mulford Biological Exploration of the Amazon Basin 1228 (4); Muller, B.L. 173 (6); Müller, F. 41 (6); Mullin, J.M. 12 (12); Munis, C.F. CFSC 7884 (2).

Nadeaud, J. P 4830295 (4), P 4831479 (3); Nagelkerken, W.P. 121 (12), 137 (12), 302 (12); Nascimento, A.F.S. 190 (5); Navarro, G. 362 (6); Neé, L. MA 249996[2] (6); Nee, M. 17154 (12), 27754 (6), 37136 (6), 37626 (6), 37844 (9), 44336 (6), 44578 (6), 45109 (6), 46383 (6), 47424 (6), 47913 (6), 56934 (6); Nelson, C. 4429 (6); Nelson, E.W. 2902 (6); Neuwied, M.A.P.W. BR (5); Neves, S.P.S. 31 (9), 52 (9), 91 (9), 153 (9), 175 (9); Nevling 69 (6), 809 (6); Newid, Mikan & Pohl s.n. G (5); Noblick, L.R. 2141 (5), 2840 (9), 3706 (12), 4448 (5); Nogueira, E. 104 (9); Nogueira, R.E. 124 (2); Nolazco, E.G. 3289 (6); Novais, J.S. 24 (4); Novelo, R.A. 1575 (12); Noyara, L.J. 3056 (6); Nunes, A. EAC 5691 (12); Nunes, T.S. 1354 (5), 1414 (5); Núñez, J.C.S. 901 (6), 930 (6), 2335 (6), 2954 (6), 3053 (6), 4264 (6), 4377 (6), 9643 (6); Nusbaumer, L. 3980 (9).

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Queiroz, E. HRB 30896, RB 482298 (12); Queiroz, E.P. 1400 (5), 1473 (3), 1588 (5), 2173 (3), 2474 (12); Queiroz, L.P. 1900 (9), 3187 (12), 5161 (9), 5179 (9), 7434 (9), 9121 (12), 9926 (9); Queiroz, R.T. 300 (12), 695 (12); Quentin, R.P. 372 (12); Questel, A. 188 (12), 412 (12), 579 (12), P 4831535 (12), P 4831536 (12).

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R (12); Silva, J.L. 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EAC 17901 (12); Silverstone-Sopkin, P.A. 6102 (6); Sinani, T.R.F. 102 (1); Sintenis, P. 939 (12), P 4831518 (12); Siqueira, R.C. 10 (12); Sladen, W.J.L. JB236/15 (12); Smith, H. R 100532 (9); Smith, H.H. 703 (13), 1476 (12); Smith, L.B. 6355 (5), 9734 (6); Smith, O.H. 309 (6); SN III TOGO 3107 (13); Snethlage, E.H. 145 (12); Sobral, M. 7601 (9), 11126 (6), 14570 (8), 15266 (8); Sobral-Leite, M. 647 (12); Soeiro, R. 07/89 (5), 38/89 (12), 43/89 (5); Soeprata K, RB 27248 (12); Sol, A.R.A. 45 (6); Sosa, M.M. 102 (6); Soto, D. 969 (9); Soto-N., J.C. 14071 (6), 15148 (6), 16022 (6), 16827 (6), 16843 (6); Soubirou P 4831472, P 4831472

(12); Sousa, E. 2550 (13); Sousa, L.O.F. 160 (5); Sousa, M.A. 1155 (12), 1290 (12); Sousa, V.F. 8 (12); Souza, A. 14 (5), 537 (5), 636 (5), 1465 (8), 1467 (8), 1468 (8), 1469 (8), 1551 (5), 1585 (5), 1645 (5), 1701 (5), 1740 (5), 1776 (5), 1835 (5), 1875 (5), 1921 (5), 1948 (5), 2171 (12), 2287 (5), 2335 (5), 2787 (5), 3553 (12), 4517 (5), R (5), (12), R 151574 (5), R 161059 (12), R 161128 (12), R 174276 (5), R 202602 (5); Souza, A.C. 149 (5); Souza, F.S. 2111 (2), 2126 (2); Souza, G. 348 (8); Souza, H.C. 60 (12); Souza, J.O. 15 (5); Souza, M.C. 2546 (6); Souza, R.S. 6 (12); Souza, V.C. 3431 (2), 9753 (12), 10025 (2), 17129 (9), 25506 (2), 26557 (12), 35738 (9), CFCR 13818 (2); Souza-Silva, R.F. 156 (12); Sperling, C.R. 5654 (9); Spichiger, R. RS2789 (6); Spies, A. PACA 36031 (6); Splitgerber, F.L. L 2202981 (12); Spruce, R. 192 (12), 462 (12), K 1210173, TCD 4971 (12); Standley, P.C. 20766 (6), 22098 (6), 24092 (6), 54785 (6); Stannard, B.L. CFCR 6675 (2), H51838 (9); Staviski, M.N.R. 442 (5), 939 (5), 1030 (5); Steere, W.C. 1356 (6), 1671 (6); Stehle, H. 427 (12), 77/119 (12); Stehlé, H. 493 (12); Stehmann, J.R. 3559 (11), BHCB 28351 (2); Steinbach, J. 3273 (6), 5072 (6), 6203 (6), 6815 (4); Steinmann, V.W. 1919 (6), 2024 (12); Stern, W.L. 346 (6); Sternnson, J.A. 2462 (6); Sterringa, J.T. 12446 (12); Stevens, W.D. 2674 (6), 9444 (6), 22266 (6); Steyermark, J.A. 88925 (12); Stockdale, F.A. 8848 (12); Stoffers, A.L. 12 (12), 83 (12), 102 (12), 188 (12), 420 (12), 542 (12), 1705 (12), 2303 (12), 2377 (12), 2908 (12), 3801 (12), 3849 (12), 3880 (12), 5050A (12); Stranghetti, V. 460 (4); Stuckert, T. 9151 (6), 15171 (6), 15495 (6), 20101 (6); Sucre, D. 427 (9), 994 (4), 1058 (5), 1061 (5), 1807 (4), 2057 (4), 2359 (8), 3371 (4), 3926 (4), 7440 (5); Suringar, W.F.R. L 2202941 (12), L 2202951 (12), L 2202952 (12), L 2202953 (12), L 2202954 (12), L 2202955 (12), L 2202956 (12), L 2202957 (12), L 2202958 (12), L 2202959 (12), L 2202960 (12), L 2202961 (12), L 2202962 (12), L 2202963 (12), L 2202966 (12), L 2202967 (12), L 2202968 (12), L 2202969 (12), L 2202970 (12), L 2202976 (12), L 2202977 (12), L 2202978 (12), L 2202979 (12); Svenson, H.K. 11294 (12); Swarbrick, J.T. 2904 (13).

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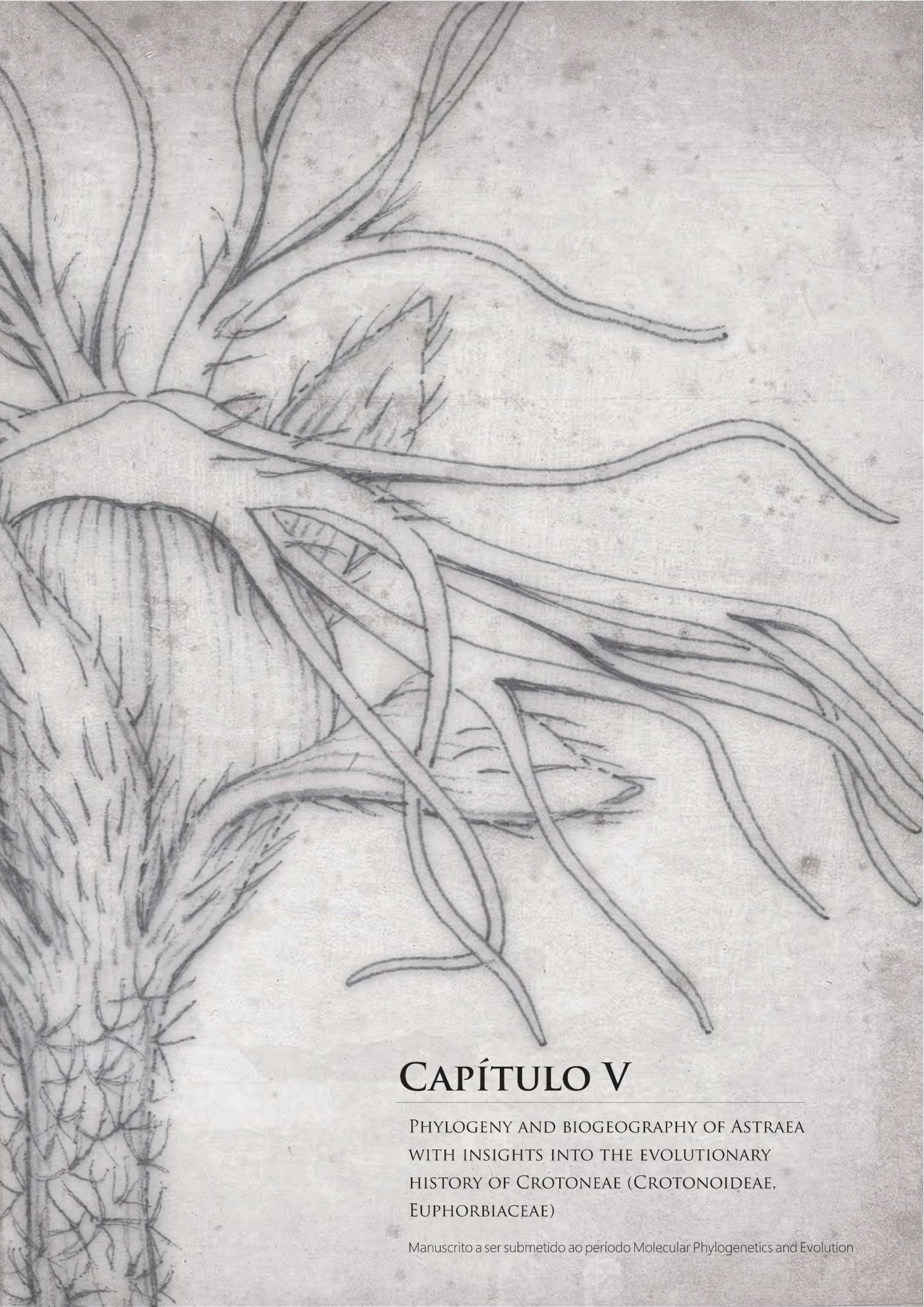
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**Y**ates, C.C. BM (13); Yunckers, T.G. 8111 (6).

**Z**afra, A.N. 1045 (6), 1251 (6), 1497 (6); Zambom, O. 187 (5); Zamith SP 490663 (5); Zamora-C., P. 4513 (12); Zamudio-R., S. 700 (6); Zanoni, T. 33287 (12), 44159 (12); Zappi, D.C. CFSC9985 (2); Zardini, E.M. 46655 (1), 51037 (1); Zerny, H. 459 (9); Zolá-B., M.G. 1814 (6); Zuloaga, F.O. 3647 (4), 6842 (6).

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## CAPÍTULO V

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PHYLOGENY AND BIOGEOGRAPHY OF *ASTRAEA*  
WITH INSIGHTS INTO THE EVOLUTIONARY  
HISTORY OF CROTONEAE (CROTONOIDEAE,  
EUPHORBIACEAE)

Manuscrito a ser submetido ao período Molecular Phylogenetics and Evolution



## PHYLOGENY AND BIOGEOGRAPHY OF *ASTRAEA* WITH INSIGHTS INTO THE EVOLUTIONARY HISTORY OF CROTONEAE (CROTONOIDEAE, EUPHORBIACEAE)

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**Abstract**—In this work we evaluate the infrageneric relationships in *Astraea* based on molecular data from the nuclear ribosomal ITS and *trnL-trnF* and *psbA-trnH* plastid spacers, sampling all species currently recognized for the genus. The biogeographic history of the genus is inferred through divergence times estimates and reconstruction of ancestral distribution ranges. With a comprehensive sampling of Crotonae, the evolutionary history of *Astraea* is also interpreted in a broader framework, including reconstructions of ancestral distribution ranges and morphological character states. Our results show that *Astraea* is monophyletic and consists of three main clades. We also infer that the putative ancestor of *Astraea* had a wide distribution range in South America, and diverged from its sister genus, *Acidocroton*, by the end of the Eocene. Most of diversification within *Astraea* took place from the Oligocene to the Pliocene, likely influenced by the formation of the South American dry diagonal. We identified the absence or strong reduction of petals in pistillate flowers as a putative morphological synapomorphy for Crotonae, and the biogeographic history inferred for the tribe suggests a putative ancestor widely distributed in moist forests, which covered great part of South America in the late Paleocene to early Eocene. Finally, we discuss the position of *Brasilicroton*, *Sagotia* and *Sandwithia* within the tribe in the light of divergence time estimates and reconstruction of ancestral characters states and geographic ranges.

**Keywords**—*Croton*, Crotonoideae, Neotropics, *Brasilicroton*, *Sagotia*, *Sandwithia*

## INTRODUCTION

Crotoneae is one of the largest tribes within Euphorbiaceae once it includes *Croton* L., the second largest genus of the family, with about 1,200 species (Webster, 2014). Recent phylogenies based on molecular data (Berry et al., 2005a; Wurdack et al., 2005) transferred *Acidocroton*, *Sagotia* and *Sandwithia* from Codiaeae and Aleuritideae to Crotoneae and recovered *Brasilicroton* P.E. Berry & Cordeiro as most closely related to *Croton*. The phylogenetic position of *Brasilicroton* separated *Croton* sect. *Astraea* (Klotzsch) Baill. from the remaining *Croton* and, therefore, Berry et al. (2005a) elevated that section to the genus level reestablishing *Astraea*. Wurdack et al. (2005) and Berry et al. (2005a) also showed that *Astraea* was most closely related to *Acidocroton* Griseb. (including *Ophellantha* Standl.), a genus from Central America, West Indies and northern South America (Webster, 2014), instead of sister to the clade formed by *Croton* and *Brasilicroton*, based on morphological similarities in flowers and inflorescences with these two genera. There are however, differences in distribution between *Astraea* and *Acidocroton*. *Astraea* is found throughout the neotropical region, reaching its highest species diversity in eastern Brazil, and with one of the weedy species reaching the Old World tropics (Gaikwad et al., 2012; Caruzo et al., 2014; Das et al. 2016; Silva et al., [Capítulo III]). Recent studies on the taxonomy of *Astraea* have contributed to clarify species circumscriptions and to resolve nomenclatural problems (Silva and Cordeiro, 2017, Silva et al., 2017, Silva et al., [Capítulo III]; Silva and Cordeiro, [Capítulo IV]).

Morphologically, *Astraea* was included in *Croton* due mainly to two features: anthers inflexed in bud and the presence of stellate and simple trichomes (Berry et al., 2005a). However, as Webster (1993) stated, *Croton* sect. *Astraea* was one of the most sharply defined sections within *Croton* due to its usually deeply lobed leaves, staminate flowers with imbricate perianth and glabrous receptacle, pistillate flowers with slender cylindrical multifid styles and tetragonal seeds in cross section, with rugulose testa and a large caruncle. However, recent morphological studies revealed that in some *Astraea* species the seeds are cylindrical in cross section and can bear small caruncles (Silva and Cordeiro, [Capítulo IV]). Miller and Webster (1966) also mentioned that *Astraea* apparently had a unique chromosome number ( $n = 9$ ) when compared to *Croton* ( $n = 10, 14, 32$ , according to Webster, 2014).

Recent phylogenetic studies on Crotoneae (Berry et al., 2005a; Wurdack et al., 2005; Riina et al., 2014) sampled only 2 or 3 species of *Astraea* and, and these species were always recovered in a clade with high support. Given the previous sampling of *Astraea* in phylogenies, phylogenetic relationships among its species remains unknown and the monophyly of the genus needs further testing, using a more representative taxon sampling spanning the morphological diversity and distribution of the genus. In this work, we present a new phylogenetic framework for *Astraea* sampling all the species in the genus and representing the other members of Crotoneae to investigate infrageneric relationships within *Astraea* and and unveil its biogeographic history. The inferred phylogeny also allowed us to explore the evolution of morphological traits in the genus and provide new insights into the evolutionary history of this tribe.



## MATERIALS AND METHODS

**Taxon sampling**— Species and voucher information, along with GenBank accession numbers, are presented in Table I. For *Astraea*, we sampled all species recognized by Silva and Cordeiro (Capítulo IV). For species with a wide distribution range we used more than one accession aiming to cover most of their genetic variability and morphologic plasticity. However, only a few samples from Central America yielded viable DNA. In South America most of the sampling effort was concentrated in Brazil due to difficulties in gathering samples and/or extracting viable DNA from herbarium specimens from other South American countries.

Regarding the most widely distributed species of *Astraea*, we included seven samples of *A. lobata*: one from North America (Mexico), two from Central America (both from Costa Rica) and four from South America (Argentina, Bolivia, and western and southern Brazil). For *A. surinamensis* five samples were included: one from Puerto Rico and the other four from Brazil (Rio Grande do Norte, Bahia, Espírito Santo and Mato Grosso do Sul). In the case of *A. trilobata*, which is widely distributed in Africa (Silva et al., Capítulo III), due to difficulties to get viable DNA from African herbarium samples, we could only include one accession from Ivory Coast.

Two species distributed mainly throughout the South American dry diagonal, *Astraea gracilis* and *A. paulina* were represented in our sampling as follows: three samples of *A. gracilis* from Bahia, Espírito Santo and Minas Gerais (Brazil), and six samples of *A. paulina* from the Brazilian states of Bahia, Ceará, Goiás, São Paulo and Pará, and one sample from Bolivia. Also, the sampling of *A. paulina* covered the morphology-based synonymization of *A. gardneri* and *A. comantha* into *A. paulina* (corresponding to the samples from Ceará and Goiás, respectively) by Silva & Cordeiro (Capítulo IV). The same applies to *A. cincta*, which in its new delimitation (Silva and Cordeiro, [Capítulo IV]) includes, as synonyms, *A. aureomarginata* and *A. hauthalii*, and is represented by four samples from the Brazilian states of Goiás, Mato Grosso do Sul, Minas Gerais and Paraná, besides one sample from Bolivia.

We also followed Silva & Cordeiro (Capítulo IV) in recognizing *Astraea macroua*, but without including *A. klotzschii* as its synonym as proposed by Moraes et al. (2014) due to differences in indumentum of leaves and calyx of pistillate flowers. In this work, we included one sample for *A. macroua* (from Espírito Santo, Brazil) and six samples of *A. klotzschii*: two from Rio de Janeiro (one from the coastal seashore vegetation and another from montane moist forests), two from Bahia, one from Alagoas and another one from Pernambuco. This sampling aimed to cover the leaf shape variation used by Müller Argoviensis (1865; 1866; 1873) to recognize infraspecific taxa.

For *Astraea comosa* and *A. manihot*, the inclusion of more than one sample was due to availability of viable DNA which allowed a better covering of the distribution range of these species. The remaining species (*A. digitata*, *A. praetervis* and *A. subcomosa*) were represented by only one sample.

Müller Argoviensis (1866) included *Croton humilis* L., *C. panduriformis* Müll.Arg. and *C. bonplandianus* Baill. (= *C. pauperulus* Müll.Arg.) in his treatment of *C. sect. Astraea* in De Candolle's *Prodromus*. However, *C. humilis* has 25–35 stamens and both *C. panduriformis* and *C. bonplandianus* have bifid styles. Although Webster (1993) only doubted the position of *C. bonplandianus* within *C. sect. Astraea*, these three species are now included in *C. sect. Adenophylli* by van Ee et al. (2011). Therefore, based on morphological characters mentioned above and the position of them in *Croton* (van Ee et al., 2011), these species are not included in this work.

For the outgroup (Nixon and Carpenter, 1993) we selected representatives from all genera included in *Crotoneae* by Webster (2014), based on previous studies (Berry et al., 2005a; Riina et al., 2014): one accession from each of the small genera (*Brasiliocroton*, *Sagotia* and *Sandwithia*), two samples of *Acidocroton* (one of them representing the recently synonymized *Ophellantha*), and 21 species of *Croton*, representing the four subgenera and some of the sections recognized by van Ee et al. (2011). All trees were rooted with one sample of *Jatropha*, which belongs to *Jatrophaeae*, the sister tribe of *Crotoneae* (Wurdack et al., 2005).

**Molecular procedures and sequence alignment**—DNA extraction, amplification of the selected markers (one coding nuclear region, *ITS* [comprehending *ITS1*, the *5.8S* gene and *ITS2*] and two non-coding plastid spacers: *trnL-trnF* and *psbA-trnH* [hereafter referred as *trnLF* and *psbA*, respectively]), sequence assembling, and alignment followed the methodology described in Silva et al. (Capítulo III).

**Datasets and phylogenetic inference**—We analyzed the nuclear and plastid datasets separately to evaluate topology incongruence between the two genetic markers using maximum likelihood (ML) and Bayesian inference. For ML we used RaXML 1.5b2 (Stamatakis, 2014) with 10,000 bootstrap replicates, employing GTR model for substitution sites with gamma distribution. Bayesian inference was conducted using MrBayes v3.2.5 (Ronquist and Huelsenbeck, 2003) with substitution models estimated through functions implemented since version 3.2 (Ronquist et al., 2012). We applied four independent runs, each with four simultaneous chains (one cold and three heated), for ten million generations, sampled every 1000<sup>th</sup> generation. Burn-in was initially set to 25% in MrBayes and checked in Tracer v.1.6 (Rambaut and Drummond, 2007) for convergence and stationarity through effective sample size (ESS) values (> 200). Trees generated by RaXML and MrBayes were visualized in FigTree (Rambaut, 2010) and assembled in vector editing software. For support values we adopted  $\geq 75$  to < 95% BS or  $\geq 0.75$  to < 0.95 PP as moderate support and  $\geq 95$  BS or 0.95 PP as strong support. Sequences newly generated were deposited in GenBank (see Appendix I for accession numbers) and alignment files are available as supplementary files.

**Variation among sequences within *Astraea***—For this work we also evaluated similarity among samples from a same species and among clades within *Astraea*. To do so, we calculated mean number of pairwise character differences using PAUP\* 4.0b10 (Swofford, 2002) function *dset* under the GTR evolutionary model.

Table I. Voucher information for the samples utilized in this work. Sequences newly generated for this study are labeled as NG.

Sample	Species	Specimen	Origin	trnLF	psbA	ITS
AcidocrotonACID	<i>Acidocroton tricophyllus</i>	HAJB 81844 (MICH)	Cuba: Holguin	EF408087	-	-
	<i>Acidocroton verrucosus</i>	G.L. Webster 8463 (DAV)	Jamaica	-	-	AY971171
AcidocrotonOPH	<i>Acidocroton spinosus</i>	Gentry 74385 (MO)	Mexico: Jalisco	AY971344	-	-
		Breedlove 46994 (NY)	Mexico: Chiapas	-	-	AY971263
AcinctaBOL	<i>Astraea cincta</i>	O.L.M. Silva 207	Santiago de Chiquitos, Bolívia	NG	NG	NG
AcinctaGO	<i>Astraea cincta</i>	M.B.R. Caruzo 182	Parque Nacional de Emas, GO	NG	NG	NG
AcinctaMG	<i>Astraea cincta</i>	O.L.M. Silva 263	Joaquim Felício, MG	NG	NG	NG
AcinctaMS	<i>Astraea cincta</i>	O.L.M. Silva 238	Corguinho, MS	NG	NG	-
AcinctaPR	<i>Astraea cincta</i>	O.L.M. Silva 196	Campo Mourão, PR	NG	NG	NG
AcomosaCAR	<i>Astraea comosa</i>	O.L.M. Silva 318	Santa Bárbara, MG	NG	NG	NG
AcomosaDIAM	<i>Astraea comosa</i>	O.L.M. Silva 273	Diamantina, MG	NG	NG	NG
Adigitata	<i>Astraea digitata</i>	O.L.M. Silva 228	Ilhéus, BA	NG	NG	NG
AgracilisBA	<i>Astraea gracilis</i>	O.L.M. Silva 225	Arataca, BA	NG	NG	NG
AgracilisES	<i>Astraea gracilis</i>	O.L.M. Silva 283	Nova Venécia, ES	NG	NG	NG
AgracilisMG	<i>Astraea gracilis</i>	A.R. Rezende 222	Ituitaba, MG	NG	NG	NG
AklotzschiiAL	<i>Astraea klotzschii</i>	O.L.M. Silva 341	Marechal Deodora, AL	-	NG	NG
AklotzschiiL	<i>Astraea klotzschii</i>	O.L.M. Silva 229	Ilhéus, BA	NG	NG	NG
AklotzschiiTA	<i>Astraea klotzschii</i>	O.L.M. Silva 220	Itacaré, BA	NG	NG	NG
AklotzschiiMAR	<i>Astraea klotzschii</i>	I. Cordeiro 3384	Maricá, RJ	NG	NG	NG
AklotzschiiPE	<i>Astraea klotzschii</i>	O.L.M. Silva 340	Tamandaré, PE	NG	-	NG
AklotzschiiSMM	<i>Astraea klotzschii</i>	R.C. Forzza 2831	Santa Maria Madalena, RJ	NG	NG	NG
AlobataAQU	<i>Astraea lobata</i>	O.L.M. Silva 119	Aquidauana, MS	NG	NG	NG
AlobataARG	<i>Astraea lobata</i>	R. Riina 1890	Argentina	NG	NG	NG
AlobataBAG	<i>Astraea lobata</i>	U. Chavarria 2199	Bagaces, Costa Rica	NG	NG	NG
AlobataBAT	<i>Astraea lobata</i>	C.E.B. Fernandes 197	Batayporã, MS	NG	NG	NG
AlobataBOL	<i>Astraea lobata</i>	R. Riina 1502	Bolívia	-	NG	NG
AlobataGUA	<i>Astraea lobata</i>	B.W. Van Ee 296	Costa Rica: Guanacaste	EF408089	-	EF421720
AlobataMEX	<i>Astraea lobata</i>	C.A. Maya-Lastra 621	Múgica, México	NG	NG	NG
AmacrouraES	<i>Astraea macroura</i>	O.L.M. Silva 137	Linhares, ES	NG	NG	NG

Sample	Species	Specimen	Origin	trnLF	psbA	ITS
AmanihotARU	<i>Astraea manihot</i>	O.L.M. Silva 139	Arujá, SP	NG	NG	NG
AmanihotJUQ	<i>Astraea manihot</i>	O.L.M. Silva 233	Franco da Rocha, SP	NG	NG	NG
AmanihotMG	<i>Astraea manihot</i>	O.L.M. Silva 237	Poços de Caldas, MG	NG	NG	NG
ApaulinaBA	<i>Astraea paulina</i>	O.L.M. Silva 184	Mucugê, BA	NG	NG	NG
ApaulinaBOL	<i>Astraea paulina</i>	O.L.M. Silva 205	Santiago de Chiquitos, Bolívia	NG	NG	NG
ApaulinaCE	<i>Astraea paulina</i>	B.M.T. Walter 6581	Crato, CE	-	NG	NG
ApaulinaGO	<i>Astraea paulina</i>	O.L.M. Silva 113	São Jorge, GO	NG	NG	NG
ApaulinaPA	<i>Astraea paulina</i>	L. Rossi 2503	Novo Progresso, PA	NG	NG	NG
ApaulinaSP	<i>Astraea paulina</i>	O.L.M. Silva 213	Botucatu, SP	NG	NG	NG
Apraetervisa	<i>Astraea praetervisa</i>	J.R. Pirani 2938 (SPF)	Ilhéus, BA	AY971266	NG	AY971173
Asubcomosa	<i>Astraea subcomosa</i>	R. Mello-Silva 689	Botumirim, MG	NG	NG	-
	<i>Astraea subcomosa</i>	E. Barboza 3808	Serranópolis de Minas, MG	-	-	NG
AsurinamensisBA	<i>Astraea surinamensis</i>	O.L.M. Silva 217	Ilhéus, BA	NG	NG	NG
AsurinamensisES	<i>Astraea surinamensis</i>	O.L.M. Silva 132	Guarapari, ES	NG	NG	NG
AsurinamensisMS	<i>Astraea surinamensis</i>	O.L.M. Silva 117	Campo Grande, MS	NG	NG	NG
AsurinamensisPR	<i>Astraea surinamensis</i>	B.W. Van Ee 549	Puerto Rico	EU497699	HM044809	EU497727
AsurinamensisRN	<i>Astraea surinamensis</i>	O.L.M. Silva 338	Serra Caiada, RN	NG	-	NG
AtrilobataC	<i>Astraea trilobata</i>	J. Koning 4937	Costa do Margim	NG	NG	NG
Bmamoninha	<i>Brasiliocroton mamoninha</i>	Lobo 340 (NY)	?	AY794691	-	-
		J.R. Pirani 4947 (SPF)	Brazil: Espírito Santo	-	HM044810	EU586944
Calchorneicarpus	<i>Croton alchorneicarpus</i>	M.B.R. Caruzo 71 (SP)	Brazil: São Paulo ou RJ?	HM044769	-	HM044788
		R. Riina 1529 (WIS)	Brazil: Rio de Janeiro	-	HM044811	-
Castroites	<i>Croton astroites</i>	B. van Ee 537 (WIS)	Puerto Rico	EU586955	HM044812	EU586901
Ccuneatus	<i>Croton cuneatus</i>	P.E. Berry 7589 (PORT)	?	AY794698	-	-
		R. Riina 1491 (MICH)	?	-	HM044816	EU407735
Ccupreatus	<i>Croton cupreatus</i>	R. Riina 1408 (WIS)	Ecuador	EU586974	HM044817	EU586919
Cechinocarpus	<i>Croton echinocarpus</i>	R. Riina 1371 (WIS)	Brazil	EU586979	-	EU586922
		R. Riina 1519	Brazil: Rio de Janeiro	-	HM044819	-
Cechioides	<i>Croton echioides</i>	Santos 795 (HUEFS)	Brazil	EU586967	HM044818	EU586907
Cglandulosus	<i>Croton glandulosus</i>	B. van Ee 512 (WIS)	USA: Wisconsin	EU497713	HM044822	EU478066

Sample	Species	Specimen	Origin	trnLF	psbA	ITS
Cgossypiifolius	<i>Croton gossypiifolius</i>	R. Riina 1261 (WIS)	Venezuela: Trujillo	AY971301	-	AY971212
Cgracilipes	<i>Croton gracilipes</i>	M. Nee 47412 (NY)	Bolivia	EU586962	HM044823	EU586909
Cheterocalyx	<i>Croton heterocalyx</i>	M.B.R. Caruzo 108 (SP)	Brazil: Bahia	HM044775	HM044825	HM044794
Cjacobinensis	<i>Croton jacobinensis</i>	D.S. Carneiro-Torres 789 (HUEFS)	Brazil: Bahia	HM044776	HM044827	HM044795
Cmanampetsae	<i>Croton manampetsae</i>	B.W. van Ee 950 (MICH)	Madagascar: Toliar	HM044777	HM044829	HM044796
Cnobilis	<i>Croton nobilis</i>	B.W. van Ee 938 (MICH)	Madagascar: Toliar	HM044778	HM044831	HM044797
Cpalanostigma	<i>Croton palanostigma</i>	R. Riina 1492 (WIS)	Peru	EU586997	HM044835	EU586943
Cpiptocalyx	<i>Croton piptocalyx</i>	1533	?	EF408148	-	-
		M.B.R. Caruzo 54 (SP)	Brazil	-	HM044836	EF421791
Crotterifolius	<i>Croton rottlerifolius</i>	M.B.R. Caruzo 56 (SP)	Brazil: São Paulo	-	HM044838	-
		R. Riina 1534	Brazil: São Paulo	HM044781	-	HM044801
Csapiifolius	<i>Croton sapiifolius</i>	Lima 667 (CEPEC)	?	EF408150	HM044841	-
		?	?	-	-	EF421754
Cschiedeanus	<i>Croton schiedeanus</i>	B.W. van Ee 458	Mexico: Yucatan	EU478156	HM044842	EU478051
Ctrichotomus	<i>Croton trichotomus</i>	B.W. van Ee 991	Madagascar: Toamasina	HM044787	HM044845	HM044808
Ctroncosoi	<i>Croton troncosoi</i>	M. Belgrano 423 (SI)	Argentina	EU586994	HM044846	EU586940
Cvelutinus	<i>Croton velutinus</i>	D.S. Carneiro-Torres 902	Brazil: Bahia	HM044786	-	HM044807
Jatropha	<i>Jatropha integerrima</i>	K.J. Wurdack D047 (US)	cultivated	AY794685	-	-
		Strain JCGLD-01	cultivated	-	-	EU340795
		PS0176MT01	cultivated	-	GQ434947	-
Sagotia	<i>Sagotia racemosa</i>	Smith 253 (US)	Peru: Madre de Dios	AY794687	-	AY971264
	<i>Sagotia brachysepala</i>	T.E. Carvalhes in PFBG_CF466)	Brazil: Vitória do Xingu, PA	-	NG	-
Sandwithia	<i>Sandwithia guyanensis</i>	E.Y. Kataoka 347	Brazil: Manaus, AM	-	-	NG
		Ek 906 (NY)	?	AY794688	-	-

**Morphological character state mapping**—Sixteen morphological characters (Table II) were coded based on the taxonomic revision of *Astraea* (Silva et al., [Capítulo IV]), van Ee et al. (2011) for the New World sections of *Croton*, Webster (1993) for the Old World species of *Croton* and Webster (2014) for the remaining Crotonaeae genera (complemented by observation of collections of *Sagotia* and *Sandwithia*) and *Jatropha*. All character states were treated as unordered and mapped onto the phylogeny using parsimony as implemented in Mesquite v. 3.02 (Maddison and Maddison, 2009).

**Table II:** Morphological characters mapped for Crotonaeae in this study and coding of their respective states.

Character	Coding
1. Habit	0 = perennial trees, 1 = annual or biannual herbs, 2 = perennial shrubs, 3 = lianas
2. Underground system	0 = not xylopodiferous, 2 = xylopodiferous
3. Type of trichomes	0 = simple, 1 = stellate, 2 = lepidote, 3 = stellate-porrect, bearing a central ray much longer than the lateral ones
4. Stipules	0 = not modified in spines, 1 = modified in spines
5. Leaf blade	0 = entire, 1 = lobed, 2 = partite/deeply lobed, 3 = compound
6. Extrafloral nectaries	0 = absent, 1 = present (acropetiolar or basilaminar)
7. Inflorescence position	0 = terminal, 1 = axillary
8. Axes of lateral cymules	0 = not reduced, 1 = reduced
9. Moniliform trichomes at the base of staminate petals	0 = absent, 1 = present
10. Staminate petal size	0 = longer than the calyx, 1 = equal or shorter than the calyx
11. Staminate flowers nectary	0 = absent, 1 = present
12. Stamens in bud	0 = erect, 1 = inflexed
13. Number of stamens	0 = 0–15, 1 = 16–20, 2 = 21–30, 3 = 31–50, 4 = 51+
14. Pistillate petals	0 = present, 1 = absent or very reduced
15. Pistillate nectary	0 = absent, 1 = present, annular, 2 = present, segmented
16. Styles	0 = bifid, 1 = entire, 2 = 2-bifid, 3 = multifid

**Divergence time estimates**—We used BEAST (version 1.8.4, Drummond et al., 2012) to produce an ultrametric tree based on our molecular data. The input file was generated through BEAUti graphical interface with the following settings. To reflect the results of the phylogenetic inference (see below) and the currently phylogenetic framework of Crotonaeae we adopted two taxon sets (forced as monophyletic groups): Crotonaeae (containing all samples except for *Jatropha* to force the tree to be rooted with this taxon) and Core Crotonaeae (hereafter used to facilitate when designating the clade containing *Acidocroton*, *Astraea*, *Brasiliocroton* and

*Croton*). Two additional taxon sets were used as secondary calibration points, following the crown ages given by van Ee (2008) for *Croton* (normal distribution, mean = 39.3 mya and stdev = 1) and *CrotonCAG* (the group containing subgenera *Croton*, *Adenophylli* and *Geiseleria*; normal distribution, mean = 32.33 and stdev = 1). One last taxon set (*Crotoneae\_Jatrophaea*) was created with all the samples to allow more accurate estimates for ages of early diverging nodes in Crotoneae, since no estimates for this group are available to use as calibration point. To avoid that the early diverging nodes in our tree come too close to the age of Euphorbiaceae, we adopted an exponential distribution with mean = 6.5 and offset = 55, resulting in a maximum age of about 90 mya to agree with the age of Euphorbiaceae (89.9 mya) estimated by Xi et al. (2012).

Among the evolutionary models available in BEAST, we choose GTR, with estimated base frequencies, gamma model for site heterogeneity and four gamma categories. We adopted a lognormal uncorrelated relaxed clock and for tree prior we used birth-death model with a random starting tree. Although birth-death models may be problematic when applied to datasets with multiple samples per species (Heled & Drummond 2010), we utilized the full dataset once the samples of same species were usually not monophyletic. We used four independent MCMC runs with 100 million iterations each, saving trees every 1000<sup>th</sup> iteration. Log files from these runs were combined with LogCombiner (version 1.8.4), followed by inspection of ESS estimates in Tracer (version 1.6; Rambaut and Drummond, 2007) to check convergence and stationarity. Trees files from the MCMC runs were also combined in LogCombiner with a 25% burnin and resampled at a lower frequency of 5000 iterations to prevent memory crashes, and then assembled in TreeAnnotator (version 1.8.4) to produce an extended majority rule consensus tree (Felsenstein, 2004). The tree assembled was visualized and edited in FigTree (version 1.4.2), followed by vectorial editing.

**Biogeographic analysis**—We adopted nine geographical areas to code the distribution range of *Astraea* and the remaining genera of Crotoneae (Table III). Within *Astraea*, we coded the distribution range of subclades considering the range of all the species they contained. For *Croton* the terminals used in our sampling were coded using information from van Ee et al. (2011), according the section to which they belong. For *Acidocroton*, *Brasiliocroton*, *Sagotia* and *Sandwithia* we coded their distribution ranges using information from Webster (2014).

We reconstructed ancestral distribution ranges using statistical dispersal-vicariance analysis (S-DIVA) implemented in RASP 4.0 (Yu et al., 2015) over the chronogram produced in TreeAnnotator (as the condensed tree) and the trees resulting from the four different runs from the divergence time estimates in BEAST to allow evaluation of uncertainty over a set of trees. We set the maximum number of areas at each node to 3, 4 and 5 to examine the effects of this constraint on wide ancestral distribution ranges. We also removed sets of areas which were not linked by at least one area (as CDEG, for example, in which G are separated from CDE by F and H). Among the remaining areas, we did not use any constraint between A and B and the remaining areas



because of the intermittent connections between Central America and South America due to the Proto-Great Antilles and GAARLandia and Isthmus of Panama during the geological history of South America. With this approach we intended to allow the reconstruction of widely distributed ancestors in these areas.

**Table III:** Geographical areas adopted in this work for the reconstruction of the biogeographic history of *Astraea*, with the species of *Astraea* found in each one of them. Species are indicated within brackets when only a few records for such species are known within this area.

Code	Area	Description	Species of <i>Astraea</i>
A	Mesoamerica	Mexico, Central America and northern islands of West Indies (Cuba, Bahamas and Jamaica)	<i>A. lobata</i> [ <i>A. surinamensis</i> ]
B	Lesser Antilles	West Indies, excluding Cuba, Bahamas and Jamaica	<i>A. surinamensis</i> [ <i>A. lobata</i> ]
C	W South America	Andes and Pacific coast of South America	<i>A. lobata</i> , <i>A. surinamensis</i> , <i>A. trilobata</i>
D	Amazon Basin	Lowland moist forests in N Brazil and neighboring countries	<i>A. surinamensis</i>
E	N South America	N Venezuela and non-Amazon portion of Suriname, Guyana and French Guiana	<i>A. surinamensis</i>
F	Central and NE Brazil	Central Cerrado and Caatinga	<i>A. digitata</i> , <i>A. gracilis</i> , <i>A. klotzschii</i> , <i>A. paulina</i> , <i>A. surinamensis</i> [ <i>A. lobata</i> ]
G	SE Brazil	Moist and seasonally dry forest in SE Brazil and Bahia, including the Espinhaço Range	<i>A. cincta</i> , <i>A. comosa</i> , <i>A. gracilis</i> , <i>A. klotzschii</i> , <i>A. macrourea</i> , <i>A. manihot</i> , <i>A. paulina</i> , <i>A. praetervisa</i> , <i>A. subcomosa</i> , <i>A. surinamensis</i> [ <i>A. lobata</i> ]
H	Chaco and SW Brazil	Cerrados from S Goias and Mato Grosso do Sul, Chaco and southern grasslands of Brazil and Uruguay	<i>A. cincta</i> , <i>A. lobata</i> , <i>A. paulina</i> , <i>A. surinamensis</i>
I	Africa	Africa and Madagascar	<i>A. trilobata</i> [ <i>A. surinamensis</i> ]

## RESULTS

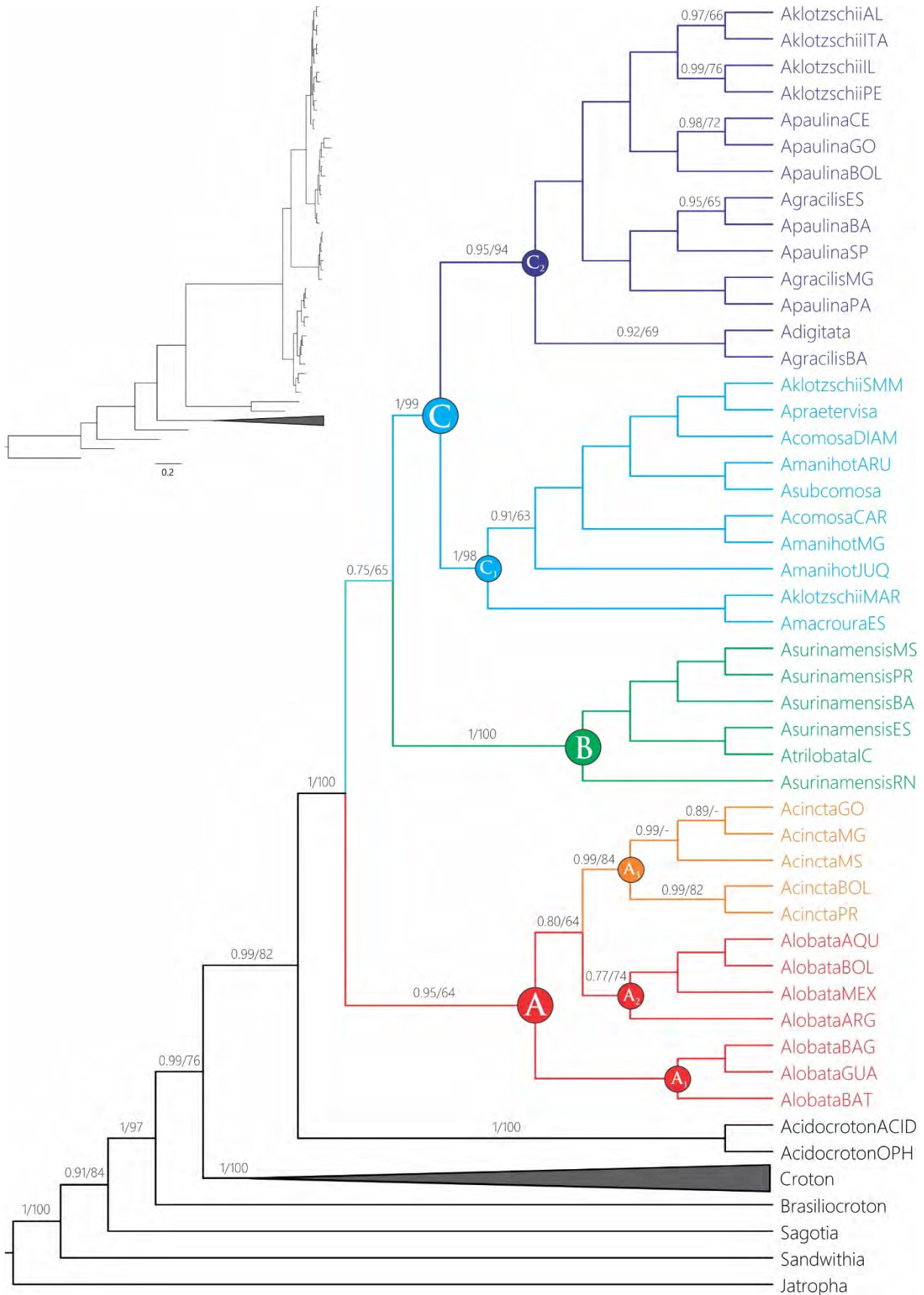
**Analysis of ITS dataset**—Summary statistics for this dataset are presented in Table IV. The ITS phylogeny (Fig. 1) recovered *Sandwithia* as the earliest genus to diverge within Crotonaeae, and the remaining genera were recovered in a moderately supported clade (0.90 PP, 84 BS). *Sagotia* was recovered as sister to Core Crotonaeae, which emerged as a clade with high support (1 PP, 97 BS). *Brasiliocroton* was recovered as sister to the clade formed by *Croton* + (*Acidocroton* + *Astraea*), and the latter clade showed moderate (76 BS) to high (0.99 PP) support. Both *Acidocroton* and *Croton* were recovered as monophyletic groups with high support (1 PP / 100 BS).

**Table IV:** Summarized statistics for the regions and datasets analyzed in this work.

	trnLF	psbA	chloroplast	ITS
Number of samples	66	59	69	69
Aligned length (bp)	980	481	1461	591
Variable characters (%)	275 (28.06 %)	90 (18.71 %)	365 (24.98 %)	323 (54.65 %)
Parsimony-informative characters (%)	127 (12.95 %)	49 (10.18 %)	176 (12.04 %)	223 (37.73 %)
Missing data	2.51 %	0.75 %	10.00 %	1.22 %

Within *Astraea*, only the sample of *A. cincta* from Mato Grosso do Sul (AcinctaMS) was partially sequenced. *Astraea* was recovered as a monophyletic group with high support (1 PP, 100 BS), and sister to *Acidocroton* with moderate (82 BS) to high (0.98 PP) support. We obtained three main clades (Fig. 1). Clade A had low (64 BS) to moderate (0.93 PP) support and contained the samples of *A. lobata* and *A. cincta*. Samples of *A. lobata* were recovered in two distinct clades, A1 with low support, including the samples from Costa Rica and one of the Brazilian samples (AlobataBAT), and A2, with moderate (0.77 PP, 74 BS) support, containing the remaining samples of these species. The samples of *A. cincta* were recovered in clade A3 with moderate (84 BS) to high (0.99 PP) support. Within clade A3, samples from Bolivia and Paraná grouped together in a subclade that was sister to the other subclade in A3 grouping samples from Goiás, Mato Grosso do Sul and Minas Gerais. Relationships among samples of *A. cincta* are mostly highly supported (0.99 PP) in the Bayesian tree, except for the closest relationship between samples from Goiás and Minas Gerais (0.89 PP).

Clade B and C formed a clade with low support (0.75 PP, 65 BS), but clades B and C individually were recovered with high support values. Clade B, containing the samples of *Astraea surinamensis* and *A. trilobata*, was recovered with high support (1 PP / 100 BS). The only sample of *A. trilobata* was recovered amongst the samples of *A. surinamensis*. However, all internal nodes within clade B had low support (0.2–0.21 PP / 0.57 BS).



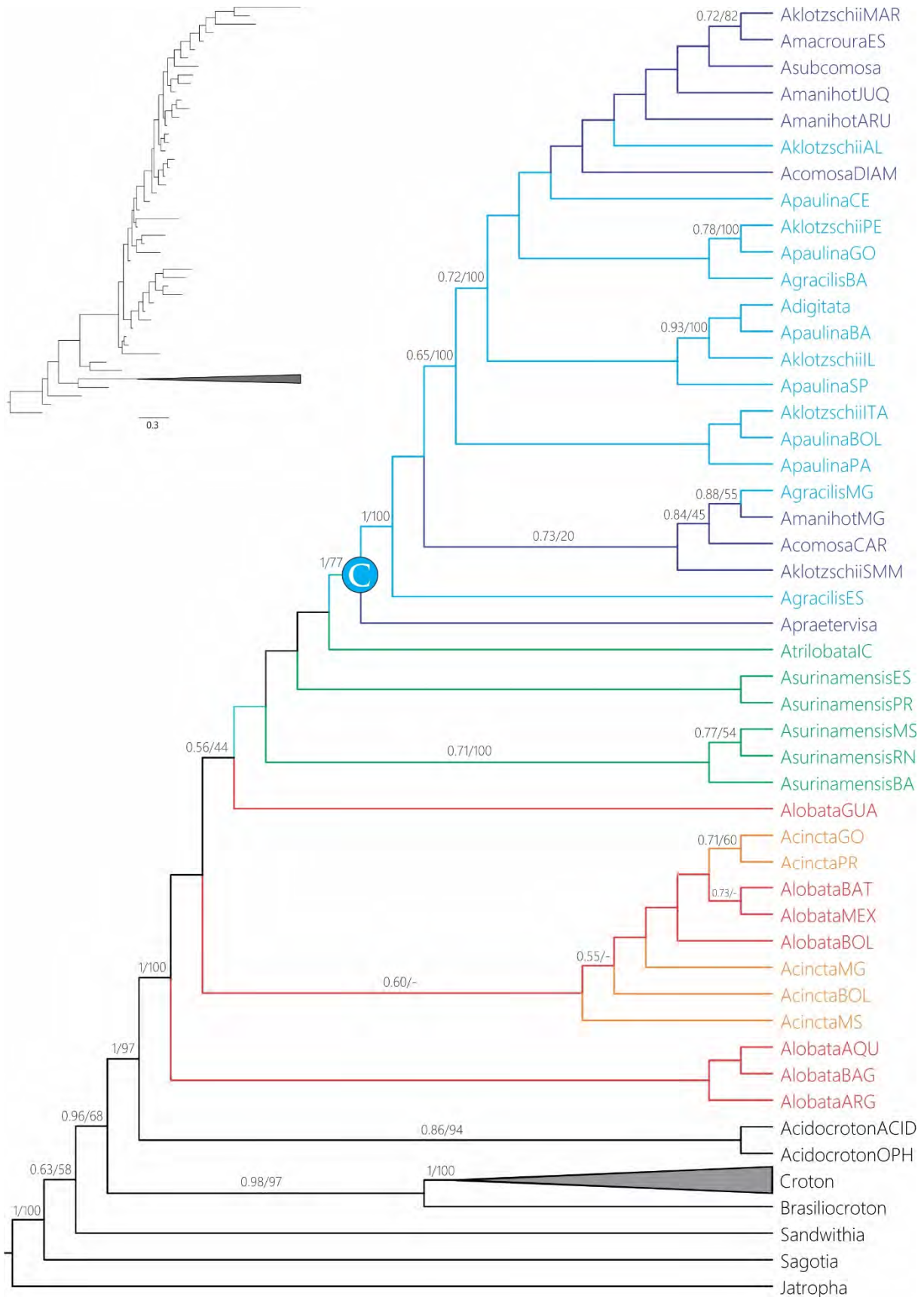
**Figure 1.** Extended majority consensus tree obtained from Bayesian analysis of ITS dataset. Values above branches correspond to Bayesian posterior probabilities / maximum likelihood bootstrap percentages. Values below 50 BS and/or 0.50 PP were omitted. On the upper left corner, the same tree is presented as phylograms and the scale bar indicates the mean number of nucleotide substitutions per site.

Clade C is the most diverse within *Astraea* including nine of the 13 species recognized by Silva & Cordeiro (Capítulo IV). This clade was recovered with high support (1 PP, 99 BS), and with two subclades: C1 showed high support (1 PP, 98 BS) and contained *A. comosa*, the samples from southeastern Brazil of *A. klotzschii*, *A. macroua*, *A. manihot*, *A. praetervisa* and *A. subcomosa*. Internal nodes were recovered with low support, except for the couplet of *Aklotzschii*MAR + *Amacroua*ES as the first diverging lineage, with the remaining relationships recovered with low (63 BS) to high (0.91 PP) support. C2 was recovered with moderate (94 BS) to high support (0.95 PP) and contained *A. digitata*, the samples from northeastern Brazil of *A. klotzschii*, *A. paulina* and *A. gracilis*. As in subclade C1, internal nodes within C2 showed low support, except for some couplets of samples with low (in ML tree) to moderate or high (in Bayesian tree) support values: *Aklotzschii*AL + *Aklotzschii*TA (0.97 PP, 66 BS); *Aklotzschii*L + *Aklotzschii*PE (0.99 PP, 76 BS); *Adigitata* + *Agracilis*BA (0.92 PP, 69 BS); *Apaulina*CE + *Apaulina*GO (0.98 PP, 72 BS); and *Apaulina*BA + *Agracilis*ES (0.95 PP, 65 BS). Despite the higher resolution in ITS tree (compared to the chloroplast phylogeny, see next section), species accessions were not recovered as exclusive lineages, except for *A. cincta*.

**Analysis of plastid dataset**—Summary statistics for this dataset are also presented in Table IV. In the case of *Astraea*, three samples (*Alobata*ARG, *Apaulina*CE, and *Aklotzschii*AL) for the *trnL*F dataset, and three for the *psbA* dataset (*Alobata*GUA, *Aklotzschii*PE and *Asurinamensis*RN) failed to amplify. Likewise, *psbA* sequences of *Acidocroton* and *Sandwithia* are missing due to amplification failure. In the *psbA* dataset, we only included sequences of *Astraea*, *Croton* and *Brasiliocroton*, and excluded available sequences of *Sagotia* and *Jatropha* because they could not be aligned probably because of the low confidence of primary homology in face of known problems regarding this marker (Borsch and Quandt, 2009). For this reason, the plastid dataset has the highest percentage (10 %) of missing data (Table IV).

The analysis of the plastid dataset (Fig. 2) recovered *Sagotia* as the earliest genus to diverge within Crotonaeae, with the remaining genera (*Sandwithia* and Core Crotonaeae) grouped in a clade with low support (0.63 PP, 58 BS). The core Crotonaeae clade was recovered with low (68 BS) to high (0.96 PP) support, and included two subclades: *Brasiliocroton* + *Croton*, with high (0.98 PP, 97 BS) support, and *Acidocroton* + *Astraea*, with high support (1 PP, 97 BS). *Croton* was recovered as monophyletic with high support (1 PP, 100 BS) and the two *Acidocroton* accessions also formed a clade, but with moderate (0.86 PP, 94 BS) support.

*Astraea* was recovered as monophyletic with high support (1 PP / 100 BS). However, the chloroplast phylogeny is poorly resolved and lacks phylogenetic structure - internal clades were mostly low supported, and they did not correspond to the clades and subclades recovered in the ITS tree, except for clade C, which emerged with moderate (77 BS) to high (1 PP) support. Within this clade, *A. praetervisa* was recovered as sister to the remaining samples, which were grouped in a highly supported (1 PP, 100 BS) clade. Also, species accessions were not grouped in distinct clades.



**Figure 2.** Extended majority consensus tree obtained from Bayesian analysis of plastid (*trnL*F and *psbA-trnH*) dataset. Values above branches correspond to Bayesian posterior probabilities / maximum likelihood bootstrap percentages. Values below 50 BS and/or 0.50 PP were omitted. On the upper left corner, the same tree is presented as phylograms and the scale bar indicates the mean number of nucleotide substitutions per site.

Variation of sequences within species of *Astraea*—We observed considerably higher variation in *trnLF* and ITS sequences, when compared to the *psbA* ones. Also, we found relatively low variation among clades. There were also many examples of no variation among sequences of the same species, for all three markers, and the highest variation was observed among sequences of *A. klotzschii* (recovered in two clades) and other widely distributed species in clade C2 (*A. gracilis* and *A. paulina*). Summary results of the variation of sequences within and among clades of *Astraea* are presented in Table V, while sequence variation among and within species are presented in Supplementary Tables I (ITS), II (*trnLF*) and III (*psbA*).

**Table V:** Variation of sequence within and between clades of *Astraea*

	ITS	<i>trnLF</i>	<i>psbA</i>
<b>Within clades</b>			
Astraea	3.61% (0.00–6.96)	2.13% (0.00–9.48)	0.94% (0.00–3.22)
Clade A	1.12% (0.00–1.89)	1.96% (0.14–4.73)	0.07% (0.00–0.39)
Clade A1	0.82% (0.57–1.25)	0.57% (0.29–0.86)	0.00%
Clade A2	0.47% (0.00–0.94)	2.18% (1.59–2.91)	0.00%
Clade A3	0.53% (0.19–0.94)	2.26% (0.43–3.97)	0.15% (0.00–0.39)
Clade B	0.19% (0.00–0.37)	1.95% (0.00–4.28)	0.15% (0.00–0.38)
Clade C	1.31% (0.19–3.04)	1.93% (0.14–8.70)	0.29% (0.00–1.54)
Clade C1	0.74% (0.19–1.69)	2.75% (0.14–8.70)	0.32% (0.00–0.77)
Clade C2	0.43% (0.00–1.12)	0.97% (0.14–2.46)	0.29% (0.00–1.54)
<b>Between clades</b>			
A x B	6.06% (5.42–6.96)	2.01% (0.00–6.61%)	0.89% (0.76–1.57)
A x C	4.99% (4.27–6.56)	2.35% (0.56–7.40)	1.78% (1.55–3.22)
B x C	5.67% (5.02–6.68)	2.26% (0.32–9.48)	1.01% (0.78–2.32)
A1 x A2	1.25% (0.94–1.52)	1.42% (0.14–2.47)	0.00%
A1 x A3	1.45% (1.13–1.85)	1.74% (0.29–4.12)	0.08% (0.00–0.39)
A2 x A3	1.32% (0.94–1.89)	2.54% (0.43–4.73)	0.08% (0.00–0.39)
C1 x C2	2.06% (1.36–3.23)	2.15% (0.28–7.15)	0.35% (0.00–1.89)

**Character state mapping**—We carried out the character state mapping and posterior analyzes (divergence time estimates and reconstruction of ancestral areas) using the ITS phylogeny because it was better resolved and supported in their internal clades than the plastid phylogeny. Overall, the topology and branch support obtained from BEAST was congruent with the topology obtained from MrBayes, recovering the same clades and subclades, except for the recovery of a clade with *Sagotia* and *Sandwithia* (the ITS tree from MrBayes recovered *Sandwithia* as sister to the remaining *Crotoneae*). Coded characters are presented in the Supplementary Table IV.

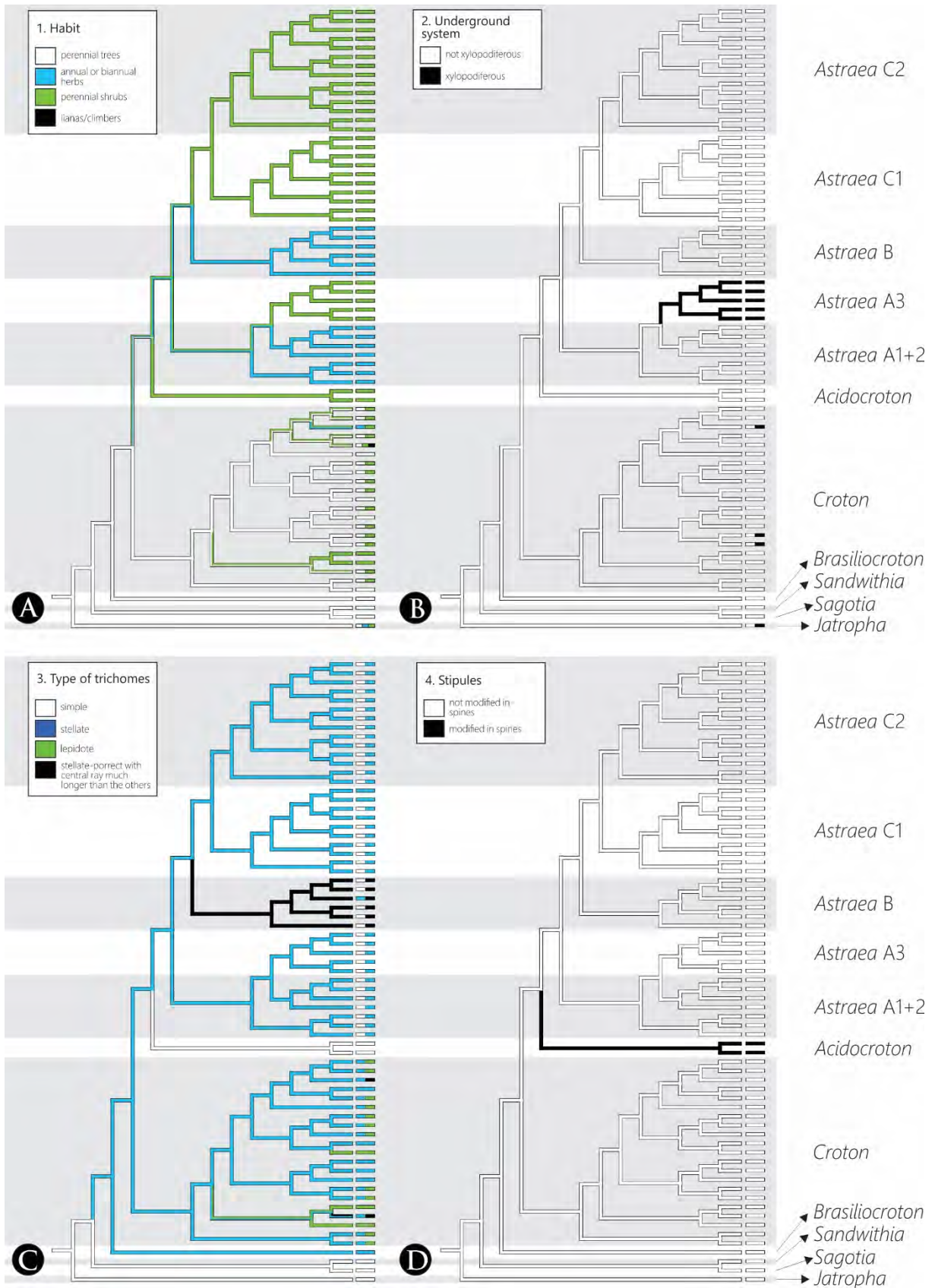
Habit in *Crotoneae* varies from annual or biannual herbs to perennial trees (Fig. 3A), although the shrubby habit is the dominant life form in the tribe. Lianescent habit is rare, and only present within *Croton*, for example, in some representatives of *Croton* sects. *Cleodora* and *Luntia* (e.g. *C. pseudofragrans* Croizat and *C. pullei* Lanj.). *Jatropha* shows the same variety of habit but shrubs are also more common, while the other two genera of *Jatrophaeae* (*Joannesia* and *Vaupesia*) are trees. Xylopodia (Fig. 3B) are observed in *Astraea cincta* (clade A3), in some groups within *Croton* (e.g., *C. antisiphiliticus* Mart., in *C. sect. Geiseleria*, and *C. didrichsenii* G.L. Webster, in *C. sect. Julocroton*) and also in *Jatropha*.

*Crotoneae* is remarkable by its diversity of trichome types, mainly due to the astonishing variety found within *Croton*, especially in subtypes of stellate trichomes (Webster, 1993). Our analysis shows that stellate trichomes are only found in *Astraea*, *Brasilicroton* and *Croton*, while the remaining genera of *Crotoneae* and *Jatropha* have only simple trichomes (Fig. 3C), whereas lepidote trichomes are restricted to *Croton*. A special type of stellate-porrect trichomes, with the central ray much longer than the lateral ones (giving the appearance of simple trichomes without the aid of a stereomicroscope) is found in two species of *Astraea* (*A. surinamensis* and *A. trilobata*, both on clade B) and some species of *Croton*, such as *Croton hirtus* (*C. sect. Geiseleria*) and *C. manampetsae* (*C. subg. Croton*).

The putative ancestor of *Astraea* had only stellate trichomes, but most species have both simple and stellate trichomes, except for *A. comosa*, *A. subcomosa* and *A. praetervisita*, which have strictly stellate trichomes. The same state was recovered for ancestors of most clades, except for the one in clade B. *Astraea surinamensis* and *A. trilobata* have remarkable stellate-porrect trichomes, in which the central ray is much longer than the lateral rays, which represent a strong putative synapomorphy for clade B.

Stipules modified as spines are mostly restricted to *Acidocroton* and represent a probably strong putative synapomorphy for this genus (Fig. 3D). A few species of *Croton* in *C. sect. Eluteria* subsect. *Cubenses*, such as *C. bispinosus* C. Wright and *C. brittonianus* Carabia, have spine-like structures (van Ee et al., 2011). However, the nature of these structures is unclear, as in *C. brittonianus* they seem to be modified branches.





**Figure 3.** Evolution patterns of habit (A), underground system (B), type of trichomes (C) and stipules (D) mapped with parsimony onto the tree obtained from the divergence time estimates. Legends for character states are represent on the upper left corner of each tree.

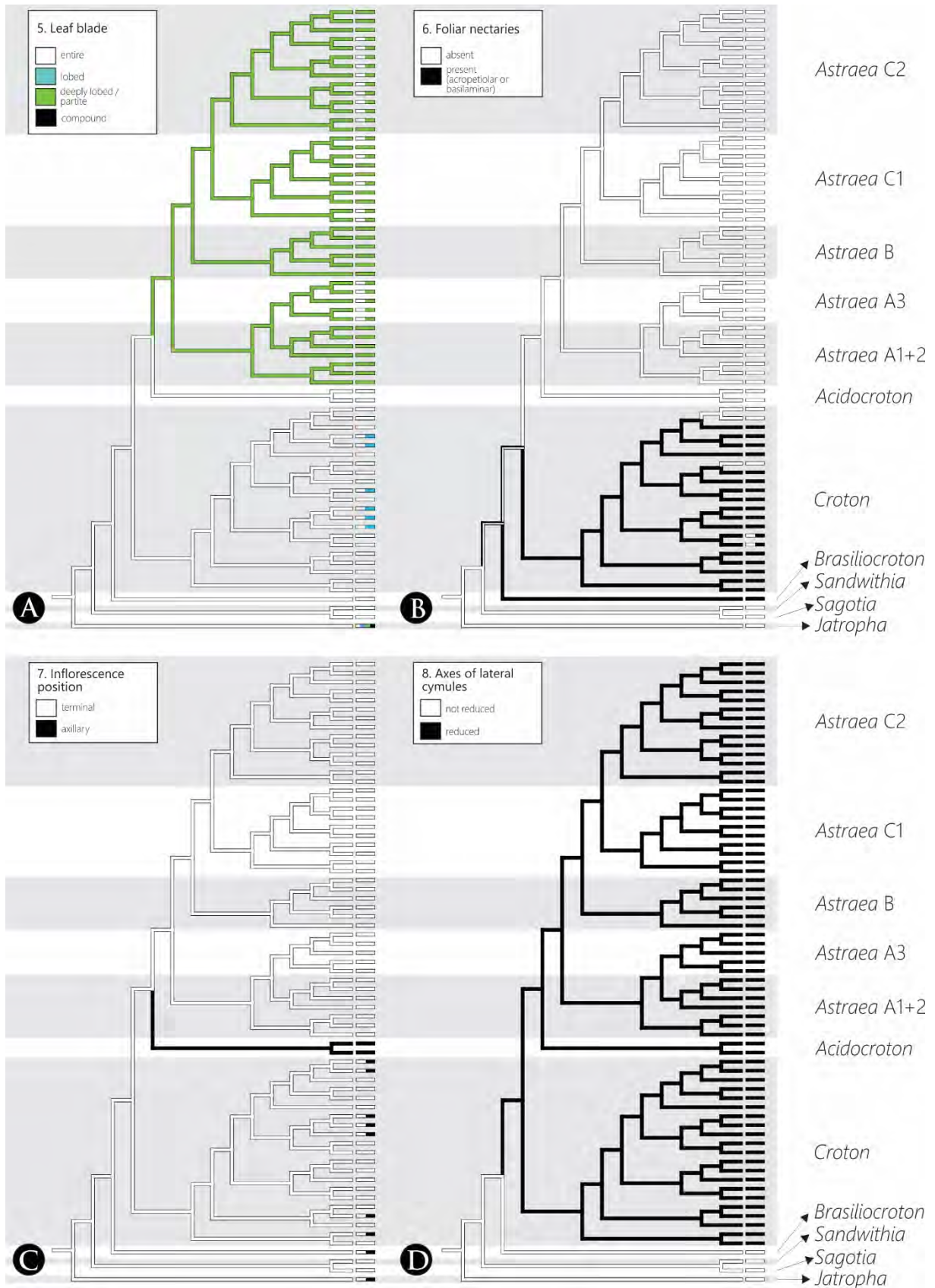
Leaf blade is mostly entire among genera of Crotonaeae (Fig. 4A), with a few not closely related species of *Croton* presenting lobed leaves, such as *C. gossypifolius* Vahl. (*C.* sect. *Cyclostigma*) and *C. palanostigma* Klotzsch (*C.* sect. *Luntia*). On the other hand, species of *Astraea* usually have deeply lobed or partite leaves, but individuals of some species, like *A. klotzschii* or *A. subcomosa*, may have only entire leaves. In *Jatropha*, leaves may be entire or, more commonly, lobed to partite or compound, while *Vaupesia* has entire leaves and *Joannesia* compound leaves.

Acropetolar or basilaminar foliar nectaries are well-known characteristics of *Croton*, although they are missing in some species or entire sections of the genus, as for example, *C.* sect. *Lamprocroton* and *C.* sect. *Julocroton* (Fig. 4B). Within Crotonaeae, these structures are only present in *Croton* and *Brasilicroton*. In *Jatropha*, only glandular trichomes are present along the leaf margin, but well-developed glands occur in *Joannesia* and *Vaupesia*.

Inflorescences are mostly terminal in Crotonaeae (Fig. 4C), and strictly axillary only in *Acidocroton*. However, inflorescences may be both terminal and axillary in some not closely related species of *Croton*, as in *C. sellowii* Baill. (*C.* sect. *Medea*), *C. hemiargyreus* Müll.Arg. (*C.* sect. *Cleodora*) and *C. sapiifolius* Müll.Arg. (*C.* sect. *Quadrilobi*), while in *Brasilicroton*, one species (*B. mamoninha*) has terminal inflorescences, while the other (*B. muricatus*) has axillary inflorescences. In Jatrophaeae, *Jatropha* has both axillary and terminal inflorescences, while *Joannesia* and *Vaupesia* have terminal inflorescences.

Regarding the structure of the inflorescence, in *Acidocroton*, *Astraea* and *Croton* the cymules have the central axis reduced (Fig. 4D). In *Croton* and *Astraea*, the inflorescences have a spiciform appearance, while in *Acidocroton* the main axis is also reduced, giving a glomerulate appearance, but some species of *Croton*, e.g., *C.* sect. *Lamprocroton*, have very short axis that look similar to the ones of *Acidocroton* or, more rarely, the axis of lateral cymules are developed, as in *C. rusbyi* Britton & Rusby (*C.* sect. *Cyclostigma*). On the other hand, in *Brasilicroton*, *Sagotia* and *Sandwithia* the cymules do not have the central axis reduced (with a paniculiform or racemose appearance). In Jatrophaeae, when the inflorescence are not dichasia (in *Jatropha*), the lateral axes are never reduced.

Staminate flowers are unique in *Astraea* because of the presence of moniliform trichomes at the basal portion of petal margin (Fig. 5A). *Sagotia*, *Sandwithia* and *Acidocroton* the petals are longer than the calyx, while in *Brasilicroton*, *Croton* and *Astraea* the petals are shorter or equal to the calyx (Fig. 5B). In Jatrophaeae, the petals are usually longer than the calyx. In Jatrophaeae and most Crotonaeae, the staminate flowers have nectaries, the only exception is *Sagotia*, in which staminate flowers lack these structures (Fig. 5C). Another remarkable characteristic of *Sagotia* is the sessile anthers, although they are also found in a few species of *Croton*, such as *C. ekmanii* Urb. Stamens inflexed in bud are exclusive of *Astraea* and *Croton* (Fig. 5D), while in the remaining genera of Crotonaeae and Jatrophaeae the stamens are erect in bud. In Jatrophaeae, the staminate



**Figure 4.** Evolution patterns of leaf blade (A), foliar nectaries (B), inflorescence position (C) and axes of lateral cymules (D) mapped with parsimony onto the tree obtained from the divergence time estimates. Legends for character states are represent on the upper left corner of each tree.

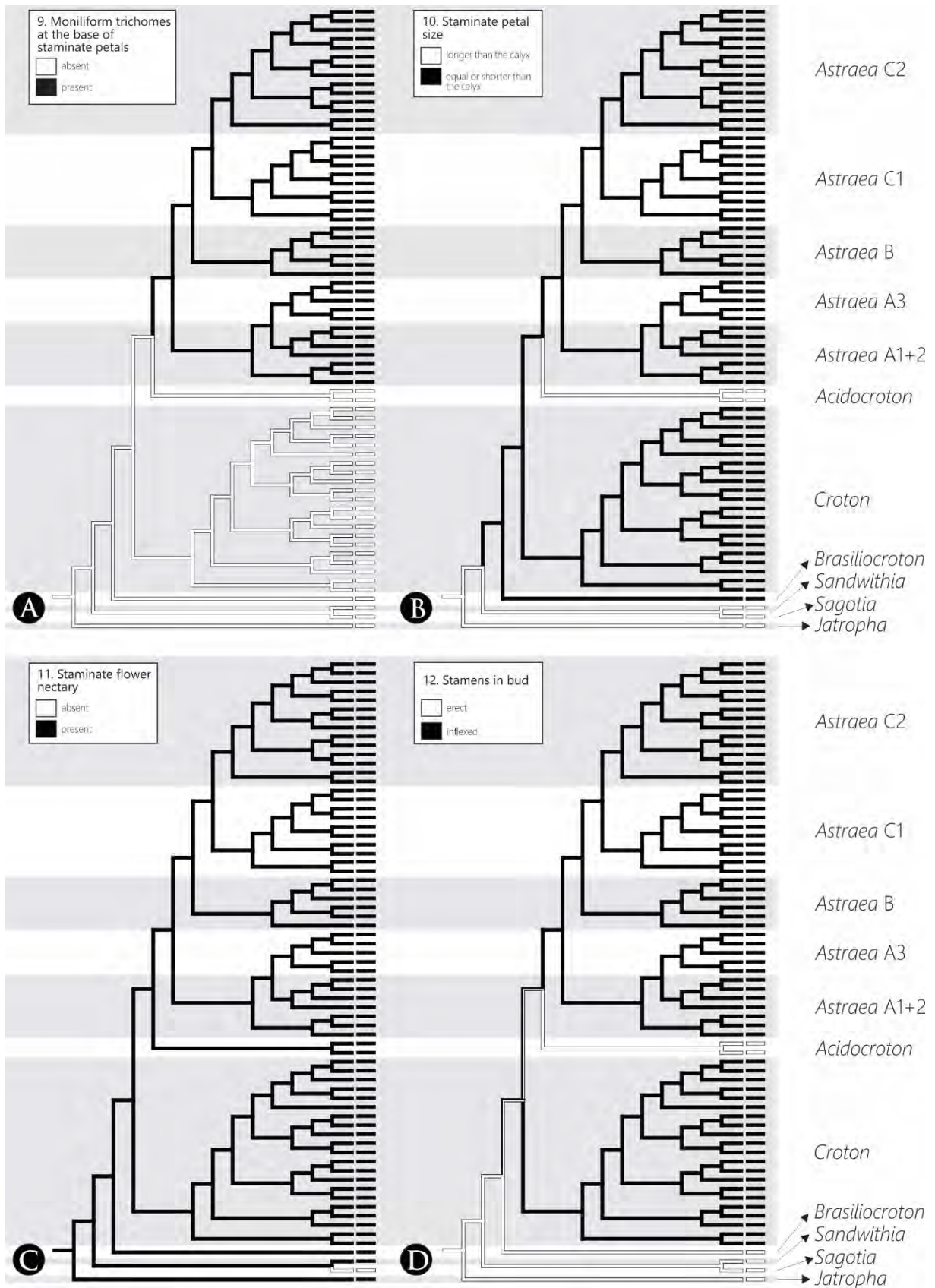
flowers have 6–12 stamens, while within Crotonaeae the number of stamens vary from three to more than 50 stamens (reaching up to 400 according to Webster, 2014) (Fig. 6A).

Pistillate flowers include one putative synapomorphy for Crotonaeae: while in Jatrophaeae the pistillate flowers have well-developed petals, in Crotonaeae, petals are generally absent or very-reduced (Fig. 6B), with a few exceptions as in *Croton* sect. *Eluteria* subsect. *Eluteria* in which petals are well-developed. As the staminate flowers, the pistillate flowers of *Sagotia* do not have nectaries (Fig. 6C), and in the remaining genera of Crotonaeae, the nectary may be annular (in *Acidocroton*, *Croton* and *Sandwithia*) or segmented (in *Brasiliocroton* and *Astraea*). In Jatrophaeae, the nectary of pistillate flowers is segmented in *Joannesia* and *Vaupesia*, while in *Jatropha* it may be annular or segmented. Finally, styles (Fig. 6D) are always bifid in *Brasiliocroton*, *Sagotia* and *Sandwithia*, while in *Acidocroton* they may be entire or bifid, in *Astraea* they are always multifid, and in *Croton* they may be bifid, 2-bifid or multifid (entire styles are only observed in *C. setiger* Hook.).

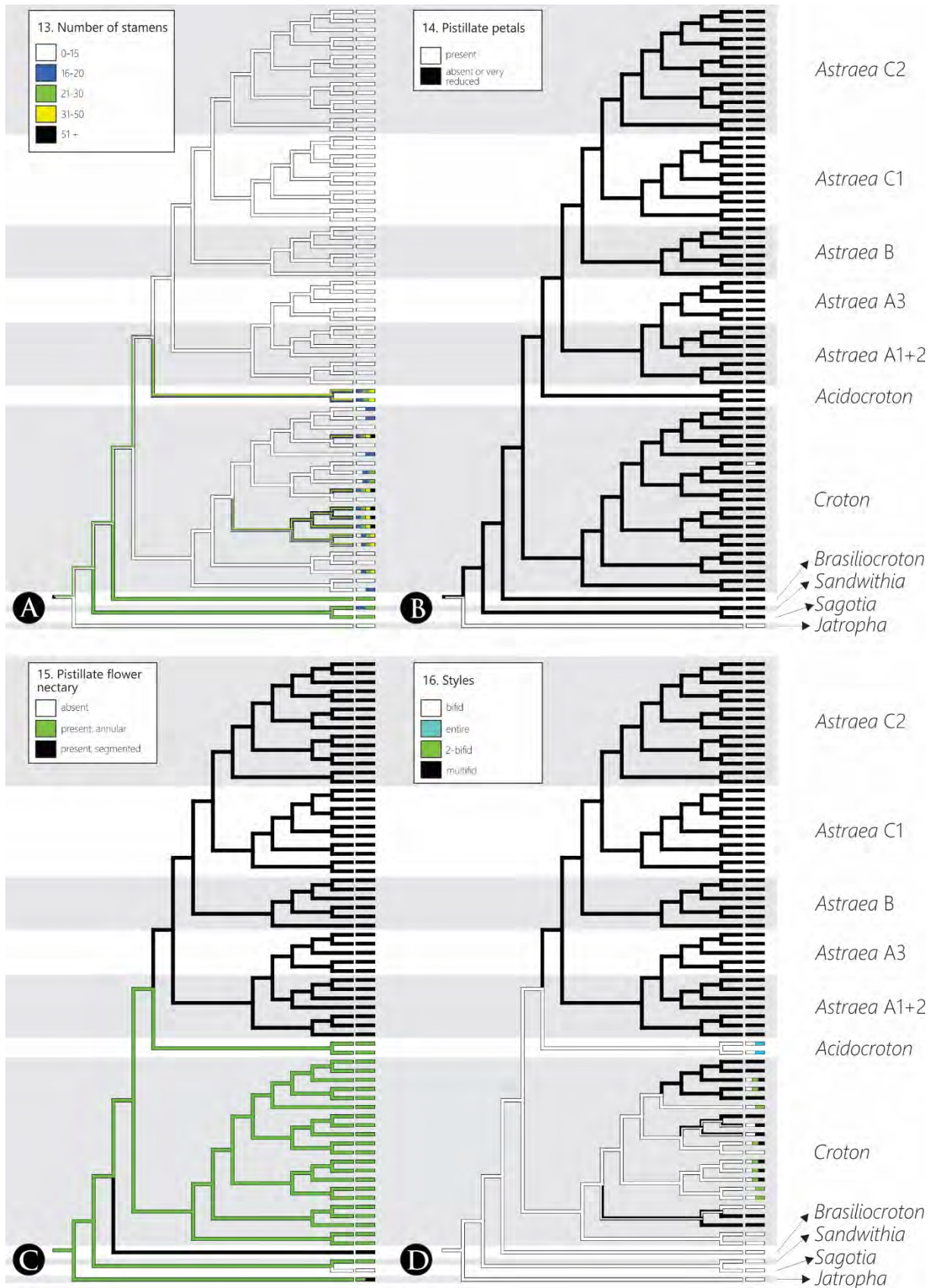
**Divergence times in Crotonaeae**—The chronogram based on the ITS dataset (Fig. 7) shows that our prior definition strategy resulted in a mean age of 59.99 Ma (95% HPD confidence interval: 55.73–69 Ma) for the divergence between Jatrophaeae and Crotonaeae, with a mean crown age of 54.71 Ma (95% HPD confidence interval: 42.26–67.35 Ma) for Crotonaeae. Under this scenario, the crown age for the clade *Sagotia* + *Sandwithia* was set to 8.22 Ma (95% HPD confidence interval: 0.16–41.37 Ma), while the divergence of *Brasiliocroton* was estimated to be 48.13 Ma (95% HPD confidence interval: 39.58–58.42 Ma), and that between *Croton* and *Acidocroton* + *Astraea* was estimated at 43.71 Ma (95% HPD confidence interval: 38.3–52.81 Ma).

*Astraea* diverged from *Acidocroton* at approximately 34.57 Ma (95% HPD confidence interval: 15.38–48.26 Ma), with crown age for *Acidocroton* set to 6.11 Ma (95% HPD confidence interval: 0.09–25.71 Ma). The crown age of *Astraea* (and the divergence between clade A and clades B + C) was estimated at about 25.7 Ma (95% HPD confidence interval: 9.09–42.73 Ma), followed by the split between clades B and C at 19.05 Ma (95% HPD confidence interval: 4.46–34.38 Ma). Crown age of clade A was set to 14.58 Ma (95% HPD confidence interval: 2–30.34 Ma), with the diversification of subclade A1 from A2 + A3 at 5.17 Ma (95% HPD confidence interval: 0.06–18.13 Ma), A2 from A3 at 8.8 Ma (95% HPD confidence interval: 0.65–21.95 Ma). Crown ages for clades A2 and A3 were at 3.81 Ma (95% HPD confidence interval: 0.13–13.08) and 4.7 Ma (95% HPD confidence interval: 0.27–14.46), respectively. Crown age for clade B and C were set to 6.87 Ma (95% HPD confidence interval: 0.29–20.3 Ma) and 14.22 Ma (95% HPD confidence interval: 3.02–28.58 Ma), respectively. Within clade C, the diversification of subclade C1 was set to 8.68 Ma (95% HPD confidence interval: 1.05–20.56 Ma) and C2 at 9.45 Ma (95% HPD confidence interval: 1.22–21.36 Ma).





**Figure 5.** Evolution patterns of moniliform trichomes at the base of staminate petals (A), staminate petal size (B), staminate flower nectary (C) and stamens in bud (D) mapped with parsimony onto the tree obtained from the divergence time estimates. Legends for character states are represent on the upper left corner of each tree.



**Figure 6.** Evolution patterns of number of stamens (A), pistillate petals (B), pistillate flower nectary (C) and styles (D) mapped with parsimony onto the tree obtained from the divergence time estimates. Legends for character states are represent on the upper left corner of each tree.

**Reconstruction of ancestral distribution ranges**—We found few differences among the reconstructions with 3, 4 and 5 areas as maximum areas at each node. However, when setting 5 maximum areas at each node, the results showed fewer areas with < 0.05 probability avoiding a higher degree of uncertainty in the results, besides allowing wide distribution ranges, especially for nodes including widespread species as *Astraea* clade B and the node uniting *Astraea* and *Acidocroton*, for example. For these reasons, we choose the results from the reconstruction allowing 5 areas at each node.

The reconstruction (Fig. 7) showed the Amazon Basin (D) or N South America (E) as the most likely stated (MLS) for the ancestor of all Crotonaeae members, but also a wider area formed by the those two, and Chaco and southwestern Brazil (H). MLS for the ancestor of *Sagotia* and *Sandwithia* was the Amazon Basin (D), but other scenarios include Western South America and northern South America (CDE) or only northern South America (DE). For the Core Crotonaeae, the MLS for the ancestral distribution range was southeastern Brazil (G), while for *Croton* it was a wider area (GH), including the Chaco and SW Brazil. For the clade containing *Acidocroton* and the two most widespread genera within Crotonaeae (*Astraea* and *Croton*), the MLS recovered in our analysis was set to southeastern Brazil (G), while for the node uniting *Acidocroton* and *Astraea* a much wider area was recovered (ACGH), containing Mesoamerica (A), western South America (C), southeastern Brazil (G) and Chaco and southwestern Brazil (H). The MLS recovered for *Acidocroton* node was Mesoamerica (A), while for *Astraea* its was western South America (C), southeastern Brazil (G) and Chaco and southwestern Brazil (H).

Within *Astraea*, MLS recovered for clade A was Chaco and southwestern Brazil (H), while MLS the for the node uniting clades B and C is inconclusive, with many possible scenarios involving western South America, central and northeastern Brazil (F), southeastern Brazil (G) and Chaco and southwestern Brazil (H). For clade B the MLS recovered in our analysis is western South America (C), or this area in combination with Chaco and southwestern Brazil (CH), northern South America (CE) or Amazon Basin (CD), but with lower probability values. Finally, the MLS for clade C is either southeastern Brazil (G) alone or with central and northeastern Brazil (FG), while for subclade C1 is only southeastern Brazil (G) and for subclade C2 is either southeastern Brazil (G), central and northeastern Brazil (F) or both (FG).

## DISCUSSION

**Topology incongruence between nuclear and chloroplast datasets**—The two datasets disagree regarding the earliest genus to diverge from the remaining Crotonaeae: the chloroplast points to *Sagotia*, while the nuclear points to *Sandwithia*, but the nuclear scenario is better supported when compared to the chloroplast topology: the clade containing *Sandwithia* and the remaining Crotonaeae genera in the ITS scenario genera has 0.91 PP and 84 BS support, while in the chloroplast the remaining genera are separated from *Sagotia* in a low supported



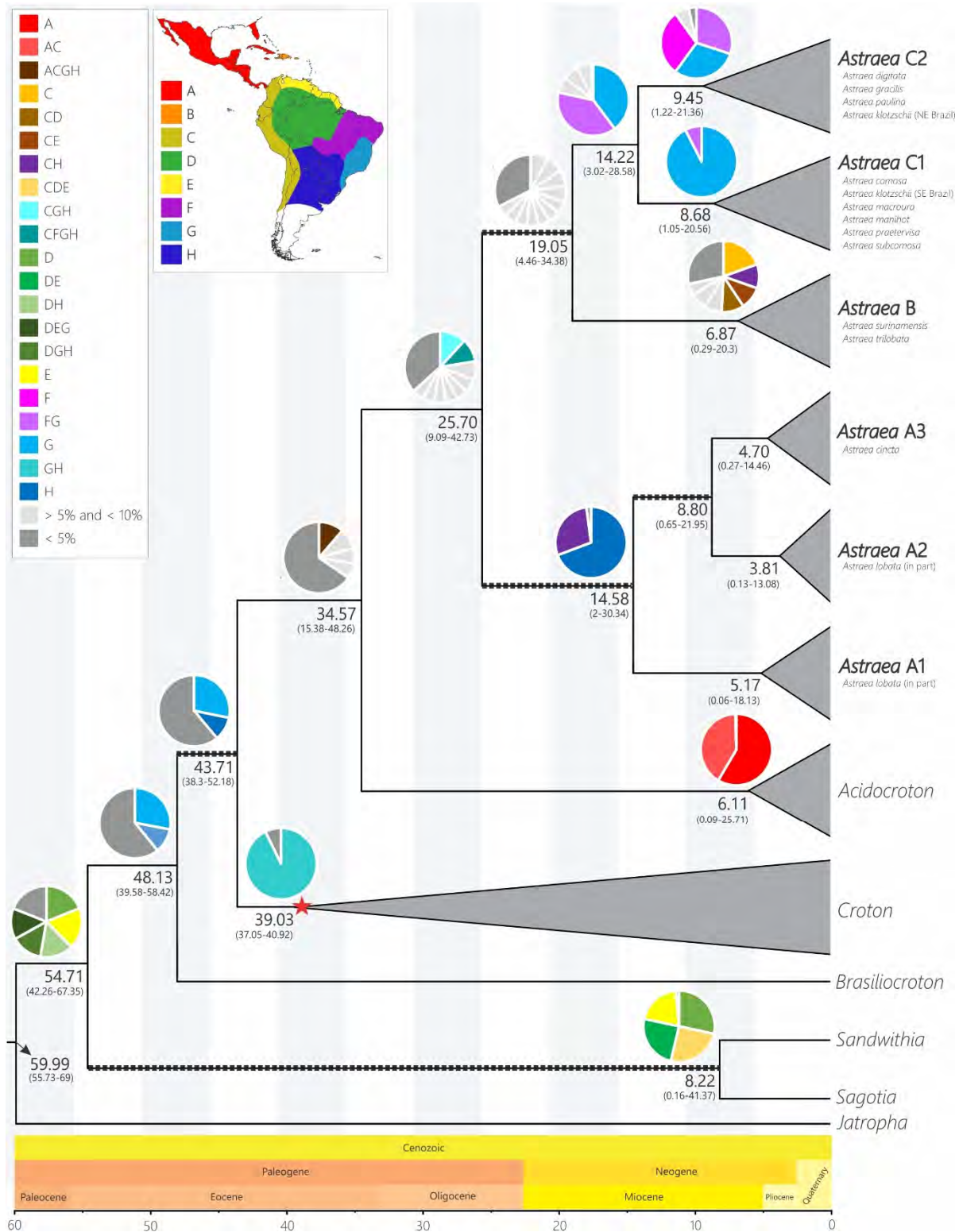


Figure 7. Chronogram resulting from the divergence time estimates of the ITS dataset with most likely states for the reconstruction of ancestral distribution ranges. Values near nodes correspond to ages with the 95% HPD confidence interval below and between parenthesis. Pie charts near nodes represent the most likely states of ancestral distribution range (color codification is represented on the upper left corner and areas are represented next to it). Low supported branches (0.75-0.94 PP) are indicated with thick dashed branches. All other branches have 0.95 PP or higher support.

clade (0.68 PP, 58 BS). Another strong incongruence regarding the relationships among Crotonae genera is the position of *Brasiliocroton*, with the chloroplast dataset recovering it as the sister genus of *Croton* in a highly supported clade (1 PP, 97 BS), while in the ITS dataset it is recovered as sister to a clade containing *Croton* + (*Acidocroton* + *Astraea*), with moderate (76 BS) to high (0.99 PP) support. Within *Astraea*, the two datasets agree only on clade C, while the species recovered in the clades A and B from the ITS dataset are recovered as successive sisters/clades do each other in the chloroplast dataset. Therefore, we did not concatenate plastid and nuclear datasets for our analysis.

Incongruence between plastid and nuclear markers is a common pattern found in plant phylogenies (Degnan and Rosenberg, 2009). Factors causing incongruence between gene trees may be of analytical (substitution model applied or taxon sampling, for example) or biological nature, such as hybridization (Smith et al., 2017), incomplete lineage sorting, horizontal gene transfer, heterotachy (variation on a give nucleotide throughout time) and rate heterogeneity (Som, 2015). Finding the cause of the incongruence is challenging (Smith et al., 2017), but one of the possibilities is the poor support in one or more partitions (Farris et al., 1994) as we observed when comparing the plastid tree with the nuclear one in our analysis. Also, incomplete lineage sorting may be associated to recent radiations (Som, 2015), which could be the case of species of *Astraea* in eastern Brazil which appear to have diverged between the Miocene and Pliocene.

The three genetic markers we used were insufficient to fully resolved species relationships within *Astraea*, probably because of the relatively recent origin and diversification of its main lineages. Additional markers or most likely genomic data will be necessary to improve phylogenetic resolution at the shallow nodes of the *Astraea* phylogeny, to better understand the reticulate pattern of evolution we have detected, and ultimately to understand the evolutionary history of this genus in the Neotropics.

**The putative synapomorphy of Crotonae**—As Wurdack et al. (2005) expanded the circumscription of Crotonae to include within it genera not previously related from Aleuritideae (*Sandwithia*) and Codiaeeae (*Sagotia* and *Acidocroton*), no macromorphological characters were indicated to distinguish Crotonae from its most closely related tribe, Jatropeae. Wurdack et al. (2005), however, indicated as one of the synapomorphies for the inaperturate crotonoids the petals present at least in the staminate flowers. In our morphological study (Fig. 6C), we found that all genera of Jatropeae (*Jatropha*, *Joannesia* and *Vaupesia*) have petals on both pistillate and staminate flowers, while in Crotonae petals are lacking or are very reduced in pistillate flowers, with rare exceptions (see below). Thus, we interpret the absence and/or reduction of petals in pistillate flowers as a putative synapomorphy for Crotonae.

Although in the original description of *Sandwithia* (Lanjouw, 1932) and in Webster (1994a), this genus is described as having petals, studies by Secco (1987; 1988) and a more recent taxonomic treatment by Webster (2014) stated that petals are very reduced, not surpassing 1 mm in length. In *Croton* there are also a few species

in *C. sect. Eluteria* subsect. *Eluteria* in which pistillate petals are well-developed (van Ee et al., 2011) and may represent an independent reversal event.

**Evolution of Crotonaeae**—The moist forests in South America, dated from at least 58 Ma (Morrone, 2006), occupied a wide range throughout the continent, up to Patagonia, from 50 to 55 Ma (Wilf et al., 2013). This timing corresponds to the time when Crotonaeae diverged from Jatropheae, at 59.99 Ma (HPD confidence interval: 55.73–69 Ma). Also, our analyzes indicate as putative ancestral areas for Crotonaeae either the Amazon Basin or northern South America, regions in which both *Sagotia* and *Sandwithia*, the first lineages to diverge within Crotonaeae, are found today (*Sagotia* also extends to part of western South America, and has very few collections in Central America, close to the Isthmus of Panama, that were not considered in the biogeographic analysis).

We found uncertainty regarding whether *Sagotia* or *Sandwithia* is the first diverging lineage within Crotonaeae due to different positions of these genera in the ITS and chloroplast datasets (see next section). However, in the tree resulting from the divergence time estimates in BEAST, *Sagotia* and *Sandwithia* would have diverged from the remaining Crotonaeae at 54.71 Ma (95% HPD confidence interval: 42.26–67.35 Ma), when South America was widely covered by moist forests (Morrone, 2006; Wilf et al. 2013). Divergence between *Sagotia* and *Sandwithia* is recovered as to have occurred only at 8.22 Ma, but with a large confidence interval (0.16–41.37 Ma) and low support (0.78 PP). However, this age would be congruent with the recent diversification from 10 Ma onwards in other forest groups, as found for *Guatteria* (Annonaceae; Erkens et al., 2007) and *Inga* (Fabaceae; Lavin, 2006).

Alternative scenarios involving an ancestral of Crotonaeae distributed in a wider area, reaching SW South America and SE Brazil were recovered in our analysis. From middle Eocene to early Oligocene a decline in the diversity of forest groups is observed in South America (Jaramillo, 2006). In the case of Crotonaeae, the putative ancestor of *Sagotia* and *Sandwithia* was distributed in the Amazon Basin, and western and northern South America, while for the remaining Crotonaeae the most likely state for the putative ancestor is the SE Brazil. This is interpreted as a vicariance event between northern and eastern South America. Nevertheless, in this scenario, the distribution ranges of *Brasiliocroton* in southeastern Brazil also corroborates that moist forests were once a unique and continuous formation, slowly separated with the increasing aridity from the Paleogene-Neogene which formed the South American diagonal of dry formations (Bigarella et al., 1975). In the present, this is reflected in an Amazon-Atlantic Forest disjunction pattern, documented for many plant groups (Fiaschi and Pirani, 2009), such as *Glycydendron* Ducke (Euphorbiaceae), *Byrsonima laevigata* (Poir.) DC. (Malpighiaceae), *Trichilia lepidota* Mart. (Meliaceae), *Philodendron ornatum* Schott (Araceae) and *Peperomia rhombea* Ruiz & Pav. (Piperaceae), besides some groups within Crotonaeae, such as *Croton* sect. *Cleodora* (Caruzo et al., 2011, Caruzo and Cordeiro 2013, Riina et al., in press).

The area of the putative ancestor of the clade containing *Acidocroton*, *Astraea* and *Croton* is the same of the one including these genera and *Brasiliocroton* (southeastern Brazil), indicating a sympatric speciation between these groups by 48.13 Ma (95% HPD confidence interval: 39.58–58.42 Ma). Our analysis indicated that the divergence between *Croton* and *Acidocroton* + *Astraea* occurred at 43.71 Ma (95% HPD confidence interval: 38.3–52.81 Ma), with a putative ancestor distributed in southeastern Brazil. Our sampling of *Croton* does not cover all the sections of this giant genus, since we were not focusing on this clade, so the divergence time estimates for internal nodes within this genus are not relevant for further discussion. However, in the reconstruction of ancestral areas, the putative ancestor of *Croton* is set to SW South America and SE Brazil, indicating that the expansion of *Croton* towards the Amazon basin could have followed the southern (through Paraná River basin) or northeastern (through the Caatinga; Rizzini, 1963) routes or across the paths of gallery forests throughout the Central Brazilian Plateau (Oliveira-Filho and Ratter, 1995). The high diversity of *Croton* in both Cerrado and Caatinga, reinforces that colonization of different biomes and new geographic areas (Pennington et al., 2004, Gonçalves et al., 2007, Saslis-Lagoudakis et al., 2008) could have played an important role in the diversification of the genus in Brazil.

From 50 to 33 Ma, South American lineages could spread to the Antilles through the Proto-Greater Antilles (Guyer and Savage, 1986) and GAARlandia (Iturralde-Vinent and MacPhee, 1999) before the closure of the Isthmus of Panama. This scenario may have played a role in the range expansion of the putative ancestor of *Acidocroton* and *Astraea*, which diverged in the two lineages at 34.57 Ma (95% HPD confidence interval: 15.38–48.26 Ma), when South America was connected to the emergent Greater Antilles during the Late Eocene-Early Oligocene transition (35–33 Ma; Gutiérrez-García and Vásquez-Domínguez, 2013). This connection between Greater Antilles and South America before the closure of the Isthmus of Panama appears to have been involved in the range expansion of *Croton* and its posterior dispersal to Africa following Laurasian migration hypothesis (van Ee et al., 2008; Davis et al., 2002).

The putative ancestor of *Acidocroton* was most likely found in Mesoamerica, and the divergence between its two sections at 6.11 Ma (95% HPD confidence interval: 0.09–25.71 Ma), indicates a vicariance event separating *A. sect. Acidocroton* (endemic to the Antilles) from *A. sect. Ophellantha* (Central America and northern South America). The recent divergence between the two sections of *Acidocroton* (when compared to the divergence between *Acidocroton* and *Astraea*) suggests that much of the diversity of this clade could have been lost due to climate changes (from warmer conditions in Eocene to cooler in Oligocene) that caused the great extinctions in marine invertebrates from late Oligocene-early Miocene (Ivany et al., 2000). Also, the relatively higher diversity of *Acidocroton sect. Acidocroton* (9 spp.) compared to that of *A. sect. Ophellantha* (4 spp.) is congruent with the increase in diversification in groups adapted to arid environments that took place in the Miocene, such as, for example, the Cactaceae (Arakaki et al., 2011), which started to diversify at around 15 Ma. As most species in that family, species in section *Acidocroton* are also strongly xeromorphic.

**The earliest diverging lineage in Crotonaeae**—Although Secco (1988) stated that *Sagotia* and *Sandwithia* would be related to each other, they were classified in different tribes by Webster (1994a). These two genera were recovered sister to each other, with high support, as the earliest diverging clade within Crotonaeae by Wurdack et al. (2005), based in two plastid regions (*rbcl* and *trnLF*), while the remaining genera were united in a moderately supported clade. A similar scenario was observed in the plastid tree of Silva et al. (Capítulo III), but the clade with *Sagotia* and *Sandwithia* was not highly supported, probably due to the inclusion of only one of plastid regions, *trnLF* (Silva et al., [Capítulo III]), used in Wurdack et al (2005).

In our Bayesian and ML analyses using a wider sampling of Crotonaeae than that of Silva et al. (Capítulo III), the clade with *Sagotia* and *Sandwithia* was not recovered (Figs. 1 and 2). Instead, *Sagotia* was recovered as the earliest diverging lineage in the plastid tree (Fig. 2), while in the nuclear tree (Fig. 1), this position was occupied by *Sandwithia*. However, in the plastid tree, the node uniting *Sandwithia* with the remaining Crotonaeae has low support (0.63 PP, 58 BS), whereas, in the nuclear tree, the clade uniting *Sagotia* and the remaining Crotonaeae has higher support values (0.91 PP, 84 BS). In the topology obtained in BEAST the clade with *Sagotia* and *Sandwithia* was recovered, but with low support (0.78 PP).

All genera in Crotonaeae have nectaries in both staminate and pistillate flowers, except for *Sagotia*. Under this scenario, one could interpret the absence of such structures as a plesiomorphic state within Crotonaeae and favor the low supported topology of the plastid tree, in which this genus is the earliest diverging lineage in the group. All genera of Jatropheae also have nectaries in both pistillate and staminate flowers, and our reconstruction of ancestral character states recovered a putative ancestor of Crotonaeae with nectaries in both pistillate and staminate flowers. The better supported position of *Sandwithia* as the earliest diverging lineage in Crotonaeae observed in the ITS tree, along with the character state recovered for the putative ancestor of Crotonaeae, supports the interpretation of *Sandwithia* as the earliest diverging lineage in Crotonaeae and that the absence of floral nectaries in *Sagotia* are derived states.

In its original description (Lanjouw, 1932), *Sandwithia* was described as having pistillate flowers with sepals united almost up to the apex, while Webster's (2014) description for the genus indicates that the sepals of pistillate flowers are more or less connate. However, the second species of *Sandwithia*, *S. heterocalyx* Secco (1988), has the pistillate sepals almost free from each other, and in one clade of *Croton* (*C.* sect. *Cleodora*), pistillate sepals can be connate up to half of their length (Caruzo et al., 2011). Therefore, connate sepals in pistillate flowers represent a very uncommon character state within Crotonaeae, rather than a putative plesiomorphic state in Crotonaeae, since this is not observed in Jatropheae and is only present in a few representatives of Crotonaeae

**The position of *Brasiliocroton***—With our taxon sampling, including all *Astraea* species, *Brasiliocroton* was recovered as sister to *Croton* with high support (1 PP, 97 BS) in the plastid tree, while in the nuclear tree it

emerged as sister to a highly (0.99 PP) to moderate (76 BS) supported clade containing *Acidocroton*, *Astraea* and *Croton*. The relationships in the plastid tree corroborate previous phylogenetic studies (Berry et al., 2005a; Wurdack et al., 2005; van Ee et al., 2011; Riina et al., 2014), while the topology of the ITS tree is the same recovered by Silva et al. (Capítulo III).

The sister relationship between *Brasiliocroton* and *Croton* has low to moderate support in the phylogeny of Wurdack et al. (2005) based on the combined *trnLF* and *rbcL* markers (68 BS and  $\leq 0.95$  PP, respectively). Similarly, this relationship was low supported in the ITS tree by Berry et al. (2005a; 57 BS), and in the ITS and *EMB2765* trees by van Ee et al. (2011; 75–90 BS). Besides the molecular data, this relationship is also supported by the presence of acropetiole/basilaminar nectaries in both genera (Riina et al. 2014), although these structures have been lost in several sections of *Croton* (van Ee et al., 2011).

The topological differences observed in our ITS tree with respect to all published ITS phylogenies including taxa of Crotonae could be explained by our use of bidimensional alignment in RNASalsa. This methodology is not widely used in phylogenetic studies yet. It was developed for regions which include transcribed spacers (as the ITS), embedding biological information on the alignment through estimation of putative secondary structure of the transcribed RNA. RNASalsa identify regions which are likely to be more conserved (stems) and more prone to indels and mutations (loops) and use this information to guide the alignment of sequences. This results in a relative higher proportion of conserved sites, which may affect directly the topology and branch support.

To support the position of *Brasiliocroton* in our ITS tree as sister of the *Croton-Acidocroton-Astraea* clade, this genus shares with the earliest diverging lineages of Crotonae (*Sagotia* and *Sandwithia*) the arborescent habit - all the species in these three genera are trees - and the inflorescences with axes of lateral cymules not reduced, which give the thyrse a paniculiform appearance. However, there are several tree lineages within *Croton*, so the arborescent habit is not unique to those genera. On the other hand, observations of wood anatomy in *Brasiliocroton mamoinha* (Berry et al., 2005b) showed the presence of distinctly elongated procumbent cell in the body of the multiseriate rays setting this genus apart from *Acidocroton*, *Astraea* and *Croton*, which have all uniseriate rays with only upright cells or upright and square cell in the body of the ray. However, these authors indicated that a better sampling within *Croton* was needed to further explore these anatomical differences.

Riina et al. (2014) suggested that the distribution range of *Brasiliocroton* and the early diverging *Croton* lineages in eastern Brazil in addition to the arborescent habit in these groups support the sister relationship between these two genera, but as we said above, the arborescent habit is also shared with *Sagotia* and *Sandwithia*. Regarding geographical distribution, many lineages in *C.* subg. *Quadrilobi* reach northern South America and Central America or Antilles, such as *C.* sect. *Pachypodi*, *C.* sect. *Moacroton* and *C.* sect.

*Corylocroton* (van Ee et al., 2011). However, considering the timing of the diversification of *Croton* and *Brasiliocroton*, the presence of the early diverging lineages of *Croton* in northern South America, Central America and Antilles is most likely explained by a later expansion with diversification of *Croton* lineages with the increasing aridity from the Paleogene-Neogene which slowly formed the diagonal of dry formations of South America (Bigarella et al., 1975), resulting in the Amazon-Atlantic Forest disjunction pattern observed in, for example, *C. sect. Sampatik* (van Ee et al., 2011). Nevertheless, our reconstruction of ancestral distribution ranges confirms the putative ancestor of Core Crotonaeae in southeastern Brazil as suggested by Riina et al. (2014).

The position of *Brasiliocroton* in our ITS tree also gives support to the recognition of this genus as distinct from *Croton*. While the paniculiform inflorescences are more similar to *Sagotia* and *Sandwithia*, the presence of acropetiole/basilaminal nectaries would still be an interesting novelty in Crotonaeae, possibly representing an apomorphy of the Core Crotonaeae, but lost in the *Acidocroton* + *Astraea* clade, and in other independent events within *Croton*, as in *C. sect. Julocroton* or *C. sect. Lamprocroton* (Caruzo et al. 2011, van Ee et al. 2011). The presence of inflexed stamens, therefore, could be interpreted as a apomorphy of *Croton* + (*Astraea* + *Acidocroton*), lost in *Acidocroton*, instead of two independent events. Finally, the same applies to trichome diversity as stellate (including its subforms and lepidote) would also be an apomorphy of the Core Crotonaeae, lost in the *Acidocroton*.

**Evolution within *Astraea***—Sampling all species morphologically assigned to the genus by Silva et al. (Capítulo IV), we recovered a highly supported monophyletic *Astraea*. Previous phylogenetic studies did not have enough sampling of *Astraea* that could allow a strong test of its monophyly (Berry et al., 2005a; Riina et al., 2014). The closest relationship of *Astraea* with *Acidocroton* identified in previous phylogenies (Berry et al., 2005a; Wurdack et al., 2005) is corroborated here with high support.

Within *Astraea*, the first divergence was estimated at 25.7 Ma (95% HPD confidence interval: 9.09–42.73 Ma), by the time when most of the Andean uplift occurred. Considering that by the time when *Astraea* diverged from *Acidocroton* the GAARlandia was available, but not when clade A diverged from clades B and C, it is likely that the species within these clades which are now distributed in Central America and Antilles have reached those areas more recently, after the closure of the Isthmus of Panama, starting from around 25 Ma (Bacon et al., 2015; Montes et al., 2015). This is also supported by the resulting putative ancestral range of *Astraea* covering an extensive area within South America (either western South America, plus southern Brazil, Chaco and Pampas [CGH] or extending to northeastern and central Brazil [CFGH]).

Diversification of the clades and subclades of *Astraea* (as well as the diversification within *Acidocroton*) started to increase ca. 15 Ma onwards, congruent with the diversification of groups adapted to arid conditions, such as Cactaceae and Poaceae, in the middle Miocene (Arakaki et al., 2011). Also, the intensification of the



Andean uplift since 15 Ma promoted a rain shadow which caused the expansion of dry areas on the eastern portion of South America, favoring the diversification of groups distributed along the northeastern-southwestern diagonal of dry areas in that continent (Werneck, 2016).

The putative ancestor of clade A was most likely distributed in southwestern Brazil, Chaco and Pampas [H]. Still in the middle Miocene, widespread lineages adapted to temperate or subtropical climates may have survived the progressive global cooling and now are mostly found in areas outside the tropical zone. In this scenario, such lineages would be restricted to meridional areas or montane habitats with cooler temperatures within the tropical belt (Fiaschi et al., 2016). This is the case of *Astraea lobata*, with its distribution concentrated in southwestern South America and Central America (from 10° north and southwards away from the Equator) and occurring mostly in higher elevations as it gets closer to the Equator (within the 10° N and S).

The divergence of *Astraea cincta* from its most closely related clade of *A. lobata* was estimated at 8.8 Ma (95% HPD confidence interval: 0.65–21.95 Ma) and, therefore, it is also likely to be influenced by the origin of the neotropical savannas, since *A. cincta* is restricted to open cerrado vegetation. Simon et al. (2009) indicated that some of the lineages characteristic of this vegetation would have originated at around 4 Ma from neighboring biomes through adaptations to specific conditions of the Cerrado, as tolerance to fire. This is the case of *A. cincta* and the occurrence of *A. lobata* along neighboring biomes and for the estimated diversification within this species set to 4.7 Ma (95% HPD confidence interval: 0.27–14.46). Also, this species is unique within *Astraea* by the presence of a well-developed underground system (probably xylopodiferous), a clear adaptation to cerrado, which allows individuals to fully regrown after fire.

Our analysis could not recover a clear distribution area for the putative ancestor of clade B + C. Instead, likelihood of all states for this clade are < 10 %, but mostly involve southeastern Brazil (G, 7.9%), or widely distributed scenarios in South America. However, the divergence within clade B (containing the both widely distributed *Astraea surinamensis* and *A. trilobata*) is recovered to have occurred at 6.87 Ma (95% HPD confidence interval: 0.29–20.3 Ma), and the most likely distribution range for the putative ancestor of this clade is western South America (C). With the recent origin of this clade and the putative ancestral distribution range, allied to the weedy nature of *A. lobata* and *A. surinamensis*, it is likely that their wide distribution range throughout the Neotropics could be result of anthropogenic factors. Human activities also are the most reasonable explanation for the occurrence of these species in Africa and Asia. In support of this view, we also have the notes from Gaikwad et al. (2012), which registered *A. lobata* through a famous place of pilgrimage in India (Maharashtra, in district of Solapur). But most importantly, the age for Crotonaeae itself is much younger than the final break-up of Gondwana at about 100 Ma (Pitman et al., 1993) to consider a putative ancestral distributed on both continents since long dispersal is not likely to occur in most Euphorbiaceae (Webster, 1994b), in which most species are usually autochoric with seed reaching up to 43 m far from the mother plant

in *Hura crepitans* L. (Hureae, Euphorbioideae), the most remarkable example in Euphorbiaceae (Swaine and Beer, 1977).

The putative ancestor of clade C either occupied southeastern Brazil (G) or eastern Brazil (FG), and the diversification within both subclades most likely was influenced by the origin of the neotropical savannas (*Cerrado*) and the diagonal of dry areas in South America with the dry climates from the Miocene (Werneck 2016). Within clade C1 are species restricted to southeastern Brazil, which reflects in a most likely area for the putative ancestor of the group in southeastern Brazil too. On the other hand, in clade C1 are species widely distributed in South America (*Astraea gracilis* and *A. paulina*), but mostly found in gallery forests (as *A. paulina* in savannas) or semideciduous dry forests or rocky outcrops (as *A. gracilis* in Atlantic Forest). The ancestral area recovered for the putative ancestor of clade C2 is either the northeastern and central Brazil (F), southeastern Brazil (G) or a combination of these areas (eastern-central Brazil, FG), all equally probable. Considering the present distribution of taxa within clade C2, the distribution of its putative ancestor in eastern-central Brazil is more likely. Also, the diagonal of dry areas in South America already existed by the time this clade diversified, around 15 Ma, which reinforces this interpretation. Under this scenario, clade C1 would be the result of sympatric speciation, therefore isolated in southeastern Brazil.

Within both clades C1 and C2 there are examples of colonization to humid areas. In C2 are: *Astraea klotzschii*, which is mostly found in seashore vegetation along Brazilian coast and *A. digitata*, found in moist forest of northeastern Brazil. In C1 are: *A. praetervisa* restricted to southern Bahia and *A. macroura*, restricted to the seashore vegetation of Rio de Janeiro and Espírito Santo states in southeastern Brazil. Therefore, the invasion of new geographic areas and different biomes (Pennington et al., 2004; Gonçalves et al., 2007; Salsis-Lagoudakis et al., 2008; Fiaschi and Pirani 2009) most likely played a role in the diversification within clades C1 and C2.

**Character mapping in *Astraea***—Character evolution in *Astraea* was never accessed due to the lack of a comprehensive phylogenetic hypothesis and unresolved taxonomy, including the poor delimitation of *A. lobata*, recently resolved in Silva et al. (Capítulo III).

In our reconstruction of morphological character states, *Astraea* has many features that easily distinguish it from its sister *Acidocroton*: usually subulate, not spiny stipules (vs. spiny stipules in *Acidocroton*; Fig. 3D), mostly deeply lobed or partite leaves (vs. always entire in *Acidocroton*; Fig. 4A), terminal and elongated, spiciform inflorescences (vs. axillary, congested, glomeruliform inflorescences in *Acidocroton*; Figs. 4C-D), staminate flowers with petals bearing moniliform trichomes at the basal portion of the margin (vs. glabrous petals in *Acidocroton*; Fig. 5A), petals shorter or equal to the calyx (vs. petals longer than the calyx in *Acidocroton*; Fig. 5B), 11–15 stamens (vs. 20–50[–100] in *Acidocroton*; Fig. 6A), inflexed in the bud (vs. erect in *Acidocroton*; Fig. 5D), pistillate flowers with segmented nectaries (vs. annular nectaries in *Acidocroton*; Fig. 6C)

and multifid styles (vs. entire or bifid styles in *Acidocroton*; Fig. 6D). Regarding characters supporting the *Acidocroton-Astraea* clade, we could not identify any macromorphological feature uniting these two genera. Anatomical studies have long shown to be very useful in Crotonoideae and Euphorbiaceae, and perhaps such studies could reveal features shared by *Astraea* and *Acidocroton* that support their close phylogenetic relationship.

Two of the features mentioned above also distinguish *Astraea* from all other genera in Crotonoideae: the mostly deeply lobed or partite leaves (with a few species in *Croton* with lobed leaves, although their leaves are not as deeply lobed or partite as in *Astraea*; Fig. 4A) and the moniliform trichomes in the petals of staminate flowers (Fig. 5A), which are synapomorphies for this genus, allied to the presence of clustered colleters at the junction of the lamina and petiole (Vitarelli et al., 2015). Other putative synapomorphies for *Astraea* indicated by anatomical and ontogenetic studies (De-Paula et al., 2011) need further evaluation since these data are not available for *Acidocroton*, *Brasilicroton*, *Sagotia* and *Sandwithia*.

According to our reconstruction, the putative ancestor of *Astraea* could be either an annual or biannual herb or a perennial shrub (Fig. 3A). However, with the exception of clade A3 (*A. cincta*), early diverging lineages within the genus (clades A and B) are mostly annual or biannual herbs, while in clade C species are mostly shrubs (herbaceous only in *A. gracilis* and *A. digitata* [Capítulo IV]). *Astraea cincta*, besides the xylopodiferous underground system (Fig. 3B), is also unique within *Astraea* by its cartilaginous leaf margin and seeds rounded in cross section (Capítulo IV). Xylopodiferous underground system is a clear adaptation to the habitat where this species is found, and cartilaginous leaf margin could be result of accumulation of carbohydrates into a thick cuticle, a case of oligotrophic scleromorphism which could be caused by high levels of aluminum in Cerrado soils (Frank-de-Carvalho et al., 2015). Distinguishing features of this species could be explained by the strong selective pressure in savannah vegetation following recent diversification and putative ancestral distribution range recovered in our analyses.

The other characters mapped in our analysis do not show variation within the genus. There is a morphological feature that we could not map for the entire Crotonoideae, which supports the recognition of two main groups within *Astraea*. Species of clade A have opaque fruits, while the species from clade B and C have lustrous fruits. Opaque and lustrous fruits were indicated in Silva et al. (Capítulo III) as putative synapomorphies for clades A and B+C, respectively, although not considering a comprehensive sampling of *Astraea*. In this work, by sampling all species within the genus, we corroborate the findings of Silva et al. (Capítulo III) regarding the placement of *A. cincta* and *A. lobata*, which are the only species having opaque fruits within the genus. However, the nature of the lustrous surface of the fruits in the remaining species of *Astraea* is still unknown and demands further anatomical exploration.

**Sequence variation within *Astraea***—The high variation among sequences of *Astraea* combined with the low number of parsimony-informative characters in our *trnLF* dataset could be interpreted as high saturation level in *trnLF* for *Astraea*. Phillippe et al. (2011) call the attention that this high level of saturation could be caused by the employment of an oversimplified model. In our analyses the evolutionary model was estimated by MrBayes itself, but we also explored the differences when setting the evolutionary model to the most complex GTR+I+G (tree not shown) and found no considerable topological differences between these two trees.

The *psbA* is considered one of the most variable intergenic spacers of the cpDNA (Shaw et al., 2007; Timme et al. 2007). The short sequence length limits the power of this marker and due to its specific molecular architecture, Borsch and Quandt (2009) suggested it could only be used for inferences among closely related taxa. Caruzo et al. (2011) found, in their study of *C. sect. Cleodora*, 43.41 % of variable characters in their *psbA* matrix (with 138 parsimony-informative characters). However, in our dataset, this region showed very low variability and low sequence variation within *Astraea*, indicating that this region can be useful for some groups within *Croton* but not for other groups in *Crotoneae*. Allied to its low variation in our dataset, there are the difficulties in aligning the sequences of *Sagotia* and *Sandwithia* in this dataset, which could be explained by frequent indels, inversions and repetitions (Borsch and Quandt 2009).

Clade C includes most species of *Astraea* (nine species, while clades A and B contain two species each) and all clades include widely distributed species: *A. lobata* in clade A, *A. surinamensis* and *A. trilobata* in clade B and *A. paulina*, *A. gracilis* and *A. klotzschii* in clade C. Our results are not indicative of any correlation between intraspecific variation and size of distribution range (i.e., sequences of widely distributed species are not more variable than those of restricted species) or between variation within a clade and species richness in that clade (i.e., variation within clades A and B is not considerably lower than that of clade C). We also found no considerable difference in variation between clades A and B or A and C, which could give additional support for the low supported (0.75 PP, 65 BS) clade containing clades B and C.

## CONCLUSIONS

Our results demonstrate the monophyly of *Astraea* and recognize three main groups within the genus. Clade A contains *A. lobata* and *A. cincta* and is characterized by opaque fruits; clade B contains *A. surinamensis* and *A. trilobata* and is characterized by stellate-porrect trichomes bearing a central much longer than the lateral rays; and finally, clade C, the most diverse with nine species, is characterized by the non-xylopodiferous shrubby perennial habit. Within clade C, we recognize two clades: C1 with species restricted to Bahia and Southeastern Brazil, such as *A. comosa*, *A. manihot* and *A. subcomosa*, and clade C2, which mostly includes widely distributed species in South America such as *A. gracilis* and *A. paulina*. We could not identify any

morphological synapomorphy for these clades (C1 and C2). *Astraea klotzschii* was the only species of C2 with accessions recovered (not monophyletic) in both clades, so it demands further investigation.

The monophyly of *Astraea* is supported by a suite of characteristics that distinguish it from its sister *Acidocroton*: mostly deeply lobed or partite leaves, terminal spiciform inflorescences, staminate flowers with petals bearing moniliform trichomes on basal portion of the margin and with up to 15 stamens inflexed in bud, pistillate flowers with segmented nectary and multifid styles. The type of trichomes on the petals of staminate flowers and the deeply lobed leaves are also unique characteristics within Crotonaeae.

The putative ancestral of the clade formed by *Astraea* and *Acidocroton*, most likely occupied a wide range in South America and Mesoamerica. The divergence between these genera was recovered at the end of the Eocene (34 Ma) before the closure of the Isthmus of Panama and by the time GAARLandia was available. The putative ancestor of *Astraea*, in turn, most likely occupied a wide area that corresponds to the present day diagonal of dry areas of South America, and diversification within the genus was likely influenced by the formation of such dry areas which in turn were driven by the Andean Uplift during the Oligocene-Pliocene. Our results also demonstrate that the wide distribution range of *A. lobata*, *A. surinamensis* and *A. trilobata*, which reach Central America, Mexico and Africa, is more likely a result of a recent range expansion after the closure of the Isthmus of Panama and likely aided by human activity.

Within Crotonaeae, character states reconstructions demonstrate that lack of petals or their strong reduction in pistillate flowers is a synapomorphy for the tribe, while reconstruction of ancestral distribution ranges indicates a putative ancestor for Crotonaeae occupying the widely distributed humid forests from South America at 60–44 Ma, which may be linked to their strictly arborescent habit. The intermittent connections of South America to Central America and Antilles via GAARlandia from 50 to 33 Ma, may have influenced the range expansion of *Croton* and the putative ancestor of *Acidocroton* and *Astraea* to the northern Neotropics. The recent divergence between the two sections of *Acidocroton* suggests that much of the diversity of this clade could have been lost during the great extinctions in the late Oligocene-early Miocene.

Regarding the position of *Sagotia* or *Sandwithia* as the earliest diverging lineage within Crotonaeae, our results are not conclusive, and inclusion of more molecular data is necessary to solve this question. Character states reconstructions are also inconclusive, with the absence of nectaries supporting the placement of *Sagotia* as the earliest diverging lineage within Crotonaeae, while the better supported position in the ITS tree and connate calyx support *Sandwithia*.

Our ITS tree recovered *Brasiliocroton* as sister to a large clade containing *Acidocroton*, *Astraea* and *Croton* contradicting previous phylogenetic hypotheses. This alternative relationship is supported by morphological features such as the branched inflorescences of *Brasiliocroton*, which represent a plesiomorphic state in

Crotoneae, shared with *Sagotia* and *Sandwithia*. Also, within Core Crotoneae, the closest relationship among *Acidocroton*, *Astraea* and *Croton* is supported by the absence of distinctly elongated procumbent cell in the body of the multiseriate rays, observed in *B. mamoinha*.

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Supplementary Table I: Variation of sequences among and within species of *Astraea* for ITS.

	<i>A. cincta</i>	<i>A. lobata</i>	<i>A. surinamensis</i>	<i>A. trilobata</i>	<i>A. comosa</i>	<i>A. klotzschii</i> (SE)	<i>A. macroura</i>	<i>A. manihot</i>	<i>A. praetervisa</i>	<i>A. subcomosa</i>	<i>A. digitata</i>	<i>A. gracilis</i>	<i>A. klotzschii</i> (NE)	<i>A. paulina</i>
<i>A. cincta</i>	0.53% (0.19–0.94)	1.37% (0.94–1.89)	6.57% (6.37–6.96)	6.73% (6.58–6.96)	5.26% (4.91–5.53)	5.66% (4.69–6.56)	5.16% (4.90–5.33)	5.44% (5.10–5.76)	6.14% (5.94–6.34)	5.57% (5.32–5.75)	4.77% (4.51–4.95)	4.76% (4.29–5.13)	4.81% (4.50–5.14)	4.79% (4.30–5.453)
<i>A. lobata</i>	1.37% (0.94–1.89)	0.96% (0.00–1.71)	5.72% (5.52–6.32)	5.89% (5.65–6.32)	5.19% (4.88–5.70)	5.57% (4.86–6.32)	5.08% (4.87–5.49)	5.37% (5.08–5.91)	5.66% (4.98–5.95)	5.50% (5.29–5.91)	4.62% (4.48–4.89)	4.59% (4.28–5.07)	4.66% (4.47–5.09)	4.63% (4.27–5.47)
<i>A. surinamensis</i>	6.57% (6.37–6.96)	5.72% (5.52–6.32)	0.15% (0.00–0.37)	0.26% (0.19–0.37)	5.83% (5.65–6.05)	6.26% (5.88–6.68)	6.12% (6.04–6.24)	6.01% (5.86–6.27)	6.37% (6.29–6.49)	6.15% (6.07–6.27)	5.31% (5.23–5.43)	5.37% (5.22–5.62)	5.35% (5.22–5.63)	5.33% (5.02–6.02)
<i>A. trilobata</i>	6.73% (6.58–6.96)	5.89% (5.65–6.32)	0.26% (0.19–0.37)	-	5.96% (5.86–6.06)	6.39% (6.10–6.68)	6.25% (6.06–6.28)	6.14% (6.06–6.28)	6.50% (6.28–6.72)	6.28% (6.07–6.49)	5.43% (5.23–5.63)	5.49% (5.43–5.62)	5.48% (5.42–5.63)	5.46% (5.23–6.02)
<i>A. comosa</i>	5.26% (4.91–5.53)	5.19% (4.88–5.70)	5.83% (5.65–6.05)	5.96% (5.86–6.06)	0.19%	0.71% (0.20–1.31)	0.47% (0.37–0.56)	0.34% (0.19–0.56)	1.03% (0.93–1.12)	0.47% (0.37–0.56)	1.79% (1.69–1.88)	1.85% (1.69–2.07)	1.83% (1.69–2.07)	1.82% (1.50–2.45)
<i>A. klotzschii</i> (SE)	5.66% (4.69–6.56)	5.57% (4.86–6.32)	6.26% (5.88–6.68)	6.39% (6.10–6.68)	0.71% (0.20–1.31)	1.36%	0.85% (0.19–1.50)	0.79% (0.39–1.31)	1.43% (1.17–1.69)	1.04% (0.59–1.50)	2.20% (1.55–2.84)	2.20% (1.55–2.84)	2.24% (1.55–3.04)	2.20% (1.36–3.03)
<i>A. macroura</i>	5.16% (4.90–5.33)	5.08% (4.87–5.49)	6.12% (6.04–6.24)	6.25%	0.47% (0.37–0.56)	0.85% (0.19–1.50)	-	0.62% (0.56–0.74)	1.31%	0.75%	1.69%	1.75% (1.69–1.88)	1.74% (1.69–1.88)	1.72% (1.50–2.26)
<i>A. manihot</i>	5.44% (5.10–5.76)	5.37% (5.08–5.91)	6.01% (5.86–6.27)	6.14% (6.06–6.28)	0.34% (0.19–0.56)	0.79% (0.39–1.31)	0.62% (0.56–0.74)	0.25% (0.19–0.37)	1.19% (1.12–1.31)	0.62% (0.56–0.75)	1.95% (1.88–2.07)	2.01% (1.88–2.26)	1.99% (1.88–2.26)	1.98% (1.69–2.64)
<i>A. praetervisa</i>	6.14% (5.94–6.34)	5.66% (4.98–5.95)	6.37% (6.29–6.49)	6.50%	1.03% (0.93–1.12)	1.43% (1.17–1.69)	1.31%	1.19% (1.12–1.31)	-	1.31%	2.65%	2.71% (2.65–2.84)	2.70% (2.65–2.84)	2.68% (2.46–3.23)
<i>A. subcomosa</i>	5.57% (5.32–5.75)	5.50% (5.29–5.91)	6.15% (6.07–6.27)	6.28%	0.47% (0.37–0.56)	1.04% (0.59–1.50)	0.75%	0.62% (0.56–0.75)	1.31%	-	2.07%	2.14% (2.07–2.26)	2.12% (2.07–2.26)	2.10% (1.88–2.64)
<i>A. digitata</i>	4.77% (4.51–4.95)	4.62% (4.48–4.89)	5.31% (5.23–5.43)	5.43%	1.79% (1.69–1.88)	2.20% (1.55–2.84)	1.69%	1.95% (1.88–2.07)	2.65%	2.07%	-	0.31% (0.00–0.56)	0.42% (0.37–0.56)	0.40% (0.19–0.93)
<i>A. gracilis</i>	4.76% (4.29–5.13)	4.59% (4.28–5.07)	5.37% (5.22–5.62)	5.49% (5.43–5.62)	1.85% (1.69–2.07)	2.20% (1.55–2.84)	1.75% (1.69–1.88)	2.01% (1.88–2.26)	2.71% (2.65–2.84)	2.14% (2.07–2.26)	0.31% (0.00–0.56)	0.50% (0.37–0.56)	0.48% (0.37–0.75)	0.45% (0.19–0.93)
<i>A. klotzschii</i> (NE)	4.81% (4.50–5.14)	4.66% (4.47–5.09)	5.35% (5.22–5.63)	5.48% (5.42–5.63)	1.83% (1.69–2.07)	2.24% (1.55–3.04)	1.74% (1.69–1.88)	1.99% (1.88–2.26)	2.70% (2.65–2.84)	2.12% (2.07–2.26)	0.42% (0.37–0.56)	0.48% (0.37–0.75)	0.34% (0.00–0.56)	0.45% (0.19–1.12)
<i>A. paulina</i>	4.79% (4.30–5.453)	4.63% (4.27–5.47)	5.33% (5.02–6.02)	5.46% (5.23–6.02)	1.82% (1.50–2.45)	2.20% (1.36–3.03)	1.72% (1.50–2.26)	1.98% (1.69–2.64)	2.68% (2.46–3.23)	2.10% (1.88–2.64)	0.40% (0.19–0.93)	0.45% (0.19–0.93)	0.45% (0.19–1.12)	0.41% (0.00–0.93)

Supplementary Table II: Variation of sequences among and within species of *Astraea* for *trnLF*.

	<i>A. cincta</i>	<i>A. lobata</i>	<i>A. surinamensis</i>	<i>A. trilobata</i>	<i>A. comosa</i>	<i>A. klotzschii</i> (SE)	<i>A. macroura</i>	<i>A. manihot</i>	<i>A. praetervisa</i>	<i>A. subcomosa</i>	<i>A. digitata</i>	<i>A. gracilis</i>	<i>A. klotzschii</i> (NE)	<i>A. paulina</i>
<i>A. cincta</i>	2.26% (0.43–3.97)	2.14% (0.29–4.73)	2.71% (0.29–6.61)	1.14% (0.58–2.69)	2.21% (0.86–4.43)	4.73% (0.86–7.53)	4.37% (3.66–5.81)	2.46% (1.01–4.58)	2.84% (1.11–5.92)	4.81% (4.13–6.45)	1.80% (0.57–3.66)	2.20% (0.73–4.58)	2.21% (0.57–4.28)	2.19% (0.57–4.43)
<i>A. lobata</i>	2.14% (0.29–4.73)	1.40% (0.14–2.91)	1.94% (0.00–4.74)	0.12% (0.00–0.71)	1.5% (0.57–3.21)	4.16% (0.86–7.53)	3.87% (3.06–5.02)	1.85% (0.86–3.67)	1.70% (0.67–2.62)	4.81% (3.83–6.45)	1.92% (0.72–3.52)	1.76% (0.43–3.22)	2.27% (0.57–4.27)	2.15% (0.56–4.43)
<i>A. surinamensis</i>	2.71% (0.29–6.61)	1.94% (0.00–4.74)	2.12% (0.29–3.68)	1.62% (0.00–4.28)	1.98% (0.57–3.67)	4.71% (0.57–9.48)	4.31% (3.37–6.28)	2.39% (0.72–4.44)	1.70% (0.67–2.62)	4.81% (3.83–6.45)	1.92% (0.72–3.52)	1.76% (0.43–3.37)	2.27% (0.57–4.27)	2.15% (0.56–4.43)
<i>A. trilobata</i>	1.14% (0.58–2.69)	0.12% (0.00–0.71)	1.62% (0.00–4.28)	-	0.92% (0.64–1.21)	1.00% (0.64–1.36)	1.90%	0.73% (0.64–0.92)	0.66%	0.61%	0.33%	0.40% (0.32–0.57)	0.99% (0.82–1.07)	0.92% (0.57–1.51)
<i>A. comosa</i>	2.21% (0.86–4.43)	1.5% (0.57–3.21)	1.98% (0.57–3.67)	0.92% (0.64–1.21)	0.71%	3.43% (0.28–6.37)	2.89%	0.88% (0.14–1.14)	0.74% (0.44–1.04)	3.42% (3.20–3.65)	0.79% (0.72–0.86)	0.69% (0.57–1.14)	1.07% (0.57–1.43)	1.02% (0.56–1.86)
<i>A. klotzschii</i> (SE)	4.73% (0.86–7.53)	4.16% (0.86–7.53)	4.71% (0.57–9.48)	1.00% (0.64–1.36)	3.43% (0.28–6.37)	6.22%	3.71% (2.73–4.68)	3.40% (0.42–6.53)	4.56% (0.41–8.70)	5.01% (3.49–6.53)	3.47% (0.72–6.22)	3.60% (0.44–6.85)	3.84% (0.57–6.84)	3.89% (0.56–7.15)
<i>A. macroura</i>	4.37% (3.66–5.81)	3.87% (3.06–5.02)	4.31% (3.37–6.28)	1.90%	2.89%	3.71% (2.73–4.68)	-	2.69% (2.45–3.04%)	3.36%	4.39%	3.19%	3.20% (3.04–3.33)	3.24% (3.19–3.33)	3.51% (3.30–3.93)
<i>A. manihot</i>	2.46% (1.01–4.58)	1.85% (0.86–3.67)	2.39% (0.72–4.44)	0.73% (0.64–0.92)	0.88% (0.14–1.14)	3.40% (0.42–6.53)	2.69% (2.45–3.04%)	1.05% (0.71–1.29)	1.31% (0.64–1.62)	3.10% (2.90–3.36)	1.00% (0.86–1.14)	1.03% (0.28–1.58)	1.51% (0.71–2.02)	1.49% (0.70–2.16)
<i>A. praetervisa</i>	2.84% (1.11–5.92)	1.70% (0.67–2.62)	1.70% (0.67–2.62)	0.66%	0.74% (0.44–1.04)	4.56% (0.41–8.70)	3.36%	1.31% (0.64–1.62)	-	4.37%	0.82%	0.55% (0.41–0.63)	1.21% (0.66–1.50)	0.97% (0.43–2.11)
<i>A. subcomosa</i>	4.81% (4.13–6.45)	4.81% (3.83–6.45)	4.81% (3.83–6.45)	0.61%	3.42% (3.20–3.65)	5.01% (3.49–6.53)	4.39%	3.10% (2.90–3.36)	4.37%	-	3.65%	3.52% (3.20–3.70)	3.79% (3.64–3.95)	3.98% (3.49–4.72)
<i>A. digitata</i>	1.80% (0.57–3.66)	1.92% (0.72–3.52)	1.92% (0.72–3.52)	0.33%	0.79% (0.72–0.86)	3.47% (0.72–6.22)	3.19%	1.00% (0.86–1.14)	0.82%	3.65%	-	0.62% (0.43–0.85)	0.95% (0.57–1.57)	0.91% (0.43–1.72)
<i>A. gracilis</i>	2.20% (0.73–4.58)	1.76% (0.43–3.22)	1.76% (0.43–3.37)	0.40% (0.32–0.57)	0.69% (0.57–1.14)	3.60% (0.44–6.85)	3.20% (3.04–3.33)	1.03% (0.28–1.58)	0.55% (0.41–0.63)	3.52% (3.20–3.70)	0.62% (0.43–0.85)	0.57% (0.43–0.71)	1.04% (0.43–1.57)	0.95% (0.43–2.01)
<i>A. klotzschii</i> (NE)	2.21% (0.57–4.28)	2.27% (0.57–4.27)	2.27% (0.57–4.27)	0.99% (0.82–1.07)	1.07% (0.57–1.43)	3.84% (0.57–6.84)	3.24% (3.19–3.33)	1.51% (0.71–2.02)	1.21% (0.66–1.50)	3.79% (3.64–3.95)	0.95% (0.57–1.57)	1.04% (0.43–1.57)	0.86% (0.85–1.00)	1.06% (0.14–2.02)
<i>A. paulina</i>	2.19% (0.57–4.43)	2.15% (0.56–4.43)	2.15% (0.56–4.43)	0.92% (0.57–1.51)	1.02% (0.56–1.86)	3.89% (0.56–7.15)	3.51% (3.30–3.93)	1.49% (0.70–2.16)	0.97% (0.43–2.11)	3.98% (3.49–4.72)	0.91% (0.43–1.72)	0.95% (0.43–2.01)	1.06% (0.14–2.02)	1.12% (0.28–2.46)

Supplementary Table III: Variation of sequences among and within species of *Astraea* for *psbA*

	<i>A. cincta</i>	<i>A. lobata</i>	<i>A. surinamensis</i>	<i>A. trilobata</i>	<i>A. comosa</i>	<i>A. klotzschii</i> (SE)	<i>A. macroura</i>	<i>A. manihot</i>	<i>A. praetervisa</i>	<i>A. subcomosa</i>	<i>A. digitata</i>	<i>A. gracilis</i>	<i>A. klotzschii</i> (NE)	<i>A. paulina</i>
<i>A. cincta</i>	0.15% (0.00–0.39)	0.08% (0.00–0.39)	0.97% (0.76–1.57)	0.87% (0.76–1.18)	1.89% (1.56–2.41)	2.09% (1.95–2.41)	1.68% (1.56–1.99)	1.82% (1.56–2.41)	0.85% (0.76–1.16)	1.68% (1.56–1.99)	2.11% (1.98–2.43)	1.68% (1.56–1.99)	1.68% (1.56–2.00)	1.95% (1.56–3.22)
<i>A. lobata</i>	0.08% (0.00–0.39)	0.00%	0.85% (0.76–1.14)	0.76%	1.75% (1.55–1.96)	1.95% (1.94–1.96)	1.55%	1.69% (1.55–1.96)	0.76%	1.55%	1.97% (1.97–1.98)	1.55%	1.55% (1.55–1.56)	1.82% (1.55–2.74)
<i>A. surinamensis</i>	0.97% (0.76–1.57)	0.85% (0.76–1.14)	0.19% (0.00–0.38)	0.09% (0.00–0.38)	1.07% (0.78–1.55)	1.26% (1.16–1.54)	0.87% (0.78–1.15)	1.00% (0.78–1.55)	0.10% (0.00–0.38)	0.87% (0.78–1.15)	1.29% (1.19–1.57)	0.87% (0.78–1.15)	0.87% (0.78–1.16)	1.13% (0.78–2.32)
<i>A. trilobata</i>	0.87% (0.76–1.18)	0.76%	0.09% (0.00–0.38)	-	0.98% (0.78–1.18)	1.17% (1.16–1.18)	0.78%	0.91% (0.78–1.18)	0.0%	0.78%	1.19%	0.78%	0.78% (0.78–0.79)	1.04% (0.78–1.93)
<i>A. comosa</i>	1.89% (1.56–2.41)	1.75% (1.55–1.96)	1.07% (0.78–1.55)	0.98% (0.78–1.18)	0.38%	0.57% (0.38–0.77)	0.19% (0.00–0.38)	0.32% (0.00–0.77)	0.95% (0.76–1.14)	0.19% (0.00–0.38)	0.59% (0.39–0.78)	0.19% (0.00–0.38)	0.19% (0.00–0.38)	0.45% (0.00–1.54)
<i>A. klotzschii</i> (SE)	2.09% (1.95–2.41)	1.95% (1.94–1.96)	1.26% (1.16–1.54)	1.17% (1.16–1.18)	0.57% (0.38–0.77)	0.77%	0.38%	0.38% (0.00–0.77)	1.14%	0.38%	0.39% (0.00–0.77)	0.38%	0.38%	0.57% (0.00–1.54)
<i>A. macroura</i>	1.68% (1.56–1.99)	1.55%	0.87% (0.78–1.15)	0.78%	0.19% (0.00–0.38)	0.38%	-	0.13% (0.00–0.38)	0.76%	0.00%	0.39%	0.00%	0.00%	0.26% (0.00–1.15)
<i>A. manihot</i>	1.82% (1.56–2.41)	1.69% (1.55–1.96)	1.00% (0.78–1.55)	0.91% (0.78–1.18)	0.32% (0.00–0.77)	0.38% (0.00–0.77)	0.13% (0.00–0.38)	0.25% (0.00–0.38)	0.89% (0.76–1.14)	0.13% (0.00–0.38)	0.26% (0.00–0.39)	0.13% (0.00–0.38)	0.13% (0.00–0.38)	0.34% (0.00–1.54)
<i>A. praetervisa</i>	0.85% (0.76–1.16)	0.76%	0.10% (0.00–0.38)	0.0%	0.95% (0.76–1.14)	1.14%	0.76%	0.89% (0.76–1.14)	-	0.76%	1.14%	0.76%	0.76%	1.01% (0.76–1.89)
<i>A. subcomosa</i>	1.68% (1.56–1.99)	1.55%	0.87% (0.78–1.15)	0.78%	0.19% (0.00–0.38)	0.38%	0.00%	0.13% (0.00–0.38)	0.76%	-	0.39%	0.00%	0.00%	0.26% (0.00–1.15)
<i>A. digitata</i>	2.11% (1.98–2.43)	1.97% (1.97–1.98)	1.29% (1.19–1.57)	1.19%	0.59% (0.39–0.78)	0.39% (0.00–0.77)	0.39%	0.26% (0.00–0.39)	1.14%	0.39%	-	0.39%	0.39%	0.52% (0.00–1.54)
<i>A. gracilis</i>	1.68% (1.56–1.99)	1.55%	0.87% (0.78–1.15)	0.78%	0.19% (0.00–0.38)	0.38%	0.00%	0.13% (0.00–0.38)	0.76%	0.00%	0.39%	0.00%	0.00%	0.26% (0.00–1.15)
<i>A. klotzschii</i> (NE)	1.68% (1.56–2.00)	1.55% (1.55–1.56)	0.87% (0.78–1.16)	0.78% (0.78–0.79)	0.19% (0.00–0.38)	0.38%	0.00%	0.13% (0.00–0.38)	0.76%	0.00%	0.39%	0.00%	0.00%	0.26% (0.00–1.15)
<i>A. paulina</i>	1.95% (1.56–3.22)	1.82% (1.55–2.74)	1.13% (0.78–2.32)	1.04% (0.78–1.93)	0.45% (0.00–1.54)	0.57% (0.00–1.54)	0.26% (0.00–1.15)	0.34% (0.00–1.54)	1.01% (0.76–1.89)	0.26% (0.00–1.15)	0.52% (0.00–1.54)	0.26% (0.00–1.15)	0.26% (0.00–1.15)	0.51% (0.00–1.54)

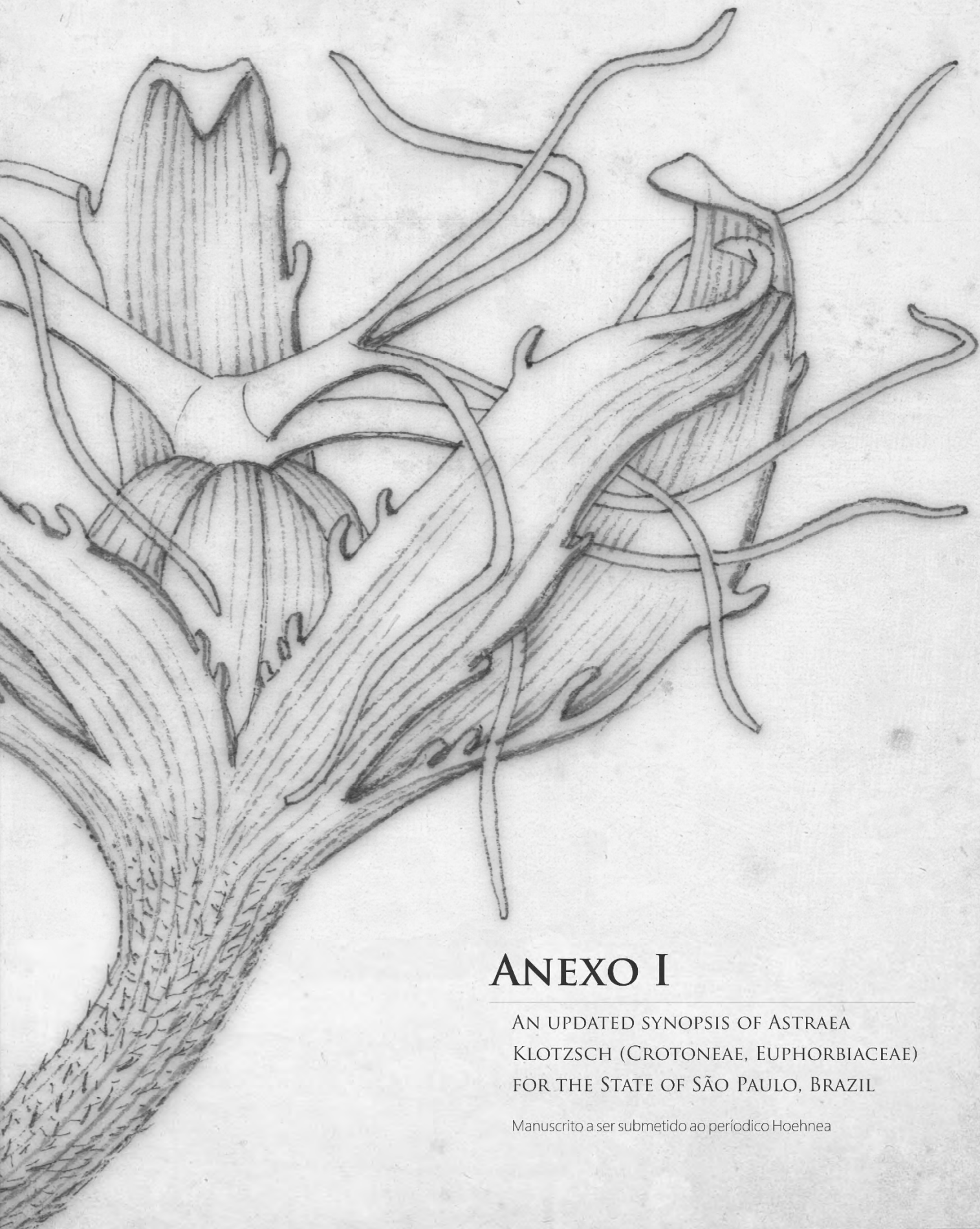
Supplementary Table IV: Codification for reconstruction of ancestral morphological character states. For characters and states codification, see Table II.

Terminal\Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
AcidocrotonACID	2	0	0	1	0	0	1	1	0	0	1	0	{1 2 3}	1	1	{0 1}
AcidocrotonOPH	2	0	0	1	0	0	1	1	0	0	1	0	{1 2 3}	1	1	{0 1}
AcinctaBOL	2	1	{0 1}	0	{0 2}	0	0	1	1	1	1	1	0	1	2	3
AcinctaGO	2	1	{0 1}	0	{0 2}	0	0	1	1	1	1	1	0	1	2	3
AcinctaMG	2	1	{0 1}	0	{0 2}	0	0	1	1	1	1	1	0	1	2	3
AcinctaMS	2	1	{0 1}	0	{0 2}	0	0	1	1	1	1	1	0	1	2	3
AcinctaPR	2	1	{0 1}	0	{0 2}	0	0	1	1	1	1	1	0	1	2	3
AcomosaCAR	2	0	1	0	2	0	0	1	1	1	1	1	0	1	2	3
AcomosaDIAM	2	0	1	0	2	0	0	1	1	1	1	1	0	1	2	3
Adigitata	{1 2}	0	{0 1}	0	2	0	0	1	1	1	1	1	0	1	2	3
AgracilisBA	{1 2}	0	{0 1}	0	2	0	0	1	1	1	1	1	0	1	2	3
AgracilisES	{1 2}	0	{0 1}	0	2	0	0	1	1	1	1	1	0	1	2	3
AgracilisMG	{1 2}	0	{0 1}	0	2	0	0	1	1	1	1	1	0	1	2	3
AklotzschiiAL	2	0	{0 1}	0	{0 2}	0	0	1	1	1	1	1	0	1	2	3
AklotzschiiIL	2	0	{0 1}	0	{0 2}	0	0	1	1	1	1	1	0	1	2	3
AklotzschiiITA	2	0	{0 1}	0	{0 2}	0	0	1	1	1	1	1	0	1	2	3
AklotzschiiMAR	2	0	{0 1}	0	{0 2}	0	0	1	1	1	1	1	0	1	2	3
AklotzschiiPE	2	0	{0 1}	0	{0 2}	0	0	1	1	1	1	1	0	1	2	3
AklotzschiiSMM	2	0	{0 1}	0	{0 2}	0	0	1	1	1	1	1	0	1	2	3
AlobataAQU	1	0	{0 1}	0	2	0	0	1	1	1	1	1	0	1	2	3
AlobataARG	1	0	{0 1}	0	2	0	0	1	1	1	1	1	0	1	2	3
AlobataBAG	1	0	{0 1}	0	2	0	0	1	1	1	1	1	0	1	2	3
AlobataBAT	1	0	{0 1}	0	2	0	0	1	1	1	1	1	0	1	2	3
AlobataBOL	1	0	{0 1}	0	2	0	0	1	1	1	1	1	0	1	2	3
AlobataGUA	1	0	{0 1}	0	2	0	0	1	1	1	1	1	0	1	2	3
AlobataMEX	1	0	{0 1}	0	2	0	0	1	1	1	1	1	0	1	2	3
AmacrouraES	2	0	{0 1}	0	{0 2}	0	0	1	1	1	1	1	0	1	2	3
AmanihotARU	2	0	{0 1}	0	2	0	0	1	1	1	1	1	0	1	2	3
AmanihotJUQ	2	0	{0 1}	0	2	0	0	1	1	1	1	1	0	1	2	3
AmanihotMG	2	0	{0 1}	0	2	0	0	1	1	1	1	1	0	1	2	3
ApaulinaBA	2	0	{0 1}	0	{0 2}	0	0	1	1	1	1	1	0	1	2	3
ApaulinaBOL	2	0	{0 1}	0	{0 2}	0	0	1	1	1	1	1	0	1	2	3
ApaulinaCE	2	0	{0 1}	0	{0 2}	0	0	1	1	1	1	1	0	1	2	3
ApaulinaGO	2	0	{0 1}	0	{0 2}	0	0	1	1	1	1	1	0	1	2	3

Supplementary Table IV: Codification for reconstruction of ancestral morphological character states. For characters and states codification, see Table II.

ApaulinaPA	2	0	{0 1}	0	{0 2}	0	0	1	1	1	1	1	0	1	2	3
ApaulinaSP	2	0	{0 1}	0	{0 2}	0	0	1	1	1	1	1	0	1	2	3
Apraetervis	2	0	1	0	{0 2}	0	0	1	1	1	1	1	0	1	2	3
Asubcomosa	2	0	{0 1}	0	{0 2}	0	0	1	1	1	1	1	0	1	2	3
AsurinamensisBA	1	0	{0 3}	0	2	0	0	1	1	1	1	1	0	1	2	3
AsurinamensisES	1	0	{0 3}	0	2	0	0	1	1	1	1	1	0	1	2	3
AsurinamensisMS	1	0	{0 3}	0	2	0	0	1	1	1	1	1	0	1	2	3
AsurinamensisPR	1	0	{0 3}	0	2	0	0	1	1	1	1	1	0	1	2	3
AsurinamensisRN	1	0	{0 3}	0	2	0	0	1	1	1	1	1	0	1	2	3
AtrilobataC	1	0	{0 3}	0	2	0	0	1	1	1	1	1	0	1	2	3
Brasilicroton	0	0	1	0	0	1	{0 1}	0	0	1	1	0	2	1	2	0
Calchorneicarpus	0	0	1	0	{0 1}	1	0	1	0	1	1	1	{1 2 3 4}	1	1	{0 2 3}
Castroites	{0 2}	0	{1 2}	0	0	0	{0 1}	1	0	1	1	1	{0 1}	1	1	3
Ccuneatus	0	0	{1 2}	0	0	1	0	1	0	1	1	1	{0 1}	1	1	{0 2}
Ccupreatus	0	0	2	0	0	1	0	1	0	1	1	1	0	1	1	0
Cechinocarpus	{0 2}	0	1	0	{0 1}	1	0	1	0	1	1	1	{1 2 3 4}	1	1	{0 2 3}
Cechioides	{0 2}	{0 1}	{1 2}	0	0	{0 1}	0	1	0	1	1	1	{0 1 2 3}	1	1	{0 2}
Cglandulosus	{1 2}	{0 1}	{1 3}	0	0	1	0	1	0	1	1	1	0	1	1	{0 2 3}
Cgossypifolius	{0 2}	0	1	0	{0 1}	1	0	1	0	1	1	1	{1 2 3 4}	1	1	{0 2 3}
Cgracilipes	{0 2}	{0 1}	{1 2}	0	0	{0 1}	0	1	0	1	1	1	{0 1 2 3}	1	1	{0 2}
Cheterocalyx	{0 2}	0	{1 2}	0	0	1	{0 1}	1	0	1	1	1	{0 1 2}	1	1	{0 3}
Cjacobinensis	{0 2}	0	{1 2}	0	0	0	{0 1}	1	0	1	1	1	{0 1}	1	1	3
Cmanampetsae	2	0	{1 3}	0	0	1	{0 1}	1	0	1	1	1	0	1	1	3
Cnobilis	{0 2}	0	2	0	0	1	0	1	0	1	1	1	{0 1 2 3}	1	1	3
Cpalanostigma	{0 2 3}	0	{1 2}	0	{0 1}	1	0	1	0	1	1	1	0	1	1	3
Cpiptocalyx	0	0	{1 2}	0	0	1	0	1	0	1	1	1	{0 1}	1	1	0
Crotterifolius	{0 2}	0	{1 2}	0	0	1	{0 1}	1	0	1	1	1	{0 1 2}	1	1	{0 3}
Csapiifolius	{0 2}	0	{1 2}	0	0	1	{0 1}	1	0	1	1	1	0	1	1	0
Cschiedeanus	{0 2}	0	{1 2}	0	0	0	{0 1}	1	0	1	1	1	0	{0 1}	1	3
Ctrichotomus	2	0	2	0	0	1	0	1	0	1	1	1	0	1	1	0
Ctroncosoi	{0 2}	0	1	0	{0 1}	1	0	1	0	1	1	1	{1 2 3 4}	1	1	{0 2 3}
Cvelutinus	{0 2}	0	1	0	{0 1}	1	0	1	0	1	1	1	{1 2 3 4}	1	1	{0 2 3}
Jatropha	{0 1 2}	{0 1}	0	0	{0 1 2 3}	0	{0 1}	0	0	0	1	0	0	0	{1 2}	0
Sagotia	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0
Sandwithia	0	0	0	0	0	0	0	0	0	0	1	0	{1 2}	1	1	0





## ANEXO I

AN UPDATED SYNOPSIS OF *ASTRAEA*  
KLOTZSCH (CROTONEAE, EUPHORBIACEAE)  
FOR THE STATE OF SÃO PAULO, BRAZIL

Manuscrito a ser submetido ao periódico *Hoehnea*

## AN UPDATED SYNOPSIS OF *ASTRAEA* KLOTZSCH (CROTONEAE, EUPHORBIACEAE) FOR THE STATE OF SÃO PAULO, BRAZIL

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**Abstract**—Euphorbiaceae is one of the richest families in the state of São Paulo, with 37 genera and around 150 species. A synopsis of one of its genera, *Astraea*, was published as part of the treatment for Crotonae, which contains the giant *Croton*, the richest genus in the state of São Paulo and second largest in Euphorbiaceae. Recent taxonomic and systematic advances with *Astraea* brought a more refined knowledge about the genus, especially for *A. lobata*. This species had its morphological delimitation poorly defined until very recently, and as result of the taxonomic advances with the genus, about five species were distinguished from *A. lobata* based on morphological characters. In this work, we aim to update the synopsis published by *Astraea*, as part of the taxonomic revision of the genus and studies with Euphorbiaceae for the Flora Fanerogâmica do Estado de São Paulo project. We present an identification key for the six species of *Astraea* found in the state of São Paulo, along with photographs of diagnostic characters and an update distribution map and list of specimens of *Astraea* in the state of São Paulo.

**Keyword**—*Astraea lobata*, flora, taxonomy

## INTRODUCTION

*Astraea* Klotzsch is a small genus in Euphorbiaceae with 13 species (Silva & Cordeiro [Capítulo IV]), widely distributed throughout the Neotropics, but especially diverse in eastern Brazil, and also found in Paleotropics, where it is represented by weedy species (Caruzo et al. 2014, Silva & Cordeiro 2017, Silva et al. 2017, Silva et al. [Capítulo III]). The genus was traditionally recognized as a section of the giant *Croton* L., due to spiciform inflorescences and stamens inflexed in bud, but was considered one of the best morphologically defined groups within *Croton* by its usually deeply lobed/partite leaves, lack of basilar nectaries or acropetal nectaries and glabrous receptacle of staminate flowers (Webster 1993). Recent phylogenetic studies (Berry et al. 2005a, Wurdack et al. 2005) recognized *Astraea* again as a distinct genus, once it was separated from the remaining *Croton* with the positioning of *Brasilicroton* P.E. Berry & Cordeiro, a recent described genus with two species (Berry et al. 2005b, Riina et al. 2014), as most closely related to *Croton*. These studies also showed that *Astraea* is sister to *Acidocroton* Griseb. (including *Ophellantha* Standl. According to Webster [2014]), a genus found in Greater Antilles, Central America and northern South America (Webster 2014).

Recent advances with the taxonomy of *Astraea* (Silva & Cordeiro 2017, Silva et al. [Capítulo III]), have shown that *Astraea lobata* s.l., the most widespread species within the genus, hid under its poorly defined morphological delimitation other species, such as *Astraea digitata* (Müll.Arg.) O.L.M. Silva, *Astraea manihot* (Müll.Arg.) O.L.M. Silva and *Astraea surinamensis* (Miq.) O.L.M. Silva & Cordeiro. The distinction of such species is also supported by a phylogenetic framework build for the genus by Silva et. al. (Capítulo III, Capítulo V).

In this work, our aim is to present an update for the synopsis of *Astraea* in the state of São Paulo, published by Caruzo & Cordeiro (2007), accounting for the recent taxonomic changes mentioned above, with illustrations and photographs of diagnostic characters and an update distribution map of *Astraea* in the state of São Paulo.

## MATERIALS AND METHODS

Herbarium specimens analyzed for the purpose of this work includes the full database for the taxonomic revision of *Astraea*, containing ca. 5200 specimens from more than 90 herbaria - A, ALCB, AMD, ASE, B, BHCB, BHZB, BM, BOTU, BR, C, CEN, CEPEC, CESJ, CGMS, COL, CTES, CVRD, DAV, E, EAC, ESA, F, FHI, FLAS, FSU, FTG, FUEL, G, GH, HAL, HB, HBG, HCF, HEPH, HNBU, HRB, HRCB, HUEFS, HUEM, HUFU, IAC, IBGE, IEB, INPA, IPA, JPB, K, L, LE, LINN, M, MA, MAC, MBM, MBML, MG, MEXU, MICH, MO, MPU, NY, OUPR, P, PACA, PAMG, PEUFR, R, RB, RSA, S, SJRP, SP, SPF, SPSF, TCD, TOGO, TUB, U, UB, UC, UEC, UESC, UFG, UFP, UFRN, US, USF, USZ, VIC, VIES, W, WAG and WIS (abbreviations according to Thiers 2018, continuously updated). For the state of São Paulo, 74 specimens were analyzed, along with collecting trips for observation of populations in the field.

The conservation status for each species is accessed following the criteria established by Mamede et al. (2007). The distribution map was elaborate with QGIS v.2.18 (Quantum GIS Development Team 2017). Specimens were georeferenced using original coordinates obtained from herbarium labels (converted to decimal degrees when necessary through *conversor* [available at: [splink.cria.org.br/conversor](http://splink.cria.org.br/conversor)]). When original coordinates were not available we used approximate coordinates from municipalities or localities obtained from *geoLoc* (available at: [splink.cria.org.br/geoloc](http://splink.cria.org.br/geoloc)).

As this stands as an update to the synopsis of *Astraea* by Caruzo & Cordeiro (2007) and as part of the ongoing taxonomic revision of the genus, we do not present full headings or newly designated lectotypes for any of the names contemplated in this work.

## RESULTS AND DISCUSSION

In the state of São Paulo, *Astraea* is represented by six species: *Astraea cincta*, *A. gracilis*, *A. lobata*, *A. manihot*, *A. paulina* and *A. surinamensis*. This represents an addition of four species to the work Wanderley et al. (2012) checklist of Spermatophyta of São Paulo, which, for *Astraea*, is based on the synopsis of Caruzo & Cordeiro (2007). Most of these novelties are recent combinations by Silva & Cordeiro (2017) and Silva et al. (Capítulo III) based on previously recognized varieties by Müller Argoviensis (1866, 1873), except for *A. paulina*, which was considered as a synonym of *A. lobata* by Caruzo & Cordeiro (2007) and is now recognized as a distinct species (see comments under *Astraea paulina*). *Astraea* is found in all regions and main vegetations types present in the state of *São Paulo*, except for mangroves, where Euphorbiaceae is also not represented (Fig. 1; Caruzo & Cordeiro 2007).

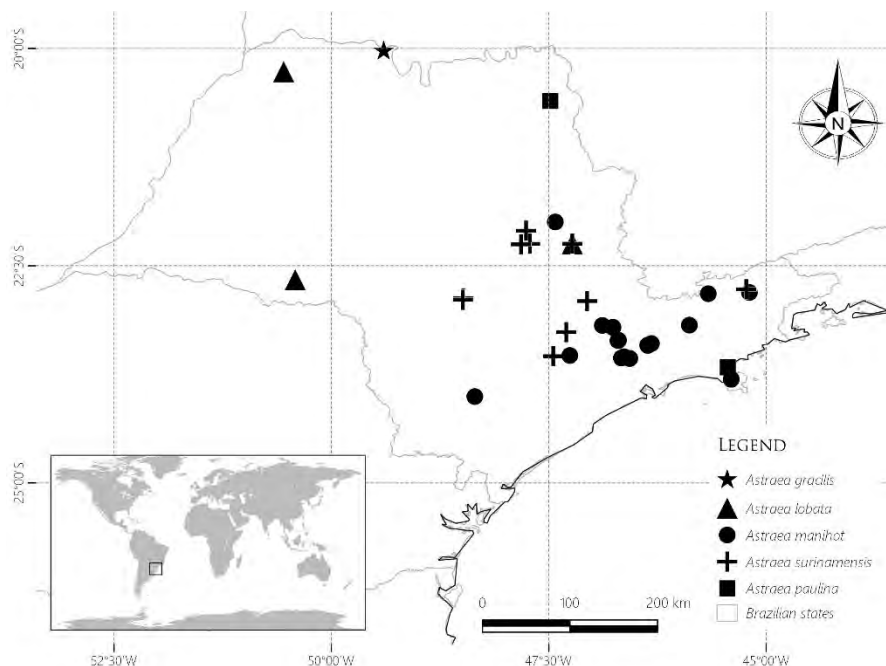


FIGURE 1: Distribution map of the species of *Astraea* in the state of São Paulo

Identification key to the species of *Astraea* in the state of São Paulo

1. Plants with a well-developed underground system (xylopodiferous). Leaves with cartilaginous margin. Seeds rounded in cross section ..... *A. cincta*
- 1'. Plants without a well-developed underground system (non-xylopodiferous). Leaves without cartilaginous margin. Seeds tetragonal in cross section.
2. Young portions of stems and petioles with stellate-porrect trichomes bearing a central ray much longer than the lateral rays, surpassing 1.5 mm long (giving an appearance of a hirsute indumentum composed by simple long trichomes) ..... *A. surinamensis*
- 2'. Young portion of stems and petioles with short (< 0.5 mm) simple, stellate or stellate-porrect trichomes bearing a central ray equal or slightly longer than the lateral rays, not surpassing 1 mm long.
3. Fruits opaque. Plants from disturbed environments ..... *A. lobata*
- 3'. Fruits lustrous. Plants from edge of humid or seasonally dry forest or gallery forest within Cerrado.
4. Pistillate flowers long-pedicellate (pedicel with 3-5 mm long). Staminate cymules with 6-8(-10) flowers ..... *A. manihot*
- 4'. Pistillate flowers sessile to short-pedicellate (pedicel not surpassing 2.5 mm long). Staminate cymules with up to 5(-6) flowers.
5. Leaves chartaceous, adaxial surface with short (< 0.5 mm) simple or stellate trichomes ..... *A. paulina*
- 5'. Leaves membranaceous, adaxial surface with long (> 0.5 mm) simple trichomes ..... *A. gracilis*

*Astraea cincta* (Müll.Arg.) Caruzo & Cordeiro, *Hoehnea* 34: 573. 2007.

Figure 2A-C.

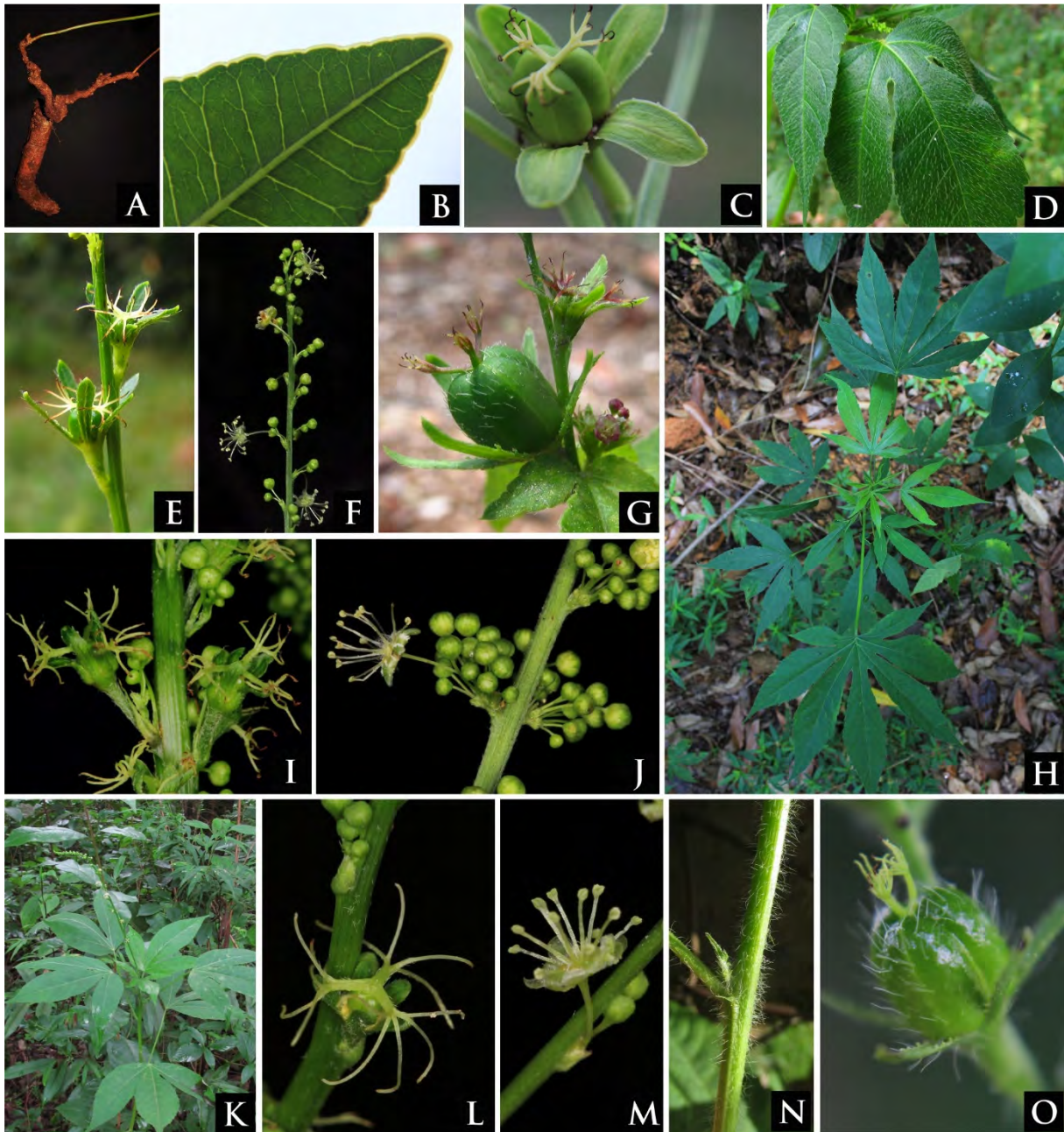
Selected material: BRAZIL. SÃO PAULO: Rio Pardo, without date, *L. Riedel 608* (G!, LE [photo!]).

Additional examined material: BRAZIL. PARANÁ: Campo Mourão, Cerrado ao lado da Agricase, na rodovia Avelino Piacentini, margem esquerda (sentido Campo Mourão-Peabiru), acesso pela Rua Alfonso Germano Hruschka, 19-X-2017, *O.L.M. Silva et al. 308* (SP). MATO GROSSO DO SUL: Corguinho, MS-352, no sentido Taboco-Cipolândia, cerca de 10 km após a entrada para o Instituto Quinta do Sol, 8-III-2016, *O.L.M. Silva et al. 238* (SP).

*Astraea cincta* is found in open cerrado vegetation from central and southwestern Brazil, Bolivia and Paraguay. Its only occurrence in the state of São Paulo is represented by its type, without an exact locality, so it is not represented in the map. However, *A. cincta* is found in all neighboring states (Paraná, Mato Grosso do Sul and Minas Gerais). Among all species of *Astraea*, *A. cincta* may be distinguished by its unique well-developed xylopodiferous underground system (Fig. 2A), cartilaginous leaf margin (Fig. 2B) and seeds rounded in cross section.



According to Mamede et al. (2007) *Astraea cincta* is considered as “Presumably Extinct” since it was collected for the last time more than 50 years ago.



**FIGURE 1:** Diagnostic characters of the species of *Astraea* in the state of São Paulo. A-C. *Astraea cincta*. A. well-developed (xylopodiferous) underground system. B. cartilaginous leaf margin. C. immature fruit. D-F. *Astraea gracilis*. D. adaxial surface of leaf. E. immature fruit (below) and pistillate flower (above). F. staminate cymules. G. pistillate flowers and immature fruit of *Astraea lobata*. H-J. *Astraea manihot*. H. young individual with 3-, 5- and 7-partite leaves. I. pistillate flowers in basal bisexual cymules. J. staminate cymules with one mature flower. K-M. *Astraea paulina*. K. young individual. L. pistillate flower. M. staminate cymules with one mature flower. N-O. *Astraea surinamensis*. N. young portion of a branch. O. immature fruit. Photos: O.L.M. Silva.

*Astraea gracilis* (Müll.Arg.) O.L.M. Silva & Cordeiro, Phytotaxa 317(4): 299. 2017

Figure 2D-F.

Selected material: BRAZIL. SÃO PAULO: Paulo de Faria, Estação Ecológica de Paulo de Faria, 17-I-2002, F. Tomasetto et al. 212 (HRCB, HSJRP, SP).

In the state of São Paulo, *Astraea gracilis* is only found in the northern portion of the state, nearby the limits with Minas Gerais. However, *A. gracilis* is a widely distributed throughout the South American dry diagonal, with few collections also in French Guiana, occurring mostly in edge of humid and seasonally dry forest or rocky outcrops (Silva & Cordeiro 2017). Morphological features that may distinguish *A. gracilis* from *A. lobata* include the lustrous fruit (vs. opaque in *A. lobata*), adaxial surface of leaves with long (>0.5 mm) simple trichomes (Fig. 2D; vs. short [ $< 0.5$  mm] simple or stellate trichomes in *A. lobata*) and geographical distribution and habitat, since *A. lobata* is found on disturbed environments along western and northwestern South America, Central America, Antilles, Mexico and Florida.

*Astraea gracilis* has a restricted distribution in the state of São Paulo, with all specimens collected in the municipality of Paulo de Faria, within a protected area (Paulo de Faria Ecological Station) and only in seasonally dry forest. Therefore, *Astraea gracilis* is considered here as “Endangered” once it qualifies for criteria 3, 5 and 9 of Mamede et al. (2007).

*Astraea lobata* (L.) Klotzsch, Arch. Naturgesch. 7(1): 194. 1841.

Figure 2G.

Selected material: BRAZIL. SÃO PAULO: Assis, Estação Experimental, região da serra velha, 15-V-1995, V.S. Moura 24 (SPSF).

Additional examined material: BRAZIL. MATO GROSSO DO SUL: Três Lagoas, Rodovia CESP, próximo ao início da ponte sobre o Rio Paraná (BR-262), 31-I-2014, O.L.M. Silva & R.F. Almeida 121 (SP).

*Astraea lobata* is one of the most widely distributed species of *Astraea*, occurring in western and northwestern South America, Central America, Antilles, Mexico and Florida. However, in the state of São Paulo it is represented by a few collections. Under its more refined morphological delimitation presented by Silva et al. (Capítulo III), this species is mainly characterized by its opaque fruits (Fig. 2G), shared only with *Astraea cincta* (Fig. 2C) and pistillate flowers usually with strongly accrescent calyx lobes, which surpass the mature fruit, reaching up to 1(-2) cm long. (Fig. 2G) Among the species found in São Paulo, this strongly accrescent calyx lobes in pistillate flowers are observed only in *Astraea gracilis* (Fig. 2E), from which it may be distinguished by the irregularly serrate margin of such lobes (vs. entire in *Astraea gracilis*), beyond habitat preferences (see comments on *Astraea gracilis*).

*Astraea lobata* is here considered as “Least Concern” following the exclusion criterium of Mamede et al. (2007), in which ruderal or invasive species are included.



***Astraea manihot*** (Müll.Arg.) O.L.M. Silva & Cordeiro, Phytotaxa 317(4): 299. 2017

Figure 2H-K.

Selected material: BRAZIL. SÃO PAULO: Santo Antonio do Pinhal, Início do Roteiro Turístico das Flores, na subida, cerca de 100 m antes do início do trecho em estrada de terra, 11-I-2017, O.L.M. Silva et al. 328 (SP).

*Astraea manihot* is found in southern Brazil in the states of Minas Gerais, Espírito Santo, Rio de Janeiro and Paraná, besides São Paulo, where it is found mostly in the southeastern portion of the state. This species grows on edges of humid forests and in gallery forests in Cerrado. The shrubby habit, predominantly 5-partite leaves with narrow lobes (Fig. 2H), and long-pedicellate pistillate flowers (Fig. 2I) and staminate cymules with more than 6 flowers (Fig. 2J) distinguishes this species from *Astraea lobata*, which has herbaceous habit, 3(-5)-partite leaves with elliptic lobes and subsessile pistillate flowers (Fig. 2G). Such characteristics also help on the differentiation between *Astraea manihot* and the remaining species of *Astraea* in the state of São Paulo (Fig 2F, 2L, 2M).

*Astraea manihot* does not qualify for any of the inclusive or exclusive criteria of Mamede et al. (2007) and, therefore, is considered as “Least Concern”.

***Astraea paulina*** Didr., Vidensk. Meddel. Dansk. Naturhist. Foren. Kjobenhavn part 9-10: 138. 1857.

Figure 2K-M.

Selected material: BRAZIL. SÃO PAULO: Botucatu, Caminho para Igreja Santo Antonio no distrito Rubião Júnior. Curva antes da subida final, logo após o portão, margem esquerda, 30-I-2015, O.L.M. Silva et al. 213 (SP).

*Astraea paulina* was included as synonym of *Astraea lobata* by Caruzo & Cordeiro (2007), but they may be distinguished mainly by habit (shrubby in *A. paulina* [Fig. 2K] vs herbaceous in *Astraea lobata*) and fruits (lustrous in *A. paulina* and opaque in *A. lobata*). Also, while *A. paulina* is widely distributed along the diagonal of dry areas of South America, occurring in habitats such as rocky grasslands (*campos rupestres*), seasonally dry forests or gallery forests along Cerrado domain, *A. lobata* is found from Mexico to southern Brazil, but more commonly on western South America and is a weedy species, occurring mainly on disturbed areas.

*Astraea paulina* does not qualify for any of the inclusive or exclusive criteria of Mamede et al. (2007) and, therefore, is considered as “Least Concern”.

***Astraea surinamensis*** (Miq.) O.L.M. Silva & Cordeiro (Chapter III)

Figure 2N-O

Selected material: BRAZIL. SÃO PAULO: Caraguatatuba, Bairro dos Golfinhos, 21-I-2018, U.G. Fernandes & A.P. Della 483 (SP).

*Astraea surinamensis* is another widespread species in *Astraea* found throughout Brazil. However, while *Astraea lobata* is mainly found in western South America, Central America, Greater Antilles and North America (Mexico and Florida), *Astraea surinamensis* is mainly distributed on eastern and northern South America and

Lesser Antilles, with very few specimens in Central America and Africa. In the state of São Paulo, this species is represented by very few collections, most likely due to a lack of collections rather than a narrow distribution.

These two species may be distinguished by the characteristic stellate-porrect trichomes bearing a central much longer than the lateral rays (surpassing 1.5 mm long) found on young portion of branches and petioles (Fig. 2N) in *Astraea surinamensis*, while, although stellate-porrect trichomes may also be found in *Astraea lobata*, they do not surpass 1.5 mm long. Also, fruits of *Astraea surinamensis* are lustrous and possesses long (> 1 mm) simple trichomes (Fig. 2O), while in *Astraea lobata* fruits are opaque and have stellate or short (< 0.5 mm) simple trichomes.

*Astraea surinamensis* is here considered as “Least Concern” following the exclusion criterium of Mamede et al. (2007), in which ruderal or invasive species are included.

#### Specimen list:

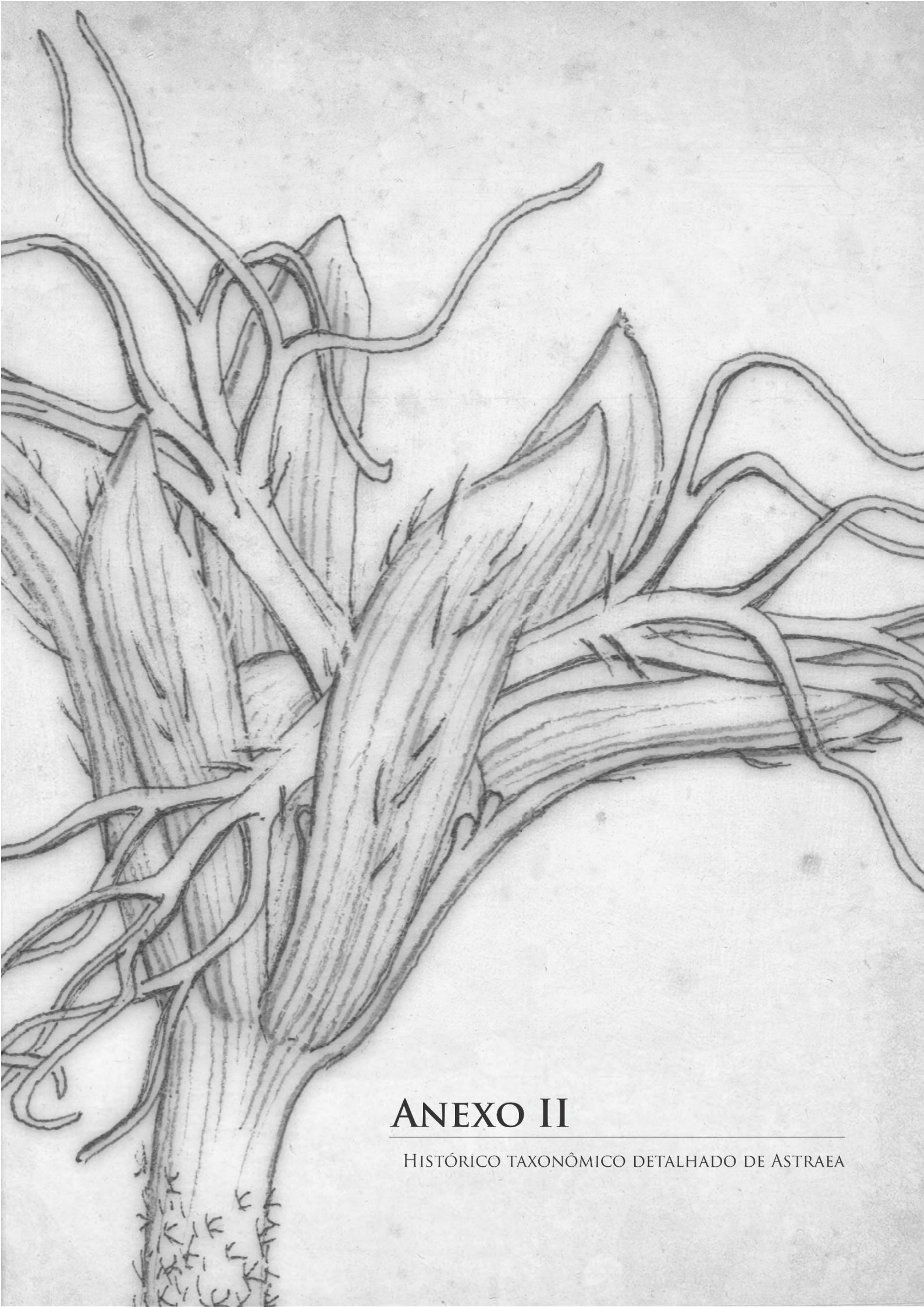
Almeida-Scabbia, R.J. 713 (manihot); Amaral-Júnior, A. 2052 (paulina), 2075 (paulina); Barreto, K.D. 1462 (paulina); Barros, A.A.M. 518 (manihot); Bicudo, L.R.H. 1 (paulina); Brade, A.C. 7336 (manihot), 7337 (manihot); Braga, L.M. 1 (paulina); Caruzo, M.B.R. 55 (paulina), 77 (paulina); De-Paula, O.C. 10 (paulina); Dinato, D.O. 271 (paulina), Fernandes, U.G. 483 (surinamensis); Ferreira, V.F. 3303 (paulina); Fina, B.G. 57 (manihot); Gemtchújnicov, I.D. BOTU 9826 (paulina); Giannotti, E. 8379 (paulina); Hoehne, F.C. s.n. SP 1521 (manihot); Hoehne, W. R 149074 (lobata), R 149075 (manihot); Jung, S.L. 32 (manihot), 33 (manihot), 34 (manihot), 35 (manihot), 36 (manihot); Kuhlmann, M. 3700 (lobata); Lamand, A. 20 (paulina); Loefgren, A. 263 (manihot); Luederwaldt, H. SP 13819 (manihot); Makino, H. MG 129114, SP 146648, UEC 4658, UEC 111065 (manihot); Martius, C.F.P. von M 233649 (manihot); Mattos, J.R. 8512 (paulina); 13935 (manihot); Mosén, H. 1628 (paulina); Moura, V.S. 24 (lobata); Rabelo, J.C. 42 (paulina); Rossi, L. 1073 (manihot), 2396 (manihot); Russel, A. 129 (paulina); Silva, O.L.M. 139 (manihot), 213 (paulina), 233 (manihot), 234 (manihot), 235 (manihot), 236 (manihot), 328 (manihot); Souza, V.C. 35738 (surinamensis); Stranghetti, V. 460 (gracilis); Tomasetto, F. 212 (gracilis); Tozzi, A.M.G.A. 313 (manihot).

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## ANEXO II

HISTÓRICO TAXONÔMICO DETALHADO DE ASTRAEA

HISTÓRICO TAXONÔMICO DETALHADO DE *ASTRAEA*

## I. Período Pré-Muelleriano (1753-1865)

Compreende o período anterior à primeira revisão mais abrangente de *Astraea*. Durante este período, o grupo foi reconhecido como parte de *Croton* até 1841, quando Klotzsch propôs o gênero *Astraea*, mas que não foi bem aceito. A partir de 1858, o grupo foi tradicionalmente reconhecido como uma seção de *Croton* (*Croton* sect. *Astraea*). Apesar de não ser reconhecido como um gênero segregado de *Croton*, Klotzsch sempre descrevia as espécies em *Astraea*. Esse período inclui a descrição de diversos nomes por uma grande variedade de autores, de diferentes regiões. O período termina com o trabalho de Müller Argoviensis na *Linnaea*, em 1865, no qual o autor apresenta algumas novidades taxonômicas para *Croton* sect. *Astraea*, preliminares do tratamento do gênero para o *Prodromus* de Candolle. Ao final do período temos 22 nomes aceitos

- 1753 A primeira espécie de *Astraea* a ser descrita, ainda como *Croton*, foi ***Croton lobatus* L.** no *Species Plantarum* de Linnaeus. Na obra, Linnaeus cita três trabalhos: Hort. Cliff. 445. e Roy. Ingb. 201 para *Croton foliis inermiserratis; inferioribus quinquelobis, superioribus trilobis*, e - Mart. Cent. 46, t. 46, para *Ricinoides herbaceum, foliis trifidis f. quinquefidis & serratis*.  
Até esse momento, *Croton lobatus* é visto como uma espécie de folhas com margem serreadas, 3- ou 5-lobadas, sem qualquer detalhe sobre as flores, inflorescências ou indumento das estruturas. Apesar das poucas informações no *Species Plantarum* e no *Herbarium Cliffortianus*, na obra de John Martyn é possível encontrar uma descrição morfológica detalhada, com comentários e uma ilustração.
- 1775 Forsskal descreve ***Croton trilobatus* Forssk.**, sem informações suficientes para diferenciá-la de *Croton lobatus* L. (as características fornecidas no protólogo incluem folhas curto-pecioladas, 3-5-lobadas, lanceoladas e serreadas), porém há um comentário de que as flores teriam apenas 10 estames, não monadelfos.
- 1797 Willdenow descreve *Schradera*, contendo ***Schradera scandens* Willd.**, uma planta escandente de Guiné, com ramos jovens tomentosos e vilosos, com tricomas alvos, folhas 3-lobadas (ternadas) e, de acordo com a descrição genérica de *Schradera*, o ovário e o fruto seriam vilosos. Não há indicação de material tipo e nenhuma coleção foi encontrada no Jstor, porém na publicação existe uma ilustração, mas muito pobre em detalhes.
- 1805 No *Species Plantarum* Editio Quarta de Linnaeus, Willdenow descreve ***Croton trilobatus* Willd.**, indicando como sinônimos o *Croton trilobatum* de Forsskal (interrogado) e a *Schradera scandens* do próprio Willdenow. O autor mantém a ocorrência da espécie para Guiné, e indica que as principais diferenças desta espécie para *Croton lobatus* L. seriam o caule lignificado, as folhas incano-pubescentes na face abaxial e os pecíolos pubescentes em *Croton trilobatus*.
- 1817 Kunth descreve, no *Nova Genera et Species Plantarum*, com Humboldt e Bonpland, ***Croton riparius* Kunth**, como uma espécie ocorrendo na Venezuela. No protólogo a espécie é descrita como possuindo ramos glabros, folhas longo-pecioladas, 3(-5)-lobadas, com indumento de tricomas estrelados dispersos na face adaxial e incano-tomentoso na face abaxial, pecíolos glabros, flores estaminadas com cerca de 15 estames, flores femininas curto-pediceladas, com cálice tomentoso na face exterior com tricomas estrelados e alvos e lobos oblongo-lanceolados, ovário hirsuto com tricomas alvos e estrelados e fruto com cálice persistente, duas vezes maior que o cálice.  
Nos comentários, os autores indiquem que o *Croton trilobatus* de Forsskal seria sinônimo de *Croton lobatus* L. e comparam *Croton riparius* com *Croton lobatus*, diferenciando-os principalmente pela face abaxial das folhas, tomentosa com tricomas estrelados em *Croton riparius*.

- 1836 Colla descreve *Croton macrourus* Colla, com base em um material de Martius, originado de Cabo Frio (Rio de Janeiro). A espécie é descrita como possuindo folhas inteiras, glabras na face adaxial e vilosas na face abaxial, com inflorescências longas, flores curto-pediceladas e frutos glabros.
- 1841 Neste momento Klotzsch propõe a segregação de *Croton* em diversos gêneros pequenos. Entre estes, propõe *Astraea*, nome derivado, assim como no caso de outros dos gêneros propostos pelo autor, de uma divindade da mitologia grega, neste caso, da filha de Zeus e Themis.
- Entre as características do gênero, Klotzsch chamou a atenção para a ocorrência na América do Sul, sendo ervas ou arbustos, com folhas 3-5-lobadas, raramente inteiras, pecioladas e estipuladas, com espigas longas, monóicas e terminais com flores femininas na parte inferior e masculinas na porção apical, todas esparsas. Apesar de não chamar atenção para algumas características como as flores masculinas com prefloração imbricada do cálice, estames 12-15, inflexos no botão e receptáculo glabro e flores femininas com disco em segmentos opostos aos lobos do cálice e estiletos multifidos, estas características estão na descrição do gênero.
- Klotzsch reconheceu 8 espécies em *Astraea* neste momento: *Astraea manihot*, *Astraea jatropha*, *Astraea tomentosa*, *Astraea palmata*, *Astraea lobata*, *Astraea diversifolia*, *Astraea divaricata* e *Astraea prunifolia*. Entretanto, como não forneceu diagnose ou material para a maioria destes nomes, apenas *Astraea lobata* é reconhecido como um nome válido, uma vez que possui *Croton lobatus* L. indicado como basinômio.
- 1845 Miquel descreve *Cnidocolus surinamensis* Miq. para um espécime coletada no Suriname. O autor coloca a espécie em *Cnidocolus* pelo indumento, descrito por ele como setoso, porém ressalta a semelhança com as inflorescências de *Croton* e a discrepância com as flores de *Cnidocolus*.
- 1846 Schelechtendal indica que uma das variedades formas agrupadas em *Croton lobatus* precisa de um exame mais detalhado, sendo diferente das plantas do México e Antilhas, citando como exemplo uma planta da Bahia, *Croton digitatus* Salzm. ex Schletdl, indicando como diferenças o comprimento das inflorescências e o formato das sementes.
- 1853 Klotzsch descreve uma nova espécie ocorrendo no Panamá: *Astraea seemanni* Klotzsch, caracterizada pelos ramos subglabros, folhas 3-5-lobadas, esparsamente hirsutas, pecíolos pilosos com tricomas estrelados, flores femininas com cálice esparsamente hirsuto, fruto esparsamento piloso com tricomas estrelados e duas vezes menor que o cálice.
- Entre os comentários, Klotzsch indica que, ao passo que em 1841, quando estabeleceu o gênero, *Astraea* contava com apenas 8 espécies, agora, em 1853, reconhecia 22 espécies, cada uma delas com espécimes preservadas no Herbário de Berlim. Ainda entre os comentários, Klotzsch escreve:
- "Entre as plantas vendidas pela Unio Itineraria, e coletadas por Kotschy na Nubia, nas montanhas de Cordofan, nós encontramos, sob o número 85, espécimes identificados como Croton lobatus, totalmente diferentes da espécie de Linnaeus; uma outra, distinta, encontrada na costa oeste da África em diversas localidades, também estava identificada com o mesmo nome por Palisot-Beauvois na Flora de Oware & Benin; e, apesar da real Croton lobatus Linn, não ser encontrada apenas no México e nas ilhas do Caribe, mas também em Nova Granada, Venezuela, Equador e Brasil, eu observei quatro outras espécies distintas em diferentes conjuntos de plantas secas enviadas para mim para estudo, todas elas próximas de Croton lobatus L., como Astraea seemanni. A distribuição geográfica das espécies de Astraea parece ser bastante peculiar: uma espécie na Nubia, outra na costa oeste da África, duas espécies no México, uma nas Antilhas, uma na América Central, uma nas Antilhas e América do Sul e 15 espécies no Brasil."*
- 1855 Em uma lista de sementes, Bartling descreve *Croton leiocarpus* Bartl., espécie originada de sementes da Nicarágua e caracterizada por folhas 3-lobadas, pilosa em ambas as faces, e frutos glabros, sem indicar qualquer coleção tipo.



- 1857 Didrichsenii descreve duas espécies que viriam a ser uma das mais comuns e amplilocadas do gênero. *Astraea klotzschii* Didr. Foi descrita com estípulas dentiformes, inconspícuas, folhas inteiras (as inferiores sublobadas), ovado-lanceoladas, hirtelas-ciliadas quando jovens e inflorescências longas. Já *Astraea paulina* Didr, foi descrita com um material de Itú (São Paulo), como uma espécie herbácea, com folhas trilobadas, com face abaxial tomentosa a velutina com tricomas estrelados e alvos a acizentados,, e face adaxial pubérula, com tricomas simples ou com poucos ramos e adpressos, e frutos glabros.
- 1858 Baillon propõe o reconhecimento de *Croton* sect. *Astraea* (Klotzsch) Baill., com quatro espécies: *Astraea lobata*, *Astraea divaricata*, *Astraea tomentosa* e *Astraea manihot*.
- 1860 Baillon descreve *Croton perrottetianus* Baill., uma espécie africana, de porte arbustivo, com ramos levemente pubescentes, folhas geralmente 3-lobadas, pubescentes e frutos glabros.
- 1864 Baillon descreve mais duas espécies: *Croton digitifolius* Baill. e *Croton manihot* (Klotzsch) Baill. O autor propõe *Croton digitifolius*, indicando como sinônimo *Astraea tomentosa* Klotzsch, um *nomen nudum*. *Croton digitifolius* é indicado no WorldChecklist de Kew (Govaerts et al. 2000) como *nomen nudum* devido falta de diagnose, mas são citados três materiais. Algo similar acontece com *Croton manihot* – *Astraea manihot* Klotzsch é indicado como sinônimo deste nome, não há diagnose e quatro materiais são citados, porém este nome não é indicado como *nomen nudum* no WorldChecklist de Kew (Govaerts et al. 2000).
- 1865 Müller Argoviensis, como parte de estudos prévios para o Prodrômus de Candolle, descreve propõe 9 novos nomes, 2 deles novas combinações, em duas espécies
- *Croton gardneri* Müll.Arg., com folhas 3-lobadas na porção inferior e inteiras na porção superior, estípulas subuladas e flor feminina com lobos do cálice lanceolados, ovário e estiletos com tricomas esparsos. Para esta espécie, Müller Argoviensis reconheceu duas variedades: *Croton gardneri* var. *cordatus* Müll.Arg., com folhas ovadas, de base cordada e face abaxial tomentosa quando jovem e vilosa-pubescente quando desenvolvidas, com dois materiais, um do Ceará (Gardner 1839) e outro da Bahia (Blanchet 3155); e *Croton gardneri* var. *lanceolatus* Müll.Arg., com folhas ovado-lanceoladas, de base levemente cuneada a obtusa e face abaxial denso-tomentosa, com apenas uma material de Jozé Gonzambres (Pohl s.n.).
  - *Croton klotzschii* (Didr.) Müll.Arg., com folhas profundamente 3-lobadas na porção inferior e as demais inteiras, estípulas diminutas, deltoide-ovadas, glandulosas e lobadas, flores femininas com lobos do cálice espatulado-lanceoladas e flores masculinas com estames 10-15. Para esta espécie, Müller Argoviensis reconheceu três variedades e duas formas: *Croton klotzschii* var. *latifolius* Müll.Arg., com folhas 1,5-2 vezes mais longas que largas (4-10 cm long.) e cuspidadas-tomentosas, originária da Bahia, com dois materiais citados (Martius s.n. e Blanchet 3216A); *Croton lobatus* var. *oblongifolius* Müll.Arg., com folhas na porção superior 2-4 vezes mais longas que largas e acuminadas, com duas formas: *Croton klotzschii* f. *divaricatus* (Klotzsch) Müll.Arg., com folhas cordadas, 3,5-4 cm long., do sul do Brasil, com indicação de *Astraea divaricata* Klotzsch e um material de Sellow s.n. citado, e *Croton klotzschii* f. *prunifolius* (Klotzsch) Müll.Arg., com folhas na porção superior rômbo-ovadas a rômbo-lanceoladas e base cuneada, com indicação de *Astraea prunifolia* Klotzsch e dois materiais: Riedel s.. e Sellow s.n.; e por fim, *Croton klotzschii* var. *genuinus* Müll.Arg., com as folhas da porção superior ovado-lanceoladas, longo-acuminadas e base aguda a obtusa. Para este nome, Klotzsch indica como sinônimos *Astraea diversifolia* Klotzsch e *Astraea klotzschii* Didr., indicando como tipo um material de Sellow (s.n.) coletado entre Campos e Vitória.

## II. Período Muelleriano (1866-1873)

Compreende o período no qual foram publicadas duas grandes revisões abrangentes do grupo por Müller Argoviensis: uma para o Prodrômus de Candolle, em 1866, e outra para a Flora Brasiliensis, em 1873. Por serem os primeiros trabalhos a organizar o grupo, este período é marcado por diversas sinonimizações e novidades nomenclaturais, mas também por publicações de espécies novas. Apesar de ser o período mais



curto no histórico taxonômico de *Astraea*, pode ser considerado como um dos mais importantes pelas grandes contribuições de Müller Argoviensis para a taxonomia do grupo. Ao final desse período, são reconhecidos 28 táxons, com um elevado número de táxons infraespecíficos em alguns casos como *Croton lobatus* e *Croton klotzschii*.

- 1866** A primeira revisão mais abrangente de *Astraea* foi publicada por Müller Argoviensis no Prodrumus de Candolle com muitas novidades taxonômicas que contribuíram para uma taxonomia mais sólida do grupo. Neste tratamento, o autor incluiu 8 espécies que compartilhavam o receptáculo glabro, mas três delas não fazem parte de *Astraea* atualmente: *Croton humilis*, apesar de ter os estiletos multífidos, possui flores masculinas com 25-35 estames, enquanto *Croton panduraeformis* e *Croton bonplandianus* (= *Croton pauperulus*) possuem estiletos dicotômicos.

As demais espécies (*Croton gardneri*, *Croton comosus*, *Croton jatropa*, *Croton lobatus* e *Croton klotzschii*), verdadeiramente *Astraea* por assim dizer, poderiam ser agrupadas pelo limbo foliar 3-lobado, pelo menos nas folhas da porção inferior da planta, flores femininas com flores masculinas com 10-15 estames.

Müller Argoviensis separou *Croton klotzschii* das demais espécies pelas suas estípulas pequenas e glanduloso-lobadas. No Prodrumus, Müller Argoviensis manteve a taxonomia da espécie, com três variedades e duas formas, como era de se esperar de um tratamento mais abrangente, com informações mais refinadas. Entre as outras espécies, caracterizadas pelas estípulas herbáceas, subuladas e não glandulosas, Müller separa *Croton lobatus* por possuir pecíolos mais ou menos do mesmo tamanho que o limbo (vs. 2-10 vezes menor nas demais espécies). Em *Croton lobatus*, Müller propôs oito variedades, duas delas com uma forma, cada. E é nessas variedade que o autor acomoda diversos nomes descritos antes de seu tratamento.

- *Croton lobatus* var. *paulinus* (Didr.) Müll.Arg. (= *Astraea paulina* Didr.)
- *Croton lobatus* var. *manihot* Müll.Arg. (= *Astraea manihot* Klotzsch, *Croton manihot* Baill.), com *Croton lobatus* var. *manihot* lusus *gracilis* Müll.Arg.
- *Croton lobatus* var. *digitatus* (Salzm. ex Schldl.) Müll.Arg. (= *Croton digitatus* Salzm. ex Schldl.)
- *Croton lobatus* var. *palmatus* Müll.Arg. (= *Astraea palmata* Klotzsch)
- *Croton lobatus* var. *riparius* (Kunth) Müll.Arg. (= *Croton riparius* Kunth, *Croton lobatus* na Flora de Oware e Benin, *Croton lobatus* Baill. [na mesma publicação de *Croton perrottetianus*], *Croton trilobatus* Willd., *Croton trilobatus* Schum., *Croton trilobatus* Vell., *Astraea lobata* Hook [Niger Flora], *Schradera scandens* Willd.), incluindo *Croton lobatus* var. *riparius* lusus *crispus* Müll.Arg.
- *Croton lobatus* var. *seemanii* (Klotzsch) Müll.Arg. (= *Croton lobatus* Schldl., *Astraea seemanii* Klotzsch, *Croton leiocarpus* Bartl. e Schldl.)
- *Croton lobatus* var. *intermedius* Müll.Arg.
- *Croton lobatus* var. *genuinus* Müll.Arg. (= *Croton lobatus* L., *Croton lobatus* Lam., *Croton lobatus* Geisel., *Croton lobatus* Kunth, *Croton lobatus* Schldl., *Croton lobatus* Griseb.; *Astraea lobata* (L.) Klotzsch; *Cnidocolus surinamensis* Miq.)

No outro grupo, das espécies com pecíolos 2-10 vezes menor que o limbo, Müller posicionou *Croton gardneri* e suas variedades, descritas no ano anterior por ele mesmo, junto com duas outras novas espécies: *Croton comosus* Müll.Arg., com duas variedades: *Croton comosus* var. *major* Müll.Arg. e *Croton comosus* var. *minor* Müll.Arg. (= *Astraea tomentosa* Klotzsch, e *Croton digitifolius* Baill.); e *Croton jatropa* Müll.Arg. (= *Astraea jatropa* Klotzsch)

Ao fim deste trabalho, o grupo continha 5 espécies de *Astraea*: *Croton gardneri* (2 variedades), *Croton comosus* (2 variedades), *Croton jatropa*, *Croton lobatus* (8 variedades, 2 formas) e *Croton klotzschii* (3 variedades, 2 formas). Apenas os nomes *Croton perrottetianus* Baill. e *Croton macrourus* Colla não foram ligados a qualquer um dos táxons propostos neste tratamento.

- 1866 Wawra descreve uma nova espécie sob o gênero *Astraea*, uma vez que houve a contribuição de Klotzsch para essa descrição. A espécie é *Astraea glandulifera* Klotzsch ex Wawra, descrita a partir de materiais da Bahia (Wawra & Maly 342, Gardner 1137 e Blanchet 3621). A descrição morfológica fornecida no protótipos é bastante detalhada e acompanhada por uma ilustração bastante rica de detalhes.
- 1873 Na Flora Brasiliensis, Müller Argoviensis eleva *Croton gardneri* var. *cordatus* para o nível específico como *Croton subcomosus* Müll.Arg., espécie próxima de *Croton comosus* Müll.Arg. pelas inflorescências de brácteas comosas, porém com folhas inteiras (vs. 3-lobadas em *Croton comosus*). A outra variedade de *Croton gardneri* (var. *lanceolatus*) é reconhecida apenas como sinônimo do *Croton gardneri*, porém um dos tipos, Blanchet 3155 é designado agora para um novo nome, *Croton praetervisus* Müll.Arg., espécie distinta das demais *Astraea* pelas estípulas glanduliformes. Müller Argoviensis ainda descreveu uma nova espécie, *Croton cinctus* Müll.Arg., espécie distinta das demais *Astraea* pelo sistema subterrâneo xilopodífero e folhas com margem cartilaginosa. Müller Argoviensis também elevou *Croton lobatus* var. *paulinus* ao nível específico, como *Croton paulinus* (Didr.) Müll.Arg., e reconhece a forma *gracilis* de *Croton lobatus* var. *manihot* como uma nova variedade para *Croton lobatus*: *Croton lobatus* var. *gracilis* Müll.Arg. Ainda dentro de *Croton lobatus*, Müller Argoviensis estabelece uma nova variedade, *Croton lobatus* var. *sericeus* Müll.Arg. com base em um material de Warming, coletado em Minas Gerais, caracterizada pelo indumento adpresso-seríceo nas porções jovens do caule, folhas 3(-5)-lobadas, adpresso-pubescentes com tricomas mistos. Por fim, dentro de *Croton klotzschii*, Müller incluiu a recém descrita *Astraea glandulifera* dentro de *Croton klotzschii* var. *latifolius* e propôs uma nova variedade, *Croton klotzschii* var. *intermedius* Müll.Arg., com duas formas: *Croton klotzschii* var. *intermedius* f. *major* Müll.Arg. e *Croton klotzschii* var. *intermedius* f. *major* Müll.Arg.

Em relação ao tratamento do Prodrômus, Müller Argoviensis incluiu apenas *Croton pauperulus* entre as espécies de *Croton* sect. *Astraea*, separando-a das demais pelos estíletes bipartidos. Ao fim deste trabalho, o grupo continha 9 espécies de *Astraea*: *Croton comosus* (2 variedades), *Croton subcomosus*, *Croton cinctus*, *Croton gardneri*, *Croton paulinus*, *Croton jatropa*, *Croton lobatus* (7 variedades) e *Croton klotzschii* (4 variedades, 4 formas). Assim como no Prodrômus, os nomes *Croton perrottetianus* Baill. e *Croton macrourus* Colla não foram ligados a qualquer um dos táxons propostos neste tratamento e *Croton lobatus* var. *seemanni* e *Croton lobatus* var. *intermedius* não são mencionados por serem espécies restritas à América Central.

### III. Período Pós-Muelleriano (1874-2004)

Compreende o período após os importantes tratamentos de Müller Argoviensis no Prodrômus de Candolle e na Flora Brasiliensis. Durante este período o grupo foi tratado como uma seção de *Croton*, apesar da proposta de Pax para reconhecer o grupo como um subgênero de *Croton*. Novos táxons foram descritos e o período termina com a publicação do World Checklist of Selected Plant Families de Euphorbiaceae (Govaerts et al. 2000), onde 18 táxons são reconhecidos, sem o grande número de variedades e formas do período anterior (sinonimizadas, em grande parte em *Croton lobatus* ou *Croton klotzschii*).

- 1890 Pax propõe o reconhecimento de *Croton* subg. *Astraea* (Klotzsch) Pax. Nos comentários o autor indica a ocorrência de cerca de 12 espécies nas Américas, 10 no Brasil e duas nas Antilhas e refere como espécies notáveis *Croton lobatus* e *Croton pauperulus* (= *Croton bonplandianus*).
- 1891 Kuntze propõe *Oxydectes*, transferindo diversas espécies de *Croton* para esse gênero, incluindo todas as espécies de *Croton* sect. *Astraea*, com exceção de *Croton klotzschii*. Entretanto, *Oxydectes* é indicado como ilegítimo.

- 1892 Kuntze descreve uma nova espécie, *Oxydectes hauthalii* Kuntze para o Paraguai, descrevendo-a como uma espécie bastante delicada e fácil de distinguir das demais espécies de *Croton* sect. *Astraea* pelos estiletes multiramificados, estípulas herbáceas, subuladas e não glandulosas, com folhas lobadas, estames 10-15 e folhas curto pecioladas. Ao comparar a espécie com *Croton lobatus*, o autor indica que os pecíolos são muito menores e que os lobos laterais possuem apenas a metade do comprimento do lobo médio, porém nenhuma comparação com *Croton cinctus*, que seria a espécie mais próxima morfologicamente, é fornecida pelo autor.
- 1894 Sessé e Mociño descrevem duas novas espécies para o México: *Croton trilobatus* Sessé & Mociño e *Croton palmatus* Sessé & Mociño. *Croton trilobatus* Sessé & Mociño é indicado como nome ilegítimo o WorldChecklist por ser um nome supérfluo (*Croton trilobatus* Forssk. 1775).
- 1895 Moore descreve uma nova espécie para o Brasil, coletada em Mato Grosso: *Croton comanthus* S.Moore, próxima de *Croton gardneri*, diferindo desta pelas folhas longo-pecioladas, flores masculinas com 16 estames, flores femininas menores e com cálice mais curto.
- 1900 Schumann transfere *Oxydectes hauthalii* para *Croton*: *Croton hauthalii* (Kuntze) K.Schum., sem informações detalhadas.
- 1905 Chodat e Hassler descrever duas novas espécies para o Paraguai: *Croton aureomarginatus* Chodat & Hassler e *Croton rumicifolius* Chodat & Hassler. Os autores comparam *Croton aureomarginatus* com *Croton cinctus* indicando que são bastante semelhantes, mas que diferem pelas folhas áureo-marginadas, crenadas e longo pecioladas, além do cálice da flor feminina não rubro-marginado. Já no caso de *Croton rumicifolius*, os autores, apesar de indicarem semelhança com *Croton aureomarginatus*, comparam a espécie com *Croton jatropa*, indicando que, porém, as estípulas são maiores que os pecíolos e que os tirsos possuem uma porção nua.
- 1908 Beille publica dois novos táxons para a África: *Croton courtetii* Beille e *Croton decorsei* Beille, indicando que ambas são próximas de *Croton lobatus* var. *genuinus*, porém *Croton courtetii* se distingue pelas estípulas não lobadas, ausência de glândulas no pecíolo e nos lobos do cálice, pétalas das flores masculinas vilosas na base exterior e pelas sementes rosadas. Já *Croton decorsei* se distingue pelos pecíolos desiguais, frequentemente maiores que o limbo foliar e desprovidos de glândulas, pelas flores femininas com lobos do cálice obovado-lanceoladas e pelas pétalas ciliadas.
- 1958 Steyermark descreve *Croton douradensis* Steyer., a partir de um material coletado por Dawson na Serra Dourada (divisa Goiás – Bahia). Nos comentários, o autor indica que, apesar de se encaixar em *Croton* sect. *Astraea*, esta espécie não possui o receptáculo das flores masculinas glabro e o cálice das flores femininas 5-partidos, considerando que talvez a espécie poderia ser um membro anômalo de *Croton* sect. *Decalobium*. Entre as características importantes para o autor para distinguir esta espécie das demais *Astraea* estão as folhas dimórficas (inteiras e 2-3-lobadas), flores masculinas com receptáculo pubescente e as flores femininas com cálice irregularmente 6-partido (um lobo mais largo que os outros), 5 pétalas com 4 glândulas na base de cada uma, e cada um dos estiletes dividido em 8 porções terminais.
- 1993 Webster, em uma sinopse de *Croton*, reconhece *Croton* sect. *Astraea*, com cerca de 10 espécies, indicando que é uma das seções melhores definidas do gênero. O autor alerta que o posicionamento de *Croton bondplandianus* (que foi referida como *C. pauperulus* na Flora Brasiliensis) na seção é duvidosa, uma vez esta espécie possui glândulas proeminentes na base das folhas, estiletes bifidos e sementes lisas, sendo possível que a ausência do indumento do receptáculo, característico de *Croton* sect. *Astraea*, tenha sido uma homologia. As espécies referidas por Webster são: *Croton lobatus*, *Croton aureomarginatus*, *Croton cinctus*, *Croton comosus*, *Croton douradensis*, *Croton gardneri*, *Croton klotzschii*, *Croton paulinus*, *Croton praetervisus* e *Croton subcomosus*.
- 1997 Radcliffe-Smith e Govaerts publicam o nome *Croton mocinoi* Radcl.-Sm. & Govaerts, indicando como sinônimo *Croton trilobatus* Sesse & Moc.

1999 Govaerts publica *Croton astraeatus* Baill ex. Govaerts, e no WorldChecklist os Selected Plant Families reconhece 15 espécies de *Astraea*. Neste checklist, todas as variedades de *Croton lobatus* propostas por Müller Argoviensis são apontadas como sinônimos de *Croton lobatus*. *Croton macrourus* não é indicado ao longo do checklist, porém aparece na lista de sinônimos, mas interrogado, não sendo mencionado em nenhum outro táxon. *Croton perrottetianus*, não mencionado nos tratamentos de Müller Argoviensis, é agora incluso como sinônimo de *Croton lobatus*, junto com *Croton courtetii* e *Croton decorsei*. Ao final deste trabalho, as 15 espécies que compõem *Croton* sect. *Astraea* são: *Croton astraeatus* (incluindo *Croton klotzschii* e suas variedades e formas como sinônimos deste táxon), *Croton aureomarginatus*, *Croton cinctus*, *Croton comanthus*, *Croton comosus*, *Croton douradensis*, *Croton hauthalii*, *Croton jatropha*, *Croton lobatus*, *Croton mocinoi*, *Croton palmatus*, *Croton paulinus*, *Croton praetervisus*, *Croton rumicifolius* e *Croton subcomosus*.

#### IV. Período Contemporâneo (2000-dias atuais)

Compreende o período em que o projeto de pesquisa está sendo desenvolvido e inicia-se após o reconhecimento do grupo como um gênero novamente, com base nas hipóteses filogenéticas publicadas a partir de 2005. Após este trabalho, a maioria dos trabalhos publicados visa apenas transferir as espécies de *Croton* sect. *Astraea* para *Astraea*. Um destes trabalho, o de Van Ee (2011), ainda fornece informações importantes sobre aspectos nomenclaturais do grupo. Nenhum trabalho mais amplo foi publicado até o momento, e o grupo conta com 13 táxons (12 espécies de *Astraea* + *Croton palmatus*)

- 2005 A hipótese filogenética apresentada por Berry et al. demonstrou que, com a inclusão de *Brasiliocroton*, as espécies de *Croton* sect. *Astraea* ficavam separadas das demais espécies de *Croton* e, assim, o grupo voltou a ser reconhecido como um gênero que, de acordo com essa hipótese filogenética, seria mais próximo *Acidocroton* e *Ophellantha*, dois pequenos gêneros do Caribe, América Central e norte da América do Sul. Neste trabalho, os autores já transferem *Croton praetervisus* para *Astraea* – ***Astraea praetervisiva* (Müll.Arg.) P.E.Berry**
- 2007 Caruzo e Cordeiro, em uma sinopse das espécies de *Crotoneae* para o Estado de São Paulo, transferem *Croton cinctus* para *Astraea* – ***Astraea cincta* (Müll.Arg.) Caruzo & Cordeiro**, e incluem *Croton paulinus* (= *Astraea paulina*) entre os sinônimos de *Astraea lobata*, sem detalhes sobre os motivos desta sinonimização.
- 2007 Berry transfere *Croton aureomarginatus* para *Astraea* – ***Astraea aureomarginata* (Chodat & Hassl.) P.E.Berry** e faz o mesmo com *Croton hauthalii* – ***Astraea hauthalii* (Kuntze) P.E.Berry**, adicionando *Croton rumicifolius* como sinônimo deste táxon.
- 2011 Van Ee traz importantes contribuições para a nomenclatura de *Astraea*, dando informações sobre a tipificação do gênero, confusões com as espécies *Croton tomentosus*, *Croton divaricatus* e *Croton prunifolius*, além de efetivamente propor o lectótipo de *Astraea lobata*, com uma breve discussão sobre a procedência do tipo, e transferir *Croton comosus* e *Croton jatropha* para o gênero: ***Astraea comosa* (Müll.Arg.) B.W. van Ee** e ***Astraea jatropha* (Müll.Arg.) B.W. van Ee**.
- 2014 Caruzo e colaboradores transferem as últimas espécies de *Croton* sect. *Astraea* para o gênero: ***Astraea comantha* (S.Moore) Caruzo**, ***Astraea douradensis* (Steyerm.) Caruzo**, ***Astraea gardneri* (Müll.Arg.) Caruzo** e ***Astraea subcomosa* (Müll.Arg.) Caruzo**.
- 2014 Moraes e colaboradores propõe um nome mais antigo para o que até então era conhecido como *Astraea klotzschii* (= *Croton astraeatus* na concepção de Govaerts): ***Astraea macroura* (Colla) P.R.L. Moraes, De Smedt & Guglielmo**, com base em *Croton macrourus*, nome não incluso nos trabalhos taxonômicos anteriores.

- 2016 No WorldChecklist de Kew Online (acessado em 23.XII.2016) inclui as combinações realizadas até o momento, junto com todos os nomes abordados por Govaerts et al. (1999), constando 12 espécies de *Astraea*: *Astraea aureomarginata*, *Astraea cincta*, *Astraea comantha*, *Astraea comosa*, *Astraea douradensis*, *Astraea gardneri*, *Astraea hauthalii* (incl. *Croton rumicifolius*), *Astraea jatropha*, *Astraea lobata* (incl. *Croton mocinoi*), *Astraea macroura* (incl. *Croton astraeatus*), *Astraea praetervisiva* e *Astraea subcomosa*. *Croton palmatus* é considerado como um nome válido ainda.
- 2017 Três novas espécies são reconhecidas em *Astraea* com base em variedades de *Croton lobatus*: ***Astraea digitata* (Müll.Arg.) O.L.M. Silva**, ***Astraea gracilis* (Müll.Arg.) O.L.M. Silva** and ***Astraea manihot* (Müll.Arg.) O.L.M. Silva**. Ainda, através de investigações moleculares, *Astraea douradensis* foi sinonimizada em *Astraea paulina*, uma vez que as características diagnósticas desta espécie se demonstraram resultantes de infestação por fitoplasmas.
- 2018 *Astraea* é reconhecido como contendo 12 espécies e estudos adicionais revelam parte da história evolutiva do gênero. *Astraea paulina* é reconhecida como uma espécie distinta de *Astraea lobata*, assim como *Astraea klotzschii* de *Astraea macroura*. As espécies reconhecidas são: *Astraea cincta*, *Astraea comosa*, *Astraea digitata*, *Astraea gracilis*, *Astraea klotzschii*, *Astraea lobata*, *Astraea macroura*, *Astraea manihot*, *Astraea paulina*, *Astraea praetervisiva*, *Astraea subcomosa*, ***Astraea surinamensis* (Miq.) O.L.M. Silva** e ***Astraea trilobata* (Forssk.) O.L.M. Silva**.



CONSIDERAÇÕES FINAIS

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## CONSIDERAÇÕES FINAIS

Nesta tese são apresentados importantes avanços para o conhecimento de *Astraea*, que se refletem em contribuições para Crotonae, bem como Euphorbiaceae na região Neotropical.

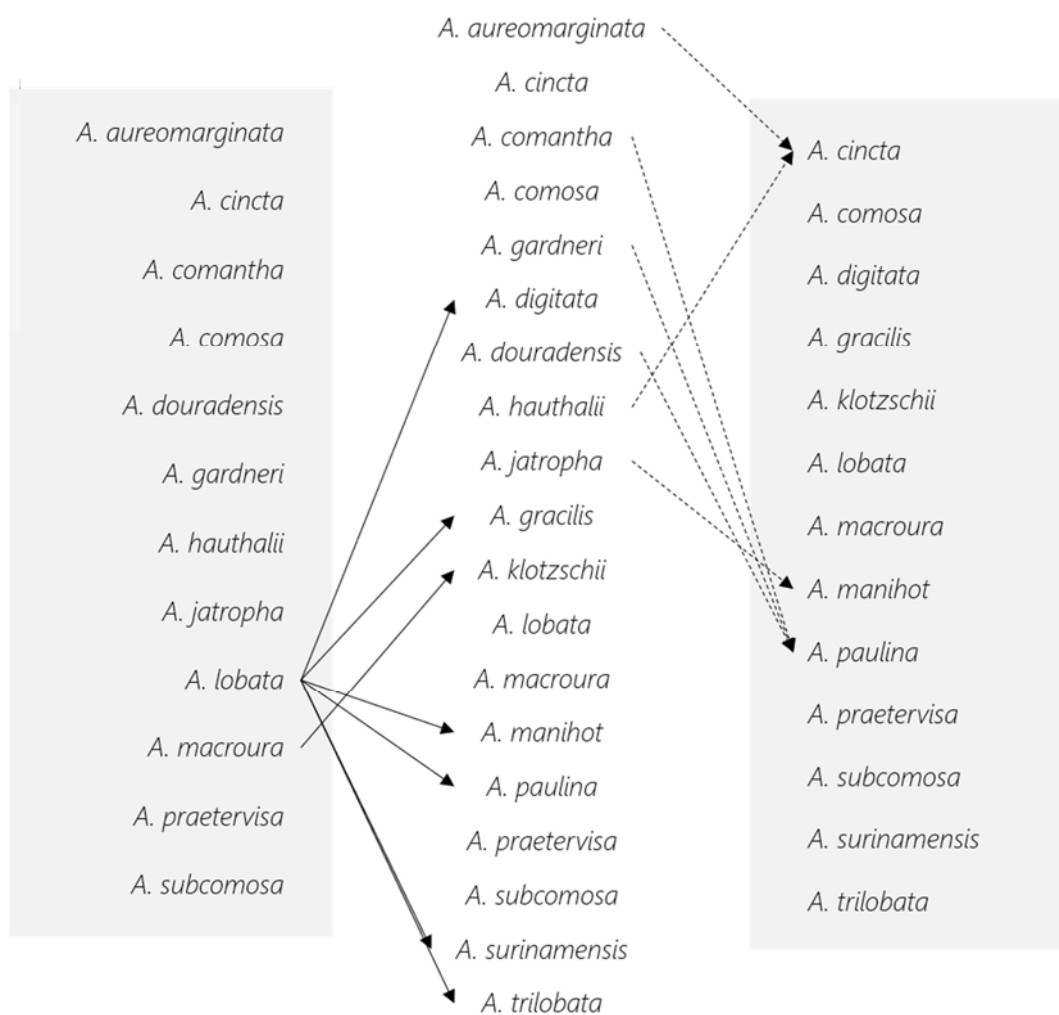
Em relação à taxonomia do grupo, o primeiro destaque refere-se à redelimitação de *Astraea lobata*, a espécie tipo do gênero. Antes dos estudos aqui apresentados, a delimitação morfológica desta espécie era pouco precisa, sem nenhum caráter diagnóstico, que se refletia em uma longa lista de sinônimos e uma ampla distribuição geográfica. Além de três espécies restabelecidas recentemente (Capítulo I), no Capítulo III propusemos ainda mais duas: *A. surinamensis* e *A. trilobata*, espécies ruderais de ampla distribuição na região Neotropical e África, respectivamente. Também apresentamos uma crítica reorganização do gênero (Fig. 1): *A. paulina*, sinonimizada recentemente por Caruzo & Cordeiro (2007) em *A. lobata*, é restabelecida como uma espécie distinta, e nela foram sinonimizadas *A. comantha* e *A. gardneri*, além de *A. douradensis*, cujos caracteres diagnósticos foram identificados como resultantes de infestação por fitoplasmas (Capítulo II). *A. aureomarginata* e *A. hauthalii* são sinonimizadas em *A. cincta*, uma vez que as principais características morfológicas que poderiam diferenciar tais espécies (tamanho e formato do limbo) foram consideradas inapropriadas para a distinção de tais espécies, apesar do alto suporte estatísticos para os subclados entre as diferentes amostras desta espécie utilizadas no estudo filogenético. Por fim, *A. jatropa* foi sinonimizada em *A. manihot*. Assim, com as alterações descritas acima, das onze espécies anteriormente reconhecidas em *Astraea*, o gênero conta atualmente com 13 espécies.

Como consequência da delimitação mais precisa de diversos táxons e do extenso número de coleções analisadas, foi possível avaliar o status de conservação de todas as espécies de *Astraea*. Apenas *A. cincta* foi incluída no Livro Vermelho da Flora do Brasil (Martinelli & Moraes 2013), sendo avaliada como “Em perigo (EN)”, categoria na qual *A. comosa* também se enquadra na nossa avaliação. Ainda, *A. macroura* é aqui classificada como “Vulnerável (VU)”, *A. praetervisa* como “ criticamente em Perigo (CR)”, enquanto as espécies ruderais (*A. lobata*, *A. surinamensis* e *A. trilobata*) são classificadas como “Menor Preocupação (LC)”. As demais espécies (*A. digitata*, *A. klotzschii*, *A. manihot*, *A. paulina* e *A. subcomosa*) se enquadram na categoria “Quase Ameaçada (NT)” uma vez que, de forma geral, possuem ampla distribuição, mas em alguns casos de forma fragmentada e em formações vegetais que atualmente sofrem forte pressão antrópica, chamando a atenção para a conservação dos campos rupestres, restingas e cerrados.

As filogenias apresentadas nos capítulos III e V demonstraram o monofiletismo do gênero com alto suporte, bem como seu posicionamento em Crotonae como irmão de *Acidocroton*, também com alto suporte. Observamos forte incongruência entre as árvores obtidas pelo conjunto de dados plastidiais (*trnL-F* e *psbA-trnH*) e nuclear (*ITS*). O conjunto plastidial recuperou uma série de terminais sucessivamente relacionados entre si, revelando muito pouco sobre as relações filogenéticas entre as espécies do gênero.



Ambas regiões plastidiais utilizadas neste trabalho demonstraram um baixo nível de caracteres informativos (10-12%). Entretanto, enquanto as sequências de *psbA-trnH* possuem pouca variação entre si (até 3,22%), as de *trnL-F* alcançam até 9,48%. A alta variação entre as sequências de *trnL-F* contrastando com o baixo número relativo de caracteres informativos indica a possibilidade de saturação deste marcador. Se por um lado, esta saturação se reflete em baixo sinal filogenético, por outro, a região pode vir a ser útil em estudos filogeográficos.



**Figura 1:** Lista de espécies de *Astraea* antes do presente estudo (esquerda) e após os resultados aqui obtidos (direita). Traços sólidos representam espécies reestabelecidas a partir de sinônimos, enquanto os tracejados indicam espécies sinonimizadas.

Na árvore baseada nas sequências de ITS, reconhecemos três grandes clados – A, B e C, que são suportados por características morfológicas e ecológicas. Os clados A e B contém, cada um, duas espécies (*Astraea lobata* e *A. cincta* no clado A, e *A. surinamensis* e *A. trilobata* no clado B), enquanto as nove espécies restantes estão no clado C, que é subdividido em subclados (C1 e C2), com espécies restritas ao sudeste do Brasil e centro e sul da Bahia (C1) e espécies de ampla distribuição na diagonal de áreas secas da América do Sul e no nordeste brasileiro (C2). Nossa estratégia de amostragem incluindo múltiplos acessos para parte das

espécies de *Astraea* (principalmente daquelas com ampla distribuição ou notável plasticidade fenotípica) resultou em não agrupamento de amostras de uma mesma espécie como monofilética. Neste clado, é interessante destacar que apenas as amostras de *A. klotzschii* foram recuperadas em subclados diferentes, com a divisão das amostras seguindo a divisão geográfica entre os clados C1 e C2 (i.e., amostras da região sudeste no subclado C1 e as do nordeste no clado C2).

Com a datação da filogenia obtida a partir do conjunto de dados nucleares, aliada à reconstrução de áreas ancestrais, foi possível avaliar a hipótese sobre a origem de *Astraea* (Hipótese D, pág. 12). Nossos resultados refutaram a nossa hipótese inicial, na qual o gênero teria se originado na Mesoamérica e, com a formação do Istmo do Panamá, teria expandido sua distribuição geográfica até o leste e sul da América do Sul, onde alcançou a maior diversidade de espécies. Ao contrário, nossas análises indicam um provável ancestral distribuído ao longo da diagonal seca da América do Sul e no leste do Brasil, que teria divergido do provável ancestral de *Acidocroton* há cerca de 35 maa, com intensificação da diversificação interna de *Astraea* entre o Oligoceno e o Plioceno, provavelmente influenciado pela formação da diagonal seca do América do Sul resultante da aridificação provocada pela sombra de chuva formada com o soerguimento dos Andes. Sob este cenário, portanto, a distribuição de *Astraea* na Mesoamérica é resultante de migração posterior à formação do Istmo do Panamá, ao passo que nos Paleotrópicos foi mediada por ações humanas.

A reconstrução dos caracteres morfológicos selecionados não foi capaz de identificar qualquer provável sinapomorfia para o clado *Acidocroton* + *Astraea*. Estes dois gêneros são bastante diversos morfológicamente: *Acidocroton* possui folhas inteiras (vs. profundamente lobadas ou partidas em *Astraea*), inflorescências axilares e fasciculadas, i.e., tanto os eixos das címulas laterais quanto a raque são reduzidos (vs. terminais e espiciformes em *Astraea*), flores estaminadas com pétalas sem tricomas moniliformes na porção basal (vs. com tais tricomas em *Astraea*) e 20-50[-100] estames (vs. 10-15 em *Astraea*) eretos no botão (vs. inflexos em *Astraea*), e flores pistiladas com um nectário anular (vs. cinco nectários em *Astraea*) e estiletos inteiros ou bifidos (vs. multífidos em *Astraea*). A longa distância de ramos entre *Acidocroton* e *Astraea*, refletida em um longo espaço de tempo entre a diversificação de *Acidocroton* e sua divergência de *Astraea*, leva à hipótese de que este cenário seja resultado de extinções na linhagem de *Acidocroton* que explicariam tais divergências morfológicas. Em suporte dessa hipótese, nossa análise biogeográfica indica um possível evento de vicariância no ancestral desses dois gêneros, congruente com o tempo em que a América do Sul sofreu outro grande isolamento após a indisponibilidade de pontes de terra (GAARLandia) com a América Central e Caribe, regiões onde a maioria das espécies de *Acidocroton* são hoje encontradas.

A amostragem de todos os gêneros de Crotonaeae, incluindo uma ampla amostragem do gigante *Croton*, permitiu avaliar as relações evolutivas de *Astraea* nesta importante tribo de Euphorbiaceae. Assim, nossos resultados também permitiram avaliar, pela primeira vez, a relação entre os gêneros de Crotonaeae após as mudanças na circunscrição desta tribo indicadas por Wurdack et al. (2005) e Berry et al. (2005), i.e., a inclusão

de *Acidocroton*, *Sagotia* e *Sandwithia*, anteriormente posicionados em outras tribos de Crotonoideae e revelaram diferentes posicionamentos para *Brasiliocroton*, *Sagotia* e *Sandwithia*. Esses casos foram discutidos sob os resultados das reconstruções de estados de caráter morfológicos de áreas ancestrais. Entretanto, cabe ressaltar que ainda são necessários estudos adicionais, com a utilização de mais marcadores moleculares ou talvez dados genômicos, para elucidar o posicionamento de *Sagotia* e *Sandwithia*, além das relações de *Brasiliocroton* com *Croton*, *Astraea* e *Acidocroton*.

Por fim, os resultados aqui apresentados representam um importante passo no conhecimento de Crotonaeae, especialmente para *Astraea*, o foco desta tese. As espécies do gênero, principalmente *Astraea lobata*, agora dispõem de delimitação morfológica mais clara e sua distribuição geográfica é melhor conhecida, resultando em um tratamento taxonômico atualizado, mais de 130 anos após o tratamento do grupo na Flora Brasiliensis. As relações filogenéticas entre suas espécies também foram estudadas pela primeira vez, e, apesar de não completamente resolvidas, permitiram reconstruir parte importante da história biogeográfica do gênero, também incluindo insights sobre a evolução de Crotonaeae.

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