

AUGUSTO FRANCENER NOGUEIRA GONZAGA

**Estudos taxonômicos em *Byrsonima* sect. *Eriolepis* Nied.
(Malpighiaceae)**

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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“Não me sinto forçado a acreditar que o mesmo Deus que nos agraciou com senso, razão e intelecto pretendeu que renunciássemos a seu uso”

Galileu

Resumo

Byrsonima Rich. ex Kunth (Malpighiaceae) possui distribuição Neotropical e ca. 135 espécies, sendo 93 ocorrentes no Brasil, principalmente em vegetação aberta como o Cerrado. As espécies do gênero são de difícil identificação, carecendo de uma revisão taxonômica atual. *Byrsonima* é monofilético, inserido dentro de um clado com *Blepharandra* Griseb. e *Diacidia* Griseb. in Mart. Dois subgêneros foram estabelecidos dentro do gênero, *Byrsonima* subg. *Byrsonima* e *Byrsonima* subg. *Macrozeugma* Nied., circunscrição baseada na morfologia dos estames. Além disso, esses dois subgêneros são divididos em cinco seções baseadas na morfologia dos estames e no indumento das brácteas e das folhas. Um importante grupo para a flora brasileira é *Byrsonima* sect. *Eriolepis* Nied. amplamente diversificada no Cerrado. O presente estudo teve como objetivo esclarecer as relações filogenéticas dentro de *Byrsonima*, com foco em *Byrsonima* sect. *Eriolepis*, resolvendo, quando possível, questões taxonômicas pendentes. Desse modo, os capítulos que compõem a presente tese têm os seguintes objetivos: o estudo filogenético de *Byrsonima* focado na seção *Eriolepis* (Capítulo 1); a revisão do grupo formado pelas espécies que originalmente pertenciam à seção *Eriolepis* e que se mantiveram num clado bem sustentado filogeneticamente (Clado *Byrsonima crassifolia*), incluindo a lectotipificação de nomes dessa seção (Capítulo 2) e a descrição de duas novas espécies para o estado de Minas Gerais, Brasil (Capítulo 3). Adicionalmente, também foi proposta uma emenda taxonômica para uma espécie rara do gênero, *Byrsonima fanshawei* (Anexo 1); e confeccionamos um guia ilustrado de espécies de *Byrsonima* ocorrentes no Brasil (Anexo 2). A filogenia de *Byrsonima* obtida, avançou a compreensão sobre as relações entre e dentro dos subgêneros e de suas seções, principalmente para a seção *Eriolepis*. Como grande parte das espécies da seção ficou dentro do clado de *B. crassifolia* (L.) Rich., esse grupo foi o alvo da revisão taxonômica, incluindo a descrição de uma nova espécie. Dentro da seção *Eriolepis*, para vários nomes não possuíam tipos determinados, assim, foi também realizada diversas lectotipificações.

Palavras-chave: *Byrsonima*, Cerrado, Filogenia, Lectotipificação, Taxonomia.

Abstract

Byrsonima Rich. ex Kunth (Malpighiaceae) has a Neotropical distribution and ca. 135 species, with 93 species occurring in Brazil, especially in open vegetation as the Cerrado. Species of the genus are difficult to identify, lacking a modern taxonomic revision. *Byrsonima* is monophyletic, within a clade with *Blepharandra* Griseb. and *Diacidia* Griseb. in Mart.. Two subgenera were established within the genus, *Byrsonima* subg. *Byrsonima* and *Byrsonima* subg. *Macrozeugma* Nied., whose circumscriptions, are based on the morphology of stamens. Furthermore, the subgenera were divided in five sections, based on the morphology of the stamens bracts and leaf indumenta. An important group for the Brazilian flora is *Byrsonima* sect. *Eriolepis* Nied. which is very diverse in the Cerrado vegetation. In this study we aimed to clarify the phylogenetic relationships within *Byrsonima*, focusing on *Byrsonima* sect. *Eriolepis*, solving, when possible, pending taxonomic issues. Thus, the chapters composing this thesis had the following aims: the phylogenetic study in *Byrsonima* focusing on sect. *Eriolepis* (Chapter 1); the taxonomic revision of the group formed by the species that originally belonged to sect. *Eriolepis* and stands in a well supported phylogenetic clade (*Byrsonima crassifolia* clade), including the lectotypification of names within this section (Chapter 2) and the description of two new species from Minas Gerais, Brazil (Chapter 3). Additionally, we propose an emend to the original description of a rare species of the genus, *Byrsonima fanshawei* (Appendix 1); and prepared a field guide of species of *Byrsonima* from Brazil (Appendix 2). The phylogeny of *Byrsonima* obtained, advanced the understanding of the relations between and within subgenera and its sections, especially for sect. *Eriolepis*. As most species of the section were within the clade of *B. crassifolia* (L.) Rich., this group was the target of the taxonomic revision, including the description of a new species. Within sect. *Eriolepis*, for several names types were not previously elected, thus, several lectotypifications was performed.

Keywords: *Byrsonima*, Cerrado, Lectotypification, Phylogeny, Taxonomy

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INTRODUÇÃO GERAL

A família Malpighiaceae possui cerca de 77 gêneros e 1300 espécies de distribuição pantropical, mas ocorre predominantemente na região Neotropical, que abrange 85% de sua diversidade (Davis & Anderson 2010). Está entre as mais diversas famílias de lianas tropicais e subtropicais (Anderson 2004). As espécies desta família podem ser facilmente reconhecidas pela presença de tricomas malpigiáceos (tricomas unicelulares apresentando uma base e duas trabéculas), por um par de elaióforos na base de cada sépala e pelas pétalas unguiculadas com uma unha muito conspícua (Anderson 1981).

Entre os gêneros de Malpighiaceae, destaca-se *Byrsonima* Rich. ex Kunth, o segundo maior da família, com cerca de 135 espécies (Anderson et al. 2006). As espécies desse gênero são caracterizadas pelo hábito arbustivo ou arbóreo, estípulas intra- e epipeciolares, ausência de nectários extra-florais nas folhas, inflorescências terminais com flores em cincínios, cálice com dez glândulas secretoras de óleo (elaióforos) ou glândulas ausentes, androceu com dez estames, três estiletes subulados e frutos do tipo drupa (Mamede 1987, Anderson 1995).

DISTRIBUIÇÃO GEOGRÁFICA

O gênero *Byrsonima* possui distribuição Neotropical (fig. 1), com a maioria das espécies ocorrendo na América do Sul, podendo ser encontradas em florestas úmidas, contudo sendo mais diverso em savanas (Anderson et al. 2006). O Brasil é o país com a maior representatividade de espécies, no qual ocorrem 97 espécies, sendo os Domínios do Cerrado (49 spp.) e da Floresta Amazônica (50 spp.), os mais diversos (Mamede et al. 2016).



Figura 1 - Distribuição de *Byrsonima* (Modificado de Anderson et al. 2006)

Podem ser destacados dois centros de diversidade para Malpighiaceae e também para *Byrsonima*: Planalto das Guianas, uma região que compreende o planalto do Sudoeste da Guiana, com a inclusão de partes dos territórios de Roraima, Venezuela e Colômbia, com 160 espécies da família e 42 espécies de *Byrsonima* (Anderson 1981). O segundo centro de diversidade é a região central do Brasil, especialmente na Cadeia do Espinhaço em Minas Gerais e na Bahia e também na Chapada dos Veadeiros em Goiás (Mamede 1987, Mamede et al. 2015, Sebastiani et al. 2015), especialmente em campos de altitude.

HISTÓRICO TAXONÔMICO DE *Byrsonima* – Categorias Supragenéricas

Na última revisão taxonômica para as Malpighiaceae, Niedenzu (1928) incluiu *Byrsonima* na subfamília Planitorae, que abrange as espécies que não possuem frutos alados. O gênero foi inserido dentro da tribo *Malpighieae* ao lado de *Malpighia* L., *Bunchosia* Kunth, *Burdachia* A. Juss., *Diacidia* Griseb., *Dicella* Griseb., *Glandonia* Griseb. e *Alcoceratothrix* Nied., sendo o último sinonimizado em *Byrsonima* por Anderson (1981).

Posteriormente, Morton (1968), baseado no Código Internacional de Nomenclatura Botânica, que determina que o nome das subfamílias deve incluir os nomes de gêneros nela incluídos, propôs a mudança do nome, de Planitorae para Malpighioideae. Anderson (1977), entretanto, observou que certos gêneros da subfamília Malpighioideae *sensu* Morton (1968) não eram proximamente relacionados. Anderson (1977) supunha que alguns tipos de frutos carnosos representavam exemplos de convergência na família e seriam provavelmente derivados de ancestrais com frutos alados. Dessa forma, o autor propôs a exclusão de alguns gêneros da subfamília Malpighioideae, dentre eles *Byrsonima*, reconhecendo uma nova subfamília, Byrsonimoideae, caracterizada pelo hábito arbustivo-arbóreo, frutos não alados, presença de três estiletes subulados com estigmas muito pequenos, grãos de pólen tricolporados e número cromossômico $n=6$ ou $n=12$. *Byrsonima*, foi incluída na tribo *Byrsonimeae*, ao lado de *Blepharandra* Griseb., *Burdachia*, *Diacidia* e *Glandonia*.

Com as primeiras análises filogenéticas realizadas para as Malpighiaceae, foi evidenciado que a subfamília Byrsonimoideae e a tribo *Byrsonimeae* eram polifiléticas, mas que o gênero *Byrsonima* era um grupo monofilético e basal dentro de Malpighiaceae, um clado bem suportado tendo como gêneros próximos *Blepharandra* e *Diacidia*, chamado *byrsonimoids* (Davis et al. 2001) (fig. 2). Recentemente Davis & Anderson (2010) confirmaram o monofiletismo desse clado, com a inclusão de mais terminais na análise (fig. 3).

ndhF + trnL-F

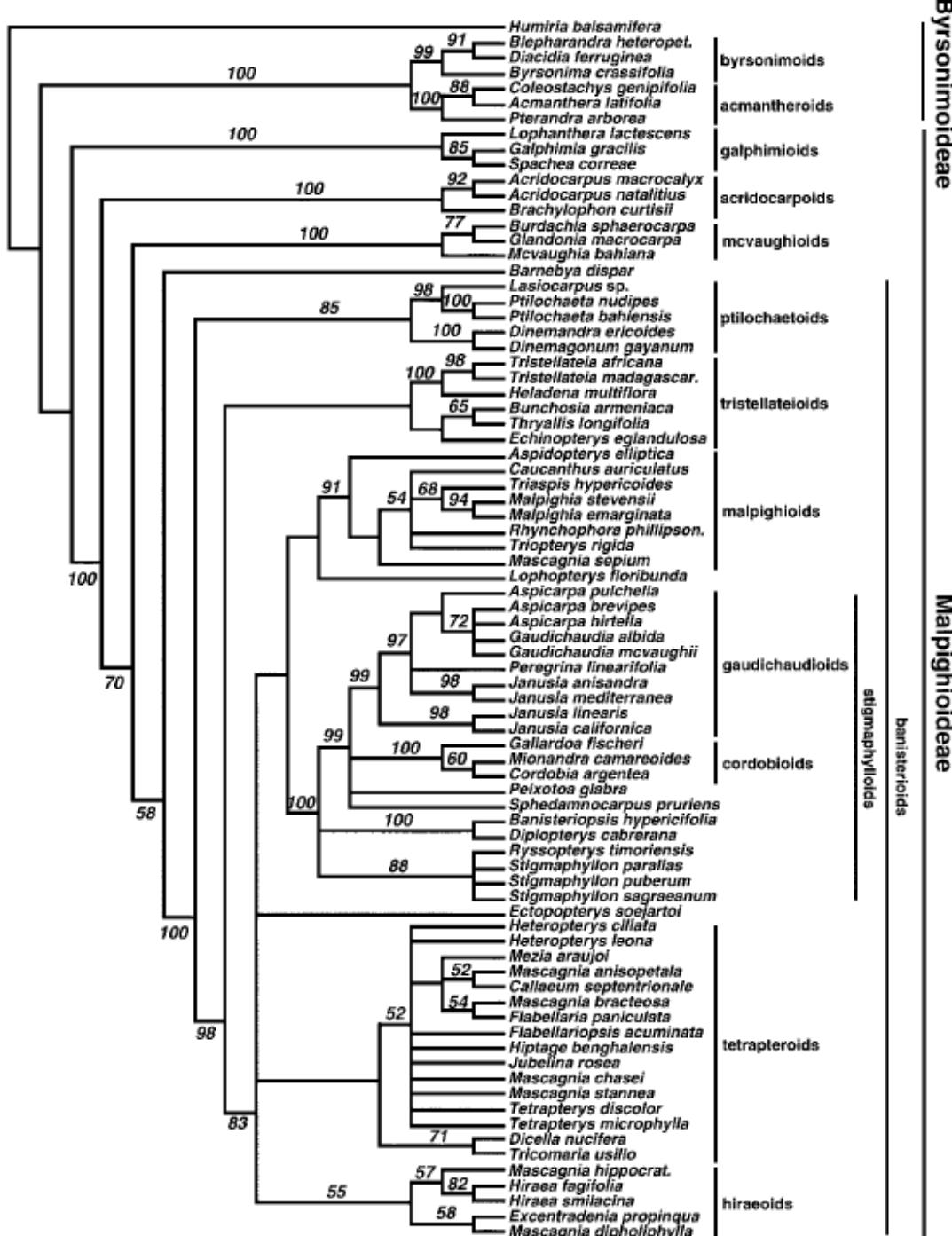


Figura 2- Davis et al. (2001) - Árvore filogenética de Malpighiaceae contendo espécies da família Malpighiaceae [Análise baseada em dados combinados de *ndhF/trnL-F*].

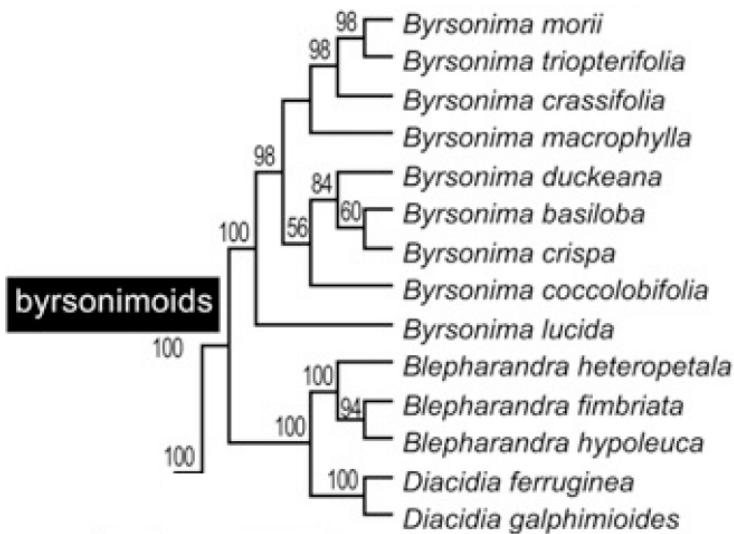


Figura 3 - Árvore filogenética extraída de Davis & Anderson (2010), evidenciando apenas o clado *byrsinomoids* baseada em dados combinados de *ndhF*, *matK*, *PHYC* e *rbcL*.

HISTÓRICO TAXONÔMICO DE *Byrsonima* – Categorias Infragenéricas

O nome *Byrsonima* foi validamente publicado pela primeira vez em 1811, no trabalho de Jussieu sobre as Ranunculaceae-Malpighiaceae, no qual este autor faz a seguinte referência: “*Malpighia spicata*, *M. lucida*, *M. crassifolia* e *M. verbascifolia*, têm flores dispostas em ramos terminais soltos, três estiletes e um fruto tricarpelar, portanto formariam um novo gênero, nomeado por Louis Claude Marie Richard de *Byrsonima*, pois essas espécies seriam utilizadas em seu país de origem no curtimento de couro” (*byrsa* = couro e *nimus* = muito usada) (Jussieu 1811). No entanto, Richard não publicou nenhum trabalho descrevendo *Byrsonima* como um novo gênero, e seu único trabalho publicado fazia referência a algumas espécies de *Malpighia* que poderiam formar três gêneros distintos (Richard 1808). Assim, Jussieu (1811) atribuiu a autoria do novo gênero a Richard, mas a primeira diagnose do gênero só foi elaborada por Kunth (1821), no “*Nova Genera et Species Plantarum*”. Nesse trabalho, o autor aceitou a delimitação do gênero feita por Jussieu (1811), bem como as combinações propostas para *Malpighia verbascifolia* L. [= *Byrsonima verbascifolia* (L.) DC.], *M. crassifolia* L. [*B. crassifolia* (L.) Kunth], *M. lucida* Mill. [= *B. lucida* (Sw.) DC.] e *M. spicata* Cav. [= *B. spicata* (Cav.) DC.]. Kunth (1821) propôs também a transferência de *M. moureila* Aubl., *M. coriacea* Sw., *M. altissima* Aubl. e *M. rufa* Poir. para o novo gênero, descrevendo ainda nove espécies novas: *Byrsonima coccobifolia* Kunth, *B.*

rhopalaefolia Kunth, *B. montana* Kunth, *B. laurifolia* Kunth, *B. chrysophylla* Kunth, *B. ferruginea* Kunth, *B. conitifolia* Kunth, *B. nitidissima* Kunth e *B. angustifolia* Kunth.

O primeiro trabalho no qual constam apenas espécies brasileiras foi realizado por Jussieu, na “*Flora Brasilieae Meridionalis*” uma descrição mais detalhada do gênero e diagnoses detalhadas de 11 espécies novas (Jussieu 1832). Sete anos depois, Grisebach publicou cinco espécies novas de *Byrsonima*: *B. psilandra* Griseb., *B. dealbata* Griseb., *B. brasiliensis* Griseb., *B. laxiflora* Griseb. e *B. perseifolia* Griseb. (Grisebach 1839).

No ano seguinte, Jussieu publicou em sua obra “*Malpighiacearum Synopsis*” 67 espécies de *Byrsonima* com descrições sucintas, dentre as quais 30 eram novas para a ciência (Jussieu 1840). Somente três anos mais tarde foi publicada a primeira monografia de Malpighiaceae por esse mesmo autor, com descrições mais detalhadas das espécies de *Byrsonima* (Jussieu 1843).

Posteriormente, Grisebach (1858) publicou na “*Flora Brasiliensis*” a descrição de 55 espécies de *Byrsonima* das quais seis eram novas. Mais tarde, Grisebach fez uma nova contribuição para o conhecimento da Flora do Brasil Central, em especial dos cerrados de Lagoa Santa, em Minas Gerais, identificando as espécies de Malpighiaceae coletadas por E. Warming. Nesse trabalho, Grisebach (1875) refere 17 espécies de *Byrsonima*, dentre as quais uma nova espécie, *B. myricifolia* Griseb.

Niedenzu apresentou em um volume da obra “*Die natürlichen Pflanzenfamilien*” uma pequena descrição do gênero, referindo a existência de cerca de 90 espécies de *Byrsonima* para América tropical (Niedenzu 1896). No entanto, o primeiro trabalho que tratou exclusivamente do gênero *Byrsonima* foi publicado por este autor somente um ano mais tarde, quando Niedenzu apresentou a primeira parte de sua dissertação sobre o gênero. Neste trabalho, o autor criou um novo gênero, *Callyntranthele*, baseando-se em duas espécies de *Byrsonima*: *B. dispar* Griseb. e *B. angustifolia* Kunth. (Niedenzu 1897). Este gênero foi posteriormente sinonimizado em *Byrsonima* pelo próprio Niedenzu, em sua monografia das Malpighiaceae (Niedenzu 1928), e então, finalmente sinonimizado em *Blepharandra* (Anderson 1981).

Quatro anos mais tarde, Niedenzu (1901) publicou a segunda parte de sua dissertação sobre o gênero *Byrsonima*, da qual constam uma chave de identificação para 97 espécies, 14 das quais espécies novas. Neste mesmo trabalho, Niedenzu subdividiu o gênero em dois subgêneros, *Brachyzeugma* (=*Byrsonima*, segundo Morton 1968) e *Macrozeugma*, que foram por sua vez subdivididos em várias seções, subseções, séries e subséries.

Grande parte das espécies do subgênero *Macrozeugma* possuem flores alvas ou róseas e conectivos muito alongados que ultrapassam as tecas da antera. Possuem distribuição predominantemente amazônica, com algumas espécies, como *B. triopteryfolia* A. Juss., *B. cocolobifolia* Kunth, *B. bahiana* W.R. Anderson e *B. cacaophyla* W.R. Anderson, ocorrendo no Cerrado brasileiro e na Floresta Atlântica, enquanto outras, como *B. wadsworthii* Little e *B. trinitensis* A. Juss., ocorrendo nas Antilhas (Elias 2004).

Por sua vez, no subgênero *Byrsonima* grande parte das espécies possui flores amarelas e estames com conectivos que não ultrapassam as tecas da antera ou raramente os ultrapassam em até um quarto de seu comprimento. Esse subgênero possui distribuição predominantemente brasileira, com grande parte de suas espécies distribuindo-se pelo cerrado, como *B. dealbata* Griseb., *B. basiloba* A. Juss. e *B. intermedia* A. Juss.

Além disso, o gênero possui cinco seções: *Acrotheca*, *Colobotheca*, *Eriolepis*, *Kerozeugma* e *Sericolepis*, divididas de acordo com a morfologia dos estames e o indumento das brácteas e das folhas (Cuatrecasas 1958, Niedenzu 1901, 1928). As seções *Acrotheca*, *Colobotheca* e *Kerozeugma*, pertencem ao subgênero *Macrozeugma*, sendo que a sua separação está baseada especialmente na morfologia do ápice das anteras. Já as seções *Sericolepis* e *Eriolepis* pertencem ao subgênero *Byrsonima*, sendo separados especialmente pelo indumento das brácteas, bractéolas e folhas. As cinco seções ainda são divididas em subseções e séries.

Niedenzu (1928), publicou o trabalho “*Das Pflanzenreich*”, com a monografia completa de Malpighiaceae, na qual o gênero *Byrsonima* contava então com 120 espécies, sendo um dos trabalhos mais completos com descrições e distribuição geográfica de todas as espécies conhecidas até aquele momento. Este trabalho é de

grande importância para a família, todavia Niedenzu (1928) teve problemas devido à baixa representatividade de várias floras, bem como por nunca ter conhecido as espécies em campo e por nunca ter visitado os herbários de Paris, Londres ou na América (Anderson 1981).

Posteriormente a essa data, novas espécies de *Byrsonima* foram publicadas por diversos autores: Standley (1930), Gleason (1931), Pilger (1937), Moldenke (1941), Sandwith (1943), MacBride (1949), Steyermark (1952), Little (1953), Cuatrecasas (1958), Lewis (1973), Mamede (1980) e Anderson (1981, 1982, 1990, 1992, 1993, 1995, 1997, 1999, 2001). Porém, nenhum desses autores apresentou uma revisão completa do gênero, resultando em uma difícil compreensão taxonômica de suas espécies.

Trabalhos filogenéticos foram realizados para *Byrsonima*, mas com o objetivo de compreender sua relação com outros gêneros da família Malpighiaceae, demonstrando que é monofilético (Cameron et al. 2001, Davis et al. 2001, Davis & Anderson 2010) (fig. 2 e 3). Todavia nenhum trabalho foi publicado para entender as suas relações infragenéricas. Davis & Anderson (2010) incluíram em sua análise nove terminais de *Byrsonima*. Apesar de representar uma amostragem insuficiente, uma vez que o gênero possui mais de 135 espécies aceitas (Anderson et al. 2006), pode-se inferir o polifiletismo dos subgêneros *Byrsonima* e *Macrozeugma* (fig. 4), os quais já haviam sido considerados como grupos artificiais por diversos autores (Cuatrecasas 1958, Anderson 1981, Mamede 1987, Elias 2004).

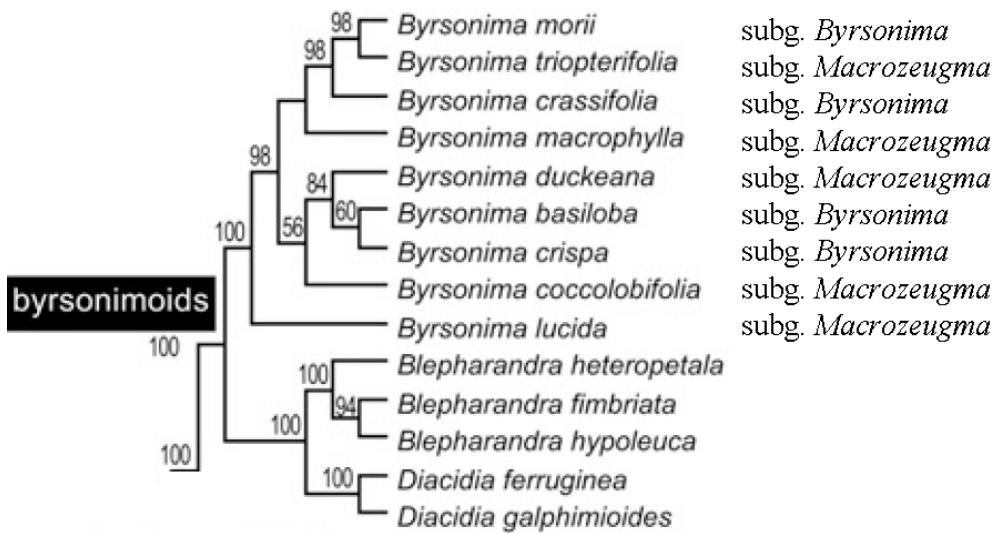


Figura 4 - Árvore filogenética da família Malpighiaceae extraída e modificada do estudo de Davis & Anderson (2010), evidenciando apenas o clado byrsonimoids e os subgêneros de *Byrsonima* evidenciados para cada espécie, demonstrando seu polifiletismo. Análise baseada em dados combinados de ndhF, matK, PHYC e rbcL.

HISTÓRICO TAXONÔMICO DE *Byrsonima* sect. *Eriolepis*

Byrsonima subg. *Byrsonima* sect. *Eriolepis* foi proposta por Niedenzu (1901) na obra “*De genere Byrsonima*”. A seção é caracterizada principalmente pela forma e indumento da bráctea e da bractéola, sendo estas de base alargada, ápice acuminado, com a face adaxial glabra e a face abaxial tomentosa e bractéolas caducas. Além disso suas folhas são coriáceas ou cartáceo-coriáceas e a drupa minutamente verrucosa. Posteriormente, Cuatrecasas (1958) ainda incluiu como característica da seção o indumento tomentoso da folha e da raque da inflorescência.

A seção foi inicialmente descrita incluindo 28 espécies, distribuídas em duas subseções: *Brachypus* Nied. e *Macropus* Nied., sendo que a subseção *Brachypus* possuiria a série *Pachybotrys* Nied., enquanto que a subseção *Macropus* possui as séries *Eriodes* Nied. e *Pyrrhos* Nied. (Niedenzu 1901). Posteriormente, Niedenzu (1928) ampliou o número de espécies, incluindo *B. pulchra* DC., *B. roigii* Urb. e *B. smalii* Fawc. & Rendle. Posteriormente algumas espécies foram descritas, mas não foram classificadas dentro de nenhuma categoria infragenérica em *Byrsonima*, mas são morfologicamente próximas de espécies pertencentes à seção *Eriolepis* sendo elas: *B. affinis* W.R. Anderson, *B. cipoensis* Mamede, *B. lanulosa* W.R. Anderson, *B. stannardii* W.R. Anderson e *B. subterranea* Brade & Markgr., totalizando assim 36 nomes de espécies na seção, sendo que 25 são nomes aceitos (tab. 1).

Tabela 1 – Espécies descritas dentro de *Byrsonima* sect. *Eriolepis*. Nomes aceitos estão marcados com asterisco (*)

<i>Byrsonima affinis</i> W.R. Anderson *	<i>Byrsonima martiana</i> A. Juss. *
<i>Byrsonima basiloba</i> A. Juss. *	<i>Byrsonima oaxacana</i> A. Juss. *
<i>Byrsonima clauseniana</i> A. Juss. *	<i>Byrsonima orbignyana</i> A. Juss. *
<i>Byrsonima cotinifolia</i> Kunth	<i>Byrsonima pachyphylla</i> A. Juss. *
<i>Byrsonima crassa</i> Nied.	<i>Byrsonima pinetorum</i> Griseb. *
<i>Byrsonima crassifolia</i> (L.) Kunth *	<i>Byrsonima psilandra</i> Griseb. *
<i>Byrsonima cumingiana</i> A. Juss.	<i>Byrsonima pulchra</i> DC.
<i>Byrsonima cydoniifolia</i> A. Juss. *	<i>Byrsonima rhombifolia</i> A. Juss.
<i>Byrsonima cipoensis</i> Mamede *	<i>Byrsonima roigii</i> Urb. *
<i>Byrsonima dealbata</i> Griseb. *	<i>Byrsonima salzmanniana</i> A. Juss. *
<i>Byrsonima eriopoda</i> DC.	<i>Byrsonima smalii</i> Fawc. & Rendle *
<i>Byrsonima fagifolia</i> Nied.	<i>Byrsonima stannardii</i> W.R. Anderson *
<i>Byrsonima grisebachiana</i> Nied.	<i>Byrsonima subterranea</i> Brade & Markgr. *
<i>Byrsonima guilleminiana</i> A. Juss. *	<i>Byrsonima tenuifolia</i> Urb. & Nied. *
<i>Byrsonima karwinskiana</i> A. Juss.	<i>Byrsonima variabilis</i> A. Juss. *
<i>Byrsonima lanulosa</i> W.R. Anderson *	<i>Byrsonima verbascifolia</i> (L.) DC. *
<i>Byrsonima laurifolia</i> Kunth	<i>Byrsonima viminifolia</i> A. Juss. *
<i>Byrsonima linearifolia</i> A. Juss. *	<i>Byrsonima whrightiana</i> Nied.

As espécies da seção *Eriolepis* estão distribuídas desde o México e Antilhas, até o sul da América do Sul (fig. 5), ocorrendo principalmente em áreas abertas como os cerrados brasileiros e as áreas savânicas do norte da América do Sul e da América Central. Apesar da ampla distribuição dos gêneros, a maioria das espécies está localizada no Brasil, principalmente no planalto central brasileiro.



Figura 5 - Distribuição de *Byrsonima* sect. *Eriolepis*

A seção *Eriolepis* ainda não passou por um tratamento taxonômico recente, mas algumas espécies foram amostradas em trabalhos de flora (Anderson 1982, Cuatrecasas 1958, Mamede 1987). E em estudos filogenéticos, quase nada pode ser evidenciado, mas a análise do trabalho realizado por Davis e Anderson (2010), no qual apenas duas espécies pertencentes da seção foram utilizadas, *Byrsonima basiloba* e *B. crassifolia* podemos inferir que a seção é polifilética (fig. 4).

MORFOLOGIA GERAL DE *Byrsonima*

Byrsonima é um gênero que possui plantas predominantemente hábito arbóreo, mas podemos destacar também o hábito arbustivo e subarbustivo em áreas savânicas, como o Cerrado brasileiro e o Planalto das Guianas. O caule pode ser ereto ou tortuoso, mas em espécies de hábito subarbustivo, o caule é subterrâneo, embora nunca formando xilopódio, como ocorre em *Heteropterys* ou *Banisteriopsis*.

As estípulas em *Byrsonima* são intrapeciolares, sendo dois pares por nó, geralmente esse par é conado, mas em algumas espécies pode ser parcialmente conado ou até livres. Seu formato também é utilizado na delimitação de espécies e se são decíduas ou não. A morfologia foliar é importante para a caracterização de espécies, podendo-se destacar especialmente a forma das folhas que são importantes para algumas espécies ou bastante variáveis especialmente em espécies de ampla distribuição. As nervuras também podem ser utilizadas, sendo broquidódromas, mas o seu número e o padrão das nervuras secundárias e terciárias são importantes.

Um dos caracteres mais importantes é o indumento foliar, bem como a forma dos tricomas malpigiáceos. São tricomas unicelulares com uma trabécula e um estipe (base). O comprimento do pedúnculo e das trabéculas define os diferentes tipos e densidades de indumentos presentes em *Byrsonima*, assumindo as formas básicas de Y, T ou V, ou ainda podem ser estrelados ou não ramificados. Em algumas espécies, por exemplo, eles são sinuosos, consistindo então de indumento tomentoso ou lanoso, enquanto em outras são retos, sendo o indumento seríceo. Além disso, o indumento pode variar num mesmo órgão (p. ex. folhas) ou em diferentes órgãos.

A inflorescência em *Byrsonima* é sempre terminal podendo ser dividida em tirso de cincínios unifloros, ou com até 4 flores, sendo esta uma característica útil na separação das espécies. As inflorescências também possuem tricomas e indumentos variados, ou podem ser completamente glabras. O comprimento da inflorescência, bem como a posição das flores na raque, é variável, e podem ser utilizados na identificação das espécies, especialmente a distribuição das flores por toda a raque, ou apenas na porção mediana e basal ou ainda apenas no ápice.

As flores podem ser sésseis ou apresentar pedicelos articulados (pedunculados) ou sésseis, pilosos ou glabros. O pedicelo e o pedúnculo podem ser circinados ou eretos, e seu comprimento e espessura podem variar. As brácteas e bractéolas estão presentes na base dessas estruturas. Quando as flores são pedunculadas, o par de bractéolas emerge na base do pedicelo, e a bráctea na base do pedúnculo, mas nas flores sésseis as bractéolas emergem no mesmo nível da bráctea. Estas estruturas foram utilizadas por Niedenzu (1901) na delimitação de Séries e Seções. Geralmente são similares na forma, sendo a bráctea maior que as bractéolas, e podem ser glabras ou pilosas, e decíduas ou não na floração ou na frutificação.

O cálice é geralmente uniforme em *Byrsonima*, sendo as sépalas ovadas ou triangulares, com seu ápice deflexo ou ereto. Na frutificação, as sépalas podem ser concrescidas com o fruto, em algumas espécies adquirirem formatos linguiformes ou ainda podem ser carnosas. Na base das sépalas é comum a presença de um par de elaióforos, por sépala, podendo estar ausentes completamente em algumas espécies, ou em indivíduos de uma mesma população, característica presente em outros gêneros de Malpighiaceae.

A corola é zigomorfa, formada por cinco pétalas, e cada pétala possui um limbo desenvolvido e uma base estreita denominada unha. A zigomorfia da corola é definida por uma pétala posterior distinta, duas pétalas látero-anteriores e duas látero-posteriores semelhantes. A pétala posterior é geralmente ereta, com um limbo patente e unha mais espessa que a das pétalas laterais. As pétalas laterais apresentam unha deflexa e limbo cupuliforme ou plano. A coloração das pétalas é variável podendo ser todas elas róseas, brancas, ou amarelas, tornando-se róseo intenso, alaranjadas a avermelhadas com o tempo, ou apresentarem pétala posterior amarela e laterais róseas ou brancas. Nas pétalas a presença de indumento é rara, ocorrendo em apenas poucas espécies (p. ex. *B. altissima*).

O androceu representa a estrutura mais importante para a taxonomia de *Byrsonima*. São sempre dez estames, presentes em uma série ao redor do ovário. Os filetes são aplanados, com tricomas na base da face adaxial, e geralmente glabros na face abaxial. Além disso, os filetes podem ser coalescentes ou não na base. Os tricomas podem ser eretos ou sinuosos e são simples.

O conectivo apresenta morfologia variável, sendo o seu comprimento em relação às tecas importante para a separação de espécies. As espécies de flores róseas ou brancas, geralmente do subgênero *Macrozeugma* usualmente possuem o conectivo desenvolvido, ultrapassando significativamente o ápice das tecas, normalmente em mais de $\frac{1}{4}$ do comprimento delas, enquanto que nas espécies de flores amarelas, geralmente do subgênero *Byrsonima*, o conectivo não ultrapassa o ápice das tecas em mais de $\frac{1}{4}$ do comprimento das tecas. A forma do conectivo também é variável, podendo ser cônica, obovoide ou globosa. Algumas espécies possuem o ápice do conectivo agudo ou acuminado. Em algumas espécies podemos encontrar tricomas nos conectivos, mas na grande maioria delas o conectivo é glabro. As anteras podem ser lineares ou oblongas, com ápice das tecas arredondado, agudo, acuminado, mucronado ou caudado. Além

disso, as tecas podem possuir projeções aladas lateralmente. A presença de tricomas nas tecas também é importante, podendo elas ser glabras, ou apresentarem tricomas seríceos, entre as tecas ou em sua lateral.

O gineceu é um caráter conservativo em *Byrsonima*. O estigma é sempre subulado e o estilete ereto, arqueado no ápice. O ovário apresenta indumento variável, podendo ser glabro ou seríceo. Os óvulos são anátropes e glabros.

Os frutos são sempre drupas, que variam entre as espécies principalmente por sua coloração e tamanho. Quando maduros os frutos podem ser amarelos, vermelhos ou negros. O tamanho varia entre espécies desde 3 mm de diâmetro até mais de 20 mm de diâmetro. Além disso, o pedicelo pode variar no fruto maduro, podendo ser ereto, patente ou circinado. O formato dos frutos possui pouca variação, podendo ser globosos ou ovóides, com um pirênio e três sementes.

OBJETIVOS

O presente trabalho teve como objetivos:

- Confirmar o monofiletismo de *Byrsonima*, dos subgêneros *Byrsonima* e *Macrozeugma*, bem como de suas seções, em especial da seção *Eriolepis* com base em caracteres moleculares;
- Realizar a revisão taxonômica de *Byrsonima* sect. *Eriolepis*.
- Contribuir com o conhecimento da biodiversidade brasileira

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Capítulo 1

Compreendendo a diversificação de *Byrsonima* (Malpighiaceae): filogenia molecular datada e evolução de caracteres morfológicos

Formatado de acordo com o periódico Systematic Botany

FRANCENER ET AL.: BYRSONIMA PHYLOGENY

Insights into the diversification of *Byrsonia* (Malpighiaceae): a dated molecular phylogeny and morphological character evolution

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Abstract—Here we present a dated molecular phylogeny to the new world genus *Byrsonima* Rich. ex Kunth (Malpighiaceae). We sampled 41 species of *Byrsonima* and four species of the outgroups *Blepharandra*, *Diacidia* and *Pterandra* in order to test the monophyly of the infrageneric classification of the genus. Maximum parsimony (MP) and Bayesian inference (BI) analysis were performed for a combined dataset of two chloroplast (*psbA-trnH* and *trnL-F*) and two nuclear regions (ITS and ETS). Five characters were optimized (four morphological and one biogeographic) on the majority rule consensus. Our results corroborate the monophyly of *Byrsonima* subg. *Byrsonima*, as well as the monophyly of its sections. *Byrsonima* subg. *Macrozeuma* is paraphyletic, with pink to white corollas being plesiomorphic in the genera, and probably in all Byrsonimoids.

Keywords—*Byrsonima* sect. *Eriolepis*, Malpighiales, Phylogenetics, Taxonomy

INTRODUCTION

Byrsonima Rich. ex Kunth is the second largest genus in Malpighiaceae, comprising ca. 135 species, endemic to the Neotropical region (Anderson 1981, Anderson *et al.* 2006). It is easily recognized by its shrubby to tree habit, intrapetiolar stipules, eglandular leaves, bracts and bracteoles, elongated thyrsi with 1-4-flowered cincinni, slender styles subulate at the apex, minute stigmas, and fleshy indehiscent drupes, with 3-locular pyrenes (Anderson 1981, Mamede 1987). The first infrageneric classification for the genus was proposed by Niedenzu (1901), including two subgenera (*B.* subg. *Brachyeuma* Nied. and *B.* subg. *Macrozeuma* Nied.) further divided in several sections, subsections, series and subseries. Most infrageneric ranks were delimited based on the type of leaf indumenta, petal color, shape and size of connectives, and the presence of indumenta on the anther locules Niedenzu (1901).

Byrsonima subg. *Brachyeuma* (i.e. *Byrsonima* subg. *Byrsonima*) comprises about 55 yellow-flowered species mostly distributed throughout Neotropical savannas (Cerrado domain). The subgenus is divided in two sections, mostly based on the bracts and leaf blade indumenta (Niedenzu 1901). *Byrsonima* subg. *Byrsonima* sect. *Eriolepis* Nied. comprises ca. 25 species usually covered by tomentose to velutine indumenta. While *Byrsonima* subg. *Byrsonima* sect. *Sericolepis* Nied. comprises ca. 30 species covered by sericeous to glabrous indumenta (Niedenzu 1901, 1928).

In the first phylogeny of *Byrsonima* (Davis & Anderson 2010), just around ten species were sampled, most of them belonging to *B.* subg. *Macrozeuma*. As a first step towards the reconstruction of complete molecular phylogeny of *Byrsonima*, we present a molecular study on this genus testing the monophyly of the genus and of its current infrageneric classification, with a focus on *B.* subg. *Byrsonima*.

MATERIALS AND METHODS

TAXON SAMPLING AND PLANT MATERIAL

We sampled a total of 45 taxa, including outgroups (*Blepharandra* Griseb., *Diacidia* Griseb., and *Pterandra* A. Juss.), and 41 species of *Byrsonima*. For DNA extraction, we used mainly silica-gel dried leaves (12–80 mg), and herbarium specimens when necessary. All specimens used in this study are listed in Table 1. Vouchers were specially deposited at SP herbarium from Instituto de Botânica de São Paulo.

MOLECULAR PROTOCOLS

Genomic DNA was extracted using the CTAB 2 protocol, modified from Doyle and Doyle (1987). Fragments were amplified by PCR (Polymerase Chain Reaction). We tested six regions suggested as potentially useful in phylogenetic reconstructions at the species level (Table 2). Two plastid (psbA-trnH and trnL-F intergenic spacer) and two nuclear regions (Internal and External Transcribed Spacers) were selected, based on their variability and number of parsimony-informative characters (Table 2).

Protocols to amplify and sequence the plastid region trnL-F intergenic spacer followed Taberlet et al. (1991) and the psbA-trnH followed Shaw et al. (2005, 2006). In order to amplify and sequence ITS region we followed White et al. (1990), and Baldwin and Markos (1998) for the ETS region. The amplification mix that achieved success for ETS, ITS, psbA-trnH, and trnL-F amplification, was a TopTaq (Quiagen) mix following the standard protocol in the kit manual, with the addition of 1.0 M betaine and 2% DMSO for ETS and ITS regions. PCR products were purified using PEG 11% precipitation (polyethylene glycol) (Paithankar and Prasad, 1991), and were sequenced directly with the same primers used for the PCR amplification, with the exception of the ITS region, in which we used primers 92 and ITS4. Sequence eletropherograms were produced in an automatic sequencer (ABI 3130XL Genetic Analyzer) using Big Dye Terminator 3.1 (Applied Biosystem). Additional sequences for ITS and trnL-F region were retrieved from Genbank. Newly generated sequences were edited using Geneious (Biomatters, 2015), and aligned using Muscle (Edgar, 2004), with subsequent adjustments in the preliminary matrices made manually by eye. The complete data matrices are available upon request from the first author.

PHYLOGENETIC ANALYSIS

Combined analysis of plastid, nuclear and plastid + nuclear regions were performed, as well as the ILD test (Farris et al. 1994) to investigate incongruences between the DNA data sets. Analyses using Maximum Parsimony (MP) in both matrices were carried out with PAUP 4.0b10a (Swofford, 2002). The heuristic search was performed using the algorithm TBR (tree-bisection reconnection) and 1000 random taxon-addition sequence replicates with TBR swapping limited to 15 trees per replicate in order to prevent extensive searches (swapping) in suboptimal islands, followed by TBR in the resulting trees with a limit of complete swapping in 1000 trees. In all analyses, the characters were equally weighted and the states of characters were specified as unordered (Fitch, 1971). Relative support for individual branches was assessed using non-parametric

bootstrapping (Felsenstein, 1985), with 1000 bootstrap (BS) pseudoreplicates, TBR swapping, simple taxon addition and a limit of 15 trees per replicate. Bootstrap percentages (BP) of 50%–70% were considered as weak, 71%–85% as moderate, and >85% as strong (Kress et al., 2002). For the model-based approach, the model was selected using hierarchical likelihood ratio tests, using J Modeltest 2 (Darriba et al., 2012). Best fit models for all used regions are presented in table 2. The Bayesian inference analysis (BI) was conducted with a mixed model and unlinked parameters, using MrBayes 3.1.2 (Ronquist and Huelsenbeck, 2003). The Markov Chain Monte Carlo (MCMC) was run using two simultaneous independent runs with four chains each (one cold and three heated), saving one tree every 1000 generations, for a total of ten million generations. We excluded as ‘burn in’ two million of them, and trees were checked for a stationary phase of likelihood. The posterior probabilities (PP) of clades were based on the majority rule consensus, using the remaining trees, and calculated with MrBayes 3.1.2 (Ronquist and Huelsenbeck, 2003). Posterior probabilities (PP) of 0.95–1.00 were considered strong, 0.85–0.94 as moderate and <0.85 as weak support. Trees were edited using FigTree v.1.3.1 (Rambaut, 2009) and Photoshop CS5 (Adobe Photoshop).

DIVERGENCE TIME ESTIMATION

Divergence time estimates were obtained using the combined dataset and the BEAST package v.1.8.2 (Drummond et al., 2012) with a GTR substitution model and gamma distribution (GTR + G + I), an uncorrelated lognormal relaxed clock model, a tree prior with a Yule speciation model, and a random starting tree. We used three calibration points based on a dated molecular phylogeny sampling all Malpighiaceae genera (Davis et al., 2014): the most recent common ancestor (MRCA) of *Byrsonima* (mean = 10.0 Mya), *Blepharandra* + *Diacidia* (mean = 28.0 Mya), and *Pterandra* (mean = 33.0 Mya), using a normal prior for each node. A BEAST file was generated in BEAUTi v.1.8.2 (Drummond et al., 2012). Four independent runs of MCMC chains were run for 10 million generations, sampling trees every 1,000 generations. Output files were visualized in Tracer v.1.6 (Rambaut and Drummond, 2013) to assess convergence of the runs. We discarded the first 400 trees from each run as burn-in and combined the time tree files in LogCombiner v.1.8.2 (Drummond et al., 2012). The results were summarized in a maximum clade credibility tree using TreeAnnotator v.1.8.2 (Drummond et al., 2012). The chronogram was visualized and edited using FigTree v.1.3.1 (Rambaut, 2009).

CHARACTER SELECTION, CODING AND MORPHOLOGICAL ANALYSIS

Characters were scored mainly from herbarium samples from ALCB, CEPEC, CGMS, CNMT, COR, CPAP, DDMS, ESA, ESAL, FUEL, HB, HCF, HERBAM, HPAN, HRC, HRCB, GTO, HUCP, HUEFS, HEPH, HEUM, HUFSJ, HUFU, HUPG, HUTO, IAN, IBGE, INPA, IPA, MBM, NY, NX, P, R, RB, SP, SPF, SPSF, TANG, UB, UEC, UESC, UFG, UFMT, UFRN, UNOP, UPCB, and US herbaria (acronyms according to Thiers, continuously updated). Character coding followed the recommendations of Sereno, 2007 for morphological phylogenies. Primary homology hypotheses (De Pinna, 1991) were proposed for leaf, floral, and biogeography characters. A total of five characters were scored, and optimized on the majority-rule (50% values) consensus tree using Mesquite 2.73 (Nixon, 2002).

RESULTS

MOLECULAR PHYLOGENY

The combined plastid + nuclear matrix for 45 taxa includes 2,364 characters analyzed, of which 257 were variable and 299 parsimony-informative. The nuclear characters represent around 48% (1117 characters) of the dataset, a little more than 80% (204 characters) of the variable characters and about 90% (264 characters) of the parsimony-informative sites (see Table 2, for a summary of regions and matrices). Regions within the same genome are congruent according to the ILD test ($p = 0.01$, among psbA-trnH and trnL-F, and $p = 0.01$, between ITS and ETS), as well as plastid and nuclear datasets ($p = 0.01$).

All selected regions showed a low rate of parsimony-informative characters for at least nine of the 45 sampled taxa. As a result, we opted to remove those taxa from the combined datasets in order to test for a better phylogenetic signal, but keeping type specimens sampled for both subgenera of *Byrsonima* (subg. *Byrsonima* and subg. *Macrozeuma*) and sections of *B.* subg. *Byrsonima* (sect. *Eriolepis* and sect. *Sericolepis*).

The combined plastid + nuclear matrix for the 36 taxa dataset includes 2,364 characters analyzed, of which 255 were variable and 296 parsimony-informative. The nuclear characters represent around 48% (1117 characters) of the dataset, a little more than 80% (203 characters) of the variable characters and about 90% (262 characters) of the parsimony-informative sites. Regions within the same genome are congruent according to the ILD test ($p = 0.01$, among psbA-trnH and trnL-F, and $p = 0.01$, between ITS and ETS), as well as plastid and nuclear datasets ($p = 0.01$).

MAXIMUM PARSIMONY

Based on the plastid dataset of 45 taxa, the heuristic search found 1 tree ($CI = 0.5054$, $RI = 0.6738$) whose majority-rule (MC) consensus presents 5 poorly supported clades (MP BSP75%). Based on the nuclear dataset, MP analysis found 1 tree ($CI = 0.6745$, $RI = 0.6463$) whose MC presents 15 well supported clades. A total of 24 clades were recovered by the combined dataset in the MC with just 15 clades supported by both analyses.

Based on the plastid dataset of 36 taxa, the heuristic search found 1 tree ($CI = 0.5515$, $RI = 0.7004$) whose majority-rule (MC) consensus presents 3 poorly supported clades (MP BSP75%). Based on the nuclear dataset, MP analysis found 1 tree ($CI = 0.7032$, $RI = 0.6930$) whose MC presents 13 well supported clades. A total of 24 clades were recovered by both datasets in the MC with just 13 clades supported by both analyses.

BAYESIAN INFERENCE

Based on the plastid dataset of 45 taxa, five clades present $PP > 50\%$, and none of them is well supported ($PP > 95\%$). Based on the nuclear dataset, 31 clades present $PP > 50\%$ and 15 well supported clades were recovered. A total of 31 clades present $PP > 50\%$ and 25 clades were well supported based on both datasets.

Based on the plastid dataset of 36 taxa, five clades present $PP = 50\%$, and one of them is well supported ($PP = 95\%$; Fig. 2). Based on the nuclear dataset, 31 clades present $PP > 50\%$ and 15 well supported clades were recovered. A total of 31 clades present $PP > 50\%$ and 25 clades were well supported based on both datasets.

PHYLOGENETICS AND DIVERGENCE TIMES OF *BYRSONIMA*

Considering only well supported clades (i.e. $BS \geq 75\%$ and $PP \geq 95\%$), the topologies produced by MP and BI analyses based on the matrix combining plastid and nuclear datasets are mostly congruent and provide higher support for more clades than results based on separate plastid or nuclear datasets. The BI tree presents all clades with $PP > 70\%$ and $PP > 95\%$ (Fig. 2). Only three clades being recovered unresolved in the majority-rule consensus of parsimony and two unresolved clades in the majority-rule consensus of the Bayesian analysis. Estimates of divergence times points that the ancestral *Byrsonima* emerged ca. 33 Mya., most likely on a savanna phytophysiognomy

in the Neotropics. All its main lineages were already established by 20 Mya. and all of them suffered radiation events from 10 Mya. to the late Holocene.

The monophyly of *Byrsonima* was tested and corroborated, with its species emerging into six major lineages, herein named: *B. triopterifolia* clade, *B. microphylla* clade, *B. melanocarpa* clade, *B. coccobifolia* clade, *B. crassifolia* clade, and *B. spicata* clade. *Byrsonima triopterifolia* clade comprises two pink-flowered species endemic to rocky outcrops in highlands of Midwest and Northeastern Brazil. *Byrsonima microphylla* clade comprises a single pink-flowered species endemic to rocky outcrops from Northeastern Brazil. *Byrsonima melanocarpa* clade comprises four white to pink-flowered species commonly found on savanna habitats in the Amazon domain. *Byrsonima coccobifolia* clade comprises seven white to pink-flowered species mostly endemic to the Espinhaço Mountain range. *Byrsonima crassifolia* clade comprises eight species widespread in Brazilian Cerrado and especially diverse in the state of Goiás, where all species co-occur. Finally, *Byrsonima spicata* clade comprises 10 species with a disjunctive distribution through the Amazon and the Atlantic Forests.

MORPHOLOGICAL ANALYSIS

We selected five different characters to optimize in the consensus tree of the Bayesian analysis. Four of them are morphological and a single one is biogeographic, all of them coded as binary or multistate (Table 5). From all those characters, three of them emerged as synapomorphies for *Byrsonima* subg. *Byrsonima*: color of petals, shape and length of connectives in relation to the locules, and presence of indumenta on anthers (Fig. 5, 6 and 7).

DISCUSSION

Our results recovered *Byrsonima* as a monophyletic group with strong support as was observed in previous studies and as sister group of *Blepharandra* and *Diacidia* (Cameron et al., 2001; Davis et al., 2001, Davis et al., 2002; Davis & Anderson, 2010), and as observed in the MP (Fig. 1). *Byrsonima* is traditionally divided in two subgenera, based on petal color and anther morphology. In *B. subg. Byrsonima* the connective does not surpass the anther locules or surpass only in $\frac{1}{4}$ of its size, while in *B. subg. Macrozeugma* the connective surpass the locules in more than $\frac{1}{4}$ of its size (Niedenzu 1897, 1901). In general, we can separate these subgenera based on petal color. *Byrsonima* subg. *Byrsonima* has the posterior petal yellow, whereas *B. subg. Macrozeugma* bears a

white or pink posterior petal. The connectives not surpassing the anther locules and yellow petals were recovered as synapomorphies for *B.* subg. *Byrsonima*. On the other hand, connectives surpassing the size of locules and white to pink petals are plesiomorphic. Our results disagree with those previously pointed by Davis and Anderson (2010), due to significant increase in species sampling.

An early diverging clade comprising *B. rigida* and *B. triopterifolia* is sister to the remaining species of *Byrsonima*. Those species are distinguished by pink or white corollas with glabrous bracts, bracteoles and anthers, and connectives not exceeding the anther locules. *Byrsonima melanocarpa* was recovered as sister to *B. umbellata*, sharing several morphological characters, but most remarkably, the globose connective surpassing the thecae.

The *B. coccobifolia* clade is composed by *B. coccobifolia*, *B. correifolia*, *B. gardneriana* and *B. vacciniifolia*. These closely related species possess pink or white petals, connectives surpassing the thecae in more than $\frac{1}{4}$ of their length. Nevertheless, *B. morii* and *B. cipoensis* diverge from the remaining species in possessing yellow posterior petals + white to pink lateral and posterior petals, and the connectives not surpassing the anther locules in more than $\frac{1}{4}$ of their length. The only characteristic shared by all species is the glabrous ovary, but it is a homoplastic condition, because other species showed this condition.

The *B. spicata* clade includes *B. stipulacea*, *B. lanulosa*, *B. crispa* and *B. spicata*. These species are commonly found in different biomes throughout Brazil (Mamede et al., 2015), with *B. stipulacea*, *B. crispa* and *B. spicata* extending to the Guyana Highlands (Anderson, 1981). It was expected *B. spicata* close related with *B. chrysophylla* and *B. laxiflora*, sharing a unique set of characters, such as posterior petal bearing two or more glands at apex of the claw or on the base of the limb and a leaf architecture with fine parallel secondary veins. According to Anderson (1982). But here its emerge as homoplastics conditions.

Furthermore, *B. stipulacea* was primarily described by Jussieu (1840), but was later transferred to *Alcoceratothrix* by Niedenzu (1901), based solely on the large unusual deciduous stipules. Based on a profound study of *Byrsonima* and on the comparison to closely related species, Anderson (1982) reestablished the name *B. stipulacea* and considered this character to be exclusive to it. Our results support the decision made by Anderson (1982), recovering *B. stipulacea* nested within Core *Byrsonima*, and closely related to *B. crispa*, *B. lanulosa* and *B. spicata*. However, no morphological

synapomorphies could be indicated for this clade based on the present sampling. The inclusion of species morphologically related to *B. stipulacea*, such as *B. fanshawei* and *B. duckeana*, in future studies may help to understand this peculiar relation.

Nevertheless, we recovered *B. poeppigiana* sister to *B. affinis* and *B. basiloba*. The first is very distinct morphologic from *B. affinis* and *B. basiloba*, very similar species being native to the Brazilian Cerrado, and part of the *B. sect. Eriolepis* (fig. 4).

The *B. crassifolia* clade includes numerous species placed in *Byrsonima* sect. *Eriolepis*. This section was circumscribed by: connectives not surpassing the anther locules (when surpassing, no more than $\frac{1}{4}$ of their length); usually deciduous, long and acuminate bracts, adaxially glabrous, abaxially lanate-tomentose; bracteoles similar to the bracts (only smaller); coriaceous to sub-coriaceous leaves; and drupes smooth or minutely verrucose (Niedenzu, 1901). The monophyly of this section was not supported by the 45 taxa dataset, due to low parsimony informative sites for the chosen genetic markers. However, when considering the 36 taxa dataset, both sections of *B. subg. Byrsonima* are recovered as monophyletic (if *B. affinis* and *B. basiloba* are transferred to *B. sect. Sericolepis*). All species in the *B. crassifolia* clade possess yellow flowers, hairy anthers and thecae with rounded apex. Nevertheless, these characters are found separately in other species outside the clade. Thus, they could be considered as homoplastic synapomorphies for this clade. Further sampling and genetic markers are needed to confirm the monophyly of *B. sect. Eriolepis*.

FINAL REMARKS

Our study is the first to test and validate the monophyly of *Byrsonima* and part of its infrageneric ranks by sampling about one third of its species. The monophyly of *B. subg. Byrsonima* was corroborated by molecular and morphological synapomorphies (e.g. yellow flowers and hairy anthers), as well as the paraphyly of its sections. Some morphological characters traditionally used to delimit infrageneric ranks were shown to be highly homoplastic (e.g. leaf indumenta and petal color). The ancestral of *Byrsonima* seems to have arisen about 33 Mya., most likely in ancient Neotropical savannas, while its main lineages begun diversifying ca. 10 Mya. As abovementioned, an increased sampling and further molecular markers are still needed for a better understanding of the morphological evolution and diversification of this genus.

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Table 1 - Voucher and GenBank accession numbers information of the species used in the study.

Species	Locality	Voucher/Herbarium	Accession Numbers (GenBank)			trnL-F
			ITS	ETS	psbA-TrnH	
<i>Acmanthera latifolia</i>	Brazil. Amazonas: Barcelos	Amorim 8575 (RB)	-	KR088167	-	No # GenBank
<i>Acmanthera parviflora</i>	Brazil. Amazonas: Barcelos	Amorim 8622 (RB)	-	No # GenBank	-	No # GenBank
<i>Blepharandra sp1</i>	Brazil. Amazonas: Barcelos	Amorim 8608 (RB)	KR087552	-	-	No # GenBank
<i>Blepharandra sp2</i>	Brazil; Amazonas: Barcelos	Amorim 8618 (RB)	KR087553	KR088210	-	No # GenBank
<i>Byrsonima affinis</i>	Brazil. Mato Grosso: Araguainha	Francener 1161 (SP)	KR087509	KR088168	KR108965	No # GenBank
<i>Byrsonima basiloba</i>	Brazil. Distrito Federal: Brasília	Francener 1132 (SP)	KR087510	KR088169	KR108966	No # GenBank
<i>Byrsonima brachybotria</i>	Brazil. Paraná: Vila Velha	Hall 818 (SP)	KR087511	KR088170	KR108967	No # GenBank
<i>Byrsonima chrysophylla</i>	Brazil. Pará: Altamira	Francener 1324 (SP)	KR087512	KR088171	KR108968	No # GenBank
<i>Byrsonima cipoensis</i>	Brazil. Minas Gerais: Santana do Riacho	Rapini 1600 (HUEFS)	KR087513	KR088172	-	No # GenBank
<i>Byrsonima clausseniana</i>	Brazil. Goiás: Aparecida de Goiânia	Francener 1207 (SP)	KR087518	KR088177	KR108972	No # GenBank
<i>Byrsonima clausseniana</i>	Brazil. Minas Gerais: Santana do Pirapama	Silva 574 (HUEFS)	-	KR088197	KR108987	No # GenBank
<i>Byrsonima coccolobifolia</i>	Brazil. Mato Grosso: Araguainha	Francener 1424 (SP)	KR087514	KR088173	KR108969	No # GenBank
<i>Byrsonima coniophylla</i>	Brazil. Amazonas: Barcelos	Amorim 8609 (RB)	KR087515	KR088174	-	No # GenBank
<i>Byrsonima correifolia</i>	Brazil. Maranhão: Brejo	Silva 192 (UFRN)	KR087516	KR088175	KR108970	No # GenBank
<i>Byrsonima crassifolia</i>	Brazil. Amapá: Serra do Navio	Hall 1024 (UFRN)	KR087517	KR088176	KR108971	No # GenBank
<i>Byrsonima crispa</i>	Brazil. Mato Grosso: Carlinda	Francener 1329 (SP)	KR087519	KR088178	No # GenBank	No # GenBank
<i>Byrsonima cydoniifolia</i>	Brazil. Mato Grosso do Sul: Rio Verde	Francener 1183 (SP)	KR087520	KR088179	KR108973	No # GenBank
<i>Byrsonima dealbata</i>	Brazil. Bahia: Rio de Contas	Francener 1397 (SP)	KR087521	KR088180	KR108974	No # GenBank
<i>Byrsonima gardneriana</i>	Brazil. Rio Grande do Norte: Natal	Almeida s.n. (HUEFS)	KR087522	KR088181	KR108975	No # GenBank
<i>Byrsonima guilleminiana</i>	Brazil. Distrito Federal: Brasília	Francener 1129 (SP)	KR087523	KR088182	KR108976	No # GenBank
<i>Byrsonima intermedia</i>	Brazil. Goiás: Mineiros	Francener 1144 (SP)	No # GenBank	KR088183	KR108977	No # GenBank
<i>Byrsonima jpurensis</i>	Brazil. Amazonas: Barcelos	Amorim 8599 (RB)	-	KR088184	-	No # GenBank
<i>Byrsonima lanulosa</i>	Brazil. Rondônia: Vilhena	Francener 1352 (SP)	KR087524	KR088185	KR108978	No # GenBank

Table 1 – Continuation...

Species	Locality	Voucher/Herbarium	Accession Numbers (GenBank)			
			ITS	ETS	psbA-TrnH	trnL-F
<i>Brysonima laxiflora</i>	Brazil. Mato Grosso do Sul: Costa Rica	Francener 1201 (SP)	KR087525	KR088186	KR108979	No # GenBank
<i>Brysonima linearifolia</i>	Brazil. Goiás: Cristalina	Almeida s.n. (HUEFS)	KR087526	KR088187	KR108980	No # GenBank
<i>Brysonima linguifera</i>	Brazil. Rondônia: Pimenta Bueno	Francener 1351 (SP)	KR087527	KR088188	KR108981	No # GenBank
<i>Brysonima macrophylla</i>	Brazil. Minas Gerais: Diamantina	Silva 515 (HUEFS)	KR087528	KR088189	KR108982	No # GenBank
<i>Brysonima melanocarpa</i>	Brazil. Rondônia: Porto Velho	Pereira-Silva 15986 (SP)	KR087529	KR088190	No # GenBank	No # GenBank
<i>Brysonima microphylla</i>	Brazil. Bahia: Salvador	Hall 959 (SP)	KR087530	KR088191	No # GenBank	No # GenBank
<i>Brysonima morii</i>	Brazil. Bahia: Palmeiras	Almeida-Silva 268 (HUEFS)	KR087531	KR088192	KR108983	No # GenBank
<i>Brysonima pachyphylla</i>	Brazil. Distrito Federal: Gama	Gomes 56 (SP)	KR087532	-	No # GenBank	No # GenBank
<i>Brysonima pachyphylla</i>	Brazil. Goiás: Alto Paraíso de Goiás	Almeida s.n. (HUEFS)	KR087533	KR088193	KR108984	No # GenBank
<i>Brysonima poeppigiana</i>	Brazil. Mato Grosso: Terra Nova do Norte	Francener 1325 (SP)	KR087534	KR088194	No # GenBank	No # GenBank
<i>Brysonima psilandra</i>	Brazil. Paraná: Vila Velha	Hall 817 (SP)	KR087535	KR088195	KR108985	No # GenBank
<i>Brysonima punctulata</i>	Brazil. Rondônia: Jaci-Paraná	Pereira-Silva 15006 (SP)	No # GenBank	-	No # GenBank	No # GenBank
<i>Brysonima rigida</i>	Brazil. Mato Grosso: Nova Mutum	Francener 1217 (SP)	KR087536	KR088196	No # GenBank	No # GenBank
<i>Brysonima sericea</i>	Brazil. Bahia: Rio de Contas	Francener 1395 (SP)	KR087539	KR088198	KR108988	No # GenBank
<i>Brysonima sp. Emas</i>	Brazil. Goiás: Mineiros	Francener 1146 (SP)	KR087541	KR088200	KR108990	No # GenBank
<i>Brysonima spicata</i>	Brazil. Mato Grosso: Tabaporã	Santos 3165 (SP)	-	No # GenBank	No # GenBank	No # GenBank
<i>Brysonima stannardii</i>	Brazil. Minas Gerais: Jequitinhonha	Almeida s.n. (HUEFS)	KR087542	KR088201	KR108991	No # GenBank
<i>Brysonima stipulacea</i>	Brazil. Espírito Santo: Conceição da Barra	Almeida 536 (SP)	KR087543	KR088202	-	No # GenBank
<i>Brysonima subterranea</i>	Brazil. Mato Grosso do Sul: Costa Rica	Francener 1195 (SP)	KR087544	KR088203	KR108992	No # GenBank
<i>Brysonima triopterifolia</i>	Brazil. Bahia: Piatã	Francener 1406 (SP)	KR087545	KR088204	No # GenBank	No # GenBank
<i>Brysonima umbellata</i>	Brazil. Mato Grosso: Araguainha	Francener 1148 (SP)	KR087546	-	No # GenBank	No # GenBank
<i>Brysonima vaccinifolia</i>	Brazil. Minas Gerais: Jequitinhonha	Almeida s.n. (HUEFS)	KR087547	KR088205	KR108993	No # GenBank
<i>Brysonima variabilis</i>	Brazil. Minas Gerais: Ouro Branco	Francener 1380 (SP)	KR087548	KR088206	KR108994	No # GenBank

Table 1 – Continuation...

Species	Locality	Voucher/Herbarium	Accession Numbers (GenBank)			
			ITS	ETS	psbA-TrnH	trnL-F
<i>Byrsonima viminifolia</i>	Brazil. Goiás: Teresina de Goiás	Francener 1259 (SP)	KR087551	KR088209	KR108996	No # GenBank
<i>Diacidia aracaensis</i>	Brazil. Amazonas: Barcelos	Amorim 8623 (RB)	No # GenBank	KR088211	-	No # GenBank
<i>Pterandra hatschbachii</i>	Brazil. Mato Grosso: Araguainha	Francener 1162 (SP)	KR087555	KR088213	No # GenBank	No # GenBank
<i>Pterandra pyroidea</i>	Brazil. Goiás: Pirenópolis	Francener 1139 (SP)	KR087556	KR088214	No # GenBank	No # GenBank

Table 2. Regions of the plastid and nuclear genome tested for species of *Byrsonima*, its success in amplification (Ampl.) and sequencing (Seq.). Quantitative traits evaluated for choice of markers: L = length of the aligned sequences; N = number of species.

Regions	Reference	Ampl.	Seq.	L(pb)	BFM (best fitting model)	N
Nuclear						
ETS	Baldwin and Markos, 1998	yes	yes	440	GTR + G	42
ITS	White et al., 1990; Sun et al., 1994	yes	yes	677	GTR + I + G	44
phyC	Davis et al., 2002	no	no	-	-	-
Combined nuclear datasets	-	-	-	1117		45
Plastidial						
ndhF	Davis et al., 2001	yes	no	-	-	-
psbA-trnH	Shaw et al., 2007	yes	yes	930	F81+G	40
trnL-F	Taberlet et al., 1991; Shaw et al., 2005	yes	yes	317	HKY	24
Combined plastid datasets	-	-	-	1247	-	45
Combined Nuclear + Plastid datasets	-	-	-	2364	-	45

Table 3. Character number, and parsimony indexes of individual and combined molecular datasets (45 taxa).

	Plastid dataset	Nuclear dataset	Combined Plastid + Nuclear datasets
Matrix length (bp)	1247	1117	2364
Analyzed characters	1247	1117	2364
Constant characters	1159	649	1808
Variable characters	53	204	257
Parsimony-informative characters	35	264	299
Consistency index	0.5054	0.6745	0.6569
Retention index	0.3285	0.6738	0.6463

Table 4. Character number, and parsimony indexes of individual and combined molecular datasets (36 taxa).

	Plastid dataset	Nuclear dataset	Combined Plastid + Nuclear datasets
Matrix length (bp)	1247	1117	2364
Analyzed characters	1247	1117	2364
Constant characters	1161	652	1813
Variable characters	52	203	255
Parsimony-informative characters	34	262	296
Consistency index	0.5515	0.7032	0.7020
Retention index	0.3621	0.7004	0.6930

Table 5. List of selected characters for optimization using ACCTRAN on Mesquite Software: **character 1)** flower, color: (0) pink or white, (1) yellow, (2) yellow and white/pink; **character 2)** leave, indumenta: (0) tomentose/velutine, (1) sericous/glabrous; **character 3)** connective, lenght: (0) exceeding more than 1/4 lenght of the locules, (1) equal or exceeding less than 1/4 the length of the locules; **character 4)** anther, indumenta (0) pilose, (1) glabrous; **character 5)** domain: (0) Amazon Forest, (1) Cerrado, (2) Caatinga, (3) Atlantic Forest

Character	1	2	3	4	5
<i>Byrsonima affinis</i>	1	0	1	0	1
<i>Byrsonima basiloba</i>	1	0	1	0	1
<i>Byrsonima chrysophylla</i>	1	1	1	0	0/1/3
<i>Byrsonima cipoensis</i>	2	0	1	1	1
<i>Byrsonima clauseniana</i>	1	0	1	0	1
<i>Byrsonima cocclobifolia</i>	0	1	0	0	1
<i>Byrsonima coniophylla</i>	0	1	0/1	1	0
<i>Byrsonima correifolia</i>	0	0	0	0	1/2
<i>Byrsonima crassifolia</i>	1	0	1	0	1
<i>Byrsonima crispa</i>	1	1	1	0	0/3
<i>Byrsonima cydoniifolia</i>	1	1	1	0	1
<i>Byrsonima gardneriana</i>	0	1	0	0	1/2/3
<i>Byrsonima guilleminiana</i>	1	1	1	0/1	1
<i>Byrsonima lanulosa</i>	1	1	1	0/1	1
<i>Byrsonima laxiflora</i>	1	1	1	0	1/3
<i>Byrsonima linearifolia</i>	1	0	1	0	1
<i>Byrsonima linguifera</i>	1	1	1	0	0
<i>Byrsonima macrophylla</i>	0	0	0/1	1	1
<i>Byrsonima melanocarpa</i>	0	1	0	1	0
<i>Byrsonima microphylla</i>	0	1	1	1	1
<i>Byrsonima morii</i>	2	1	0	0/1	1
<i>Byrsonima pachyphylla</i>	1	0	1	0	1
<i>Byrsonima poeppigiana</i>	1	0	1	0	0
<i>Byrsonima punctulata</i>	0	0/1	0	1	0
<i>Byrsonima rigida</i>	0	1	1	1	1
<i>Byrsonima spicata</i>	1	1	1	0	0
<i>Byrsonima stipulacea</i>	1	0	1	0	0/3
<i>Byrsonima subterranea</i>	1	0	1	0	1
<i>Byrsonima termitaria</i>	1	0	1	0	1
<i>Byrsonima tripterifolia</i>	0	1	1	1	1
<i>Byrsonima umbellata</i>	0	1	0	1	1
<i>Byrsonima vacciniifolia</i>	0	1	0	0	1/2
<i>Blepharandra</i> sp.	0	1	1	0	0
<i>Diacidia aracaensis</i>	1	0	1	1	0
<i>Pterandra hatschbachii</i>	0	0	1	1	1
<i>Pterandra pyroidea</i>	0	0	1	1	1

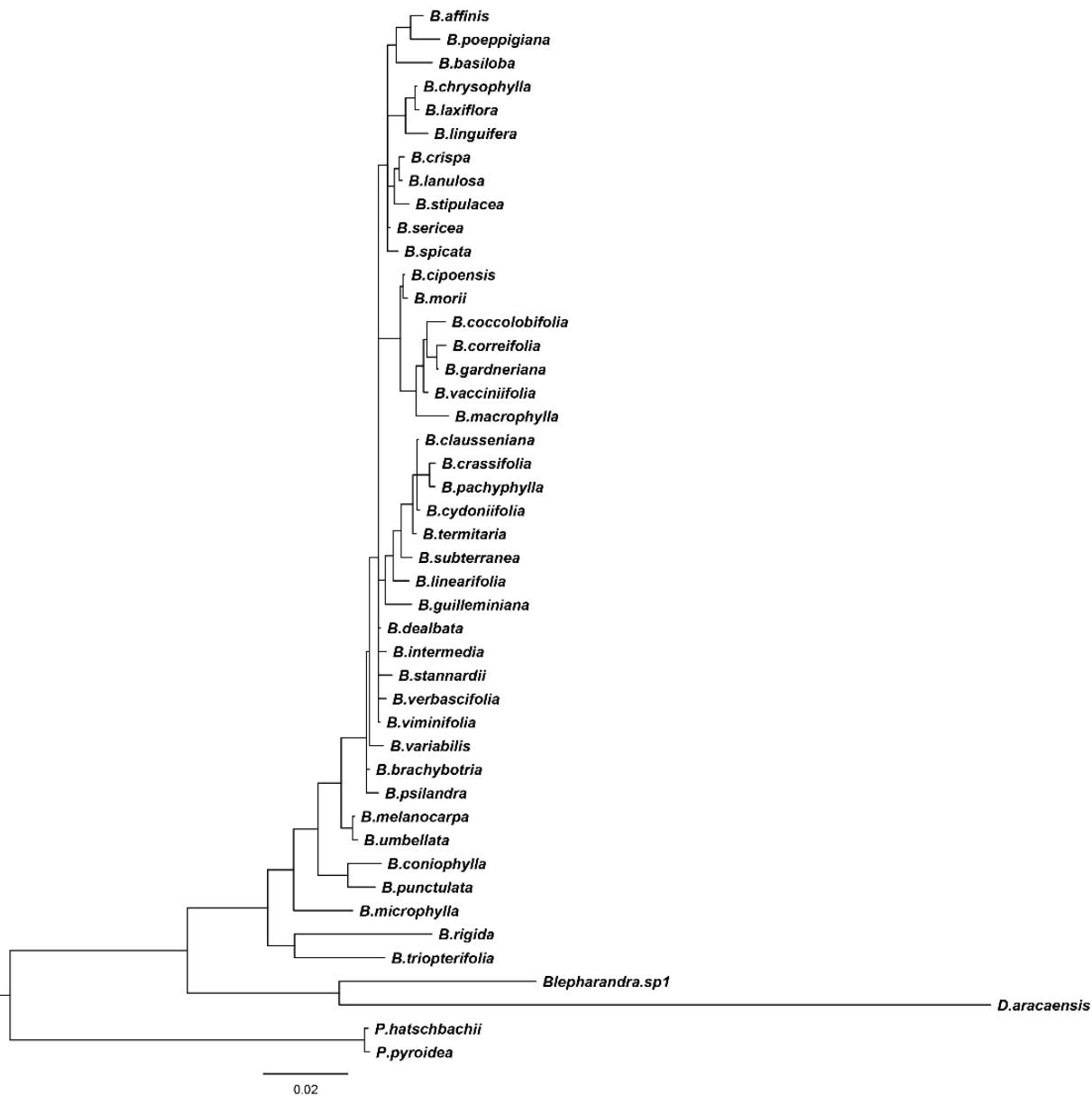


Figure 1 –Bayesian analysis of *Byrsonima* containing branch lengths, using a dataset of 45 terminals based on ETS, ITS, psbA-trnH, and trnL-F regions.

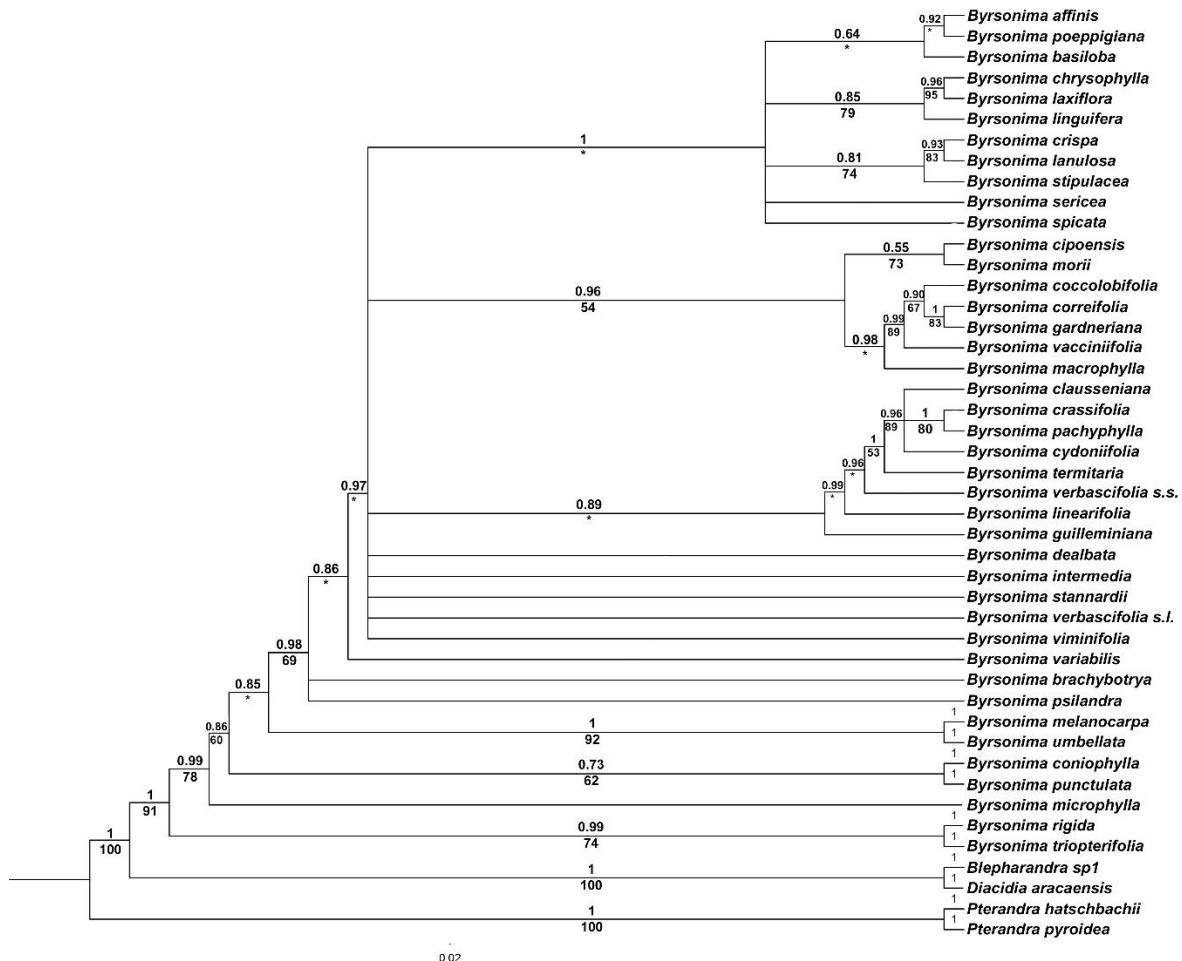


Figure 2 – Cladogram of *Byrsonima* recovered for a dataset of 45 terminals, based on ETS, ITS, psbA-trnH, and trnL-F region: value above the branch = posterior probability of the Bayesian analysis, value below the branch = bootstrap value of the Maximum Parsimony analysis.



Figure 3 – Bayesian cladogram of *Byrsonima* containing branch lengths. Recovered using a dataset of 36 terminals based on ETS, ITS, psbA-trnH, and trnL-F region.

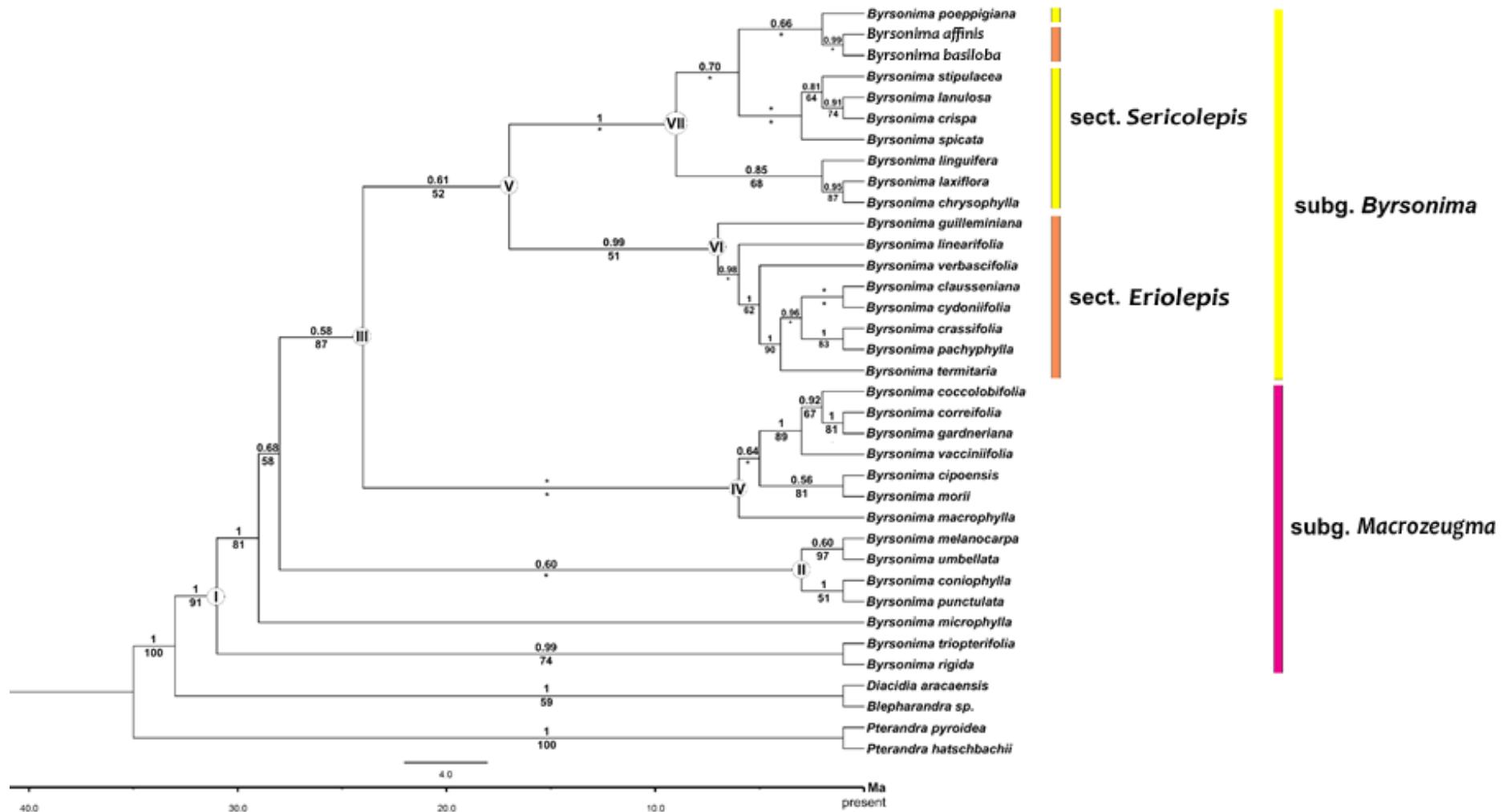


Figure 4 – Dated and calibrated cladogram of *Byrsonima*, using the dataset of 36 terminals: value above the branch = posterior probability of the bayesian analysis: value below the branch = bootstrap value of the maximum parsimony analysis. The *Macrozeugma* subgenus is paraphyletic, with its species in a basal grade. On the other hand, the *Byrsonima* subgenus is monophyletic, but its sections are paraphyletic

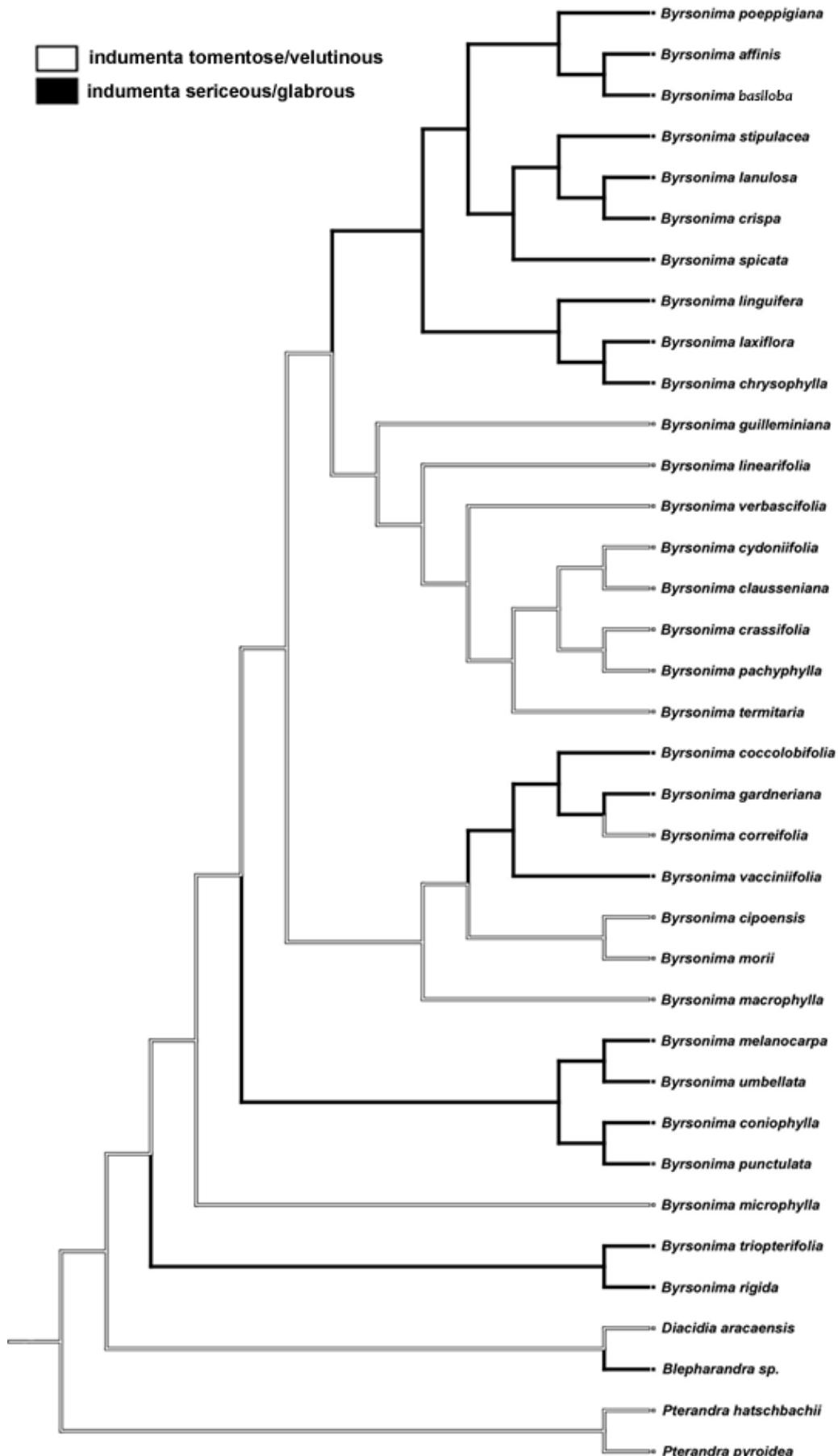


Figure 5 – Mapping of characters using ACCTRAN (topology recovered with the genus dataset of 36 terminals): leaf indumenta.

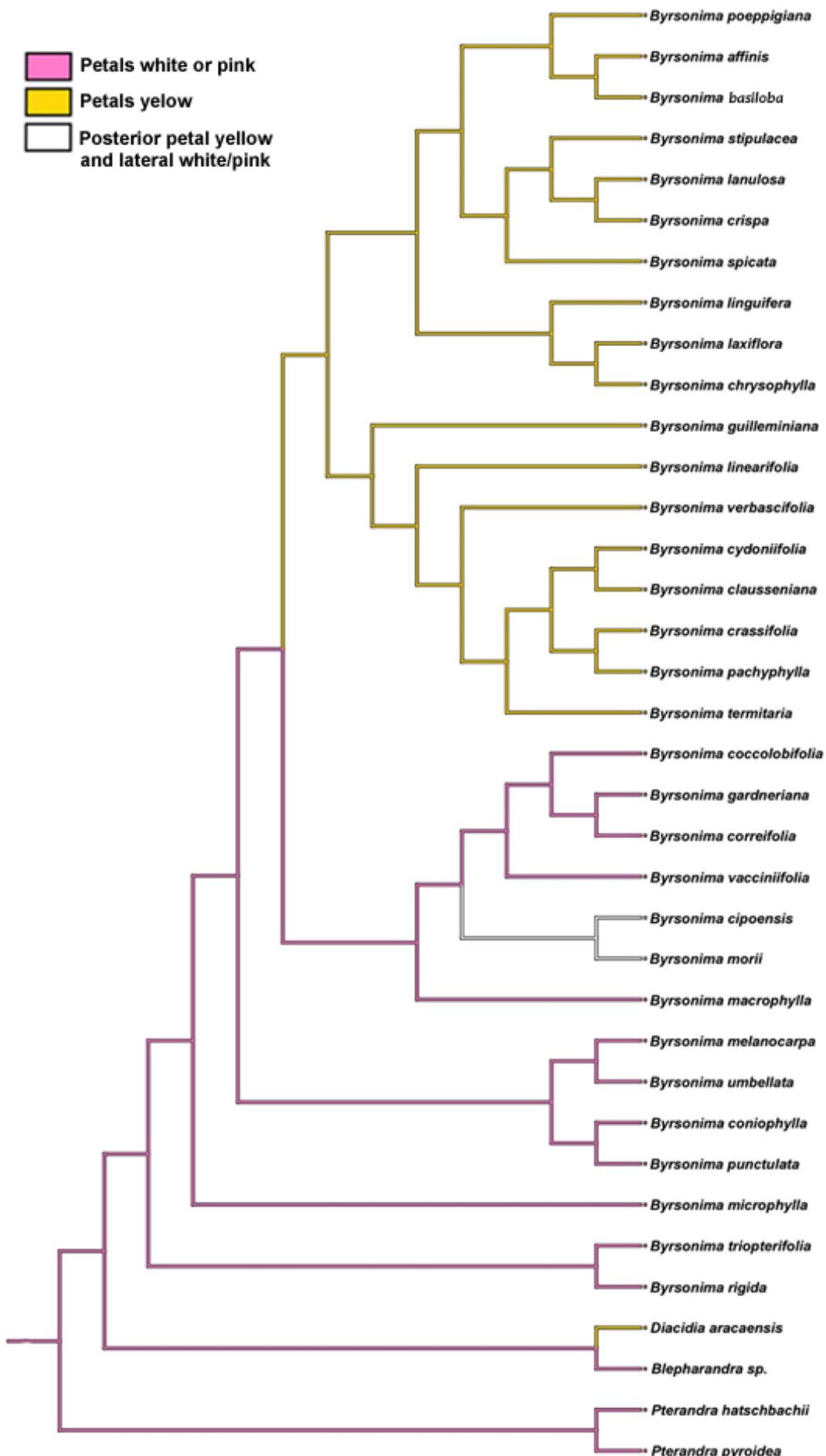


Figure 6 – Mapping of characters using ACCTRAN (topology recovered with the dataset of 36 terminals): color of the petals during anthesis.

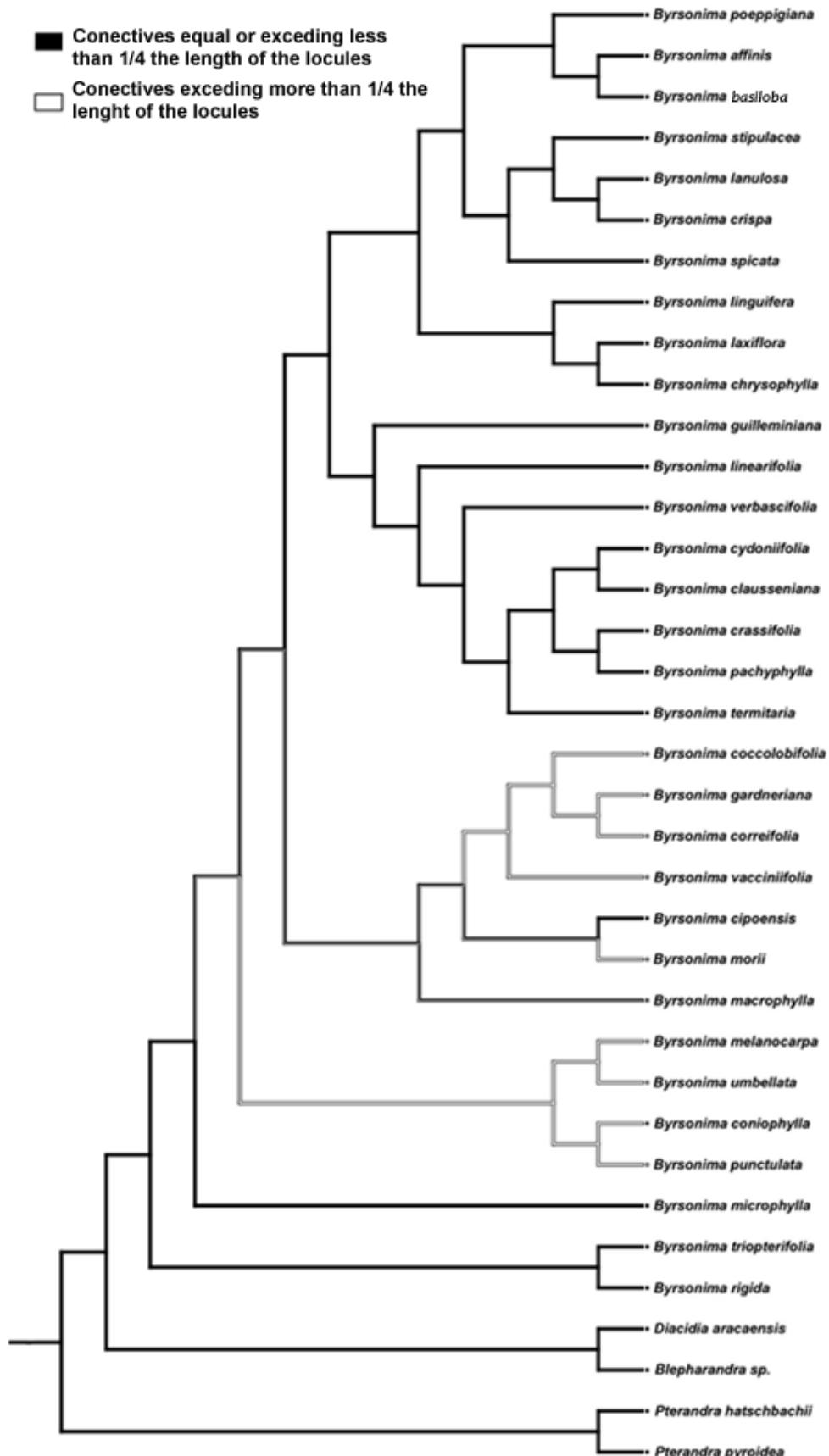


Figure 7 – Mapping of characters using ACCTRAN (topology recovered with the dataset of 36 terminals): relation between the length of the connective and the theca in the stamens.

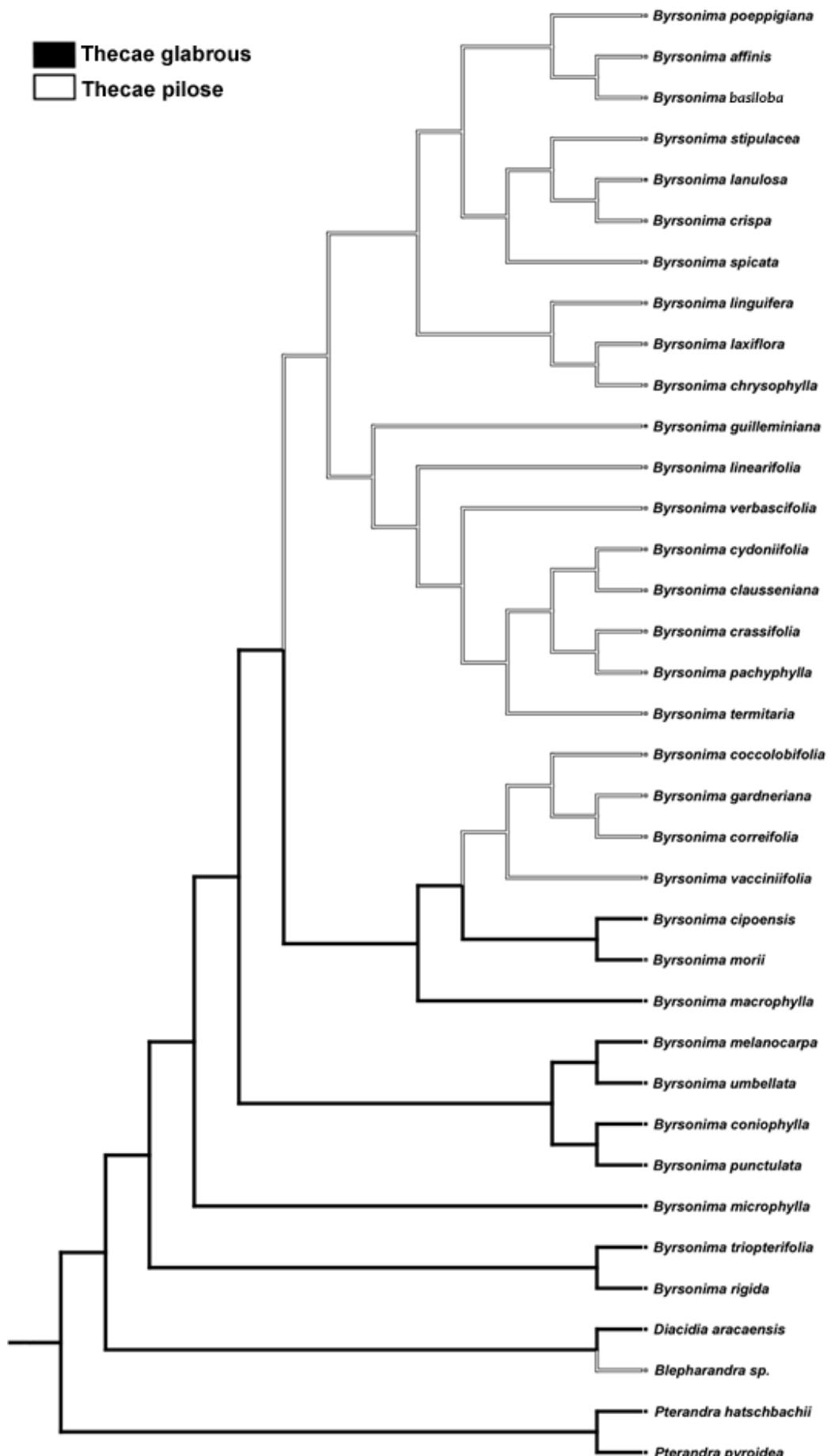


Figure 8 – Mapping of characters using ACCTRAN (topology recovered with the dataset of 36 terminals): theca indumenta.

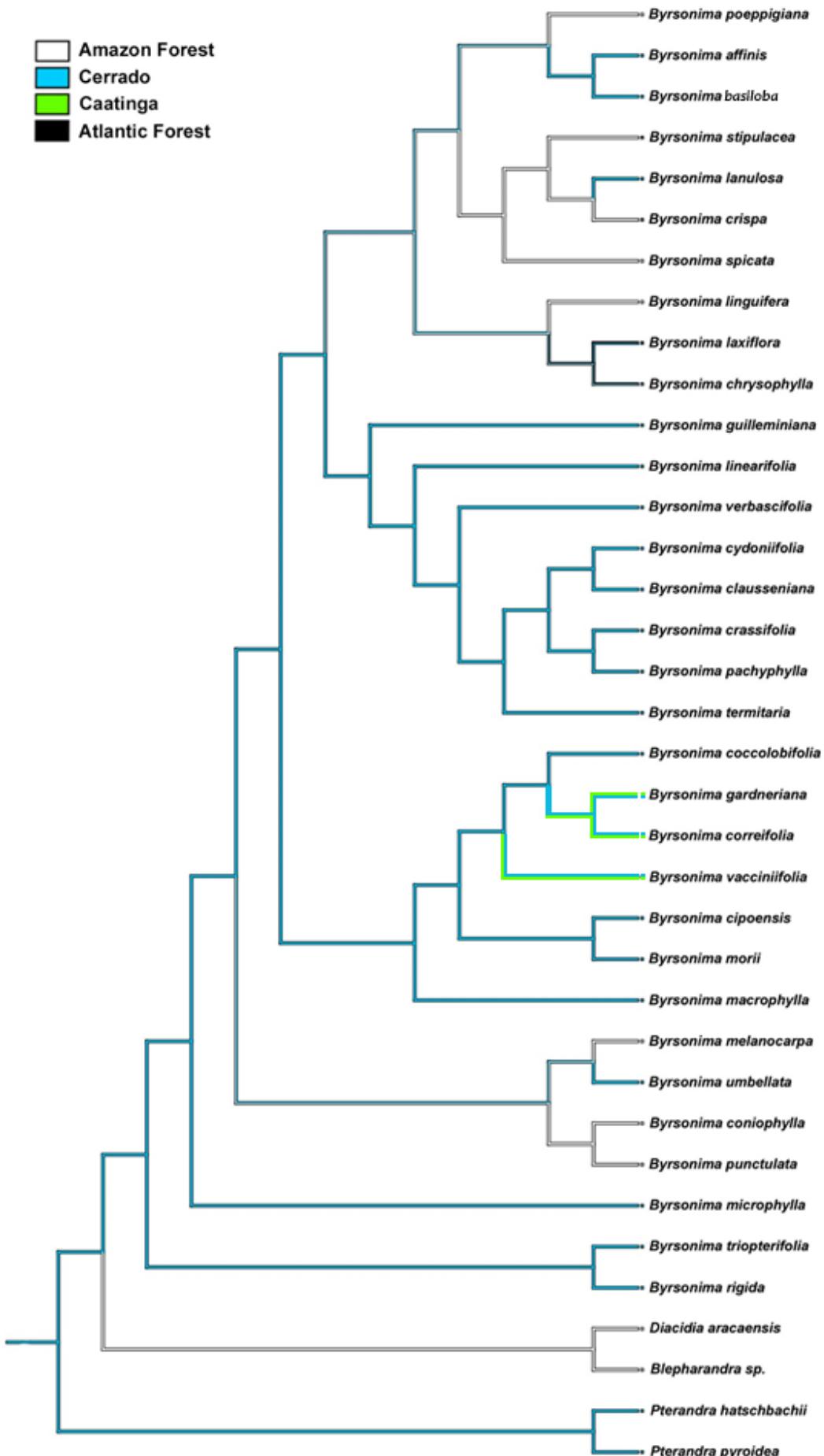


Figure 9 – Mapping of characters using ACCTRAN (topology recovered with the dataset of 36 terminals): Neotropical phytogeographic dominions.

Capítulo 2

Revisão taxonômica do clado *Byrsonima crassifolia* e lectotipificações em *Byrsonima* sect. *Eriolepis* (Malpighiaceae)

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Taxonomic revision of the *Byrsonima crassifolia* clade and lectotypifications in *Byrsonima* sect. *Eriolepis* (Malpighiaceae)

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Abstract

We present a taxonomic revision to the species belonging to the *Byrsonima crassifolia* clade, a group mainly restricted to the Brazilian Cerrado, with eight species were described: *B. clauseniana* A. Juss., *B. crassifolia* (L.) Kunth, *B. cydoniifolia* A. Juss., *B. guilleminiana* A. Juss., *B. linearifolia* A. Juss., *B. pachyphylla* A. Juss., and *B. verbascifolia* (L.) DC., including a new species endemic of Brazil.

Keywords: Cerrado, Malpighiales, Neotropics, Taxonomy

Resumo

Apresentamos uma revisão taxonômica das espécies do clado *Byrsonima crassifolia*, um grupo restrito majoritariamente ao Cerrado brasileiro, com oito espécies são descritas: *B. clauseniana* A. Juss., *B. crassifolia* (L.) Kunth, *B. cydoniifolia* A. Juss., *B. guilleminiana* A. Juss., *B. linearifolia* A. Juss., *B. pachyphylla* A. Juss. e *B. verbascifolia* (L.) DC., incluindo uma nova espécie endêmica do Brasil.

Palavras-chave: Cerrado, Malpighiales, Neotrópico, Taxonomia

Introduction

Byrsonima Rich. ex Kunth (1822: 147) is the second largest genus in Malpighiaceae, comprising ca. 135 species endemic to the Neotropical region (Anderson 1981, Anderson *et al.* 2006). It is easily recognized by its shrubby to tree habit, intrapetiolar stipules, eglandular leaves, bracts and bracteoles, elongated thyrsi of 1-4-flowered cincinni, slender styles subulate at apex, minute stigmas, and fleshy, indehiscent

drupes, with 3-locular pyrenes (Anderson 1981, Mamede 1987). The first infrageneric classification for the genus was proposed by Niedenzu (1901), including two subgenera, and several sections, subsections, series and subseries. Most infrageneric categories were delimited based on type of leaf indument, color of petals, size of connectives, and locule morphology (Niedenzu 1901). *Byrsonima* subg. *Brachyzeuma* (i.e. *Byrsonima* subg. *Byrsonima*) comprises about 55 yellow flowered (at least the posterior petal) species mostly distributed throughout neotropical savannas (Cerrado). The subgenus is divided into two sections, mostly based on the bracts and leaf blade indument (Niedenzu 1901). *Byrsonima* subg. *Byrsonima* sect. *Eriolepis* comprises ca. 25 species usually covered by tomentose to velutinous indument, while *Byrsonima* subg. *Byrsonima* sect. *Sericolepis* comprises ca. 30 species covered by sericeous to glabrous indument (Cuatrecasas, 1958, Niedenzu 1901, 1928).

In the first molecular phylogeny of *Byrsonima* (Chapter 1), both subgenera were recovered as paraphyletic, as well as the sections of subgenus *Byrsonima*. Among the 12 sampled species for *B.* section *Eriolepis*, only eight were recovered in a well supported clade comprising *Byrsonima crassifolia* (1822: 149), the type of this section. The remaining species from *Byrsonima* section *Eriolepis* were placed in a basal polity in Core *Byrsonima*. Since additional genetic markers are included in the molecular phylogeny, it is the authors' opinion that those taxa might fall within a *B. crassifolia* clade s.l., turning this section monophyletic (Francener *et al.*, Chapter 1).

As a first step towards a revisionary treatment for *B.* section *Eriolepis*, we present a taxonomic revision of all names included within the *Byrsonima crassifolia* clade, along with lectotypifications of the remaining names from the section.

Material and Methods

Fieldwork was carried out in order to collect fertile specimens of *Byrsonima* sect. *Eriolepis* in different regions of Brazilian Cerrado (Neotropical Savanna). All collections were dried according to standard botanical techniques (Bridson & Forman 1992), and readily incorporated to the Malpighiaceae collection at SP herbarium. Morphological descriptions and phenology of the studied species were based on specimens of many herbaria (ALCB, CEPEC, CGMS, CNMT, COR, CPAP, DDMS, ESA, ESAL, FUEL, HB, HCF, HERBAM, HPAN, HRC, HRCB, GTO, HUCP, HUEFS, HEPH, HEUM, HUFSJ, HUFU, HUPG, HUTO, IAN, IBGE, INPA, IPA, MBM, NY, NX, P, R, RB, SP, SPF, SPSF, TANG, UB, UEC, UESC, UFG, UFMT, UFRN, UNOP, UPCB, and US),

type collections, and spirit collections (herbaria acronyms according to Thiers, continuously updated). The indument terminology follows Anderson (1981) and Niedenzu (1928), structure shapes follows Radford et al. (1974), Harris and Harris (1994) and Beentje (2012), the inflorescence terminology and morphology follows Anderson (1981), and fruit terminology follows Anderson (1981) and Niedenzu (1928). Scanning Electron Microscope images were performed with samples fixed in Karnovsky solution (Bozzola & Russel 1992), and coated in gold. The conservation status was proposed following the recommendations of IUCN Red List Categories and Criteria, Version 3.1 (IUCN 2001). GeoCAT (Bachman et al., 2011) was used for calculating the Extent of Occurrence (EOO) and the Area of Occurrence (AOO). Maps were elaborated using QGis 2.6.0-Brighton software (2014) and geographical coordinates were obtained from herbaria specimens and fieldwork data.

Taxonomy

***Byrsonima crassifolia* clade**

Byrsonima crassifolia clade comprises eight species: *Byrsonima clausseniana* A. Juss., *B. crassifolia* (L.) Kunth, *B. cydoniifolia* A. Juss., *B. guilleminiana* A. Juss., *B. linearifolia* A. Juss., *B. pachyphylla* A. Juss., *B. termitaria* Francener & Mamede and *B. verbascifolia* (L.) DC. The clade distribution extends from Mexico and West Indies, through South America, reaching Southern Brazil and Bolivia. Its species occur in open dry areas, such as neotropical savannas (cerrados), or in gallery forests. The Brazilian Cerrado is the richest biome on species of the *B. crassifolia* clade, highlighting the state of Goiás in Brazil, in which all species from this clade co-occur. Morphology of leaf hairs (fig. 1) is one of the most important characters to distinguish the species from *Byrsonima crassifolia* clade.

Even though this work comprises just eight accepted names from a total of 28 from section *Eriolepis*, most names proposed by Niedenzu (1901) (ca. 18 names) are treated here as synonyms of one of the eight currently accepted names for this clade. The list of *insertae sedis* presented comprises the remaining accepted names from section *Eriolepis* in need of tipification.

Key to the species of the *Byrsonima crassifolia* clade

1. Subshrubs with underground trunk.....2
1. Shrubs to trees with aerial trunk.....5
2. Leaves linear, margin usually strongly revolute; nodes and leaves lax; stipules partially connate or free; thyrsi (1 flower per cincinnus), in the median to distal part of the rachis, sometimes many flowers congested at apex; filaments free.....*B. linearifolia*
2. Leaves obovate, oblanceolate, elliptic or spatulate, margin slightly revolute; nodes and leaves congested and crowded at ground level; stipules connate; thyrsi (1–2 flowers per cincinnus), in the median to distal part of the rachis; filaments connate at base.....3
3. Thyrsi usually consisting of 2-4 flowered cincinni, rachis sericeous.....*B. guilleminiana*
3. Thyrsi 1-2 consisting of flowered cincinni, rachis tomentose or velutinous.....4
4. Subshrubs up to 11 cm tall; foliar laminas up to 14.5 cm long; adaxially glabrous; petiole absent or no longer than 2 mm.....*B. termitaria*
4. Subshrubs up to 60 cm tall; foliar laminas longer than 14.5 cm; adaxially velutinous to sparsely velutinous, with hairs usually unbranched; petiole longer than 5 mm long.....*B. verbascifolia*
5. Trunk usually exfoliating, reddish brown in the exfoliationg region.....6
5. Trunk rarely exfoliating.....7
6. Leaves and rachis of inflorescence tomentose, with hairs sinuate and stalked 2-10 mm long; abaxial view of foliar lamina tomentose, with stalk 0,2-1 mm long; thyrsi of 1-flowered cincinni.....*B. pachyphylla*
6. Leaves and rachis of inflorescence sericeous, with hairs straight and stalk sessile to subsessile (0-0,2 mm long); thyrsi of 2-4 flowered cincinni.....*B. guilleminiana*
7. Abaxial face of leaves velutinous, hairs whitish with stalk usually longer than 0.4 mm long; bracts narrowly triangular to linear, longer than 4.2 mm*B. clauseniana*
7. Abaxially face of leaves sericeous-velutinous to glabrescent, hairs whitish to brown with stalk usually up to 0.2 mm long; bracts triangular, narrow triangular or rarely linear, usually up to 4.5 mm long.....8
8. Indument of abaxial face of leaves irregularly deciduous, hairs usually rusty-red or light-brown.....*B. crassifolia*
8. Indument of abaxial face of leaves usually persistent, whitish, sparsely sericeous to sericeous-velutinous, sometimes becoming glabrous with age, hairs whitish.....*B. cydoniifolia*

1. *Byrsonima clauseniana* A.Juss. (1840: 332). Type:—BRAZIL. Minas Gerais: *S.loc.*, *s.d.*, *Claussen s.n.* (lectotype designated by Anderson (2007): P barcode P02428574!; isolectotype: BR barcode BR0000008497437!, K barcodes K000426858!, K000426859!, P barcodes P02428575!, P02428576!). Figure 2A–E, 3
= *Byrsonima cydoniifolia* var. *cearensis* Nied. (1901:25), *syn. nov.* Type—BRAZIL. Ceará: Crato, *s.d.*, *Gardner 1490* (holotype: GOET?; isotypes: G!, K barcode K000426856!, S no S08-15458!, S08-15457!, US barcode US00108707!).

Trees, (0.6–) 1–8 (–12) m tall; trunk erect, cylindric, wisth by elongated lenticels, sparsely velutinous to glabrous, hairs 0.3–1 mm long, whitish, stalk sessile to up to 0.3 mm long; stems sericeous to sericeous-tomentose, hairs 0.5–1.7 mm long, whitish or light-brown, stalk 0.1–0.3 mm long, nodes lax. *Stipules* 3–5 × 2–3 mm, connate, ovate, adaxially shiny, glabrous, abaxially sericeous, hairs 0.6–1.3 mm long, whitish or light-brown, stalk sessile to up to 0.2(–0.3) mm long. *Leaves* opposite, entire, plane; petioles 4.5–15 mm long, tomentose-sericeous, hairs 0.3–1.5 mm long, whitish or light-brown, stalk sessile to up to 0.3 mm long.; leaf blades 7–12.5 × 2–8 cm, elliptic or obovate, apex acute, acuminate, mucronate or rounded, margin slightly revolute, entire to sinuose, base cuneate to attenuate, adaxially glaucous, greenish or light-brown, velutinous to sparsely velutinous, rarely glabrescent, hairs 0.5–1 mm long, whitish, stalk 0.2–0.5 mm long, abaxially whitish, greenish, or light-brown, velutinous, hairs 0.5–1 mm long, whitish, stalk (0.1–) 0.4–0.8 mm long, venation brochidodromous, 6–9 pairs of secondary veins, prominent, tertiary veins reticulate, usually hidden by indument. *Thyrses* with 1–2(–3) flowers per cincinnus 4–12 cm long, 8–20 flowered.; rachis canaliculated, hidden by the indument, sericeous to tomentose-sericeous, hairs 0.4–1.5 mm long, whitish, rarely light-brown, stalk 0.1–0.7 mm long; bracts and bracteoles at base of pedicel, deciduous or persistent in fruit; bracts 4.2–5 (–10) × 0.9–1.2 mm, narrowly triangular to linear, erect, abaxially sericeous or velutinous-sericeous, hairs 0.7–1.3 mm long, whitish or light-brown, stalk sessile to up to 0.2 (–0.5) mm long, adaxially glabrous; peduncle absent; bracteoles 2.5–3.2 (–4.4) × 0.7–1.3 mm, triangular or narrowly triangular, erect, abaxially velutinous-sericeous, hairs 0.4–1 mm long, whitish or light-brown, stalk sessile to up to 0.3 mm long, adaxially glabrous or sericeous at base, hairs 0.7–0.8 mm long, light-brown, stalk sessile; pedicels 7–10 mm long, enlarged in fruit, tomentose, hairs 0.3–1 mm long, whitish or light-brown, stalk sessile to up to 0.3 mm long. *Flowers* distributed along the median and

distal portion of the rachis; sepals $3\text{--}4.5 \times 2.1\text{--}2.8$ mm, expandend in fruits, all biglandular, adpressed, usually reflex or sometimes erect at apex, apex acute or rounded, abaxially sericeous, hairs 0.5–1 mm long, whitish or light-brown, stalk sessile to up to 0.1 mm long, adaxially glabrous; glands $1.5\text{--}2.2 \times 1\text{--}1.2$ mm, greenish in pre-anthesis, yellow to orangish in anthesis; petals yellow, turning orange with age, glabrous; lateral petals reflexed, lamina $5\text{--}7 \times 5.5\text{--}7$ mm, cupuliform, margin sinuate, claws bent or twisted, $4\text{--}4.5 \times 0.5\text{--}0.7$ mm; posterior petal patent, lamina $3\text{--}5 \times 3.3\text{--}5.6$ mm, corrugate, margin erose, claw erect, $3.5\text{--}4 \times 0.8\text{--}1.3$ mm. *Stamens* 10, connate at base, heteromorphic; filaments $1.9\text{--}2.8 \times 0.6\text{--}1$ mm, abaxially glabrous, adaxially pilose at the base, hairs simple, 0.4–3 mm long, whitish or light-brown; connectives expanded, $2.5\text{--}3 \times 0.6\text{--}0.8$ mm, glabrous, sometimes exceeding the locules (up to 0.2 mm long), apex acute or rounded; locules $2.5\text{--}3.5 \times 0.5\text{--}0.7$ mm, apex rounded, sparcely sericeous between or laterally the locules, hairs 0.8–1.4 mm long, whitish, stalk sessile. *Ovary* $1.5\text{--}1.8 \times 1\text{--}1.6$ mm, conical, glabrous or sericeous, hairs 1–1.4 mm long, whitish, stalk sessile to up to 0.1 mm long; ovules $0.6\text{--}1.0 \times 0.3\text{--}0.6$ mm, glabrous; styles $3.4\text{--}4.5 \times 0.2\text{--}0.3$ mm, linear, erect, glabrous, apex subulate, bent. *Drupes* 5.5–10 mm diam., ovoid or globose, glabrous or sericeous, hairs 0.4–1.3 mm long, whitish or light-brown, stalk sessile to up to 0.1 mm long.

Specimens selected:—**BRAZIL. Bahia:** Formosa do Rio Preto, Fazenda Lagoa de Fora, 12 October 1989, *Violatti et al.* 30 (SP). São Félix do Coribe, Faz. Futuro, 24 September 2009, *Correia* 517 (HUEFS). **Distrito Federal:** Brasília, APA da Cafuringa Fazenda Chapadinha em José Pires, 25 September 1990, *Vieira et al.* 513 (CEN, NY, SP). **Goiás:** Alexânia, Estrada entre Alexânia e Abadiânia, 10 March 2004, *Souza et al.* 29682 (ESA, RB). Alto Paraíso de Goiás, 15 November 1997, *Felfili* 374 (SP). Arenópolis, Bacia do rio Caiapó, próximo à Hidrelétrica de Mosquitão, 15 October 2007, *Aparecida da Silva et al.* 6417 (SP, UB). Caldas Novas, ca. 10 km due NW of city of Caldas Novas, several km N of N edge of Serra de Caldas, 23 December 1974, *Heringer et al.* 14218 (NY, UESC, SP). Campinaçu, Córrego Laginha, área ligada à margem do reservatório, Área de influência indireta da UHE Serra da Mesa, 9 October 1991, *Cavalcanti et al.* 900 (CEN, SP). Campos Belos, estrada velha de São Domingos para Campos Belos, entrada da fazenda Barrigudinha, 22 October 2001, *Fonseca et al.* 3009 (IBGE, SP). Niquelândia, 11 km em direção a Uruaçu, 22 May 1990, *Pedralli et al.* 3295 (CEN, SP). Padre Bernardo, Fazenda Lagoa Santa, ca. 7,5 km WSW de Padre Bernardo, 24 November

1982, *Kirkbride Jr.* 5087 (MO). **Maranhão**: Lorêto, "Ilha de Balsas" region between the Balsas & Parnaíba Rivers, 35 km S of Lorêto, East of main house of Fazenda Morros, In brook gully, "Grota do Caboré", On gully side 50 m from mouth, 15 February 1970, *Eiten et al.* 10615 (NY, SP, UB). **Mato Grosso**: Nova Brasilândia, ca. 1km NE de Riolândia (Frieira) em direção a Planalto da Serra, 7 October 1997, *Souza et al.* 20115 (ESA, RB). Rosário Oeste, ca 75km E de Rosário Oeste, Estrada entre Riolândia (Frieira) e Marzagão, 7 October 1997, *Souza et al.* 20238 (ESA, RB). **Minas Gerais**: Belo Horizonte, Estação Ecológica da UFMG, Trilha E, 2^a estação de coleta, 25 May 1990, *Bacariça et al.* 21 (BHCB, SP). Cristália, Fazenda Curral Velho, 27 November 1991, *Carvalho et al.* 747 (BHCB, ESA, SP). Diamantina, Estrada Gouveia-Curvelo, ca. de 20 km de Diamantina, 23 September 2008, *Rosa et al.* 1173 (HUFU, SP). Morada Nova de Minas, 5 Km de Morada Nova, próximo ao lado da Represa de Três Marias (Furnas), 11 November 1991, *Vieira et al.* 926 (CEN, SP). Patrocínio, Fazenda Serra Negra, 17 November 1988, *Felfili et al.* 153 (IBGE, SP). **Pará**: Conceição do Araguaia, nas cercanias do aeroporto, 5 December 2014, *Lemos-Filho et al.* s.n. (BHCB174561). **Piauí**: Campo Maior, Alto do Comandante, 27 November 2001, *Lopes et al.* 25 (SP). Piriri, Parque Nacional de Sete Cidades, 2 December 2013, *Lemos-Filho et al.* s.n. (BHCB169522). São Francisco do Piauí, Fazenda Serrinha, 29 November 1973, *Ramalho* 298 (IPA). **São Paulo**: Estreito, Perto do rio Grande, 6 November 1997, *Marcondes-Ferreira et al.* 1541 (ESA, SP, UEC). Pedregulho, Igaçaba, Morro Solteiro, 12 November 1994, *Marcondes-Ferreira et al.* 1023 (HRCB, SP). **Tocantins**: Almas, Bacia do Tocantins, Sub-bacia Manuel Alves da Natividade, 17 October 2008, *Mendonça et al.* 6286 (HUTO, IBGE, SP, UB). Formoso do Araguaia, Bacia do Araguaia, Sub-bacia do Rio Formoso, entrada para a Fazenda Três Lagos, 7 October 2008, *Mendonça et al.* 6152 (HUTO, IBGE, SP). Palmas, Serra do Lajeado, 29 October 1998, *Árbocz* 6227 (HTO, UB). São Valério da Natividade, Bacia do Tocantins, Sub-bacia do Rio Tocantins, 11 October 2008, *Mendonça et al.* 6202 (HUTO, IBGE, SP).

Distribution, habitat and phenology:—*Byrsonima clauseniana* is a widespread species in Brazilian Cerrado (fig. 4), commonly found in *cerrado sensu lato* or occasionally in seasonally dry forests. Flowering from July to March, and fruiting from August to May.

Conservation status:—*Byrsonima clausseniana* should be regarded as Least Concern due to its wide distribution and abundant populations in South America.

Etymology:—The epithet pays honor to the collector of the type specimen, M. Claussen.

Discussion:—*Byrsonima clausseniana* usually bears a greenish to whitish sericeous indument abaxially on leaves. The hairs have a long stalk (usually longer than 0.4 mm long) and the bracts are usually narrow and triangular to linear in shape. The closest species is *B. cydoniifolia*, which usually bears smaller and triangular bracts, and leaves abaxially sericeous to sericeous-velutinous, with hairs sessile to subsessile.

- 2. *Byrsonima crassifolia* (L.) Kunth (1822: 149). ≡ *Malpighia crassifolia* L., (1753: 426).**
Type:—*S. loc., s.d., s. leg.* (holotype: LINN barcode LINN588.8!). Figure 2K–O, 5.
= *Byrsonima chrysophylla* var. *lancifolia* Griseb., (1866: 42). ≡ *Byrsonima wrightiana* Nied., (1897:8). Type:—CUBA. *S. loc., 1863, Wright 2145* (holotype: GOET barcode GOET007087!; isotypes: G barcode G00352683!, GH barcode GH00045060!, K barcode K000424383!, NY barcode NY00888108!, P barcode P02428573!, YU barcode YU244626!).
= *Byrsonima cotinifolia* Kunth (1822: 152). Type:—MEXICO. Guerrero, Acapulco, *s.d., Humboldt & Bonpland s.n.* (holotype P00679981!; isotype P02428583!).
= *Byrsonima crassifolia* subsp. *insulata* Cuatrec. (1958: 611). Type:—COLOMBIA. Vaupés: Rio Karurú, 15 April 1933, *Schultes & Crámer 19164* (holotype: US barcode US00108703!).
= *Byrsonima crassifolia* f. *kunthiana* Nied. (1901: 16). **Lectotype (designated here):**— BRAZIL. Minas Gerais: Congonhas do Campo, *s.d., Glaziou 13412* (lectotype: R!).
= *Byrsonima crassifolia* var. *jamaicensis* Urb. & Nied., (1901: 18). **Lectotype (designated here):**—JAMAICA. Kingston, *s.d., Oersted 2* (lectotype: GOET barcode GOET007091!; isolectotype: GOET barcode GOET007092!).
= *Byrsonima cubensis* A.Juss. (1840: 333). ≡ *Byrsonima crassifolia* f. *cubensis* (A. Juss.) Nied., (1901:17). Type:—CUBA. *S. loc., s.d., Poeppig s.n.* (holotype: P barcode P00578075!, isotype: G barcode G00352752!).
= *Byrsonima cumingiana* A.Juss. (1840:332). Type:—COLOMBIA. *S. loc., 1837, Cuming 1207* (holotype K barcode K000426906!; isotype P barcode P02428589!, P-JU?).

- = *Byrsonima ferruginea* Kunth (1822: 446). ≡ *Byrsonima crassifolia* f. *ferruginea* (Kunth) Nied., (1901: 16). Type:—VENEZUELA. Amazonas: Rio Orinoco, s.d., *Humboldt & Bonpland s.n.* (holotype: P00647236!, isotype: P00689790!).
- = *Byrsonima laurifolia* Kunth (1822: 150). Type:—VENEZUELA. Llanos de Cumaná, s.d., *Humboldt & Bonpland s.n.* (holotype: P barcode P00679979!).
- = *Byrsonima laurifolia* var. *guatemalensis* Nied. (1928: 724). Type:—GUATEMALA. San Antonia Las Flores, 4 April 1921, *Rojas* 362 (holotype: USCG!; isotype: US barcode 01268584!).
- = *Byrsonima oaxacana* A.Juss. (1840:332), *syn. nov.* Type:—MEXICO. Guichilona: Oaxaca, 1833, *Andrieux* 491 (lectotype, designated by Anderson (2007): P barcode P02428649!; isolectotype: G barcodes G00352734!, !G00352733!, G00352732!, K barcode K000424385!, NY barcode NY00055541!, P barcode P02428650!).
- = *Byrsonima rhombifolia* A.Juss. (1840:333). Type:—BRAZIL. *S.loc.*, s.d., *Ferreira s.n.* (holotype P barcode P00310211!).
- = *Byrsonima spruceana* Nied. (in Engl. & Prantl 1897:207). ≡ *Byrsonima crassifolia* var. *spruceana* (Nied.) Nied. (1901: 18). Type:—BRAZIL. Pará: Santarém, 1849–1850., *Spruce* 244 (holotype K barcode K000426873!; isotype NY barcode NY00055564!).
- = *Byrsonima tenuifolia* Urb. & Nied. (1901: 19). Holotype:—B†. **Lectotype (designated here):**—HAITI. *S.loc.*, s.d., *Picarda* 536 (lectotype: NY barcode NY00888109!; isolectotype: GH barcode GH00254231!).
- = *Malpighia cinerea* Poir. (in Lam. 1816: 7). ≡ *Byrsonima cinerea* (Poir.) DC., (1824: 580). ≡ *Byrsonima crassifolia* var. *cinerea* (Poir.) Nied., (1901:17). Type:—FRENCH GUIANA, 1821, *Perrottet* 254 (holotype: P?, isotype: P barcode P02428552!, G barcode G00211301!).
- = *Malpighia lanceolata* Poir. (1797: 332). ≡ *Byrsonima crassifolia* var. *lanceolata* (Poir.) Griseb. (1866: 42). Type:—FRENCH GUIANA. Cayenne, 1792, *Leblond* s.n. (holotype: P barcode P00673595!; isotype: P barcodes P02428553!, P02428554!, P02428555!, P02428556!).
- = *Malpighia moureila* Aubl. (1775: 459). ≡ *Byrsonima crassifolia* var. *moureila* (Aubl.) DC., (1824: 579). Type:—FRENCH GUIANA. *S.loc.*, s.d., *Aublet* s.n. (holotype: LINN barcode LINN-HS822.3!).

Shrubs or trees, 1.5–7 m tall; trunk erect or tortuous, cillindric or gnarled, wisth by elongated lenticels, sericeous to glabrous, hairs 0.3–0.8 mm long, brown or grey, stalk

sessile to up to 0.1 mm long; stems sericeous, hairs 0.3–0.8 mm long, whitish or brown, stalk 0.1–0.3 mm long, nodes lax. *Stipules* connate, 2.6–5 × 2.1–3.2 mm, triangular to ovate, adaxially shiny, glabrous, abaxially sericeous, hairs 0.4–0.7 mm long, whitish to brown, stalk 0.1–0.2 mm long. *Leaves* opposite, entire, plane; petioles 5–19 (–22) mm long, sericeous to glabrescent, hairs 0.2–0.7 mm long, whitish, light-brown or brown, stalk sessile to up to 0.1 mm long.; leaf blades 6–12 × 2.5–7.5 cm, elliptic, obovate or lanceolate, base acute, margin entire, slightly revolute to sinuose, apex usually acuminate, occasionally acute, or rounded, adaxially light-brown or light green, shiny, sparsely sericeous to glabrous, hairs 0.3–0.8 mm long, whitish or brown, stalk sessile to up to 0.1 mm long, abaxially rusty-red, brown or greenish, sericeous to glabrescent, indument often irregularly deciduous, hairs 0.3–0.7 mm long, usually light-brown or brown, rarely whitish, stalk sessile to up to 0.2 mm long; venation brochidodromous, 7–11 pairs of secondary veins, prominent or impressed, tertiary veins reticulate. *Thyrses* of 1–2(–3)–flowered cincinni, with 15–43 flowers distributed in the median and distal portion of the rachis, sometimes with few flowers at base; rachis 6–21 cm long, canaliculate (hidden by the indument), sericeous to tomentose, hairs 0.3–0.8 mm long, whitish or light-brown, stalk sessile to up to 0.3 mm long; bracts and bracteoles deciduous in fruiting; bracts 2–4.5 × 1.2–1.5 mm, narrow triangular to triangular, erect, adaxially glabrescent, few hairs at base, hairs light-brown, 0.3–0.5 mm long, unbranched or branched, stalk up to 0.1 mm long, abaxially sericeous, hairs 0.3–0.7 mm long, light-brown, stalk sessile to up to 0.1 mm long.; peduncle sessile or up to 4 mm long.; bracteoles 1.1–2.5 × 1–1.2 mm, triangular, erect, adaxially glabrescent, few hairs at base, hairs light-brown to brown, 0.3–0.8 mm long, unbranched or branched, stalk sessile to up to 0.1 mm long, abaxially sericeous, hairs 0.3–0.7 mm long, light-brown, stalk sessile to up to 0.1 mm long.; pedicels 7–12 mm long, reflexed at fruiting, tomentose-sericeous, hairs 0.3–0.8 mm long, whitish or light-brown, stalk sessile to up to 0.2 mm long. *Sepals* 3–4 × 2–2.5 mm, expanded in fruiting, biglandular, apex acute or rounded, adpressed to reflexed at anthesis, adaxially glabrous to glabrescent, few hairs at base, hairs 0.7–0.8 mm long, whitish or light-brown, stalk sessile, abaxially sericeous, hairs 0.5–1 mm long, whitish to light brown, stalk sessile to up to 0.1 mm long.; glands 1.5–2 × 1–1.5 mm, yellow. *Petals* yellow, turning orange to red with age, glabrous; lateral petals reflexed, lamina 4.5–7 × 5.5–7 mm, cupuliform, margin sinuate, claws 3–4.5 × 0.5–0.7 mm, patent, bent or twisted; posterior petal patent, lamina 4–5 × 5–6 mm, corrugate, margin erose, claw 3–5 × 0.7–1 mm, erect. *Stamens* 10, free at base; filaments 1.5–3 × 0.5–0.7 mm, adaxially pilose at

base, hairs 0.5–2 mm long, whitish, light-brown or brown, simple; abaxially glabrous to glabrescent, few hairs at base, hairs 0.4–0.8 mm long, simple, light-brown; connective $1.5–2.2 \times 0.5–0.7$ mm, glabrous, apex acute, acuminate to rounded, exceeding or not the locules (up to 0.4 mm long); locules $2–2.8 \times 0.5–0.7$ mm, apex rounded, sericeous, few to many spreading sericeous hairs, hairs 0.7–1.5 mm long, between or on the sides of locules, whitish, stalk sessile. *Ovary* conical to globose, $1.5–1.8 \times 1–1.5$ mm, sericeous to glabrous, hairs 0.5–1.1 mm long, whitish to light-brown, stalk sessile; ovules $0.7–0.8 \times 0.4–0.5$ mm; styles linear, $3–5.3 \times 0.2–0.4$ mm, erect, subulate, bent at the apex, glabrous; stigmas minute. *Drupes* 6–10 mm diam., globose, glabrous to glabrescent at apex, hairs up to 0.5 mm long, whitish, stalk sessile.

Specimens selected:—**BELIZE.** **Cayo:** Spanish Lookout, 20 August 1986, *Ratter* 5185 (P). **BOLIVIA.** Yungas & Yuracaré, 1839, *Pentland s.n.* (P04783604). **Beni:** Moxos, San Juancito a 20 km al N de San Ignacio, 2 January 1990, *Seidel* 3166 (MBM). **La Paz:** Cereice, 3 February 1956, *Seta* 533 (HB). **Nor Yungas:** Entre Yolosa y Coroico, 13 February 1993, *Beck* 21223 (MBM). **Sud Yungas:** La Paz, Cerro Pelado Along the road between Marimonos and Quiquibey, ca 20 km NE of Palos Blancos, 10 November 1990, *Lewis* 37964 (P). **Yunquisivi:** *s.loc.*, December 1846, *Weddel* 4196 (P). **BRAZIL.** **Amapá:** Calçoene, Cunany (Guyane Brésil), 13 April 1895, *Huber* 1012 (P). Macapá, 15 km leste de Porto Santana, 23 March 1962, *Mattos* 10129 (HSJRP, SP, SPF). **Amazonas:** Cacau-Pirêra, Margem direita do Rio Negro, 28 June 1983, *Kawasaki et al.* 15 (CEPEC, INPA). **Bahia:** Barreiras, BR-020, 20 June 1986, *Hatschbach et al.* 50510 (CEPEC, MBM). **Ceará:** Fortaleza, Praia do Futuro, 16 March 2002, *Souza et al.* 28660 (ESA, RB). **Espírito Santo:** Sooretama, Reserva Natural da Vale, 2 November 2013, *Caxambu et al.* 4523 (HCF). **Goiás:** *S.loc.* probably Tocantins, 1866, *Gardner* 3058 (P). **Maranhão:** Alcântara, Vegetação pertubada a NW of Alcântara, 4 February 1984, *Carvalho et al.* 2085 (RB, SP). **Mato Grosso:** Colíder, Serra do Cachimbo, road Santarém-Cuiabá, BR-163, km 763 to 30 km of Guarantã, 19 April 1983, *Silva et al.* 40 (INPA, NY). **Minas Gerais:** Congonhas do Campo, 4 March 1883, *s.leg.* 13412 (P). **Pará:** Belém, adjacent building housing the Herbário IAN, 3 February 1974, *Anderson* 10500 (MBM, IAN). **Piauí:** *S.loc.*, Sítio Baixão-Restinga de Parnaíba, 13 July 1954, *Andrade-Lima* 54-1858 (IPA). **Roraima:** Pacaraima, Ilha San Salvador Near Lake Maiú, 40 Km NW of Boa Vista, 8 January 1969, *Prance et al.* 9148 (INPA, NY, P, R). **Tocantins:** Aguiarnópolis, Margem direita do Rio Curicaca, 8 July 2005, *Santos* 2624

(CEN). Araguaina, 21 November 2003, *Salles et al.* 2719 (UESC). **COLÔMBIA.** **Antioquia:** Rio Negro, no date, *Triana s.n.* (P04783601). **Bogotá:** San Martin, *s.d.*, *Triana s.n.* (P 05600454). **Boyaca:** Cano Cancia, 25 km SSW de Hato Yarumito, 38 km S de Mani, 23 February 1971, *Sastre* 836 (P). **Huehuetenango:** Serranía de La Macarena Márjen Izquierda del Rio Guayabero a 10 km abajo de Caño Lozada, primera Meseta sobre el campamento no. 1, 16 January 1959, *Pinto* 210 (P). **Magdalena:** Mariquita, Nouvelle-Grenade, *s.d.*, *Triana s.n.* (P05600447). **Meta:** Carretera de Puerto Gaitán a Planadas, 4 km de la carretera central, Vale del río Manacacías, margem derecha, 26 March 1971, *Pinto et al.* 1543 (P). **Orocué:** 3 November 1933, *Cuatrecasas* 4383 (P). **Vichada:** Carretera a Puerto Carreño, Hato El Tigre, Margen del caño El Tigre, 14 March 1971, *Pinto et al.* 1227 (P). **COSTA RICA.** **Puntarenas:** Cascajal, Along road from Cascajal to Pigres, 25 km ESE of Puntarenas, 6 July 1949, *Holm et al.* 283 (P). **CUBA.** **Nueva Gerona:** Isla de Pinos, 1904, *Curtiss* 216 (P). **Pinar del Rio:** Near Herradura, 23 January 1905, *Hermann* 595 (P). **Santa Clara:** Cienfuegos, 5 September 1895, *Combs* 16 (P). **DOMINICAN REPUBLIC.** **La Vega:** La Vega, June 1912, *Fuertes* 1799 (P). **Santiago Rodriguez:** Moncion, Ca. 1km W of Town along Arroyo Cinea, 24 May 1983, *Landrum* 4733 (MBM). **EL SALVADOR.** South of headquarters of Hacienda Las Tabalas, near Río Acachapa, Balsam Range, June 1942, *Tucker* 1363 (P). **FRENCH GUIANA.** Cayenne, 18 March 1961, *Aubréville* 7 (P). **GUATEMALA.** **Huehuetenango:** Huehuetenango, 20 May 1970, *Gillis* 9283 (P). **Quezaltenango:** San Jose Buena Vista, Costa, Cuca, 21 January 1980, *Rodriguez* 1709 (P). **GUYANA.** **Imbaimadai:** Cuyuni - Mazaruni Region, 2 July 2004, *Clarke et al.* 12313 (INPA). **Cuyuni-Mazaruni:** *S.loc.*, May 1863, *Appun* 1102 (P). **Demerara-Mahaica:** Along Highway to Timehri International Airport, 22 March 1987, *Boom* 7130 (P). **East Berbice-Corentyne:** Left bank upper Canje +/- 35 mi S of Torani Canal; *loc. cit.*, 3 mi SE of Digitima Creek, 18 December 1986, *Pipoly et al.* 9402 (P). **Potaro-Siparuni:** Kaieteur Savannah, Potaro River, October 1881, *Jenman* 87 (P). **Rupununi:** Kuyuwini Landing, Kuyuwini River, 10 February 1991, *Jansen-Jacob et al.* 2532 (P). **Upper Demerara-Berbice:** 15 km E of Rockston, on Linden Rockstone Road, 1 January 1987, *Pipoly et al.* 9572 (P). **Upper Takutu-Upper Essequibo:** Betwenn Takutu River and Kanuku Mountains, March 1938, *Smith* 3344 (P). **HAITI.** *S.loc., s.d.*, *Taeger* 293 (P). **HONDURAS.** **Francisco Morazan:** Zambrano, Cercanias de Parque Aurora, 14 April 1977, *Ochoa* 26 (MBM). **MEXICO.** **Chiapas:** 3.1 km E of junction with hwy 195 on hwy 190, ca. 47 km W of San Cristobal, 1 August 1989, *Landrum et al.* 6405 (MBM).

Colima: Colima, August 1897, *Palmer* 119 (P). **Guerrero:** Petatlán, abundante, 4 February 1986, *Ssoto Nuñez et al.* 12221 (MBM). **Jalisco:** Sierra du Nayarit Territoire Huichol, *Diguet* 552 (P). **Oaxaca:** San Pedro Juchatengo, Dto. Juquila, 12 km al Ne de El Vidrio, brecha a Sola de Vega, 17 August 1988, *Campos et al.* 2389 (MBM). **Tabasco:** Cárdenas, Campo Rodador (PEMEX), en camino a Cinco Presidentes, 7 October 1996, *Tenorio* 19511 (MBM). **Veracruz:** Soteapan, 2 km al N de San Pedro de Soteapan, 2 August 1982, *Ramamoorthy et al.* 3883 (MBM, UEC). **PANAMA.** Canal Zone, 23 June 1940, *Bartlett* 16301 (MBM). **Chiquiro:** Quebrada Manzanillo, Burica Peninsula, 9 km south x southwest of Puerto Armuelles, 3 March 1973, *Busey* 734 (MBM). **PUERTO RICO.** Aguada: Piedra Branca, 18 December 1886, *s.leg.* 3725 (P). **Mayagüez:** Mesa, South of Mayaguez, 8 February 1900, *Heller* 4544 (P). **SURINAM.** Sipaliwini: Tafelberg Airplane Crash Savannah. Trail up to 2 km to the south of the Augustas Falls campsite, 21 June 2001, *Hawkins* 1957 (SP). **TRINIDAD.** Wallerfield: *S.loc.*, 4 December 1973, *Phhilcox* 7360 (P). **VENEZUELA.** **Amazonas:** Puerto Ayacucho, 27 June 1942, *Williams* 15942 (P). **Apuré:** Pedro Camejo, Banks of the Río Orinoco on Isla Poyatón opposite the Serranía de Baraguán on the Apure side of Estrecho de Baraguári of the Río Orinoco, 27 April 1977, *Davidse et al.* 12225a (P). **Aragua:** Valley or Rio Limon, along the new road to Ocumare de la Costa, 18 April 1913, *Pittier* 6059 (P). **Bolívar:** Cedeño, Valley of Caño Colorado, vicinity of Panare Indian village, ca. 30 km SW of National Guard post at Maniapure, 5 April 1985, *Boom et al.* 6035 (INPA). **Venezuela:** Casiquiré, Laja da Caraça Cassiqueare, 8 October 1928, *Luetzelburg* 22862 (R).

Distribution, habitat and phenology:—*Byrsonima crassifolia* is a widespread species, from Mexico and West Indies to South America, reaching Bolivia and Southern Brazil (fig. 6). It usually occurs in open dry areas, such as neotropical savannas (cerrados), or sometimes in seasonally dry forests. Flowering and Fruiting throughout the year.

Conservation status:—*Byrsonima crassifolia* should be regarded as Least Concern due to its wide distribution and abundant populations in South America.

Etymology:—The epithet refers to the thickness of its leaves.

Discussion:—*Byrsonima crassifolia* bears leaves usually abaxially rusty-red, indument irregularly deciduous, hairs usually light-brown or brown, sessile to subsessile and leaf apex usually acuminate. Floral characters are quite constant, and similar to its closest species, as *B. clauseniana*, *B. cydoniifolia* and *B. pachyphylla*, but none of them bear a deciduous indument. In addition, the bracts are smaller than in *B. clauseniana* and *B. pachyphylla*, and differs from those of *B. cydoniifolia*, due to its leaves and inflorescences covered with rarely deciduous, whitish sericeous indument.

Byrsonima crassifolia is distributed through several countries, and many names were used to the species and later synonymized. One of this names is *Byrsonima oaxacana*, described to Mexico, and here included as synonym of *B. crassifolia* based especially on its irregularly deciduous indument.

3. *Byrsonima cydoniifolia* A.Juss. (1833: 77). Type:—BRAZIL. Minas Gerais: Contendas, s.d., Larouotte s.n. (holotype: P barcode P02428594!; isotypes: MPU barcode MPU013941!, P barcodes P02428595!, P02428596!). Figure 7F–J, 8
= *Byrsonima orbigniana* A.Juss. (1840: 332). Type:—BOLIVIA. Chiquitos: Santiago de Chiquitos, s.d., d'Orbigny 880 (holotype: P barcode P02428656!; isotypes: G barcode G00352738!, P barcode P02428657!).
= *Byrsonima cydoniifolia* var. *chiquitensis* A.Juss. (1843: 281). Type:—BOLIVIA. Chiquitos: S. Rafael, s.d., d'Orbigny 993 (holotype: P barcode P02428655!).
= *Byrsonima cydoniifolia* var. *cuneata* S.Moore (1895: 323). Type:—BRAZIL. Mato Grosso: Jangada, 1891–1892, Moore 274 (holotype: BM barcode BM000796117!).

Shrubs or trees (0.7–) 1–7.8 (–10) m tall; trunk cylindric, sometimes twisted, wisth by elongated lenticels, glabrous; stems tomentose-sericeous to glabrous with age, hairs 0.3–1 mm long, whitish, stalk sessile to up to 0.2 mm long, nodes lax. Stipules 2–4 × 3.7–4 mm, connate, broadly ovate, adaxially glabrescent to glabrous, hairs 0.3–0.7 mm long, whitish or brown, stalk sessile to up to 0.1 mm long, abaxially velutinous, hairs 0.5–1.5 mm long, whitish to rarely brown, stalk sessile to up to 0.1 mm long. Leaves opposite, entire, plane; petioles 4–9 (–15) mm long, floccose to sericeous, hairs 0.3–0.6 mm long, stalk sessile to up to 0.3 mm long.; leaf blades 5.5–11 × 2–5.2 cm, elliptic to obovate, base cuneate, margin entire, slightly revolute, sinuose, apex acuminate, cuspidate, obcordate, retuse or obtuse, adaxially brown, shiny, sericeous to floccose to glabrescent, hairs 0.3 –0.7 mm long, whitish, stalk sessile to up to 0.1 mm long, abaxially whitish,

sparselly sericeous to sericeous-velutinous, rarely glabrous with age, hairs 0.5–0.8 mm long, whitish, stalk sessile to up to 0.1 (–0.3) mm long; venation brochidodromous, 6–10 pairs of secondary veins, adaxially impressed, abaxially prominent, tertiary veins reticulate. *Thyrses* of 1-3-flowered cinni, with 10–25–flowers distributed in the median and distal portion of the rachis; rachis 4–7 cm long, canaliculated, sericeous, hairs 0.3–0.8 mm long, brown, stalk sessile to up to 0.25 mm long; bracts and bracteoles deciduous in fruiting; bracts 3–8 × 1.5–2 mm, triangular, narrowly triangular or linear, erect, adaxially, pilose to glabrous at base, hairs 0.5–1 mm long, rusty-red, stalk sessile, abaxially sericeous to velutinous, hairs 0.3–0.8 mm long, whitish, rarely rusty-red, stalk sessile to up to 0.2 mm long; peduncle sessile; bracteoles 2–2.8 × 1.2–1.8 mm, triangular, erect, adaxially, pilose to glabrous at base, hairs 0.5–1 mm long, rusty-red, stalk sessile, abaxially sericeous to velutinous, hairs 0.3–0.8 mm long, whitish, rarely rusty-red, stalk sessile to up to 0.2 mm long; pedicels 7–10 mm long, erect in fruiting, velutinous-sericeous to sericeous, hairs 0.3–0.7 mm long, whitish or light-brown, stalk sessile to up to 0.2 mm long. *Sepals* 3–4.5 × 2–3 mm, expanded in fruiting, all biglandular, apex rounded, adpressed or reflexed, adaxially glabrous, abaxially tomentose, hairs 0.4–0.5 mm long, whitish, stalk sessile to up to 0.1 mm long; glands 2.2–2.5 × 1–1.3 mm, yellow. *Petals* yellow turning orange with age; lateral petals reflexed, lamina 5–6 × 6–7 mm, cupuliform, margin slightly erose, claws 3–4.2 × 0.5–0.7 mm, twisted; posterior petal erect, lamina 3–4.5 × 3–5 mm, corrugate, patent, margin slightly erose, claw 3.5–3.8 × 0.8–1 mm, straight. *Stamens* 10, free at base; filaments 2–3 × 0.5–1 mm, adaxially pilose at base, hairs 1–3 mm long, simple, brown, abaxially glabrous; connective 2–2.5 × 0.7–0.8 mm, apex acute or rounded, glabrous, exceeding or not the locules (up to 0.5 mm long); locules 2.4–3 × 0.7–1 mm, apex rounded, sparselly sericeous, hairs 0.5–1 mm long, whitish, stalk sessile, between or on the side of the locules. *Ovary* 1.2–2 × 0.8–1 mm, conical, glabrescent to glabrous, hairs 0.5–0.7 mm long, whitish, stalk sessile to up to 0.1 mm long; ovules 0.6–1.0 × 0.4–0.5 mm; styles 3.4–3.5 × 0.2–0.3 mm, linear, erect, bent at apex, glabrous. *Drupes* 7–10 mm diam., ovoid or globose, glabrescent to glabrous at apex, hairs 0.4–0.5 mm long, whitish, stalk sessile to up to 0.1 mm long.

Specimens selected:—**BOLIVIA.** **Beni:** Iténez, S side of Rio Guaporé, Campo Verde, ca. 15 km ESSE of Costa Marques-Rondônia-Brasil, 31 March 1987, Nee 34590 (NY, SP). **Santa Cruz:** Chiquitos, 1850, d'Orbigny 880 (G, P). **Velasco,** Estâncio Flor de Oro, W side of the Rio Guapore (=Rio Itenez), 0-1 km W of airstrip, 22 June 1991, Nee 41221

(SP). **BRAZIL. Bahia:** Formosa do Rio Preto, na margem da Várzea do Anil, 24 February 2005, *Xavier* 462 (ALCB, CEPEC). **Ceará:** Crato, Serra do Araripe, 06 November 1986, *Lima* 486 (IPA). **Goiás:** Alvorada do Norte, Fazenda Estâncio Paraná. Ponto 1, 24 August 2003, *Sevilha et al.* 3038 (CEN, CEPEC). Santa Izabel, Parque Nacional do Araguaia Ilha do Bananal, 6km norte da Sede, 18 June 1979, *Silva et al.* 183 (UB). Teresina de Goiás, Rio São João, 9 November 1991, *Hatschbach et al.* 55979 (MBM). **Maranhão:** Balsas, Condominio Kissy, Lote 23, 7 March 1996, *Pereira-Silva et al.* 3408 (CEN, SP). **Mato Grosso:** Araguaiana, Rio Pindaíba, 4 October 2012, *Rego 06* (UFMT). Barão de Melgaço, Fazenda Santa Lúcia, 3 October 1979, *Allem et al.* 2491 (CEN, SP). Cáceres, Fazenda Descalvados, 4 November 1978, *Allem et al.* 2390 (CEN, SP). Nobres, 5Km ao S pela Rod. BR-163, 22 October 1995, *Hatschbach et al.* 63993 (CPAP, CEPEC, MBM, UPCB). Nova Xavantina, 20 September 1967, *Argent et al.* 6439 (P); *loc. cit.*, 16 October 2004, *Pereira et al.* 3542 (CEPEC, IBGE). Poconé, Estrada Posto Espírito Santo-São Luís, 14 September 2004, *Lima Jr. et al.* 433 (HUEFS, UFMT). **Mato Grosso do Sul:** Corumbá, Área próxima-comunidade do Amolar, 4 November 2004, *Bortolotto et al.* 1613 (CGMS, COR, HRCB, MBM). Miranda, BR-262. Próximo a Miranda, 7 October 2009, *Francener et al.* 876 (CGMS, UFG, CEPEC). **Minas Gerais:** Januária, distrito de Fabião, 24 October 1997, *Lombardi* 2036 (BHCB, MBM, SPF). **Pará:** São Geraldo do Araguaia, Margem esquerda do rio Araguaia, mata da Fundação, Fazenda Andorinhas, retiro Santa Cruz, 23 April 2004, *Pereira-Silva et al.* 8977 (CEN, CEPEC). **Pernambuco:** Vitória de Santo Antão, Engenho Pombal, 27 March 1999, *Laurênia* 1558 (UFRN). **Rio Grande do Norte:** Parnamirim, estrada do Jiqui, Barreira do Inferno, 16 February 1999, *Cestaro* 99-0049 (UFRN). **Sergipe:** Pirambu, próximo à Lagoa Redonda, 17 January 2014, *Lemos-Filho s.n.* (169492). **Tocantins:** Araguatins, Lugar Antonina, 18 August 1961, *Oliveira* 1776 (IAN, UB). Conceição do Tocantins, Bacia do Tocantins, Sub-bacia do rio Palma, Fazenda Acácia, 30 June 2009, *Oliveira et al.* 1441 (HUTO, IBGE, SP).

Distribution, habitat and phenology:—*Byrsonima cydoniifolia* occurs in Bolivia and Brazil, especially over sandy soils, reaching Chapada Diamantina (state of Bahia), and some areas of caatinga and restinga vegetation in Northeastern Brazil (fig. 9). Large populations adapted to waterflood pulses are found in Pantanal wetlands and Araguaia River. Flowering and fruiting throughout the year.

Conservation status:—*Byrsonima cydoniifolia* should be regarded as Least Concern due to its wide distribution and abundant populations in South America.

Etymology:—The epithet probably refers to the resemblance to leaves of *Cydonia* Mill. (1754: 1) (Rosaceae).

Discussion:—*Byrsonima cydoniifolia* bears a whitish sericeous indument abaxially on leaves, inflorescences usually bearing small hairs (0.3–0.8 mm), and stalk usually sessile to subsessile (up to 0.1 mm long). Populations from the states of Bahia and Minas Gerais bear superficial sericeous-velutinous indument, with stalk up to 0.4 mm long, but deep hairs with sericeous indument, and stalk sessile to subsessile. Its closest species are *B. clauseniana* and *B. crassifolia*, the first being quite common in Brazilian cerrado, and also showing whitish hairs abaxially on leaves. However, these hairs bear a long stalk (usually longer than 0.4 mm long) and longer and more linear bracts in *B. clauseniana* than in *B. cydoniifolia*. *Byrsonima crassifolia* also bears triangular to narrowly triangular, small bracts, and hairs with stalk sessile to subsessile. However, it shows a whitish deciduous indument covering the leaves abaxially.

4. *Byrsonima guilleminiana* A.Juss. (1840: 331). Lectotype (here designated):—
BRAZIL. São Paulo, February 1839, *Guillemin* 356 (P barcode P02428542!). Figure 10.
= *Byrsonima guilleminiana* var. *arborescens* Griseb. (1858: 6). Type:—BRAZIL. Piauí:
Em campos na província do Piauí, s.d., *Gardner* 2496 (holotype: P05530871!, isotypes:
B†, P!).

Subshrubs, shrubs or trees, 0.3–6.0 m tall; trunk under or above ground, erect or tortuous, cylindric, usually exfoliating, exfoliated region, reddish to brown; stems sericeous, hairs 0.3–0.5 mm long, white, stalk sessile to up to 0.1 mm long, nodes lax or crowded at ground level. *Stipules* 4–10 × 4–7 mm, connate, triangular to widely ovate, adaxially sericeous to glabrous, hairs 0.4–0.7 mm long, white or light-brown, stalk sessile to up to 0.1 mm long, abaxially sericeous to tomentose-sericeous, hairs 0.3–1 mm long, white or light-brown, stalk sessile to up to 0.2 mm long,. *Leaves* opposite, entire, plane; petioles 2–8 mm long, sericeous, hairs 0.2–0.8 mm long, white, stalk sessile to 0.3 mm long; leaf blades 9.5–21 × 2.5–8.5 cm, coriaceous, elliptic, obovate, spatulate or oblanceolate, base decurrent or acute, margin slightly revolute, sinuate, apex acuminate, acute or retuse,

adaxially greenish or brown, shiny, sericeous to glabrous, mostly in the midrib, hairs 0.2–0.5 mm long, whitish or light-brown, stalk sessile to up to 0.1 mm long, abaxially whitish or brownish, sericeous, hairs 0.3–0.8 mm long, white, stalk sessile to up to 0.2 mm long, venation brochidodromous, 6–11 pairs of secondary veins, adaxially impressed, abaxially prominent, tertiary veins reticulate. *Thyrses* of (1–)2–4-flowered cincinni, with 27–38–flowers distributed in the median and distal portion of the rachis; rachis 14–17.5 cm long, canaliculated, wisth, sericeous, hairs 0.2–0.8 mm long, whitish or light-brown, stalk sessile to up to 0.2 mm long; bracts and bracteoles deciduous or persistent in fruiting; bracts 4–8 × 2.5–3 mm, narrow triangular to triangular, erect, adaxially tomentose to glabrous at base, hairs 0.7–1 mm long, light-brown, simple or branched, stalk sessile to up to 0.1 mm long, abaxially sericeous to sericeous-velutinous, hairs 0.3–0.8 mm long, light-brown, simple or branched, stalk sessile to up to 0.3 mm long; peduncle absent; bracteoles 2.5–3.5 × 1.5–2.5 mm, triangular, erect, adaxially tomentose to glabrous at base, hairs 0.7–1 mm long, light-brown, simple or branched, stalk sessile to up to 0.1 mm long, abaxially sericeous to sericeous-velutinous, hairs 0.3–0.8 mm long, light-brown, simple or branched, stalk sessile to up to 0.3 mm long; pedicels 6–16 mm long, erect or usually twisted in fruiting, usually sericeous, sometimes tomentose, hairs 0.3–0.8(–1.5) mm long, whitish or light-brown, stalk sessile to up to 0.3 mm long. *Sepals* 3.1–4 × 2.2–2.5 mm, expanded in fruiting, all biglandular, apex acute, adpressed to erect, adaxially glabrous, abaxially sericeous, hairs 0.3–0.6 mm long, light-brown, stalk sessile to up to 0.1 mm long; glands 1.8–2.5 × 1–1.4 mm, yellow. *Petals* yellow turning orange with age, glabrous; lateral petals reflexed, lamina 5.4–6.2 × 6.7–8 mm, cupuliform, margin slightly erose, claw 3.5–4 × 0.8–1 mm, twisted; posterior petal erect, lamina 4–5.7 × 4.8–6 mm, patent, margin erose, claw 3.5–4 × 1–1.2 mm. *Stamens* 10, connate at base; filaments 2.5–3.1 × 0.5–1 mm, adaxially densely pilose at base, hairs 0.5–3 mm long, whitish to brown, simple, abaxially glabrous; connectives 1.6–2.2 × 0.7–0.8 mm, apex acute or rounded, exceeding or not the locules (up to 0.2 mm long), glabrous; locules 1.8–2.5 × 0.6–0.7 mm, apex rounded, pubescent to glabrous, hairs sericeous, 0.7–1.5 mm long, stalk sessile, white or light-brown, between or on the sides of the sides of locules. *Ovary* conical, 1–1.8 × 1–2 mm, sericeous to glabrous, hairs 0.5–1 mm long, whitish, stalk sessile to up to 0.2 mm long; ovules 0.7–1.1 × 0.6–0.7 mm; styles 2.8–3.6 × 0.2–0.3 mm, erect, linear, subulate, bent at the apex, glabrous; stigmas minute. *Drupes* 7–9 mm diam., ovoid to globose, glabrescent to glabrous at apex, hairs 0.5–1 mm long, whitish or light-brown, stalk sessile to up to 0.1 mm long.

Specimens selected:—**BRAZIL: Distrito Federal:** Brasília, APA da Cafuringa Fercal, a 38 km do Cenagen, 9 August 1990, *Cavalcanti et al.* 628 (CEN, CEPEC, SP). **Goiás:** Alexânia, BR-060, 43 km de Brasília, 5 March 1985, *Hashimoto* 9255 (SP). Cristalina, próximo a Cachoeira do Arrojado, 20 January 2013, *Francener et al.* 1272 (CEPEC, SP, UFG, UFRN). Minaçu, Estrada paralela ao rio Tocantins, entre rio Tocantins e Serra Negra, 25 July 1995, *Cavalcanti et al.* 1663 (CEN, CEPEC, SP). **Maranhão:** Balsas, about 15-20 km NE of city of Balsas, 8 September 1963, *Eiten et al.* 5481 (SP, UB). **Minas Gerais:** Cabeceira Grande, estrada de acesso ao túnel, ca. 1 Km depois do Rio, 5 September 2001, *Cavalcanti et al.* 2728 (CEPEC). Paracatu, Serra da Anta ca. 2km N of Paracatu, 5 February 1970, *Irwin et al.* 26076 (NY, UB). **Piauí:** Uruçui, Barra da Volta, 12 May 2009, *Miranda et al.* 5888 (ASE, FUEL, HST, HUEFS, UFRN). **São Paulo:** São Paulo, Monumento do Ipiranga, 27 November 1894, *Edwall* 3024 (SP). São Roque, Porta do Sol, 8 March 1997, *Hashimoto* 13259 (SP). **Tocantins:** Almas, Bacia do Tocantins, Sub-bacia Manuel Alves da Natividade, Km 9 após a placa do projeto Tamborá, 5 July 2009, *Oliveira et al.* 1546 (HUTO, IBGE, SP). Dianópolis, Bacia do Tocantins, Sub-bacia do rio Palma, 1 July 2009, *Fonseca et al.* 5971 (HUTO, IBGE, SP). Jaú do Tocantins, Bacia do Tocantins, Sub-bacia do rio Santa Tereza, 9 July 2009, *Fonseca et al.* 6221 (HUTO, IBGE, SP, UFRN). Pequizeiro, a 9 km de Pequizeiro em direção a Conceição do Araguaia, 24 May 1990, *Pedralli et al.* 3320 (CEN, SP). Porto Nacional, Estrada para Natividade, ca. 6km de Porto Nacional, 16 July 2000, *Souza et al.* 23990 (CEPEC, ESA, RB).

Distribution, habitat and phenology:—*Byrsinima guilleminiana* is a common species from Brazilian Cerrado, found in the states of, Goiás, Maranhão, Minas Gerais, Piauí and São Paulo and in the Distrito Federal (fig. 11). It occurs in different Cerrado phytophysiognomies, especially in *cerrado sensu strictu*. Some populations occur disjunctly in the Atlantic Forest, in enclaves of cerrado, but usually only in savanic phytophysiognomies. Flowering and fruiting throughout the year.

Conservation status:—*Byrsinima guilleminiana* should be regarded as Least Concern due to its wide distribution and abundant populations in Brazil.

Etymology:—The epithet pays honor to A. Guillemin, collector of the type specimen.

Discussion:—*Byrsonima guilleminiana* was traditionally divided into two varieties, *B. guilleminiana* var. *arborecens* and *B. guilleminiana* var. *guilleminiana*. Both were distinguished by habit, and anther and ovary indument: variety *guilleminiana* is represented by subshrubs to shrubs bearing glabrous anthers and ovaries, while variety *arborecens* is represented by trees, and pilose anthers and ovaries. Nonetheless, those characters are not consistent in the analyzed specimens. The only pattern corroborated by our morphological studies is that in Northern Chapada dos Veadeiros (state of Goiás), specimens of *B. guilleminiana* are trees, and southern this region they are usually shrubs.

Specimens of *B. guilleminiana* var. *arborecens* were identified as *B. pachyphylla* in most of the consulted herbaria, due to the tree habitat and exfoliating trunks. We opted by considering this varietal name a synonym of *B. guilleminiana*, based on leaf indument and inflorescence architecture.

B. guilleminiana and *B. pachyphylla* are morphologically related, showing exfoliating and reddish trunks. However, *B. guilleminiana* shows sericeous indument abaxially on leaves and on inflorescence rachis, with hairs straight and sessile to subsessile, and pseudoracemes of 2-4-flowered cinni. On the other hand, *B. pachyphylla* shows tomentose, sometimes velutinous, indument abaxially on leaves and on inflorescence rachis, with hairs sinuate and stalked (2–10 mm long), and pseudoracemes of 1-flowered cinni.

5. *Byrsonima linearifolia* A. Juss. (1843: 279). Type:—BRAZIL. Goiás: Serra dos Cristais, s.d., Pohl 1489 (holotype: CGE!; isotypes: B†, BR barcode BR0000008579539!, K barcode K000426861!, W!). Figures 7A–E, 12.

Subshrubs, 12–45 cm tall; trunk erect or reptant, underground, glabrous; stems sericeous to glabrescent, hairs 0.5–1.4 mm long, whitish to brown to whitish-grayish to rusty-red, stalk up to 0.1 mm long; nodes lax. *Stipules* 1.4–4 × 0.7–1.3 mm, triangular, partially connate or free, adaxially shiny, glabrous, abaxially sericeous to sericeous-velutinous, hairs 0.5–1 mm long, whitish or brown, stalk sessile to up to 0.1 mm long. *Leaves* opposite, entire, plane; petioles sessile; leaf blades 8.3–14 × 0.3–0.9 cm, linear, base decurrent, margin entire, strongly revolute, apex acute, adaxially shiny, greenish to brown, glabrous, rarely sparsely sericeous, hairs 1–1.3 mm long, whitish, stalk sessile to up to 0.2 mm long, abaxially sericeous to sericeous-tomentose, hairs rusty-red to whitish, 0.8–1.5 mm long, stalk 0.1–0.3 mm long, venation brochidodromous, 9–14 pairs of

secondary veins, adaxially impressed, abaxially prominent (secondary and tertiary veins hidden by the indument). Thyrse of 1-flowered cincinni, 6–11–flowers distributed in the median and distal portions of the rachis, sometimes congested at apex resembling an umbrella; rachis 3.5–9 cm long, fissured (hidden by the indument), sericeous-tomentose, hairs 0.4–1 mm long, whitish or brown, stalk sessile to up to 0.1 mm long; bracts and bracteoles deciduous or persistent in fruiting; bracts 2.8–5 × 1–1.5 mm, narrowly triangular to triangular, erect, adaxially glabrous, abaxially velutinous or tomentose, hairs 0.5–1.5 mm long, whitish or rusty-red, stalk sessile to up to 0.1 mm long; peduncle absent; bracteoles 1.8–2.7 × 0.8–1 mm, narrowly triangular to triangular, erect, adaxially glabrous, abaxially velutinous or tomentose, hairs 0.3–0.7 mm long, whitish or brown, stalk sessile to up to 0.1 mm long; pedicels 8–11 mm long, bent at fruiting, sericeous-velutinous, hairs 0.3–1 mm long, whitish or brown, stalk sessile to up to 0.1 mm long. *Sepals* 4–4.7 × 2–2.5 mm, expanded in fruiting, all biglandular, apex acute, reflexed, adaxially glabrous, abaxially sericeous, hairs brown, 0.3–0.7 mm long, stalk sessile to up to 0.1 mm long; glands 1.5–2 × 1–1.2 mm, yellow. *Petals* yellow turning orange or red with age; lateral petals reflexed, lamina 6–7 × 5–6.5 mm, cupuliform, margin sinuate, claws 4–5 × 0.5–0.6 mm, twisted; posterior petal erect, lamina 5–6 × 5–8 mm, corrugate, patent, margin erose, claw 4–5 × 1–1.1 mm. *Stamens* 10, free at base; filaments 2–2.8 × 0.5–0.9 mm, adaxially pilose at base, hairs 1.5–2 mm long, whitish, simple, abaxially glabrous; connective 1.5–2 × 0.5–0.7 mm, apex rounded or acute, glabrous, exceeding or not the locules (up to 0.2–0.5 mm long); locules 2.5–2.8 × 0.6–0.8 mm, apex rounded, few spreading sericeous hairs, 0.5–1 mm long, whitish, between or rarely on the sides of locules. *Ovary* conical, 1.5–2 × 2–2.1 mm, sericeous, hairs 0.5–1 mm long, stalk sessile to up to 0.1 mm long, light-brown; ovules 0.5–0.8 × 0.6–1 mm; styles 3.5–4.5 × 0.2–0.3 mm, erect, linear, subulate, bent at apex, glabrous; stigma minute. *Drupes* 7–9 mm diam., ovoid, sericeous at apex, hairs 0.3–1 mm long, stalk sessile to up to 0.05 mm long, whitish.

Specimens selected:—**BRAZIL: Goiás:** Cristalina, ca. 7 km E of Cristalina on Brasília-Belo Horizonte highway, 21 February 1975, Anderson 11507 (MBM); *loc. cit.*, Morro do Padre BR 040, 7 km SE de Cristalina, camino a Paracatu, 1 February 1990, Arbo *et al.* 3314 (UPCB); *loc. cit.*, ca. 4 km nordeste de Cristalina ao longo da BR-040-050, 6 December 1988, Wanderley *et al.* 1863 (SP); *loc. cit.*, Serra dos Cristais, 5 km W of Cristalina, 2 November 1965, Irwin *et al.* 9796 (UB); *loc. cit.*, Serra dos Topázios, 10

September 1972, Rizzo 8375 (UFG); *loc. cit.*, 20 km antes de Cristalina, 23 October 1972, Rizzo 8520 (UFG); *loc. cit.*, 22 August 1973, Rizzo 9183 (UFG); *loc. cit.*, ca. 5 km da cidade, estrada para Paracatu, 4 February 1987, Pirani *et al.* 1558 (ESA, SPF); *loc. cit.*, Rio das Perdizes, 20 February 1990, Hatschbach 53775 (MBM); *loc. cit.*, RPPN Linda Serra dos Topázios, 29 October 1995, Proença *et al.* 1320 (CEPEC, MBM, UB); *loc. cit.*, 19 November 1995, Moretto *et al.* 13 (UB, SP); *loc. cit.*, estrada para Salto do Arrojado, 22 January 1997, Hatschbach *et al.* 66128 (ESA, MBM, UPCB); *loc. cit.*, 15 October 1960, Heringer 7764 (UB); *loc. cit.*, 10 Km de Cristalina em direção a Unaí, GO-309, 10 August 1998, Souza *et al.* 21355 (ESA, RB); *loc. cit.*, ca. de 10 Km de Cristalina em direção a Luziânia, 10 August 1998, Souza *et al.* 21431 (ESA, RB); *loc. cit.*, ca. 7 km by road NW of Cristalina on road to Brasília, 3 April 1973, Anderson 8059 (UB). **Minas Gerais:** Paracatu, Ramal entrando a NE da BR-040, 30 October 2010, Queiroz 15060 (HUEFS, SP).

Distribution, habitat and phenology:—*Byrsonima linearifolia* is restricted to a few localities in the States of Goiás and Minas Gerais (fig. 13), especially in the region of Serra dos Cristais. It occurs in *cerrado s.s.*, *campos úmidos* and *cerrados rupestres*. Flowering and fruiting throughout the rainy season, from September to April.

Conservation status:—*Byrsonima linearifolia* should be regarded as Endangered [categories B2ab(iii)], due to its area of occupancy of <500 km² and threats related to crystal mines and farming.

Etymology:—The epithet refers to the remarkable linear shape of its leaves.

Discussion:—*Byrsonima linearifolia* is a subshrub, up to 0.5 m tall, bearing linear and revolute leaves, petioles sessile to up to 0.5 mm long, stipules partially connate or free, pseudoracemes sometimes congested at the apex of rachis, resembling an umbrella.

6. *Byrsonima pachyphylla* A. Juss. (1833: 77). Lectotype (designated here):—
BRAZIL. Goiás: Villa Boa, *s.d.*, Saint-Hilaire Catal. Cl n. 799, (P barcode P00646286!; isolectotype: P barcode P00646287!). Figures 2F–J, 14.

= *Byrsonima grisebachiana* Nied. (1901: 23). Type:—BRAZIL. Minas Gerais: França, *s.d.*, Lund *s.n.* [VII 1834] (lectotype, designated by Anderson (2007): K!).

- = *Byrsonima pachyphylla* var. *latifolia* Nied. (1901: 27). **Lectotype (designated here):**
BRAZIL. Minas Gerais: Serra do Caraça, s.d., Ule 2456 (R!).
- = *Byrsonima pachyphylla* var. *obovata* Nied. (1901: 27). Type:—BRAZIL. São Paulo,
s.d., Löfgren 861 (holotype: B?; isotype: P!).
- = *Byrsonima pachyphylla* var. *lanceolata* Nied. (1901: 27). Type:—BRAZIL. Minas
Gerais: Aiuruoca, Campo da Ayurnoca, s.d., Glaziou 14557 (holotype: B?; isotype: ?).
- = *Byrsonima pachyphylla* f. *parvifolia* Nied. (1914: 54). Type:—BRAZIL. Minas Gerais:
São João Del Rey, Serra do Lenheiro, s.d., Langsdorff & Riedel 259 (holotype: B†).
- = *Byrsonimima crassa* Nied. (1901: 30). **Lectotype (designated here):**—BRAZIL.
Goiás: Guariroba, s.d., Glaziou 20770 (P barcode P05529538!; isolectotypes: BR!, K!,
MPU!, P barcodes P05529539!, P05529540!).
- = *Byrsonima crassa* f. *leiocarpa* Nied. (1901: 30). **Lectotype (here designated):**—
BRAZIL. Minas Gerais: Serra da Moeda, s.d., Claussen 133. (lectotype: P!;
isolectotype: S!).

Trees, 3–5 m tall; trunk erect or tortuous, cylindric, usually exfoliating, exfoliation region reddish to brown, glabrescent to glabrous, hairs 0.5–0.8 mm long, whitish or light-brown, stalk sessile to up to 0.2 mm long; stem velutinous to glabrous, hairs 0.5–2 mm long, whitish or light-brown, stalk sessile to up to 0.3 mm long; nodes congested or lax. *Stipules* 5–6 × 3–5 mm, deltate, connate or partially connate, adaxially shiny, glabrous, sometimes pilose at base, hairs 0.5–2 mm long, brown, unbranched, abaxially sericeous-velutinous, hairs 0.5–2 mm long, whitish or brown, grey and brittle with age, stalk sessile to up to 0.3 mm long. *Leaves* opposite, entire, plane; petioles sessile to up to 4–10 mm long, velutinous, hairs, 0.4–1 mm long, whitish, stalk sessile to up to 0.3 mm long; leaf blades 8–23 × 3–10.5 cm, lanceolate, elliptic to obovate, coriaceous, base cuneate, margin slightly revolute, sinuate, apex acuminate, acute or mucronate, rarely rounded, adaxially shiny, greenish or brown, glabrous or sericeous-tomentose at midrib, hairs 0.5–1 mm long, whitish or light-brown, stalk sessile to up to 0.2 mm long, abaxially tomentose, hairs 0.8–2.3 mm long, whitish, stalk 0.2–1 mm long, venation brochidodromous, 6–12 pairs of secondary veins, adaxially impressed, abaxially prominent, tertiary veins reticulate, hidden by the indument. *Thyrses* of 1–2 flowered cincinni, 6–36–flowers distributed in the median and distal portion of the rachis; rachis 5.5–16.5 cm long, canaliculated, fissurate or angulate (hidden by the indument), velutinous to tomentose, hairs 0.5–2 mm long, whitish or brown, stalk sessile to up to 0.3 mm long; bracts and bracteoles deciduous

to persistent in fruiting; bracts $5–8 \times 1.5–3$ mm, narrowly triangular to triangular, erect, adaxially glabrous, abaxially sericeous-velutinous or velutinous, hairs $0.5–1.5$ mm long, whitish or light-brown, unbranched or branched, stalk sessile to up to 0.1 mm long; peduncle sessile; bracteoles $2–4 \times 1–2$ mm, triangular, erect, adaxially glabrous, abaxially sericeous-velutinous or velutinous, hairs $0.5–1.5$ mm long, whitish or light-brown, unbranched or branched, stalk sessile to up to 0.1 mm long; pedicels $7–11(–17)$ mm long, erect or twisted in fruiting, tomentose, hairs $0.5–1.5$ mm long, whitish or light-brown, stalk sessile to up to 0.4 mm long. *Sepals* $5–6.5 \times 2.5–3.2$ mm, expanded in fruiting, all biglandular, apex acute, adpressed to reflexed, adaxially glabrous, abaxially sericeous to sericeous-tomentose, hairs $0.5–1$ mm long, light-brown, stalk sessile to up to 0.2 mm long; glands $2.5–3 \times 1–1.5$ mm, yellow. *Petals* yellow turning orange with age, glabrous; lateral petals reflexed, lamina $7–8 \times 8.5–10$ mm, cupuliform, margin slightly erose, claws $5–6 \times 0.5–1$ mm, twisted; posterior petal erect, lamina $5–6 \times 6–7$ mm, patent to reflexed, margin rose, claw $4–5 \times 1–1.1$ mm. *Stamens* 10, connate at base; filaments $2.8–4 \times 0.5–1$ mm, adaxially densely pilose at base, hairs $0.5–3$ mm long, simple, whitish to brown, abaxially pilose to glabrous at base, hairs $0.5–2$ mm long, simple, whitish or light-brown; connectives $2–2.5 \times 0.6–1$ mm, apex acute or rounded, glabrous, exceeding or not the locules (up to 0.2 mm long); locules $2.5–3 \times 0.5–0.8$ mm, apex rounded, sericeous to glabrous between or on the sides of locules, hairs $1–1.5$ mm long, spreading, stalk sessile, whitish or brown. *Ovary* conical, $2–3 \times 1.5–2$ mm, sericeous-tomentose to glabrous, hairs $0.7–2$ mm long, whitish, stalk sessile to up to 0.1 mm long; *ovules* $0.7–1 \times 0.6–1$ mm; *styles* $4–5.5 \times 0.2–0.3$ mm, linear, erect, subulate, bent at apex, glabrous. *Drupes* $5–7$ mm diam., ovoid, glabrescent to glabrous at apex, hairs $0.5–1.5$ mm long, whitish, stalk sessile to up to 0.1 mm long.

Specimens selected:—**BRAZIL: Bahia:** Correntina, Fazenda Jatobá, 5 June 1992, *Aparecida da Silva et al. 1266* (RB). **Distrito Federal:** Brasília, APA da Cafuringa Saindo da DF-180 rumo Brasília pela DF-220, 4 June 1992, *Dias et al. 200* (CEN, SP). **Goiás:** Alto Paraíso de Goiás, Parque Nacional da Chapada dos Veadeiros Próximo a sede do Parque, 16 October 2010, *Francener et al. 1027* (CGMS, UFG). Aporé, ca. 65 km de Aporé, 2 August 1995, *Pietrobom-Silva 2315* (MBM). Caiapônia, Serra do Caiapó ca. 30km S of Caiapônia, road to Jataí, 29 June 1966, *Irwin et al. 17975* (IAN, MO, NY, SP, UB). Caldas Novas, Parque Estadual da Serra de Caldas Novas, 15 April 2008, *Francener et al. 591* (UFG). Cristalina, 7 km da entrada de Cristalina em direção a

Paracatu, BR-040, 17 July 2007, Monteiro *et al.* 75 (CEPEC, RB, SP). Pirenópolis, Estrada da Seda da Agência Ambiental para o Morro do Cabeludo, 26 November 2005, Delprete *et al.* 9297 (NY, UB). **Mato Grosso:** Araguainha, Fazenda Ribeirão das Pedras, próximo a sede da fazenda, 28 July 2009, Francener 815 (CGMS, UB, UFG). Barra do Garças, Serra do Roncador, 2.4 Km S of Landico's restaurant, 24 November 1969, Eiten *et al.* 9519 (NY, SP). Ponte Branca, propriedade de Laerte Nogueira de Moraes, no córrego do Marreco, divisa entre os municípios de Araguainha e Ponte Branca, 30 July 2009, Francener *et al.* 825 (CGMS, UFG). **Mato Grosso do Sul:** Aquidauana, Morro Paxixi Distrito de Camisão, 28 June 2008, Barbosa-Filho 26 (CGMS). Bataguassu, Rod. BR-267, 14 May 1970, Hatschbach 24259 (CEPEC, ESA, FLOR, MBM, SP). Corguinho, Comunidade de Taboco, no Salto do Taboco, 19 September 2009, Francener 871 (UFG). **Minas Gerais:** Joaquim Felício, Serra do Cabral Estrada para Francisco Dumont, 22 September 2005, Hatschbach *et al.* 79438 (MBM, RB). Uberlândia, Sítio Capim Branco, BR-365, Km 634, 17 July 1984, Vieira 253 (HUFU, MBM, NY, SP, UEC). **São Paulo:** Araraquara, ca. 12 km west of village of Tamoio, Fazenda Tamoyo, part called Santa Joana, 21 June 1961, Eiten *et al.* 3129 (NY, SP, UB). Bauru, Jardim Botânico Municipal de Bauru, trilha para Antiga Raia, 29 July 2003, Weiser *et al.* 258 (UEC, SP).

Distribution, habitat and phenology:—*Byrsonima pachyphylla* is a common species from Brazilian Cerrado, distributed in the states of Bahia, Goiás, Mato Grosso, Mato Grosso do Sul, Minas Gerais and São Paulo and in Distrito Federal (fig. 15). It occurs in different Cerrado phytopysiognomies, especially in *cerrado sensu strictu*. Flowering from March to January and fruiting from August to February.

Conservation status:—*Byrsonima pachyphylla* should be regarded as Least Concern, due to its wide distribution and abundant populations in South America.

Etymology:—The epithet refers to its thick leaves.

Discussion:—*Byrsonima pachyphylla* is a small tree, with usually exfoliating, reddish trunks, and thick leaves, adaxially shiny, sericeous-tomentose to glabrous along the midrib. Its closest species are *B. crassifolia* and *B. cydoniifolia*, but leaves, stipules and flowers in *B. pachyphylla* are quite larger, especially the lateral petals, filaments, ovary and styles.

7. *Byrsonima termitaria* Francener & Mamede, sp. nov.

Type:—BRAZIL. Goiás: Mineiros, Parque Nacional das Emas, 10 August 2012, fl., *Francener et al. 1146* (holotype: SP003447!; isotype: UB!). Figures 16A–F, 17.

This species is morphologically similar to Byrsonima verbascifolia, but readily distinguished by its reduced stipules and leaves, petioles adpressed, base of leaf blades cuneate, adaxial side of the leaves glabrous; and by reduced inflorescences.

Subshrubs, up to 11 cm tall; trunk gnarled, underground, sericeous-velutinous to glabrous near the leaves, hairs 0.4–1 mm long, brown, stalk sessile to up to 0.2 mm long; stems absent, nodes crowded, close to the ground. *Stipules* 4–7 × 2.1–3 mm, connate, triangular or ovate, abaxially sericeous-velutinous to velutinous, hairs 0.5–1.5 mm long, whitish to light-brown, unbranched or branched, stalk sessile to up to 0.2 mm long, adaxially shiny, glabrescent to glabrous at base, hairs 1–1.5 mm long, brown, unbranched. *Leaves* opposite, entire, plane, crowded, at ground level, sometimes deciduous; petioles sessile to up to 2 mm long, glabrous; leaf blades 8.5–14.5 × 4–9 cm, obovate, base cuneate, margin sinuate, slightly revolute, apex obtuse or mucronate, adaxially shiny, green-brown, glabrous, abaxially whitish, sericeous to sericeous-velutinous, hairs 0.5–1 mm long, whitish, stalk sessile to up to 0.2 mm long, venation brochidodromous, 6–8 pairs of secondary veins, adaxially impressed, abaxially prominent, tertiary veins reticulate. *Thyrses* of 1–2-flowered cincinni, 8–18 flowers distributed in the median to distal part of the rachis; rachis 7.5–11 cm long, canaliculate (hidden by the indument), tomentose to velutinous, hairs 0.3–2 mm long, whitish or light-brown, unbranched to branched at base, stalk sessile up to 0.2 mm long; bracts and bracteoles deciduous; bracts 5.5–8 × 1.5–1.7 mm, narrowly triangular to subulate, erect or reflexed, adaxially glabrous, abaxially sericeous-velutinous, hairs 0.3–1.5 mm long, whitish or brown, branched or unbranched, stalk sessile to up to 0.3 mm long; peduncle sessile to up to 2 mm long; bracteoles 2.5–4.8 × 0.8–1.6 mm, narrowly triangular, erect, adaxially glabrous, abaxially sericeous-velutinous, hairs 0.3–1.5 mm long, whitish or brown, branched or unbranched, stalk sessile to up to 0.3 mm long; pedicels 9–12 mm long, sericeous-velutinous, hairs 0.4–1.5 mm long, whitish or brown, branched or unbranched, stalk sessile to up to 0.3 mm long. *Sepals* 4–5 × 2.5–3.8 mm, all biglandular, apex obtuse to rounded, adpressed to erect, adaxially glabrous, abaxially sericeous, hairs 0.5–1.3 mm long, whitish or light brown, branched, stalk sessile to up to 0.2 mm long; glands 1.8–3 × 1–1.5 mm, yellow.

Petals yellow, glabrous; lateral petals reflexed, lamina $6.5–7 \times 8.9–10$ mm, cupuliform, margin sinuate, claws $3.5–5 \times 0.8–0.9$ mm, bent or twisted; posterior petal erect, lamina $4–5 \times 5–6$ mm, corrugate, patent, margin erose, claw $3.4–5 \times 0.8–1$ mm. *Stamens* 10, connate at base; filaments $2–3.2 \times 0.7–1$ mm, adaxially pilose at base, hairs 1–3 mm long, simple, whitish or brown, abaxially glabrous; connectives $2–2.8 \times 0.7–1$ mm, apex rounded, not exceeding the locules, glabrous; locules $3.1–3.5 \times 1–1.3$ mm, sericeous between or on the sides of locules, hairs 1–2 mm long, spreading, stalk sessile. *Ovary* conical, $1.8–2.1 \times 1.3–2$ mm, sericeous, hairs 0.4–1.5 mm long, whitish or light-brown, branched, stalk sessile to up to 0.2 mm long; ovules $0.8–0.9 \times 0.6–0.7$ mm; styles $2.2–4 \times 0.2–0.3$ mm, linear, erect, subulate, glabrous; stigmas minute. *Drupes* not seen.

Specimens examined (paratypes):—BRAZIL. Goiás: Parque Nacional das Emas, 22 September 1989, fl., Ferreira 2509 (UFG).

Distribution, habitat and phenology:—*Byrsonima termitaria* is endemic to Emas National Park, state of Goiás, Brazil (fig. 18). It occurs in *cerrado sensu strictu*, usually associated with termite nests, which are quite common in this area. Flowering from August to September.

Conservation status:—*Byrsonima termitaria* should be regarded as Critically Endangered [categories B2ab(iii, iv)], due to its area of occupancy be $<10 \text{ km}^2$, and for the fact that the conservation unit suffers with high rates of fires and pressure of soy farms nearby the park.

Etymology:—The epithet refers to the termite nests commonly found associated to populations of this species.

Discussion:—*Byrsonima termitaria* is a subshrub with underground trunk, bearing adpressed leaves crowded at ground level, adaxially glabrous, and short inflorescences. The closest species is *B. verbascifolia*, which is also a subshrub with crowded leaves close to the ground. They can be distinguished by the following characters: *B. termitaria* bears smaller stipules, leaves, inflorescence, bracts and bracteoles, the base of leaf blades is cuneate and adaxially glabrous, the petioles are sessile or up to 2.0 mm long. In *B.*

verbascifolia the petiole is longer than 5.0 mm, the base of the leaf blades is attenuate and adaxially hairy, with persistent unbranched hairs.

8. *Byrsonima verbascifolia* (L.) DC. (1824: 579). ≡ *Malpighia verbascifolia* L. (1753: 426). Type:—AMERICA CALIDIORE, *s.d.*, *s. leg.* (holotype: LINN588.10!). Figures 16G–I, 19.

= *Byrsonima verbascifolia* var. *petiolata* A.Juss. (1833: 75). Type:—BRAZIL. *S.loc.*, *s.d.*, *Ferreira s.n.* (holotype: P!).

= *Byrsonima verbascifolia* var. *angustifolia* A.Juss. (1833: 76). Type:—BRAZIL. Minas Gerais: *S.loc.*, *s.d.*, *Saint-Hilaire s.n.* (holotype: P!).

= *Byrsonima verbascifolia* var. *denudata* Cuatrec. (1958: 605). Type:—COLOMBIA. Vaupés: San José del Guaviare, *s.d.*, *Cuatrecasas 7713* (holotype: COL!, isotypes: F!, NY!, US!).

= *Byrsonima verbascifolia* var. *spathulifolia* A.Juss. (1833: 76). Type:—BRAZIL. Minas Gerais: Sertão, *s.d.*, *Laruotte s.n.* (holotype: P barcode P00631826!, isotypes: MPU!, P!).

= *Byrsonima verbascifolia* f. *spathulata* Nied. (1901: 29). **Lectotype (designated here):**—GUYANA. *S.loc.*, *s.d.*, *Rob Schomburgk I 91.* (MPU!, isolectotype: BR!; P barcodes P05529776!, P05529786!; P05529775!; TCD!).

= *Byrsonima subterranea* Brade & Markgr. (1950: 30). *syn. nov.* Type:—BRAZIL. Minas Gerais: Belo Horizonte, Serra Taquaril, *s.d.*, *Markgraf 3590* (holotype: RB!).

Subshrubs, up to 60 cm tall; trunk underground, gnarled, twisted, glabrescent to glabrous, hairs 1–2 mm long, stalk sessile; stems sessile; nodes congested. *Stipules* 7–13 × 4–7 mm, connate, narrowly triangular, adaxially shiny, glabrous, abaxially velutinous, hairs 1–3 mm long, simple, whitish or light-brown. *Leaves* opposite, entire, plane, congested, at ground level; petioles 0.5–4 cm long, tomentose or velutinous, hairs 0.5–3 mm long, whitish or brown, unbranched or branched, stalk sessile to up to 0.1 mm long, leaf blades 14.5–33.5(–40) × 4.5–16(–28) cm, oblanceolate, obovate or spatulate, base attenuate, margin sinuate, slightly revolute, apex acute, acuminate or obtuse, adaxially light-green to glaucous-green, velutinous, sparsely velutinous or glabrescent, hairs 0.8–1.5 mm long, simple, bright at light, rarely branched, stalk sessile to up to 0.1 mm long, abaxially whitish, densely velutinous, tomentose or rarely glabrous, hairs 0.8–1.8 mm long unbranched or branched, stalk sessile to up to 0.1 mm long, venation brochidodromous,

8–12 pairs of secondary veins, adaxially impressed, abaxially prominent, tertiary veins reticulate. *Thyrses* of 1–2-flowered cincinni, with (6)14–60 flowers distributed in the median and distal portions of the rachis, sometimes with a few flowers at base; rachis (7–)12.5–41 cm long, canaliculate (hidden by the indument), velutinous to tomentose, hairs 0.7–3 mm long, whitish, unbranched or branched, stalk sessile to up to 0.3 mm long; bracts and bracteoles deciduous or not in fruiting; bracts 9–10 × 1.5–2 mm, narrowly triangular or subulate, erect, adaxially glabrous, abaxially sericeous-velutinous, hairs 0.4–2 mm long, simple or branched, whitish or light-brown, stalk sessile to up to 0.2 mm long; peduncle sessile; bracteoles 3.5–6.5 × 0.6–1 mm, narrowly triangular or subulate, erect, adaxially glabrous, abaxially sericeous-velutinous, hairs 0.4–1.5 mm long, whitish or light-brown, unbranched or branched, stalk sessile to up to 0.2 mm long; pedicels 9–16 mm long, erect to reflexed in fruiting, velutinous, hairs 0.4–1 mm long, whitish, unbranched or branched, stalk sessile 0.1 mm long. *Sepals* 4.5–5 × 2–2.6 mm, expanded in fruiting, all biglandular, apex acute or obtuse, adpressed to reflexed, adaxially glabrous, abaxially sericeous, hairs 0.5–1 mm long, whitish, branched, stalk sessile to up to 0.1 mm long; glands 2–2.7 × 0.8–1 mm, yellow. *Petals* yellow turning orange with age, glabrous; lateral petals reflexed, lamina 5–7 × 6.5–7 mm, cupuliform, margin sinuate, claws 3.5–4.8 × 0.4–0.5 mm, twisted; posterior petal erect, lamina 4–4.2 × 5–6 mm, corrugate, patent, margin sinuate or erose, claw 3.8–4 × 0.6–1 mm. *Stamens* 10, connate at base; filaments 2–3 × 0.6–1 mm, pilose at base on both faces or usually adaxially, hairs 1–2.5 mm long, simple, whitish or brown; anthers 2.3–2.9 × 0.7–1 mm, sericeous between or on the sides of locules, hairs 0.8–1 mm long, branched, whitish, stalk sessile to up to 0.1 mm long; connective 1.8–2.2 × 0.4–0.6 mm, apex acute or rounded, exceeding or not the locules (up to 0.3 mm long), glabrous. *Ovary* conical, 1.8–2.5 × 1.4–2.3 mm, velutinous or glabrous, hairs 0.5–2.5 mm compr., unbranched, whitish or brown; ovules 0.7–1.2 × 0.4–0.7 mm; styles 3.1–5.0 × 0.2–0.3 mm, linear, erect, subulate, bent at apex, sometimes towards the posterior petal, glabrous; stigmas minute. *Drupes* ovoid or globose, 8–11 mm diam., velutinous to glabrescent, hairs 0.5–2.5 mm long, unbranched.

Specimens selected:—**BOLIVIA. Santa Cruz:** Velasco, Parque Nacional Noel Kempff Mercado, Campamento Las Gmas, 27 October 1995, *Killeen* 7799 (MEX, NY). **BRAZIL. Acre:** Rio Branco, Território Federal do Rio Branco, 6 November 1954, *Jaccoud s.n.* (IAN110850, INPA290, SP74978). **Amapá:** Calçoene, Near the rio Amapá Grande on the Amapá to Calçoene road, 30 November 1993, *Ratter et al.* 6905 (INPA,

UEC). **Amazonas:** Humaitá, 500m ao Noroeste da BR-230 Km 7, 20 August 1980, *Janssen et al.* 528 (INPA, RB). **Bahia:** Correntina, Faz. Jatobá, 8 August 1992, *Aparecida da Silva* 1613 (UB). **Distrito Federal:** Brasília, Parque Ecológico Norte Burle Marx , 18 September 2003, *Santos et al.* 54 (CEN, CEPEC, SPSF). **Goiás:** Alto Paraíso de Goiás, Chapada dos Veadeiros, Trilha da Raizama, 16 October 2010, *Francener et al.* 1032 (UFG). Aragarças, Fazenda de Geraldão, ca. 150 km on the road S of Base Camp, 8 November 1968, *Harley et al.* 10956 (IAN, NY, P, RB, UB). São João da Aliança, Fazenda Capão da Onça, 28 May 1975, *Hatschbach* 36962 (CEPEC, MBM). **Mato Grosso:** Araguainha, Domo de Araguainha, 9 November 2000, *Sousa Silva* 154 (CEPEC). Chapada dos Guimarães, Parque Nacional da Chapada dos Guimarães Morro São Gerônimo, 21 November 1999, *Amorim Neto et al.* 997 (UFMT). **Mato Grosso do Sul:** Costa Rica, Rio Sucuriú, próximo da Cachoeira da Rapadura, 26 October 2012, *Francener et al.* 1195 (SP). Três Lagoas, Fazenda Floresta. Prop. Joaquim Queirós, 17 September 1964, *Gomes Júnior* 2137 (UB). **Minas Gerais:** Coronel Xavier Chaves, Dom Silvério, 8 November 2011, *Sobral* 14429 (HUFSJ, RB). Sacramento, Estrada Sacramento-Franca, 8 June 1984, *Vieira et al.* 246 (HUFU, MBM, SP, UEC, UB). **Pará:** Salvaterra, Condeixas, Transmarajoara, estrada que vai a Cachoeira do Arari, 10 October 1982, *Rosário et al.* 123 (INPA). Ilha de Marajó, Direção a Camará de Marajó, 2 October 1995, *Ferreira* 453 (HBR, MBM). **Paraná:** Arapoti, Margem da PR-239, 4 November 2007, *Caxambu et al.* 1896 (HCF). Jaguariaíva, Fazenda Cajuru, 13 October 1968, *Hatschbach* 20059 (MBM, P). **Roraima:** Boa Vista, along Boa Vista-BV 8 road (BR-174), Km 76, by Uraricoera river, 8 October 1977, *Coradin et al.* 549 (IAN, INPA, CEN). Caumé, along Boa Vista-BV 8 road (BR-174) Km 9, 14 October 1977, *Coradin et al.* 668 (CEN, IAN, INPA). **São Paulo:** Pedregulho, Estreito Perto da Faz. Três Irmão, 5 November 1997, *Marcondes-Ferreira et al.* 1473 (ESA, SP, SPF, UEC); Estreito, Igaçaba, Cerrado com afloramentos quartzíticos, perto do Morro Solteiro, 12 November 1994, *Marcondes-Ferreira et al.* 1015 (SP, SPF, UEC). **Tocantins:** Dianópolis, 27 September 2003, *Scariot et al.* 923 (CEN, CEPEC, ESA, RB, SP). **COLÔMBIA.** **Bogotá:** San Martin, s.d., *Triana s.n.* (P05474878). **Boyacá:** *S.loc.*, Region de Sta. Elena, 26 February 1971, *Sastre* 890 (P). **Meta:** Remolino, Entre Caño Victoria y Caño Piedra de Candela, 15 February 1969, *Pinto et al.* 866 (P). **Vichada:** *S.loc.*, carretera entre Pto. Carreño y Pto. Gaitán, 20 km adelante de Monserrate, 20 March 1971, *Pinto et al.* 1404 (P). **CUBA.** Isle of Pines, 1916, *Britton et al.* 14139 (P); *loc. cit.*, Ramon de La Sagra, s.d., *s.leg. s.n.* (P05529814). **FRENCH GUIANA.** **Cayenne:** Pariacabo, 15 December

1914, *Benoist* 1696 (P). **GUYANA.** **Isherton:** Basin of Rupununi River, November 1937, *Smith* 2412 (P). **East Berbice-Corentyne:** Canje River 1 km N & S of Digitima creek, 0.5 km W of river, 15 April 1987, *Pipoly et al.* 11630 (P). **SURINAM.** *S.loc.*, December 1842, *Hostmann* 1296 (P); *loc. cit.*, 1843, *Hostmann* 1496 (P). **VENEZUELA.** Caracas, 1843, *Funk* 466 (P). **Apure:** Pedro Camejo, Along the Río Meta at the junction of the Caño Siriaco, 15.4 airline km W of Buena Vista, 15 February 1978, *Davidse et al.* 14157 (MEX, P). **Rómulo Gallegos:** area between the Laguna del Termino and the Río Capanaparo, 24-32 airline km SW of Elorza, 7 March 1979, *Davidse et al.* 16137 (P).

Distribution, habitat and phenology:—*Byrsonima verbascifolia* is widespread in the Neotropics, occurring from Cuba, and Northern South America to Southern Brazil (fig. 20). It occurs in open dry areas of neotropical savannas (cerrados). Flowering throughout the year, and fruiting from August to March.

Conservation status:—*Byrsonima verbascifolia* should be regarded as Least Concern, due to its wide distribution and abundant populations in Cuba and South America.

Etymology:—The epithet refers to the resemblance of its leaves to that of *Verbascum* L. (1753: 177) (Scrophulariaceae).

Discussion:—*Byrsonima verbascifolia* was formerly known as *B. subterranea*, a common subshrub with underground trunk, bearing adpressed large leaves crowded at ground level, unbranched hairs adaxially on leaves, and elongated inflorescences. When we analyse the type of *B. verbascifolia*, it shares the characters describe above. Thus based on the priority of names, we selected the name *B. verbascifolia*.

Its closest species is *B. termitaria*, which bears adaxially glabrous leaves, smaller stipules, leaves and inflorescences, and petioles usually sessile to up to 2.0 mm long, while in *B. verbascifolia* it is always longer than 5.0 mm long.

Tree specimens widely known as *B. verbascifolia* in Brazilian cerrado, are morphologically similar *B. verbascifolia* s.s., but further studies are needed to clarify the true identity of this taxa (*B. verbascifolia* *sensu lato*).

Incertae sedis

The remaining names placed in *Byrsonima* sect. *Eriolepis* Nied. (1901: 1), which could not be assigned to *Byrsonima crassifolia* clade, are here presented. These names were not sampled in the molecular phylogeny of *Byrsonima* or were placed in a basal polytomy in Core *Byrsonima*. We believe that most of these names should probably be placed in a *B. crassifolia* clade *s.l.* in the near future, once additional genetic markers are included in the phylogeny presented in Chapter 1. Additionally, we present lectotypifications of all names related to *Byrsonima* sect. *Eriolepis* Nied. (1901: 1).

1. *Byrsonima* sect. *Eriolepis* Nied. (1901: 15). **Lectotype (designated here):**—*Byrsonima crassifolia* A. Juss. (1822: 149). \equiv *Malpighia crassifolia* L., (1753: 426).
2. *Byrsonima* sect. *Eriolepis* subsect. *Macropus* Nied. (1901: 15). **Lectotype (designated here):**—*Byrsonima fagifolia* Nied. (1901: 20).
3. *Byrsonima* sect. *Eriolepis* subsect. *Macropus* ser. *Pyrrhos* Nied. (1901: 15). **Lectotype (designated here):**—*Byrsonima pinetorum* Griseb. (1866: 42).
4. *Byrsonima* sect. *Eriolepis* subsect. *Macropus* ser. *Eriodes* Nied. (1901: 19). **Lectotype (designated here):**—*Byrsonima fagifolia* Nied. (1901: 20).
5. *Byrsonima* sect. *Eriolepis* subsect. *Brachypus* Nied. (1901: 22). **Lectotype (designated here):**—*Byrsonima variabilis* A. Juss. (1833: 78).
6. *Byrsonima* sect. *Eriolepis* subsect. *Brachypus* ser. *Brachybotrys* Nied. (1901: 22). **Lectotype (designated here):**—*Byrsonima variabilis* A. Juss. (1833: 78).
7. *Byrsonima* sect. *Eriolepis* subsect. *Brachypus* ser. *Pachybotrys* Nied. (1901: 26). **Lectotype (designated here):**—*Byrsonima pachyphylla* A. Juss. (1833: 77).
8. *Byrsonima basiloba* A.Juss. (1840: 331). Lectotype (designated by Anderson 2007):—BRAZIL. Goiás, *s.d.*, Gardner 3617 (G!; isolectotypes: G!, K!, NY!, P!).
9. *Byrsonima dealbata* Griseb. (1839: 253). Holotype:—B†. **Lectotype (designated here):**—BRAZIL. *S.loc.*, *s.d.*, Sellow 1860 (K barcode K000426863!).

= *Byrsonima dealbata* var. *montana* Nied. (1901: 24). Type:—BRAZIL. Minas Gerais: Itacolomi, summit of Mt. Itacolumi, *s.d.*, *Martius s.n.* (holotype: B†).

10. *Byrsonima eriopoda* DC., (1824: 579). Type:—TROPICAL AMERICA. *S.loc., s.d., s. leg.* (holotype: G-DC!).

11. *Byrsonima fagifolia* Nied. (1901: 20). **Lectotype (designated here):**—BRAZIL. Bahia: Santo Antônio prope Vila de Barra, *s.d.*, *Blanchet 3139* (G!; isolectotype: F!, K!, MG!).

12. *Byrsonima karwinskiana* A.Juss. (1840: 333). Type:—MEXICO. *S.loc., s.d.* *Karwinski s.n.* (holotype: M?).

13. *Byrsonima martiana* A.Juss. (1840: 333). Type:—BRAZIL. Minas Gerais, *s.d.*, *Martius s.n.* (holotype: M?).

14. *Byrsonima pinetorum* Griseb. (1866: 42). ≡ *Byrsonima crassifolia* var. *pinetorum* (Griseb.) M. Gómez (1890: 231). Type:—CUBA, *s.d.*, *Wright 2144*, (holotype: GOET barcode GOET007105!; isotypes: GH barcode GH00045063!, JE barcode JE00004830!, K barcode K000424382!, NY barcode NY01043301!, P barcode P02428667!, S barcodes S08-15581!, S-R-10162!, US barcode US00108730!, YU barcode YU001349!).

15. *Byrsonima psilandra* Griseb. (1839: 251). Type:—BRAZIL. Southern Brazil: *s.d.*, *Sellow s.n.* (holotype: ?; isotype B†).

16. *Byrsonima salzmanniana* A.Juss. (1840: 331). Type:—BRAZIL. Bahia. *s.d.*, *Salzmann s.n.* (holotype: G barcode G00352805!; isotypes: CGE!, G!, K!, MO!, MPU!, P!).

17. *Byrsonima variabilis* A.Juss. (1833:78). Type:— BRAZIL. Minas Gerais: Serra do Caraça, *s.d.*, *Laruotte 296* (holotype: P barcode P02428630!, isotypes: P!, MPU!).
= *Byrsonima variabilis* f. *jussieuana* Nied. (1901: 23). **Lectotype (designated here):**— BRAZIL. Minas Gerais: Serra da Piedade, *s.d.*, *Lund s.n.* (P barcode P05529752!).

- = *Byrsonima variabilis* f. *lanceolata* Nied. (1901: 23). Type:—BRAZIL. Minas Gerais: Caldas, s.d., *Regnell II* 33 ½ (holotype: S!; isotype: S!).
- = *Byrsonima variabilis* f. *latifolia* Nied. (1928: 728). **Lectotype (designated here):** BRAZIL. Minas Gerais: Pico d’Itabira, s.d., *Claussen* 20 (P barcode P05529766!, isolectotype: P barcode P05529767!).
- = *Byrsonima variabilis* f. *oblongifolia* Nied. (1901: 22). Type:—BRAZIL. Minas Gerais: Caldas, s.d., *Regnell I* 36 (S barcode S08-15596!, isolectotypes: R!, S barcodes S08-15999!, S08-15601!, S08-15600!).
- = *Byrsonima variabilis* f. *ovata* Nied. (1901: 23). **Lectotype (designated here):**—BRAZIL. Minas Gerais: *S.loc.*, s.d., *Ackermann* 247. (BR barcode BR869762!; isolectotype: BR barcode BR869873!).
- = *Byrsonima variabilis* f. *subcordata* Griseb. (1839: 252). Type:—BRAZIL. Minas Gerais: Villa Rica, s.d., *s.leg.* (holotype: P?).
- = *Byrsonima variabilis* f. *vulgaris* (A.Juss.) Griseb. (1839: 252). Type:—BRAZIL. Minas Gerais: Serra do S. Antonio, s.d., *Sellow s.n.* (holotype: B?).
- = *Byrsonima variabilis* var. *glabrifolia* A.Juss. (1833: 79). Type:—BRAZIL. Minas Gerais: Villa Rica, s.d., *Saint-Hilaire Catal.* B1 no. 154 (holotype: P barcode P02428633!, isotype: MPU!, P barcode P02428634!, US!).
- = *Byrsonima variabilis* var. *lancifolia* A.Juss. (1833: 79). Type:—BRAZIL. Minas Gerais: *S.loc.*, s.d., *Laruotte s.n.* (holotype: P barcode P0248527!, isotype: MPU!, P barcode P02428528!).
- = *Byrsonima variabilis* var. *rotundata* Griseb. (1876: 123). Type:—BRAZIL. Minas Gerais: Serra da Piedade, s.d., *Warming s.n.* (holotype: C?; isotype: GOET!). ≡ *Byrsonima variabilis* A.Juss. var. *velutina* Nied. (1901: 22). *nom. superfl.*

- 18. *Byrsonima viminifolia* A.Juss.** (1833: 83). Type:—BRAZIL. Goiás: Vila Boa, s.d., *Saint-Hilaire Catal.* C1 n. 789 (holotype P barcode P02428672!, isotypes: MPU!, P barcode P02428673!).
- = *Byrsonima viminifolia* A.Juss. var. *vulgaris* Nied. (1901: 23). **Lectotype (designated here):**—BRAZIL. Goiás: Cabeceiras do Rio Gama, *Glaziou* 20773 (lectotype: P barcode P04870472!, isolectotypes: BR!, MPU!, P!, S!).

19. *Byrsonima viminifolia* A.Juss. var. *latifolia* Nied. (1901: 23). **Lectotype (designated here):**—BRAZIL. Goiás: Cabeceiras do Rio Torto, *Glaziou* 20777 (P barcode P04870473!, isolectotypes: BR!, P barcode P04870471!).

20. *Byrsonima viminifolia* A.Juss. var. *humilis* Nied. (1901: 24). **Lectotype (designated here):**—BRAZIL. Goiás: Cabeceiras do Rio Torto, *Glaziou* 20772 (P barcode P00506159!; isolectotypes: BR!, K!, MPU!, NY!, P!, S!). = *Byrsonima onishiana* W. R. Anderson, (1982: 96).

The following names are relative to *Byrsonima verbascifolia* s. l., which revealed to be distantly related to *Byrsonima crassifolia* clade in the molecular phylogeny presented in Chapter 1. Careful taxonomic studies are needed in the future for a better comprehension of this taxon, and the application of these names:

21. *Byrsonima verbascifolia* (L.) DC. var. *discolor* Griseb. (1839: 250). Type:— BRAZIL. Minas Gerais: Serra do S. Antonio, *s.d.*, *Sellow s.n.* (syntype: B?); Tapera, *s.d.*, *Sellow s.n.* (syntype: B?); Serra de Pitangui, *Sellow s.n.* (syntype: B?); Bahia, *s.d.*, *Lhotzky s.n.* (syntype: B?).

22. *Byrsonima verbascifolia* (L.) DC. var. *intermedia* A.Juss. (1833: 76). Type:— BRAZIL. Minas Gerais: Serra das Carrancas, *s.d.*, *Saint-Hilaire Catal. D no. 423* (holotype: P?, isotype: P barcode P00631832!).

23. *Byrsonima verbascifolia* (L.) DC. var. *lanata* A.Juss. (1843: 280). Type:— BRAZIL. Minas Gerais: Chapada do Paranã, *s.d.*, *Martius s.n.* (holotype: P?; isotype: P barcode P00673564!).

24. *Byrsonima verbascifolia* (L.) DC. var. *latifolia* A.Juss. (1833: 76). **Lectotype (designated here):**—BRAZIL. São Paulo: Taubaté, *s.d.*, *Saint-Hilaire Catal. D 744bis.* (P barcode P00631828!; isolectotypes: P barcodes P00631830!, P00631829!).

25. *Byrsonima verbascifolia* (L.) DC. var. *villosa* Griseb. (1839: 250). Type:— BRAZIL. *S.loc.*, *s.d.*, *Sellow s.n.* (syntype: BR barcode BR0000008696939!); San João das Gaitas, *s.d.*, *Sellow s.n.* (syntype: BR barcode BR0000008696571!); Minas Gerais, *s.d.*, *Lhotzky s.n.* (syntype: ?).

26. *Byrsonima verbascifolia* (L.) DC. f. *brasiliensis* Nied. (1901: 28). Lectotype (designated here):—BRAZIL. São Paulo: Araraquara, caminho de Anhumas, Loefgren CGG 965. (P!; isolectotype: IPA!, SP!).

27. *Byrsonima verbascifolia* (L.) DC. f. *leiocarpa* Nied. (1901: 28). Lectotype (designated here):—BRAZIL. Minas Gerais: *S.loc.*, *s.d.*, Claussen 42 (BR barcode BR672360!; isolectotypes: BR barcodes BR672425!, BR672393!).

28. *Byrsonima verbascifolia* (L.) DC. f. *vulgaris* Nied. (1901: 28). Lectotype (designated here):—BRAZIL. Bahia: Ilhéus, Wied 87 (BR barcode BR658677!: isolectotype: BR barcode BR658644!).

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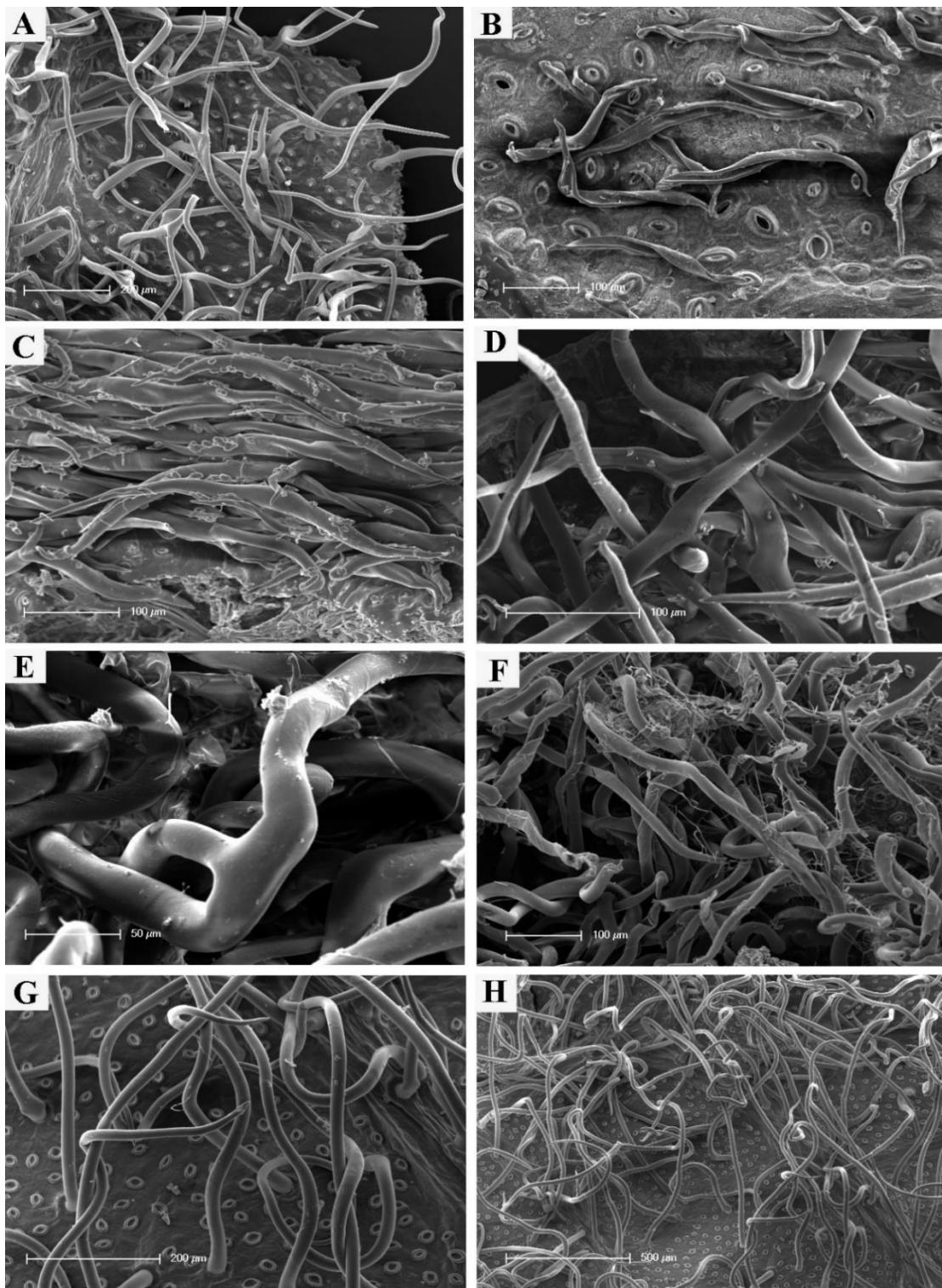


Figure 1 – Hairs in species of the *Byrsonima crassifolia* clade. A. Hairs in the abaxial side of leaves of *Byrsonima clauseniana*, B. Hairs in the abaxial side of leaves of *Byrsonima crassifolia*, C. Hairs in the abaxial side of leaves of *Byrsonima cydoniifolia*, D. Hairs in the abaxial side of leaves of *Byrsonima linearifolia*, E. Hairs in the abaxial side of leaves of *Byrsonima pachyphylla*, F. Hairs in the abaxial side of leaves of *Byrsonima termitaria*, G–H. Hairs in the adaxial side of leaves of *Byrsonima verbascifolia*.

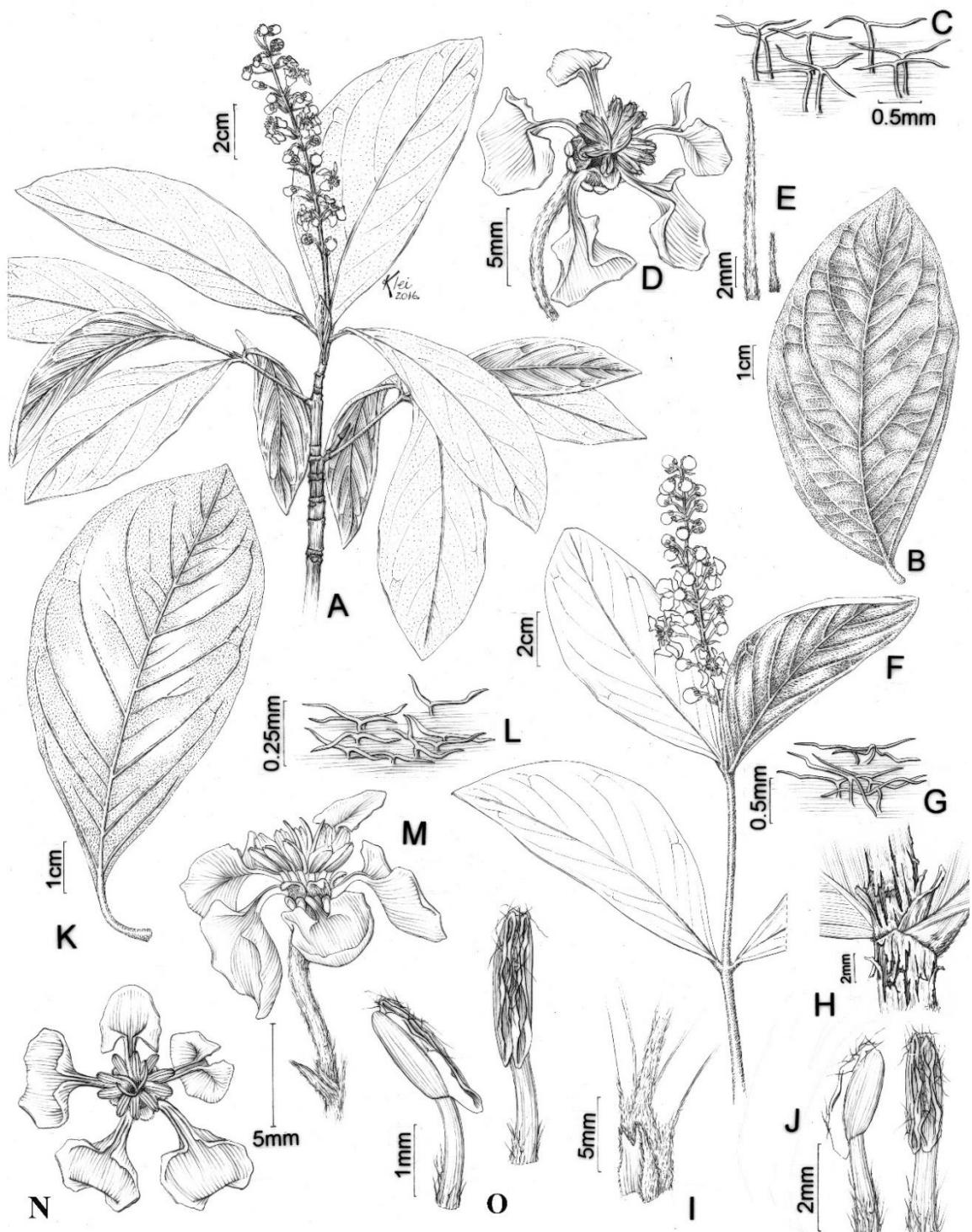


Figure 2 — *Byrsonima clauseniana* A–E: A. Habit, B. Abaxial side of leaves, C. Hairs on abaxial side of leaves, D. Frontal view of the flower, E. Abaxial view of bracts and bracteoles. *Byrsonima pachyphylla* F–J: F. Habit, G. Hairs on abaxial side of leaves, H. Exfoliating trunk, I. Stipule partially connate, J. Stamens in lateral and frontal views. *Byrsonima crassifolia* K–O: K. Abaxial side of leaves, L. Hairs on abaxial side of leaves, M. Lateral view of the flower, N. Frontal view of the flower, O. Stamens in lateral and frontal views. (A–E, Francener et al. 1207; F–J, Ratter 1925; K–O, Prata 494).

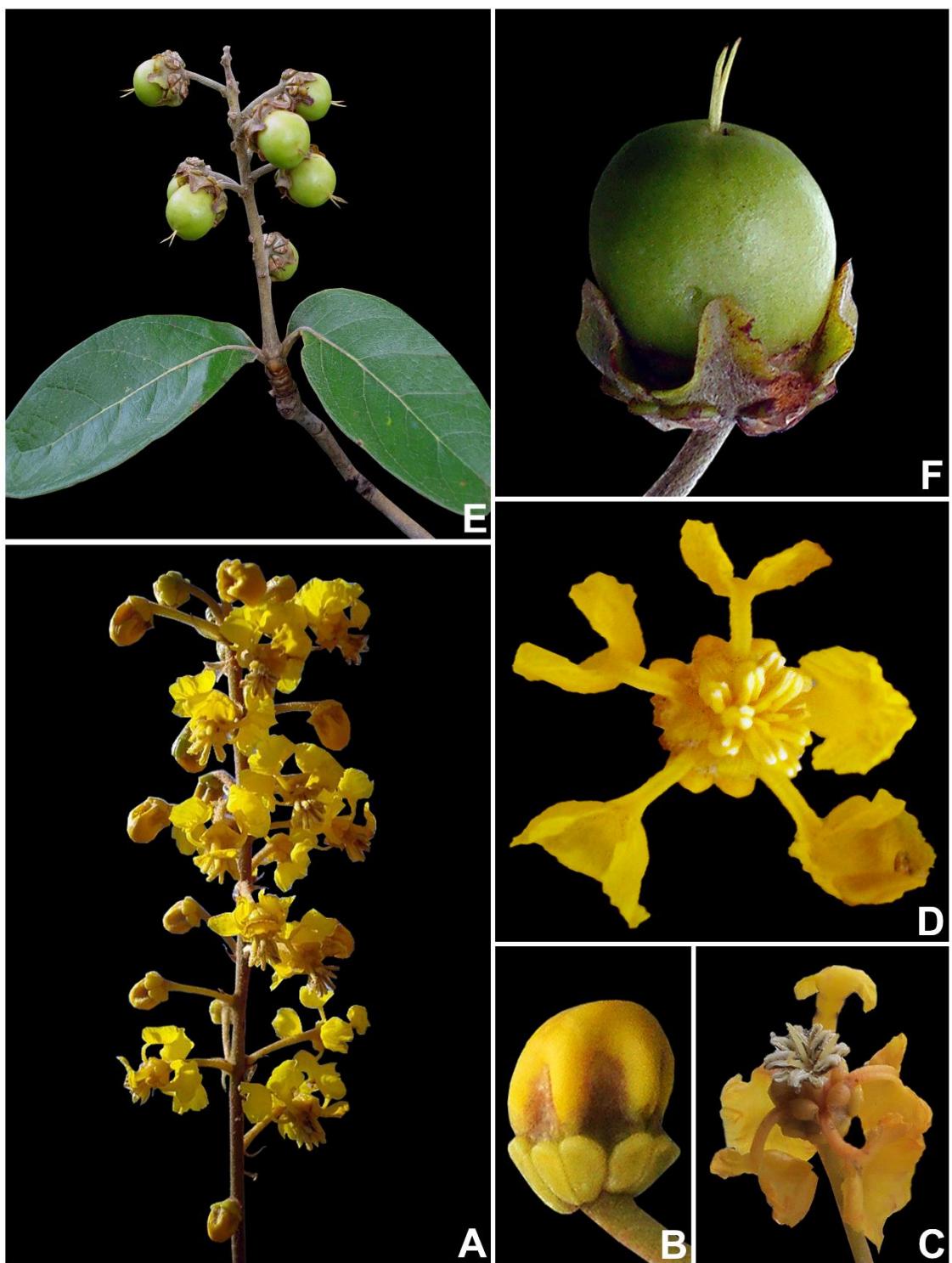


Figure 3 — *Byrsonima clauseniana* A–F: A. Inflorescence, B. Floral bud, C. Flower in lateral view, D. Flower in frontal view, E. Fruiting branch, F. Drupe (photos by C.F.Hall).

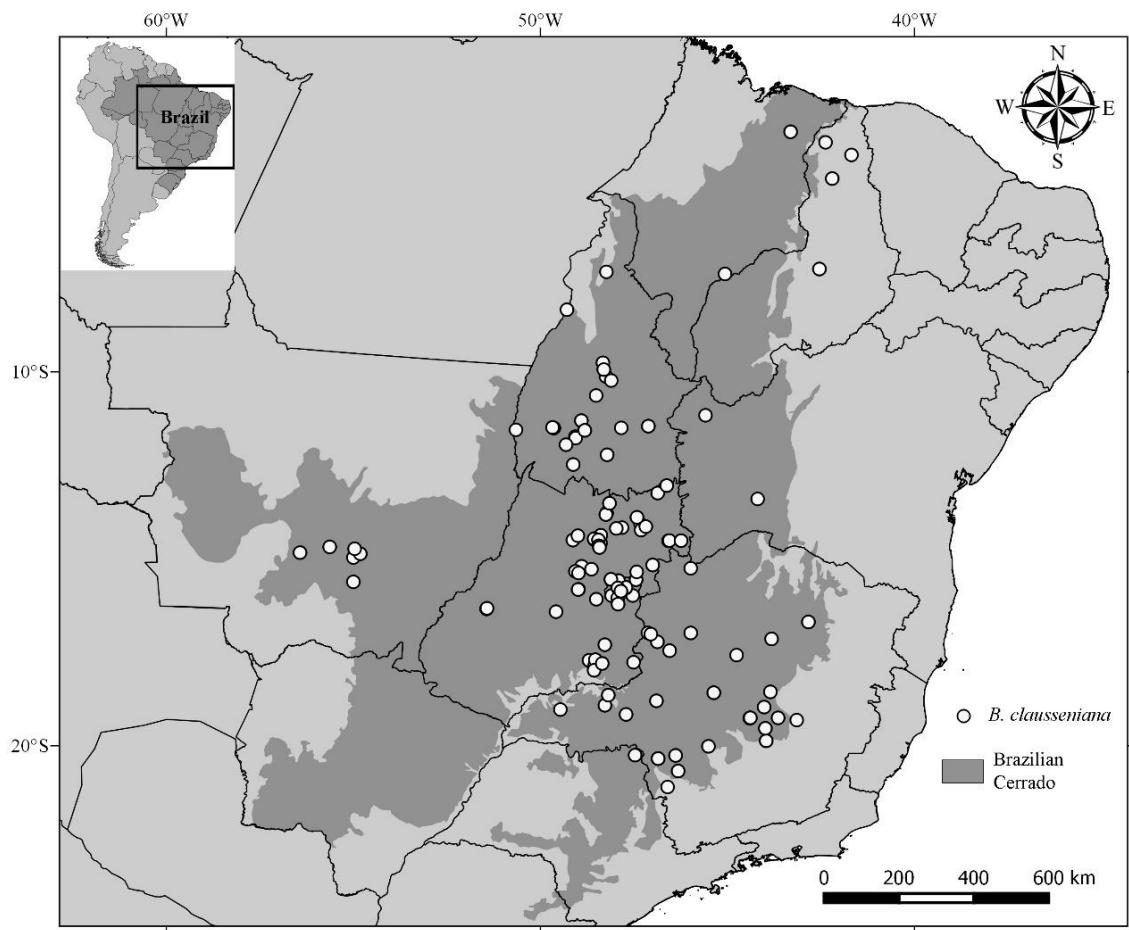


Figure 4 — Distribution of *Byrsonima clauseniana*.

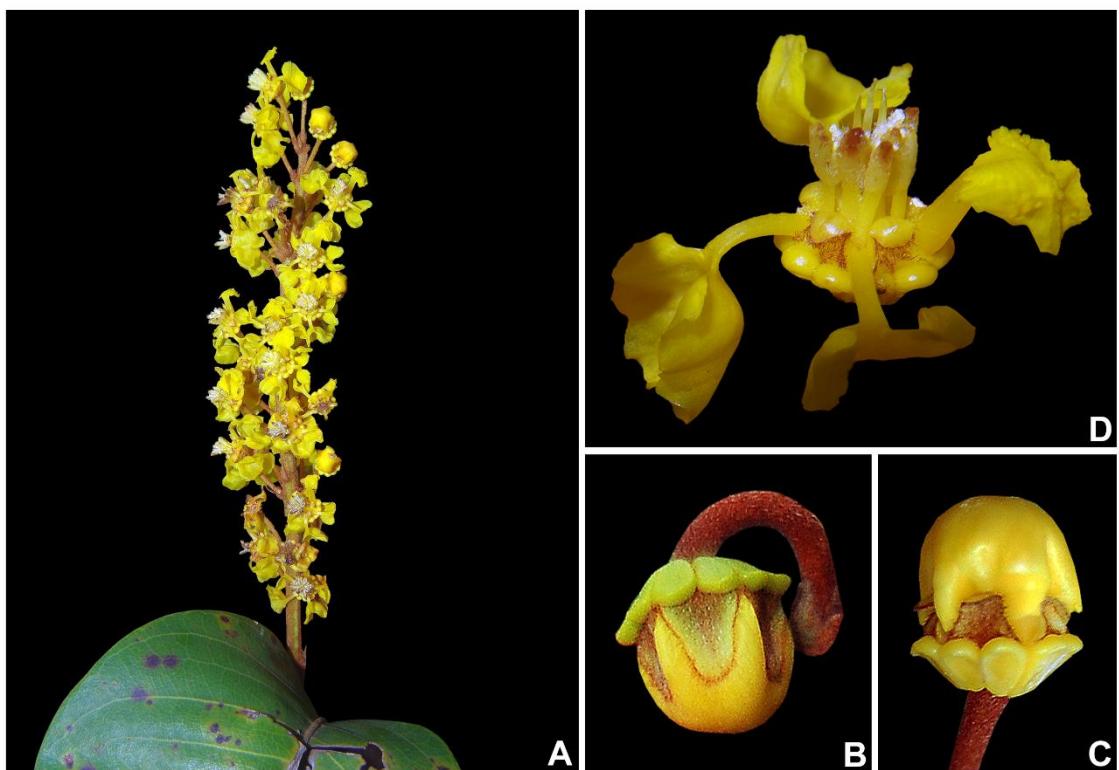


Figure 5 — *Byrsonima crassifolia*: A. Inflorescence, B. Imature floral bud, C. Mature floral bud, D. Flower in lateral view (photos by C.F.Hall).

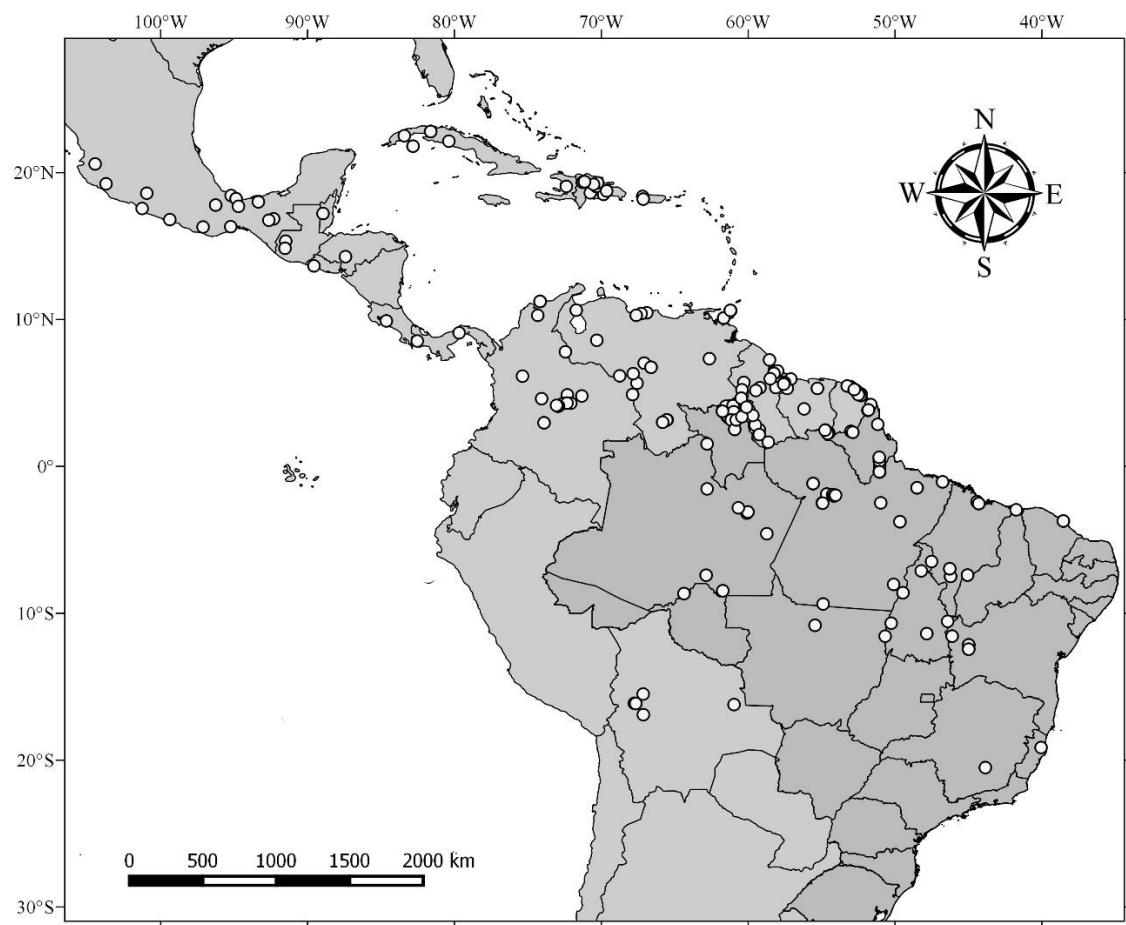


Figure 6 – Distribution of *Byrsonima crassifolia*.

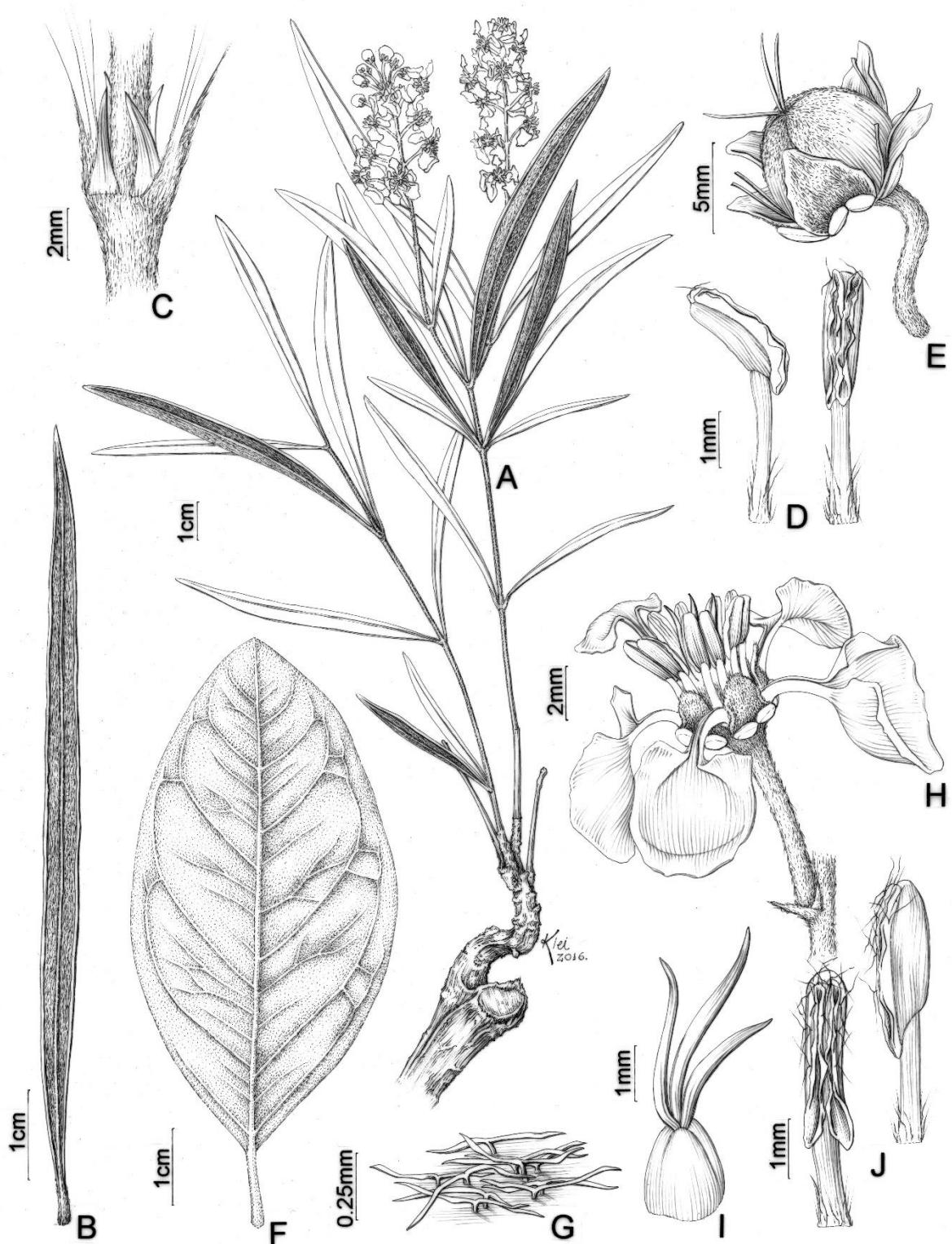


Figure 7 – *B. linearifolia* A–E; A) Habit, B) Abaxial side of leaves, C) Stipules free, D) Stamens, lateral and frontal views, E) Drupe with concrescent sepals. *B. cydoniifolia* F–J; F) Abaxial side of leaves, G) Hairs in abaxial side of leaves, H) Lateral view of the flower with bracts, I) Ovary glabrous, J) Stamens, frontal and lateral views. (A–E, Queiroz, L.P. 15080, F–J, Oliveira, F.C.A. 1612).

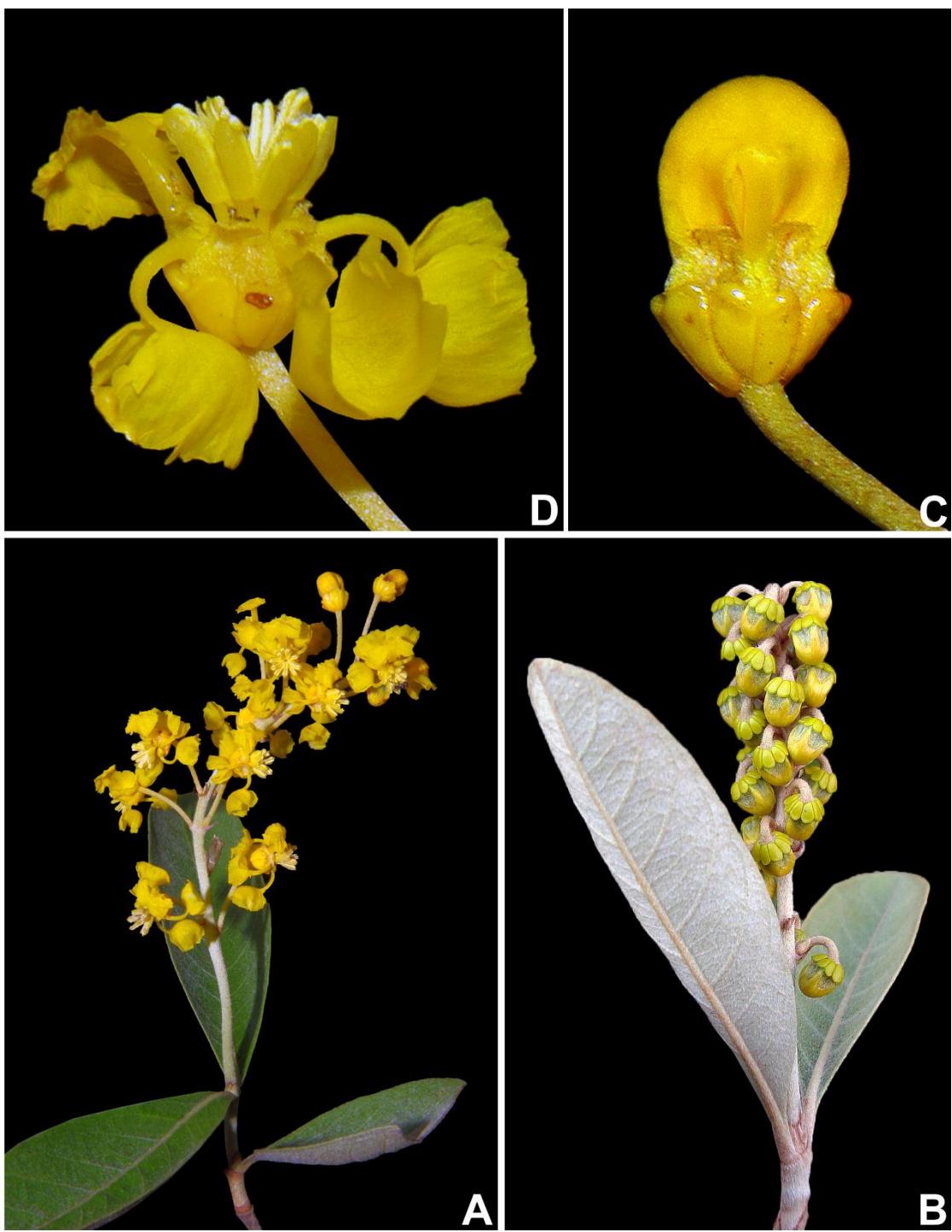


Figure 8 – *Byrsonima cydoniifolia*: A. Flowering branch with flowers in anthesis, B. flowering branch with floral buds, C. Detail of a floral bud in lateral view, D. Detail of a flower in anthesis in lateral view (photos by C.F.Hall).

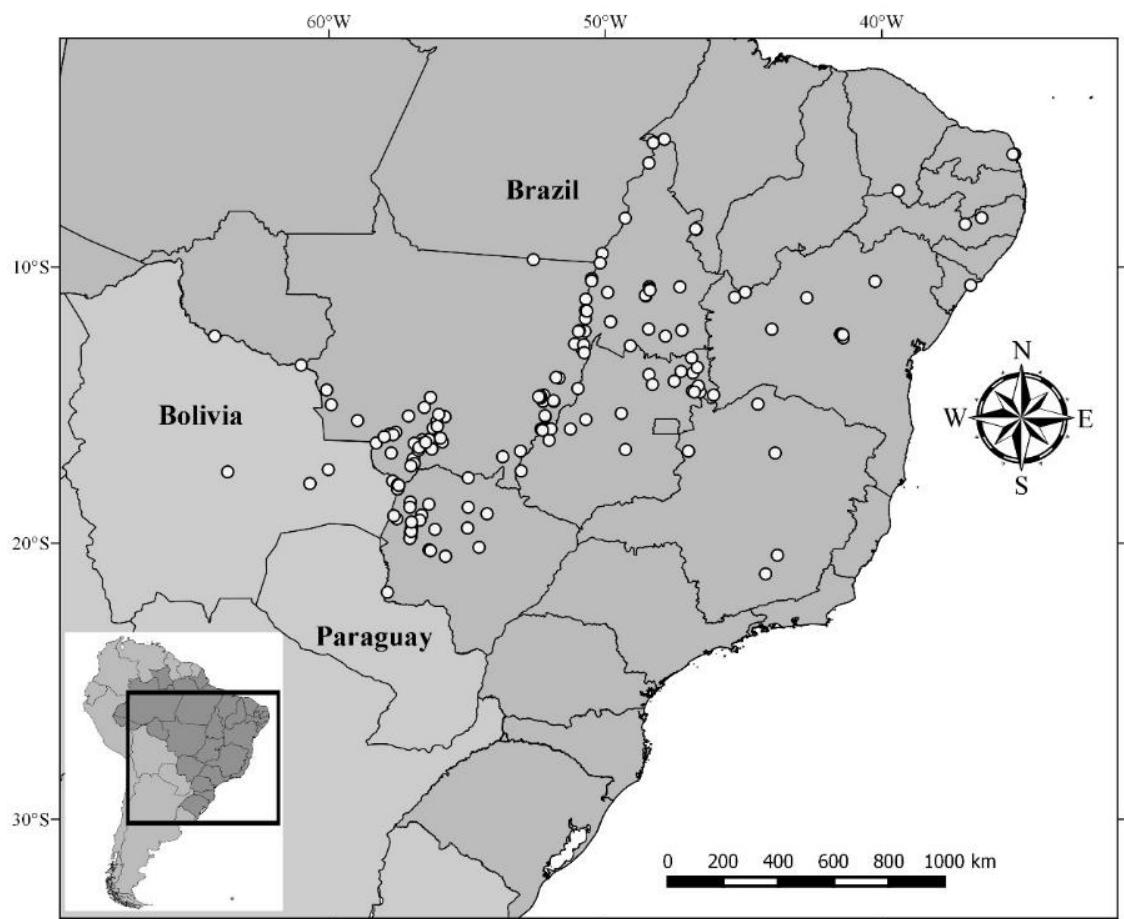


Figure 9 – Distribution of *Byrsonima cydoniifolia*.

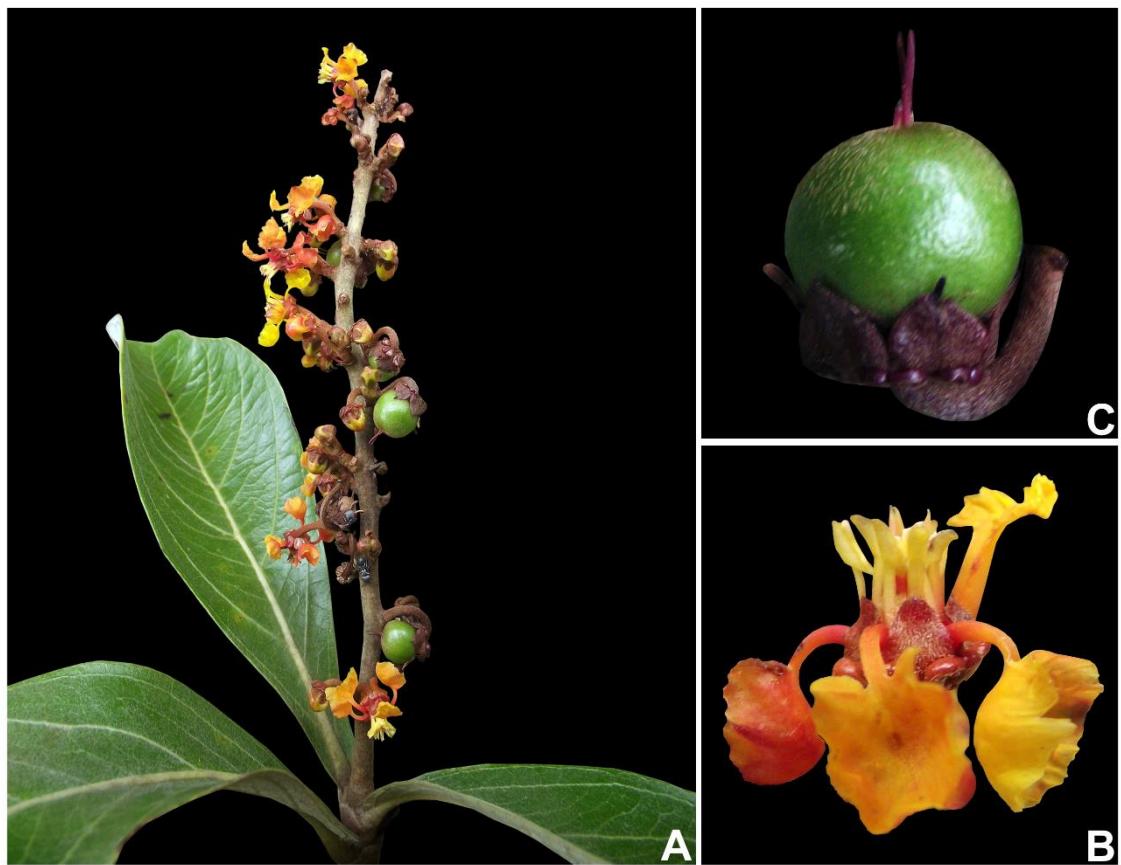


Figure 10 – *Byrsonima guilleminiana*: A. Flowering branch in lateral view showing flowers in post-anthesis and immature fruits, B. Mature flower in lateral view, C. Immature fruit in lateral view (photos by R.F.Almeida).

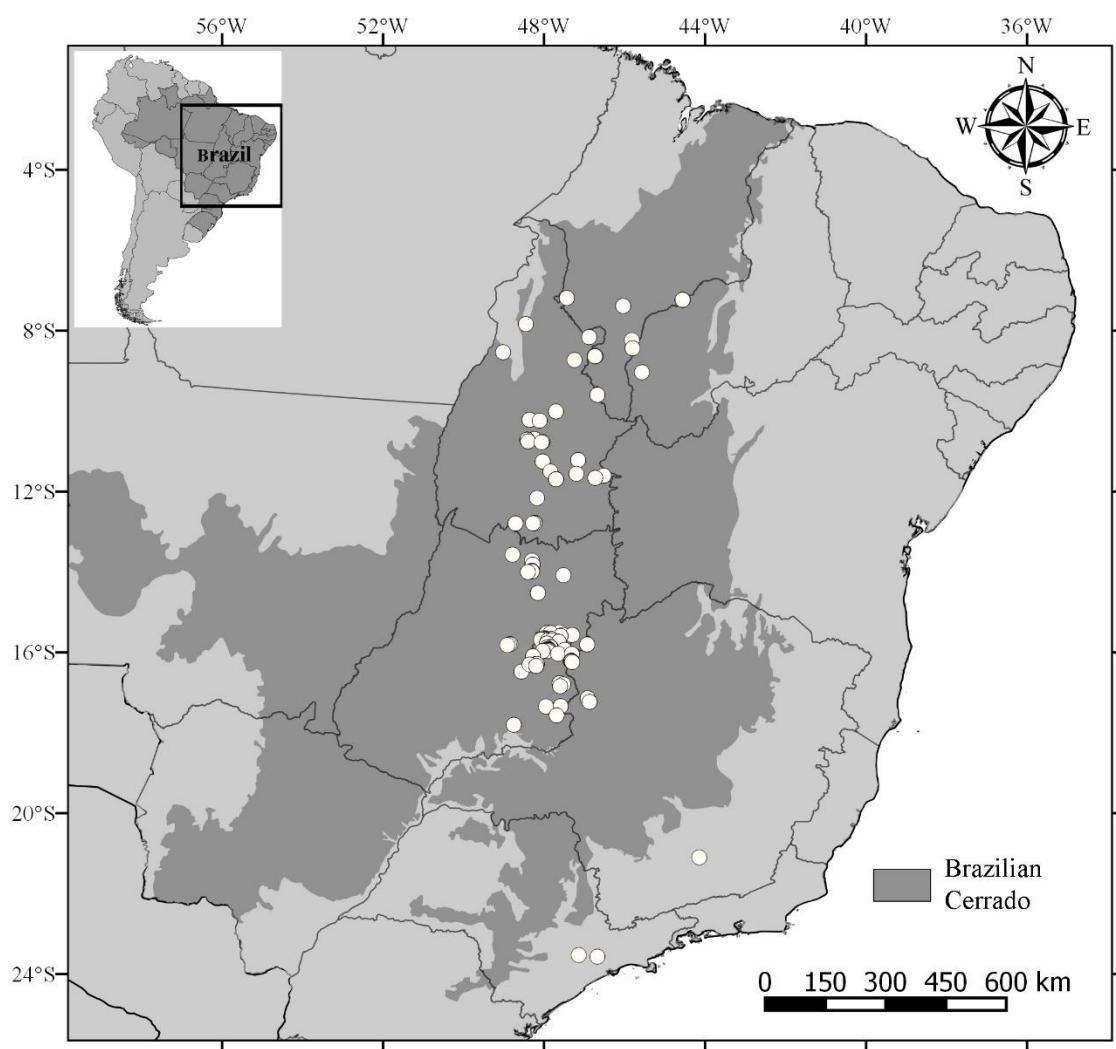


Figure 11 – Distribution of *Byrsonima guilleminiana*.

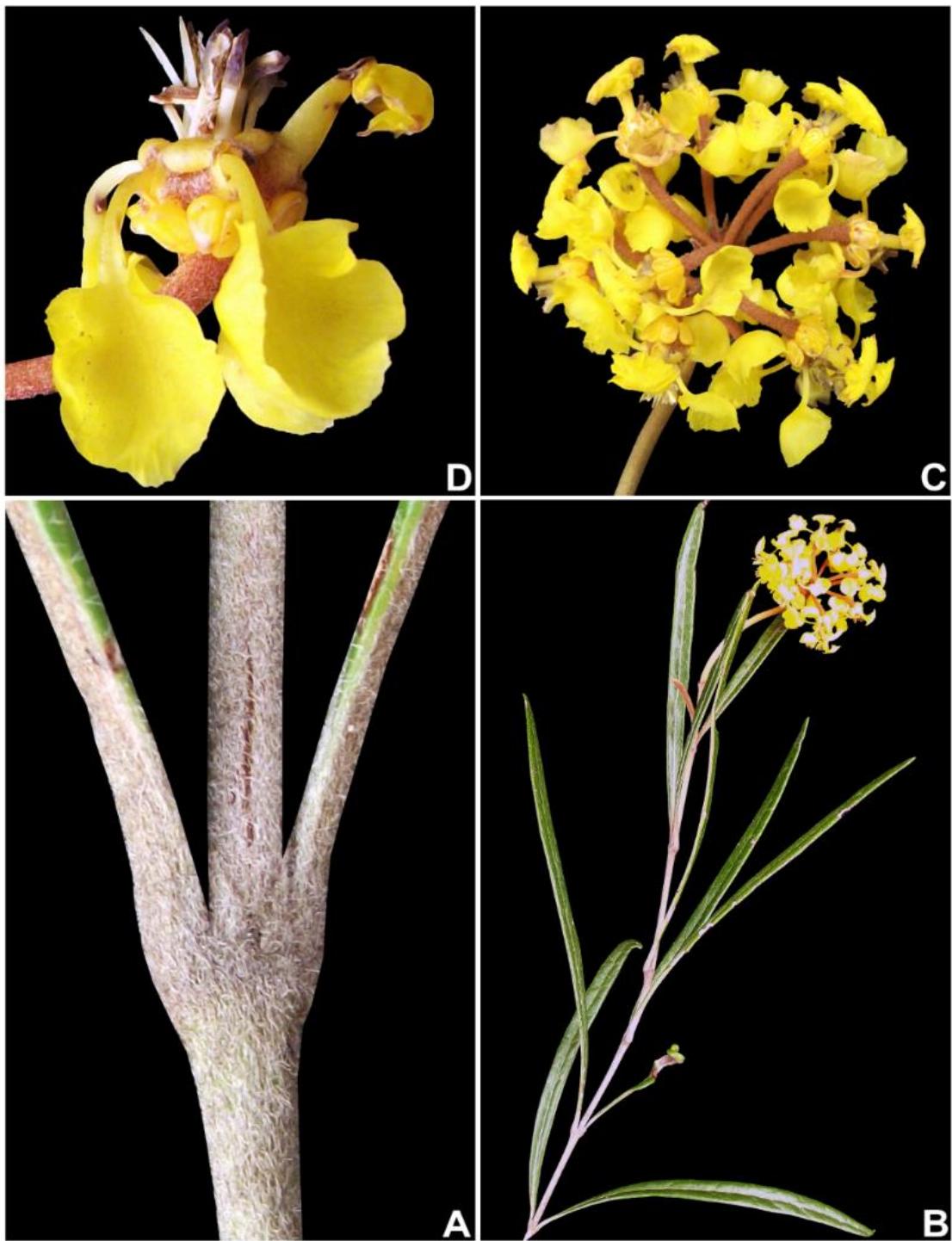


Figure 12 – *Byrsonima linearifolia*: A. Detail of a stem node covered by indument, B. Flowering branch in lateral view, C. Inflorescence in lateral view, D. Detail of a flower in lateral view (photos by R.F.Almeida).

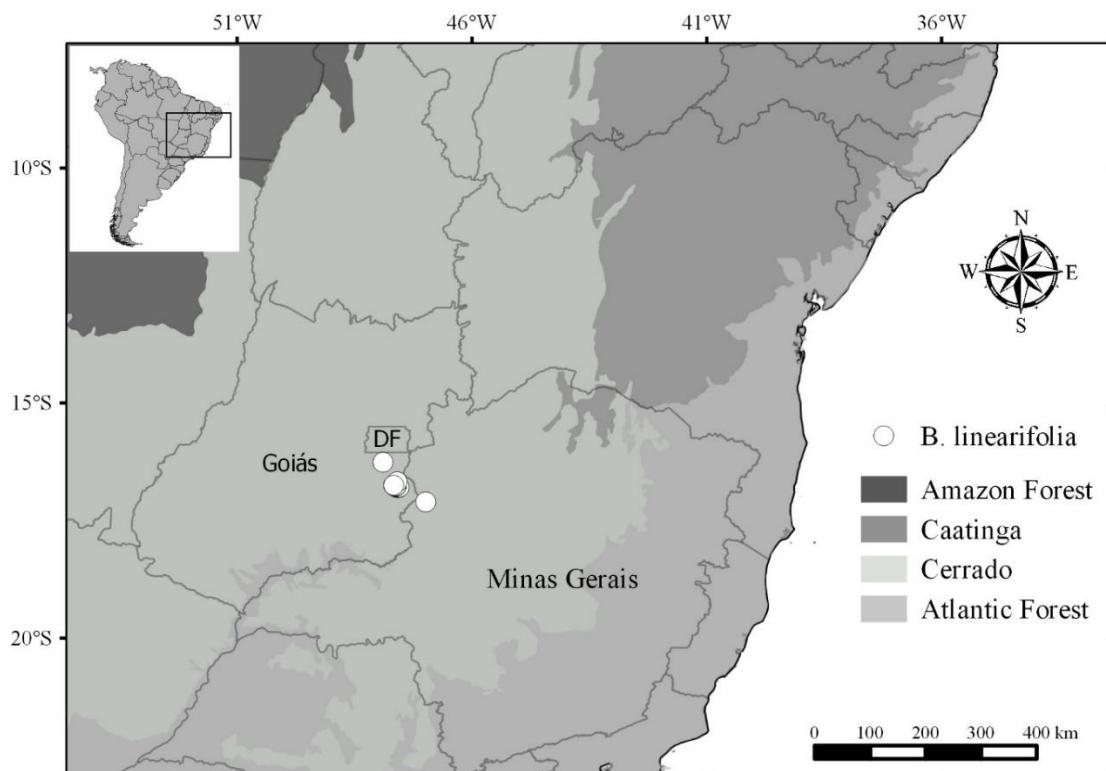


Figure 13 – Distribution of *Byrsonima linearifolia*.

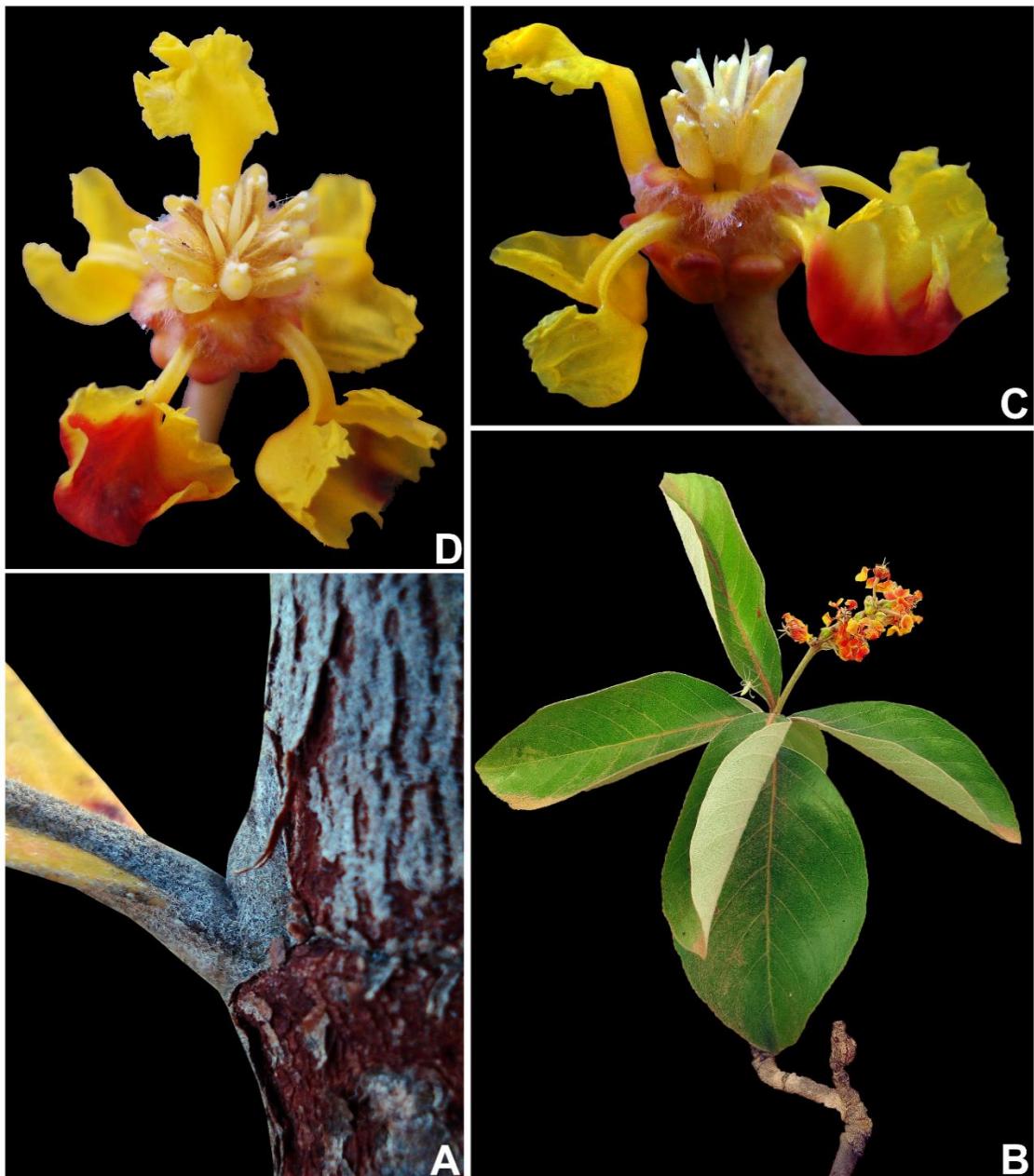


Figure 14 – *Byrsonima pachyphylla*: A. Detail of a stem node, B. Flowering branch in lateral view, C. Flower in lateral view, D. Flower in frontal view (photos by R.F.Almeida).

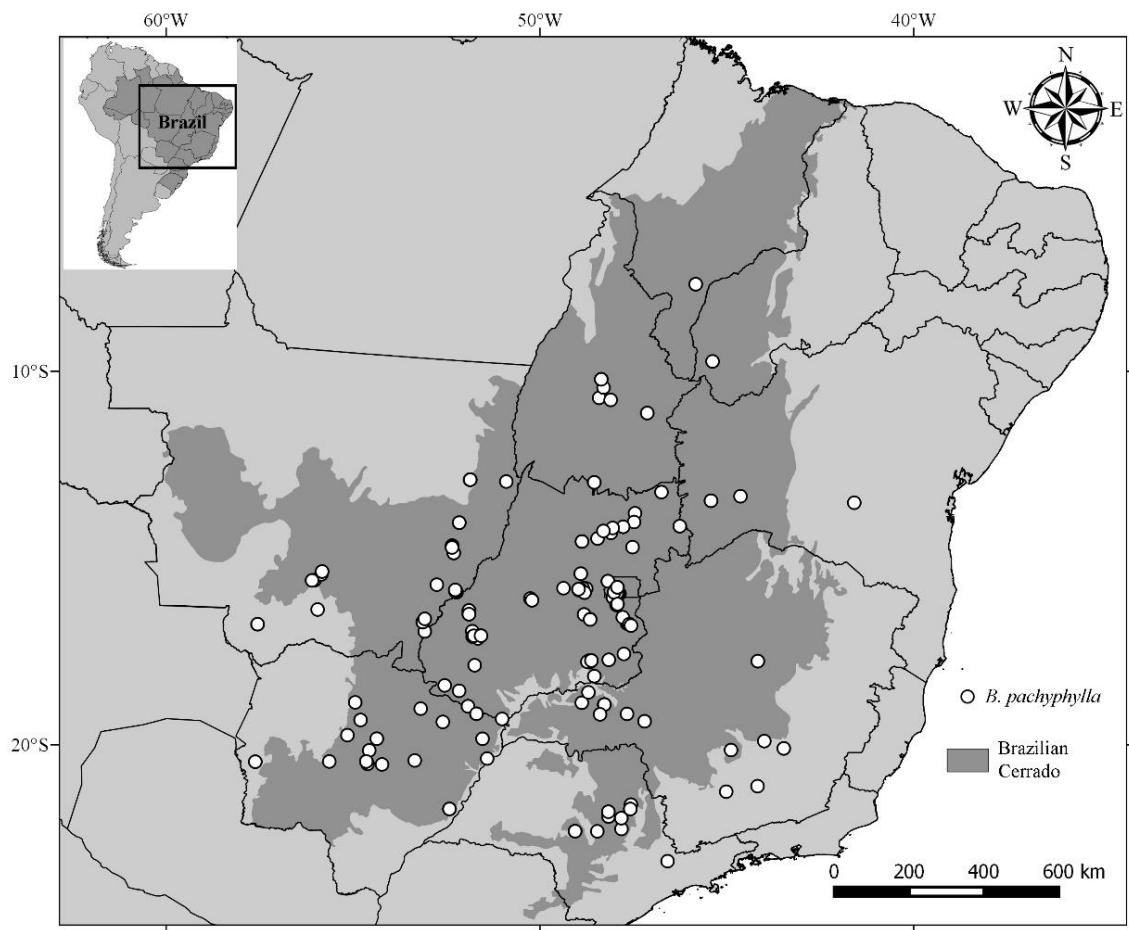


Figure 15 – Distribution of *Byrsonima pachyphylla*.

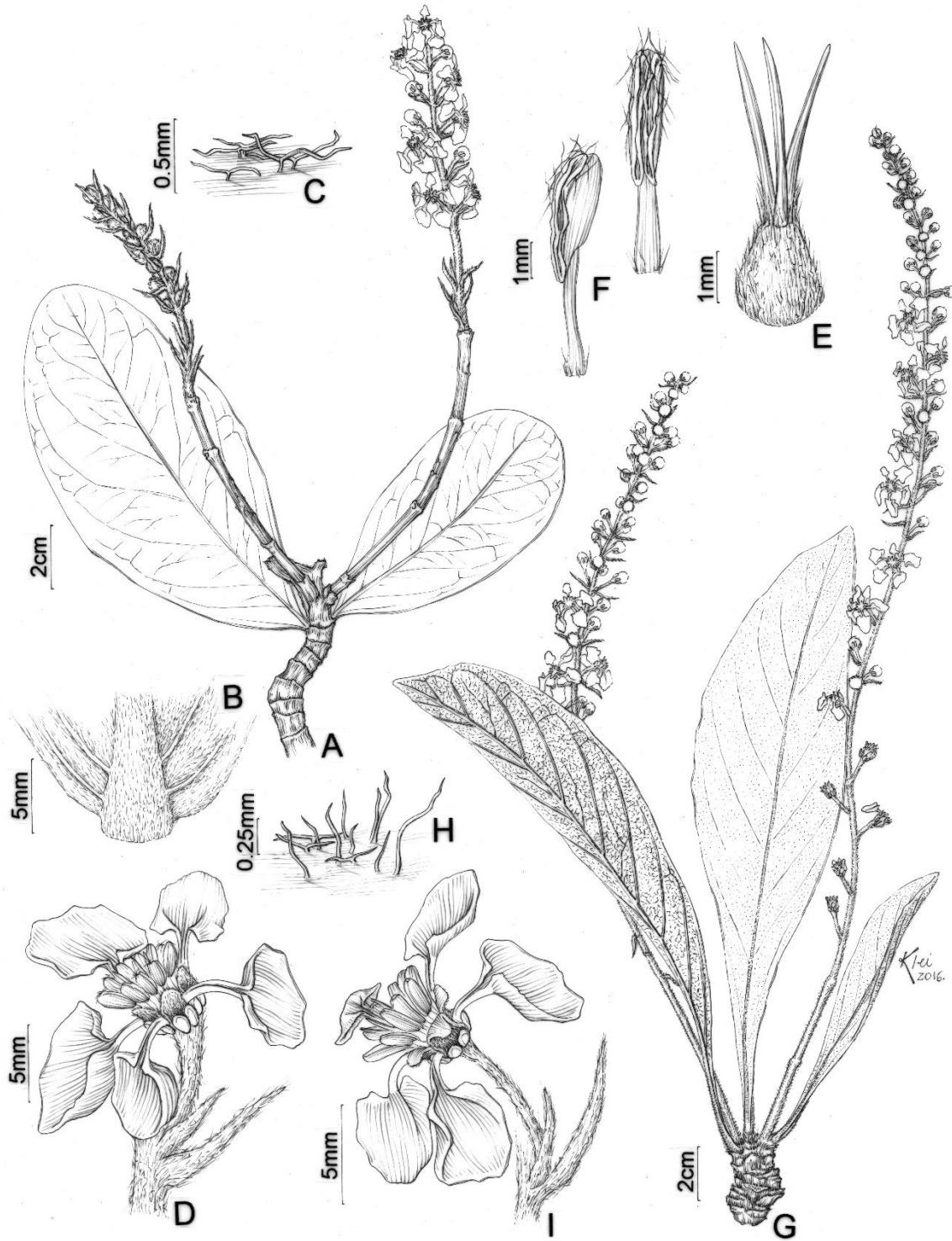


Figure 16 – *B. termitaria* A–F; A) Habit, B) Base of leaves, C) Hairs on abaxial side of leaves, D) Lateral view of the flower with bracts and bracteole, E) Ovary sericeous, G) Stamens, lateral and frontal views. *B. verbascifolia* G–I; G) Habit, H) Hairs on adaxial side of leaves, I) Lateral view of the flower with bract and bracteole. (A–F Francener, A. et al. 1146, G–I, Soares, EA. 176).

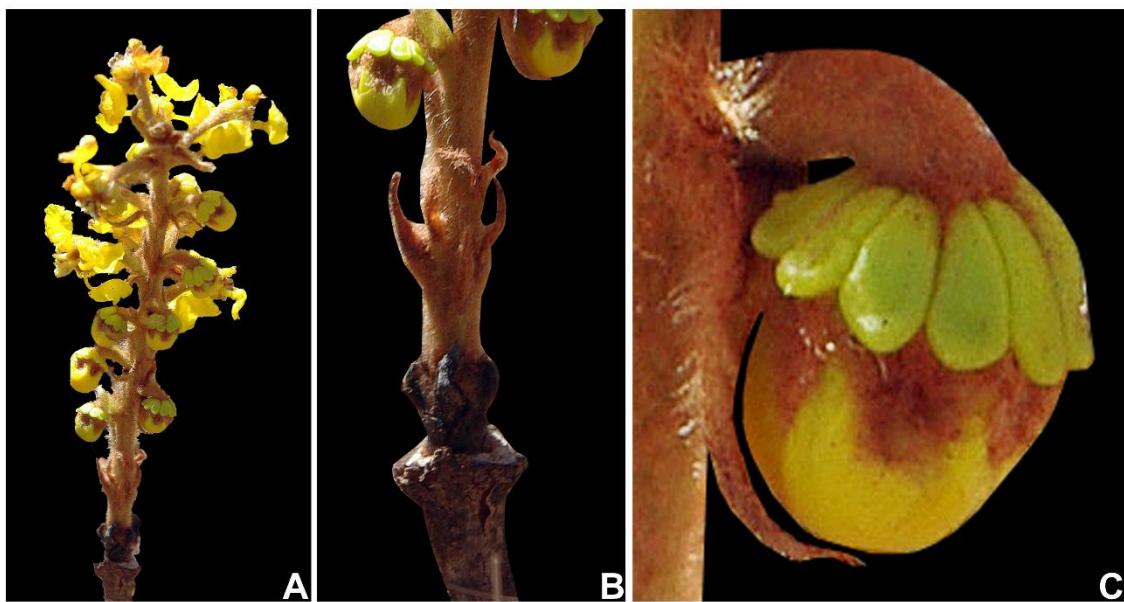


Figure 17 – *Byrsonima termitaria*: A. Inflorescence in lateral view, B. Detail of the base of the inflorescence in lateral view, C. Floral bud in lateral view (photos C.F.Hall).

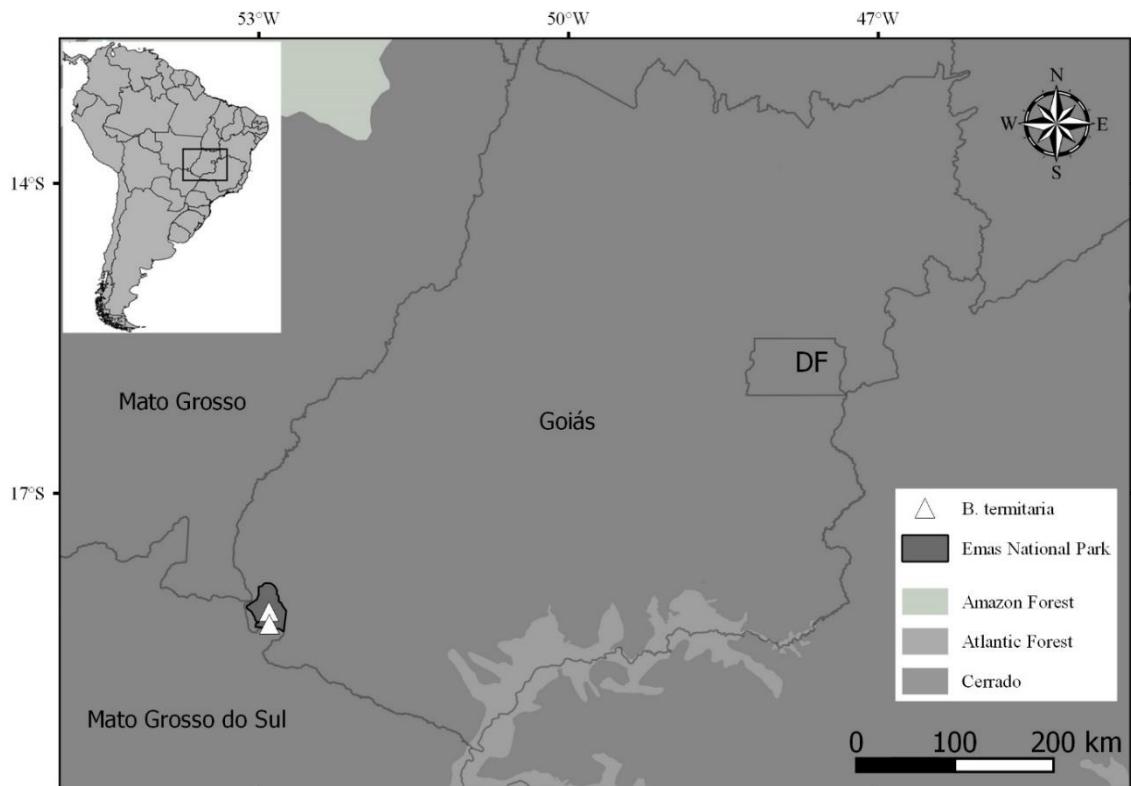


Figure 18 – Distribution of *Byrsonima termitaria*.

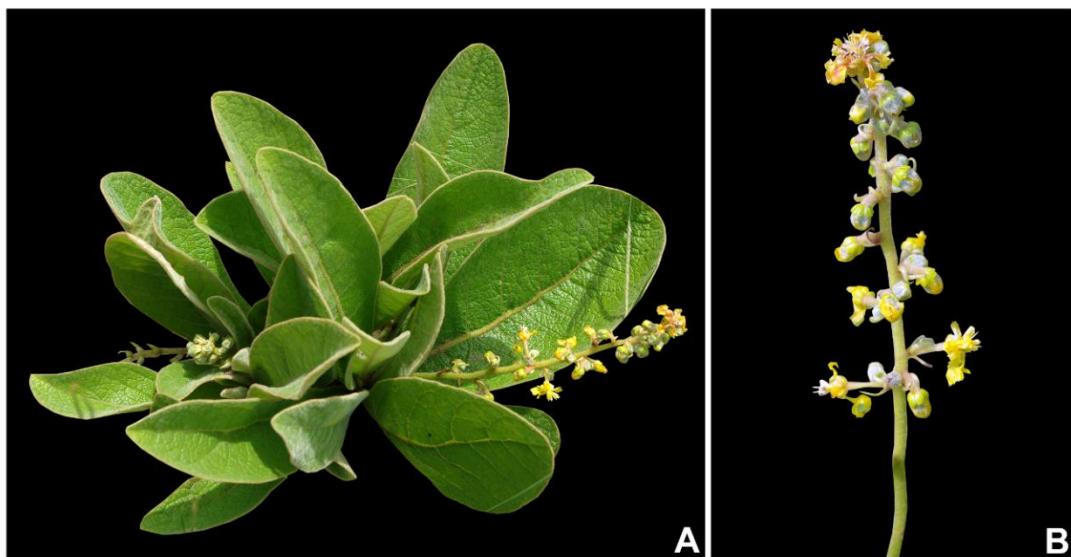


Figure 19 – *Byrsonima verbascifolia*: A. Flowering specimen in lateral view, B. Detail of the inflorescence in lateral view (photos C.F.Hall).

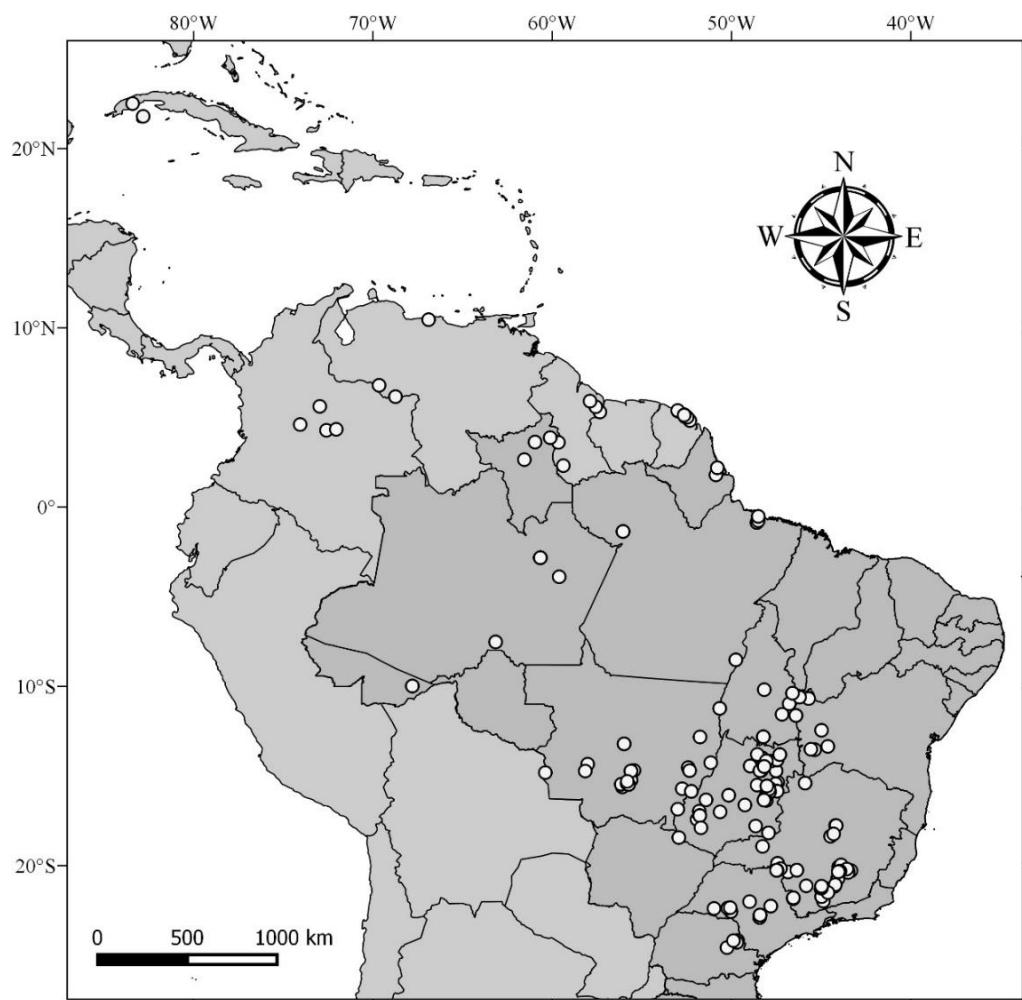


Figure 20 – Distribution of *Byrsonima verbascifolia*.

Capítulo 3

Duas novas espécies de *Byrsonima* (Malpighiaceae)

do estado de Minas Gerais, Brasil

Formatado de acordo com o periódico Phytotaxa

**Two new species of *Byrsonima* (Malpighiaceae) from the state of Minas Gerais,
Brazil**

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Abstract

Two new species of *Byrsonima*; *B. minarum* and *B. rupestris* (Malpighiaceae) endemic to rocky fields in Southwestern state of Minas Gerais are described. We present morphological descriptions, illustrations, distribution maps and comments on conservation, distribution, and taxonomic affinities to both species.

Key words: Cerrado, Malpighiales, Plant taxonomy, Rocky Fields.

Resumo

Duas novas espécies de *Byrsonima*; *B. minarum* and *B. rupestris* (Malpighiaceae) endêmicas dos campos rupestres do sudoeste do estado de Minas Gerais são descritas. São apresentadas descrições morfológicas, ilustrações, mapas de distribuição e comentários sobre conservação, distribuição e afinidades taxonômicas de ambas espécies.

Palavras-chave: Campo Rupestre, Cerrado, Malpighiales, Taxonomia Vegetal.

Introduction

Byrsonima Rich. ex Kunth, (1821: 147) is easily recognized by its shrubby to tree habit, intrapetiolar stipules, eglandular leaves, bracts and bracteoles, elongated thyrsi of 1-flowered cincinni, slender styles subulate at apex, minute stigmas, and drupes, with 3-locular pyrenes (Anderson 1981, Mamede 1987). It is the second largest genus in Malpighiaceae, comprising about 135 species endemic to the Neotropical region (Anderson 1981, Anderson *et al.* 2006). Brazil is the richest neotropical country in the

genus, with about 97 species found in all Brazilian biomes, but especially diverse in Cerrado vegetation (neotropical savannas) (BFG 2015).

Espinhaço Range is the most important mountain chain within Cerrado biome in Eastern Brazil (Giulietti *et al.* 1987, Harley 1995, Rapini *et al.* 2008). This region holds high rates of plant endemism, especially above 800 m where rocky fields are the predominant phytobiognomy (Giulietti *et al.* 1987, Harley 1995, Rapini *et al.* 2008).

During visits to Brazilian herbaria for the taxonomic revision of *Byrsonima* sect. *Eriolepsis* Niedenzu (1901: 1), we came across two new species of *Byrsonima* endemic to rocky fields from Southwestern Espinhaço Range, in state of Minas Gerais, Brazil.

Material and Methods

Morphological descriptions and phenology of the studied species were based on herbarium specimens (BR, CEPEC, HUFU, R, RB, SP and UESC), and type collections (herbaria acronyms according to Thiers, continuously updated). The indumenta terminology follows Anderson (1981) and Niedenzu (1928), structure shapes follows Radford *et al.* (1974), the inflorescence terminology and morphology follows Anderson (1981), and fruit terminology follows Anderson (1981) and Niedenzu (1928). Scanning Electron Microscope images were performed with samples fixed in Karnovsky solution (Bozzola & Russel 1992), and coated in gold. The conservation status was proposed following the recommendations of IUCN Red List Categories and Criteria, Version 3.1 (IUCN 2001). GeoCAT (Bachman *et al.*, 2011) was used for calculating the Extent of Occurrence (EOO) and the Area of Occurrence (AOO). Maps were elaborated using ArcGis version 9.3 (ESRI 2010), and geographical coordinates were obtained from herbaria specimens.

Results

Taxonomy

1. *Byrsonima rupestris* Francener & Mamede, *sp. nov.*

Type:—BRAZIL. Minas Gerais: Parque Nacional da Serra da Canastra, Estrada para Sacramento, entrada Garagem de Pedras, 20 March 1995, fl., Nakajima *et al.* 922 (holotype: HUFU!; isotypes: SP016875!, UESC!). Figure 1A–H.

Byrsonima rupestris differs from *B. cipoensis Mamede* and *B. variabilis A.Juss.* by its unusual unbranched hairs covering the entire plant, and the leaf blades with all veins strongly prominent, even the tertiary ones.

Shrubs, 0.4–1.5 m tall, trunk erect, terete, velutine, hairs 0.3–1 mm long, white or brown, unbranched, rarely branched, stalk up to 0.3 mm long; younger stems grayish white or ferruginous, older stems grayish, becoming glabrous. *Stipules* 6–7.3 x 1.8–4 mm, connate, triangular to ovate, abaxial surface velutinous, hairs 0.3–1.5 mm long, white, unbranched, rarely branched, stalk 0.5–0.8 mm long, adaxial surface shiny, glabrous or velutinous, hairs 0.5–1.5 mm long, brown, unbranched present only at the base. *Leaves* opposite, rarely verticillate; petiole 2–10 mm long, velutine, hairs 0.3–2 mm long, brown or whitish, unbranched, when branched, stalk 0.1–0.2 mm long; leaf blades 3.2–15.5 x 2.1–7 cm, ovate, elliptic, obovate or lanceolate, base acute, subcordate or obtuse, margin entire, slightly revolute, sinuose, apex acute, acuminate or obtuse, adaxial side greenish, glaucous-green or light-brown, velutinous to sparsely velutinous, hairs 0.2–1.4 mm long, whitish, unbranched, when branched, stalk up to 0.2 mm long, abaxial side usually ferruginous or white-ferruginous, densely velutinous to tomentose, hairs 0.5–1.4 mm long, whitish, unbranched, occurring mainly in the veins, rarely branched, stalk up to 0.3 mm long; venation brochidodromous, 5–12 pairs of secondary veins, strongly prominent, tertiary veins reticulate, strongly prominent. *Thyrsi* of 1-flowered cincinni, 5–43-flowered, flowers distributed in the median and distal part of the rachis; rachis 3.5–13 cm long, velutinous, hairs 0.4–1.5 mm long, whitish or brown, unbranched, when branched, stalk up to 0.2–0.3 mm long; bracts and bracteoles at the base of pedicel, deciduous or not in fruit; bracts 4.5–7 x 0.8–1.5 mm, narrowly triangular, erect, adaxial side glabrous, abaxial side sericeous-velutine, hairs 0.3–1 mm long, whitish or brown, unbranched or branched, stalk up to 0.1–0.4 mm long; peduncle sessile; bracteoles 3–4 x 0.8–1 mm, narrowly triangular, erect, adaxial side glabrous, abaxial side sericeous-velutinous, hairs 0.3–1 mm long, whitish or brown, unbranched or branched, stalk up to 0.1–0.4 mm long; pedicels 5–12 mm long, velutine, hairs 0.3–1.4 mm long, whitish or brown, unbranched or rarely branched, stalk up to 0.7 mm long. *Sepals* 3.5–4 x 2.2–2.5 mm, always biglandular, apex acute or rounded, erect, adpressed to the androecium, adaxial side glabrous, abaxial side sericeous-velutinous, hairs 0.3–1.3 mm long, whitish or brown, unbranched; *glands* 1.5–2.3 x 1–1.1 mm, white. *Petals* glabrous; lateral petals white turning pink with age, lamina cucullate, 4.5–6 x 5–6 mm, margin sinuate, claws 3–4.5 x 0.5–0.8 mm, reflexed, bent or twisted; posterior petal always yellow, lamina patent, 3–5

\times 4–5 mm, margin erose, corrugate, claw 3.5–4.2 \times 0.8–1.1 mm, erect. *Stamens* 10, connate at the base; filaments 2.4–3.1 \times 0.4–0.9 mm, adaxially pilose at base, hairs simple, 1.5–3 mm long, brown, abaxially glabrous; connectives 1.5–2.2 \times 0.5–0.7 mm, exceeding or not the locules (up to 1 mm long), glabrous; locules 2.2–2.7 \times 0.5–0.7 mm, glabrous. *Ovary* conical, 1.5–2 \times 1.7–1.8 mm, glabrous; ovules 0.8–1 \times 0.4–0.5 mm; styles linear, 3.2–4 \times 0.2–0.3 mm, subulate, bent at the apex, glabrous; stigma minute. *Drupes* 6–7 mm diam., ovoid or globose, glabrous; sepals expanded in fruit; pedicels bent or twisted.

Additional specimens examined (paratypes):—BRAZIL. Minas Gerais: São Roque de Minas, Parque Nacional da Serra da Canastra, 19 November 2002, fl., *Pacheco et al.* 287 (HUFU); *loc. cit.*, Cachoeira Casca D'Anta, parte de cima, 23 August 1997, fl., *Romero et al.* 4503 (CEPEC, HUFU); *loc. cit.*, Chapadão do Diamante, 20 November 1995, fl., *Romero et al.* 3135A (HUFU, SP016879); *loc. cit.*, Chapadão do Diamante, 15 October 1997, fl., *Nakajima et al.* 2855 (CEPEC, HUFU, UESC); *loc. cit.*, entrada para o Retiro de Pedras, 27 September 1995, fl., *Romero et al.* 2869 (HUFU, SP016882); *loc. cit.*, estrada para a Cachoeira do Rolinhos, 26 September 1995, fl., *Romero et al.* 2855 (HUFU, SP016869); *loc. cit.*, estrada para Cachoeira Casca D'Anta, 28 September 1995, fl., *Romero et al.* 2960 (CEPEC, HUFU, SP016881); *loc. cit.*, estrada para Sacramento, 3 km da sede administrativa, 17 March 1995, fl., *Romero et al.* 1951 (HUFU, SP016868, UESC); *loc. cit.*, estrada para Sacramento, 3 km da sede administrativa, 7 December 1994, fl., *Nakajima et al.* 665 (HUFU, SP016876); *loc. cit.*, estrada para Sacramento, 23 km da sede administrativa, 19 April 1994, fl., *Nakajima et al.* 300 (HUFU, SP016878); *loc. cit.*, estrada para Sacramento, entrada Garagem de Pedras, 16 October 1997, fl., *Romero et al.* 4658 (HUFU, SP003449); *loc. cit.*, Guarita de Sacramento, 18 November 1995, fl., *Romero et al.* 3109 (HUFU, SP016880); *loc. cit.*, Morro da Cachoeira da Casca D'Anta, 22 August 1994, fl., *Romero et al.* 1150 (HUFU, SP016871); *loc. cit.*, Morro próximo à sede administrativa, 15 October 1994, fl., *Nakajima et al.* 477 (HUFU, SP016877, UESC); *loc. cit.*, Morro próximo à sede administrativa, 20 August 1994, fl., *Romero* 1116 (HUFU); *loc. cit.*, Paredão da parte de cima da Cachoeira da Casca D'Anta, 29 September 1995, fl., *Nakajima et al.* 1384 (HUFU, SP016874, UESC); *loc. cit.*, paredão da parte de cima da Cachoeira da Casca D'Anta, 29 September 1995, fl., *Nakajma et al.* 1386 (HUFU, SP016973); *loc. cit.*, próximo ao córrego dos Passageiros, 19 July 1995, fl., *Romero et al.* 2624 (HUFU); *loc. cit.*, próximo à guarita de Sacramento, 14 October 1994, fl., *Romero*

et al. 1190 (HUFU, SP016870, UESC); *loc. cit.*, próximo à guarita de Sacramento, 6 December 1994, fl., *Romero* 1463 (HUFU, SP016867); *loc. cit.*, próximo ao Curral de Pedras, 18 October 1994, fl., *Romero et al.* 1313 (HUFU, SP016866); *loc. cit.*, trilha Casca D'Anta, 19 November 2002, fl. fr., *Romero* 6520 (HUFU, SP003448); *loc. cit.*, trilha da Cachoeira Casca D'Anta, 19 November 2002, fl. fr., *Duarte et al.* 52 (CEPEC, HUFU); *loc. cit.*, trilha para a parte de baixo da Cachoeira da Casca D'Anta, 29 September 1995, fl., *Nakajima et al.* 1390 (HUFU, SP016872, UESC).

Distribution, habitat and phenology:—*Byrsonima rupestris* is endemic to the Serra da Canastra region, southwestern state of Minas Gerais (fig. 1), occurring in areas of neotropical savannas and rocky fields (*cerrado* and *campo rupestre*). Flowering from August to April, and fruiting in November.

Conservation status:—*Byrsonima rupestris* should be regarded as Endangered [categories B1ab(iii) and 2ab(iii)], due to its extension of occurrence (<5000 km²), area of occupancy (<500 km²) and for the fact that the conservation unit suffers with high rates of annual fires.

Etymology:—The epithet makes reference to the occurrence of the species restricted to rocky fields (*campos rupestres*).

Discussion:—*Byrsonima rupestris* is easily recognized by its unusual unbranched hairs covering the entire plant (fig. 3), especially on the abaxial side of leaf blades, and by the strongly prominent veins on the abaxial side of leaf blades. This type of hair is very unusual within the genus, being only previously found on the leaves of *B. verbascifolia* (L.) DC (1824: 579). *Byrsonima rupestris* is very similar to *Byrsonima cipoensis* Mamede (1980: 42), *Byrsonima stannardii* W.R.Anderson (1992: 725-727) and *Byrsonima variabilis* A. Juss. (1833:78). These species are restricted to rocky fields (*campos rupestres*) over Espinhaço Range, and share four white lateral petals, and a yellow posterior petal [except in *Byrsonima stannardii* W.R. Anderson (1992: 725-727), in which all petals are yellow]. These species can be easily distinguished by the following characters:

1. Shrubs or trees; all petals yellow turning orange or red with age, anthers sericeous between locules.....*B. stannardii*
1. Subshrubs or shrubs, lateral petals white turning pink with age; posterior petal yellow, anthers glabrous.....2
2. Abaxial side of leaf blades mostly covered with unbranched hairs; primary, secondary, and tertiary veins strongly prominent.....*B. rupestris*
2. Abaxial side of leaf blades covered with branched hairs; primary, and secondary veins prominent, but usually hidden by indumenta, tertiary veins impressed.....3
3. Shrubs (0.6–) 1–2 (–3.5) m tall; leaves 3–15.5 × 2–7 cm, abaxially densely tomentose or glabrescent.....*B. variabilis*
3. Subshrubs 0.3–0.7 m tall; leaves 1.5–7 × 0.4–2 cm, abaxially sparsely tomentose.....*B. cipoensis*

2. *Byrsonima minaria* Francener & Mamede, **nom. nov.** ≡ *Byrsonima pachyphylla* var. *latifolia* Nied., (1901: 27), *non Byrsonima latifolia* (A.Juss.) Kralik, (1908: 284).

Lectotype (designated here):—BRAZIL. Minas Gerais: Serra do Caraça, *s.d.*, Ule 2456 (R!) Figure 1I-K.

Byrsonima minaria is distinguished from *B. macrophylla* by its yellow flowers, secondary veins prominent, anthers glabrous, and connectives not exceeding the locules.

Trees, trunk striate, erect, terete, glabrous; stem sericeous, hairs 0.3–1 mm long, brown, stalk sessile up to 0.2 mm long. *Stipules* 5.5–7.5 × 3.8–4 mm, connate, triangular to ovate, adaxial side shiny, glabrous to glabrescent at base, hairs 0.3–0.6 mm long, brown, stalk sessile, abaxial side sericeous, hairs 0.3–1 mm long, brown, stalk sessile. *Leaves* opposite, entire; petioles 8–12 mm long, cylindrical, sericeous, hairs 0.2–1 mm long, brown, stalk sessile to up to 0.2 mm long; leaf blades 9.5–14.2 × 4.2–6.6 cm, elliptic or obovate, base acute, margin entire, slightly revolute, sinuose, apex acute, adaxial side dark green, sparsely sericeous, hairs 0.3–0.7 mm long, whitish, stalk sessile, abaxial side ferruginous, sparsely sericeous, hairs 0.3–1 mm long, light-brown, stalk sessile to up to 0.2 mm long; venation brochidodromous, 9–12 pairs of secondary veins, adaxially impress, abaxially prominent; tertiary veins reticulate, prominent. *Pseudoracemes* (thyrsi of 1-flowered cincinni), with 6–20 flowers distributed in the median to superior part of the rachis; rachis ca. 8.5–13 cm long, tomentose-sericeous, hairs 0.2–1 mm long, brown,

stalk sessile to up to 0.2 mm long; bracts not seen; peduncle sessile to up to 1 mm long; bracteoles ca. 2×1.5 mm, triangular, adaxial side glabrous, abaxial side sericeous, hairs 0.2–0.7 mm long, light brown, stalk sessile to up to 0.1 mm long; pedicels 14–16 mm long, tomentose-sericeous, hairs 0.3–0.7 mm long, light brown to brown, stalk sessile to up to 0.2 mm long. *Sepals* 3.7–4.0 × ca. 2.0 mm, allways biglandular, adpressed to the androecium, apex rounded, revolute, adaxial side glabrous, abaxial side sericeous, hairs 0.3–0.7 mm long, whitish to light-brown, stalk sessile to up to 0.1 mm long; glands 2–2.8 × 1.2–1.4 mm, yellow. *Petals* yellow, glabrous; lateral petals reflexed, lamina cucullate, 5–6 × 5–6.5 mm, margin sinuate, claw 2.5–3 × 0.5–0.6 mm, twisted; posterior petal with lamina patent, ca. 4 × 5 mm, corrugate, margin erose, claw ca. 4.2 × 1 mm, erect. *Stamens* 10, connate at base; filaments 2–2.2 × 0.5–0.9 mm, adaxially pilose at base, hairs simple, 0.9–2.5 mm long, light brown, abaxially glabrous; connective 1.5–1.8 × 0.5–0.7 mm, not exceeding the locules, glabrous; locules 2–2.1 × 0.5–0.6 mm, apex rounded, glabrous. *Ovary* conical, ca. 1.8 × 1.8 mm, sericeous, hairs 0.5–1.1 mm long, shiny, light brown, stalk sessile to up to 0.1 mm long; ovules 0.7–0.9 × ca. 0.5 mm; style linear, 3.6–3.6 × 0.3–0.4 mm, erect, subulate, bent at the apex, glabrous; stigma minute. *Drupes* not seen.

Additional specimens examined:—BRAZIL. Minas Gerais: *S.loc.*, 18 Dezember 1837, fl., *s.leg.* (syntype BR no 857848). Serra do Caraça, March 1892, fl., *s.leg.* (syntype RB no 146817). Tiradentes, Vila de São José, *s.d.*, fl., *Pohl s.n.* (syntype BR no 857983).

Distribution, habitat and phenology:—*Byrsonima minaria* is known to Serra do Caraça, and Serra de Tiradentes in the state of Minas Gerais, Brazil (fig. 4), occurring in neotropical savannas (*cerrado*), or in rocky fields (*campo rupestre*). Flowering from December to March, and fruiting in March.

Conservation status:—*Byrsonima minaria* should be regarded as Critically Endangered [categories B2ab(iii)], due to its area of occupancy be less than 10 km² and by the continually declining habitat quality.

Etymology:—The epithet makes reference to the restricted distribution of *B. minaria* in the state of Minas Gerais.

Discussion:—*Byrsonima minaria* is a small tree with yellow flowers, prominent secondary veins, connective not exceeding the locules, and glabrous anthers. At first sight, it seems very similar to *B. macrophylla* (Pers.) W.R. Anderson (1993: 362), a common species in rocky fields from the state of Minas Gerais. However, *B. macrophylla* bears pink petals, with only the posterior petal showing a yellow claw (vs. petals with yellow limbs and claws in *B. minaria*), and connectives exceeding the locules in almost all anthers (vs. connective not exceeding the locules in *B. minaria*).

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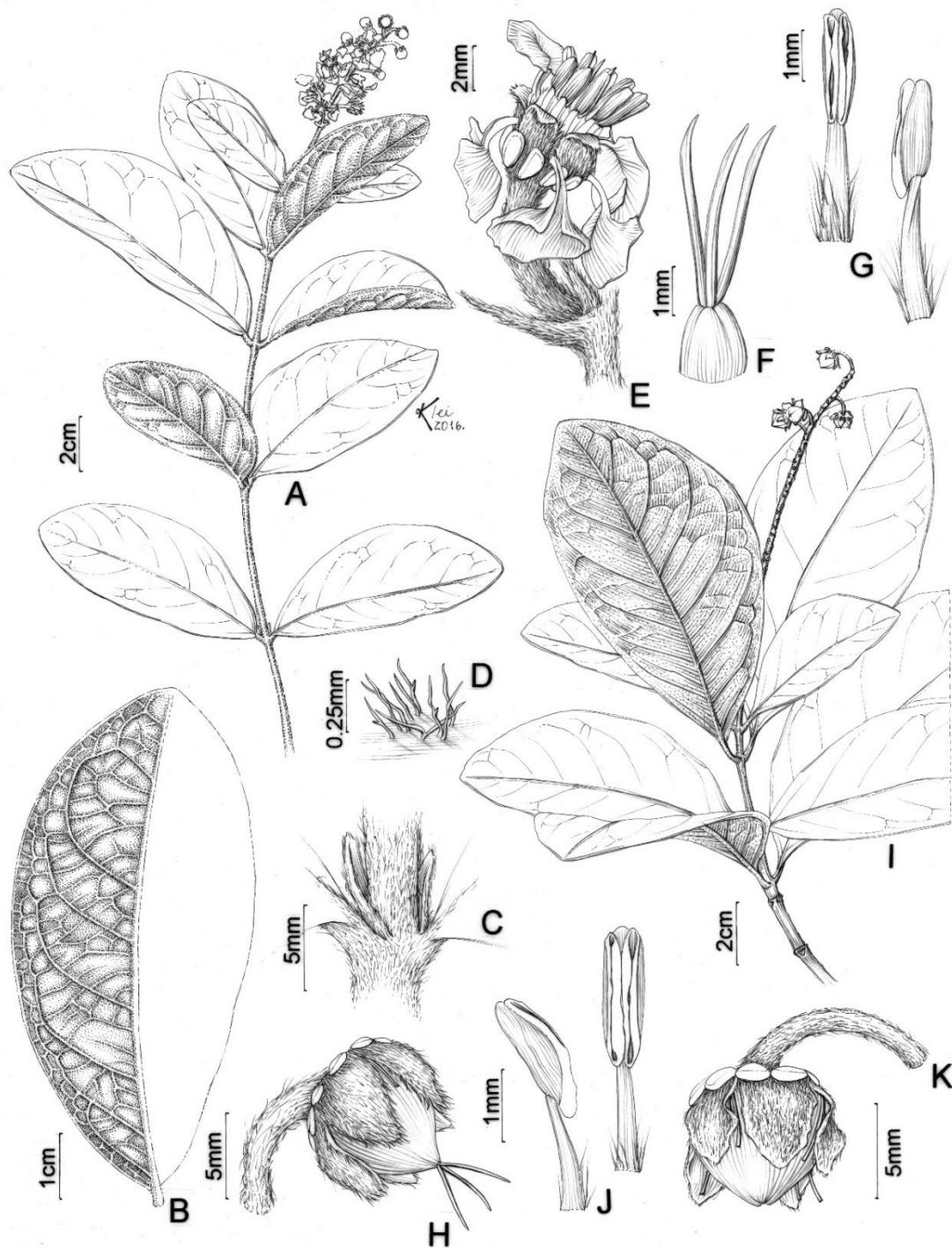


Figure 1 – *Byrsonima rupestris* A–H: A. Habit, B. Abaxial side of leaf blades, C. Stipules, D. Hairs on the abaxial side of leaf blades, E. Lateral view of the flower with the bract and bracteoles, F. Glabrous ovary, G. Stamens, frontal and lateral view, H. Drupe. *Byrsonima minaria* I–K: I. Habit, J. Stamens, frontal and lateral view, K. Lateral

view of the flower with the bract and bracteoles (A–H, Nakajima *et al.* 300, I–K, Ule 2456).

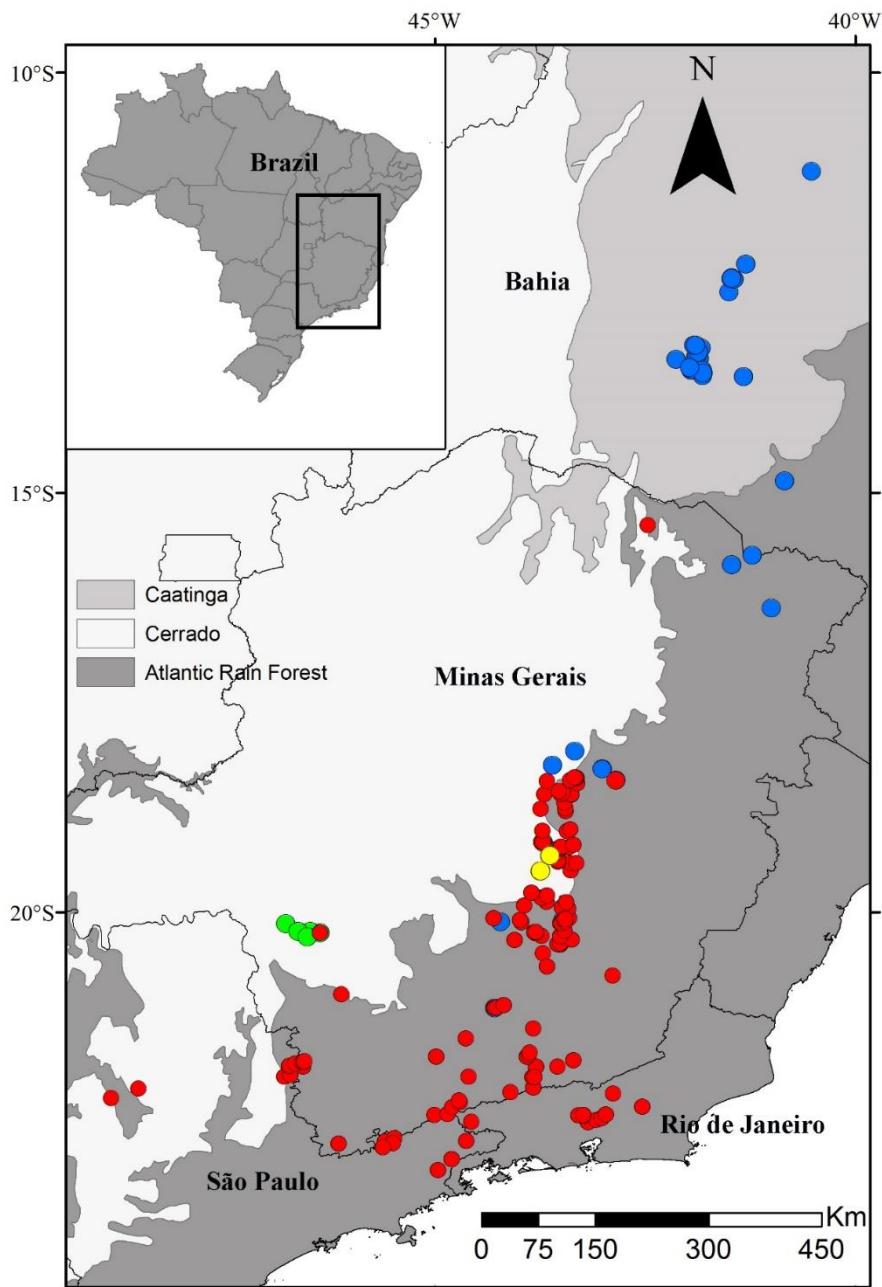


Figure 2 – Distribution of *Byrsonima rupestris* and closely related species: Green circles – *B. rupestris*; Red circles – *B. variabilis*; Yellow circles – *B. cipoensis*; Blue circles – *B. stannardii*.

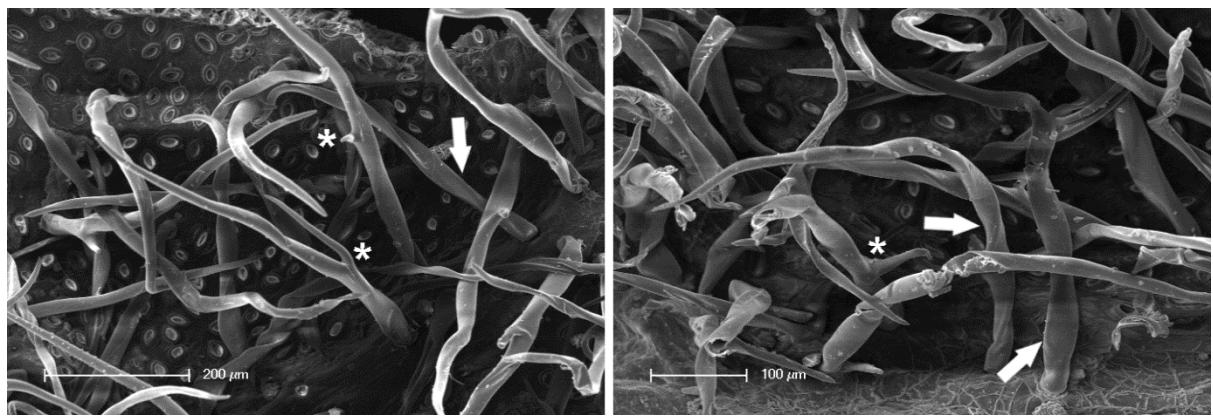


Figure 3 – Hairs from *Byrsonima rupestris*: Branched hairs marked with asterisk, and unbranched hairs marked with arrows.

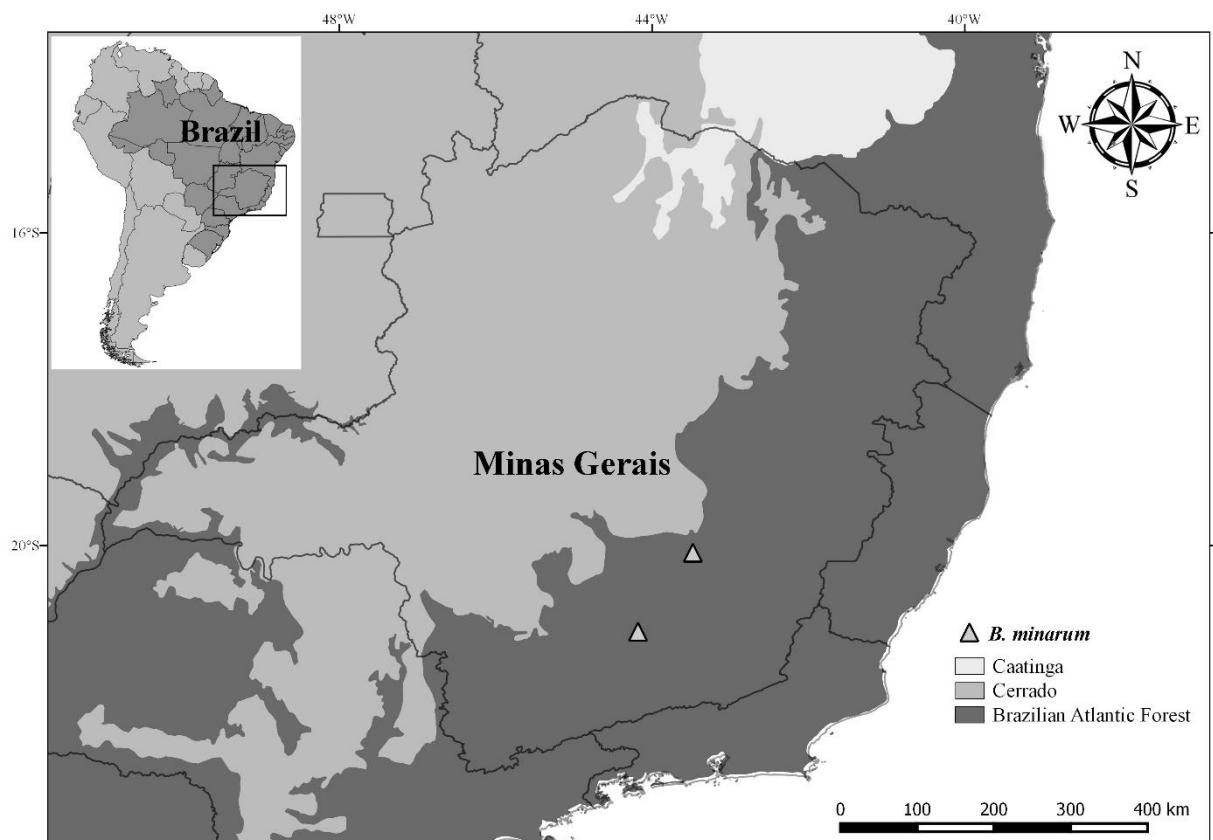


Figure 4 – Distribution of *Byrsonima minaria*.

Anexo 1

Desvendando o quebra-cabeças de *Byrsonima fanshawei* W.R. Anderson (Malpighiaceae): emenda e novos registros para uma espécie rara

Formatado de acordo com o periódico Phytotaxa

Assembling the Puzzle of *Byrsonima fanshawei* W.R. Anderson (Malpighiaceae): Emend and new records to a rare species

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Abstract

Byrsonima fanshawei is a rare species of Malpighiaceae which was described based only in a fruiting specimen from Kaieteur Plateau, Guyana. Here we provide an emend to the original description, including a complete description of floral characters, besides new records to the states of Amazonas and Espírito Santo, Brazil.

Keywords: Amazon Forest, Atlantic Forest, disjunction, Espírito Santo, Guyana

Resumo

Byrsonima fanshawei é uma espécie rara de Malpighiaceae que foi descrita baseada apenas em material com frutos do Kaieteur Plateau, Guiana. Apresentamos uma emenda para a descrição original, com a descrição completa de caracteres florais, além de novos registros para os estados do Amazonas e Espírito Santo, Brasil.

Palavras-chave: disjunção, Espírito Santo, Floresta Amazônica, Floresta Atlântica, Guiana

Introduction

Byrsonima (1821: 147) is the second largest genus in Malpighiaceae, comprising ca. 135 species endemic to the Neotropical region (Anderson 1981, Anderson *et al.* 2006). Brazil is the richest neotropical country in the genus, with ca. 97 species found in all Brazilian biomes, but especially diverse in the Cerrado vegetation and in the Amazon and Atlantic Forests biomes (Almeida *et al.* in press, Anderson 1981, BFG 2015).

Few species of *Byrsonima* present a disjunct distribution between the Amazon and Atlantic Forest (Anderson 1981). *Byrsonima fanshawei* (1981: 84-85) was recently identified as one the three known disjuncted species, with two fruiting specimens collected in the Atlantic Forest of Southern state of Bahia. This taxon was first described for the Guyana Highland, based on a single fruiting specimen (Anderson 1981). During visits to Northeastern Brazilian herbaria for the taxonomic revision of *Byrsonima* sect. *Eriolepsis* Nied. (1901: 1), we came across new records of *Byrsonima fanshawei*, including the first two flowering specimens ever recorded.

We present an emended description of this species, including a complete floral morphological description, along with an updated distribution in Brazil.

Material and Methods

Morphological descriptions and phenology of the studied species were based on herbaria specimens (CEPEC, ESA, HUEFS, INPA, MO, NY, RB, SP and U), and type collections (herbaria acronyms according to Thiers, continuously updated). The indumenta terminology follows Anderson (1981) and Niedenzu (1928), structure shapes follows Radford et al. (1974), the inflorescence terminology and morphology follows Anderson (1981), and fruit terminology follows Anderson (1981) and Niedenzu (1928). Scanning Electron Microscope images was performed with samples fixed in Karnovsky solution (Bozzola & Russel 1992), and coated in gold. The conservation status was proposed following the recommendations of IUCN Red List Categories and Criteria, Version 3.1 (IUCN 2001). GeoCAT (Bachman et al. 2011) was used for calculating the Extent of Occurrence (EOO) and the Area of Occurrence (AOO). Maps were elaborated using ArcGis version 9.3 (ESRI 2010), and geographical coordinates were obtained from herbarium specimens.

Results

Taxonomy

Byrsonima fanshawei W.R. Anderson *emend. nov.* Francener & Mamede

Type:—GUYANA. Kaieteur Plateau, 6 May 1944, Maguire & Fanshawe 23270 (holotype: NY!, isotype: K barcode K000426918!, MO barcode MO251736!, U barcode U0008172!, VEN!). Figure 1.

Tree up to 6 m tall; trunk 4 cm diam.; branches tomentose to glabrous, hairs T-shaped, sessile, reddish. *Stipules* persistent, connate, ca. 6 mm long., wide ovate, apex obtuse, abaxially sericeous-tomentose to glabrous, adaxially glabrous. *Leaves* opposite, plane; petioles 11–15 mm long, canaliculate, tomentose; leaf blades 10–12.7 × 5–7 cm, elliptic to obovate, base cuneate, margin entire, apex obtuse to rotund, adaxial side rough, tomentose along veins, hairs T-shaped, sessile, branches 1.5–2 mm long., stellate hairs absent, abaxial side tomentose, hairs T-shaped, sessile branches ca. 0.5 mm long, tortuous, to glabrous, sometimes with irregularly spaced stellate hairs bearing 2–5 unequal branches; veins impressed on both sides. *Pseudoracemes* (thyrsi of 1-flowered cincinni), with 14–20 flowers distributed in the median to superior part of the rachis; rachis ca. 6.5–10.5 cm long, tomentose-sericeous, hairs 0.5–1 mm long, brown, stalk sessile to up to 0.2 mm long; bracts and bracteoles deciduous in fruiting; bracts 3.5–5 × 1–1.5 mm, triangular, erect, abaxial side tomentose, adaxial side sparsely pilose; peduncle sessile to up to 1 mm long; bracteoles 2.4–2.5 × 1–1.2 mm, triangular, erect, abaxial side tomentose, adaxial side sparsely pilose; pedicels 9–10 mm long, bent, tomentose, hairs brown. *Sepals* 3–3.5 × 2.5–3 mm, all biglandular, apex rounded, erect or reflex at anthesis, sericeous on both sides; glands 2–2.6 mm long, yellow, glabrous. *Petals* yellow, glabrous; lateral petals reflexed, lamina 5–5.5 × 5–5.2 mm, cupuliform, margin slightly erose, claws 2.3–3 × 0.8–0.9 mm, circinate; posterior petal with lamina 3.8–4 × 3.5–4 mm, patent, corrugated, base auriculate, margin slightly erose, claw 3–3.5 × 0.9–1 mm, erect. *Stamens* 10, free at base; filaments 2–2.3 × 0.7–1 mm, pilose, hairs at base, 1–1.3 mm long, whitish; connective 2–2.7 × 0.6–1 mm, apex acute or acuminate, pilose to glabrous, exceeding or not the locules (up to 0.4 mm long); locules 2.5–3.3 × 0.7–0.8 mm, apex rounded, sericeous between the locules or laterally, hairs whitish. *Ovary* conical, 2–2.1 × 1.5–2 mm, sericeous, hairs up to 0.5 mm long, whitish; ovules 0.9–1 × 0.5–0.6 mm; styles 4–4.8 mm long, erect, subulate, apex bent, glabrous; stigmas minute. *Drupes* 8–9 mm diam., globose, apex apiculate, tomentose near apex. *Seeds* 3, 2–1 aborted, glabrous.

Examined specimens:—BRAZIL. Amazonas: Presidente Figueiredo, Rebio Uatumã, 19 May 2007, fr., Zartman *et al.* 7025 (CEPEC, INPA). Bahia: Una, Reserva Biológica de Una, 28 January 1998, fl., Carvalho *et al.* 6472 (CEPEC, NY, RB, SP); *loc. cit.*, 19 February 1998, fr., Jardim *et al.* 1716 (CEPEC, SP); Wenceslau Guimarães, Estação Ecológica, 29 May 2015, fl, Aona *et al.* 2318 (HUEFS). Espírito Santo: Linhares, Reserva

Natural da Vale, 19 June 2006, fr., *Folli* 5303 (CEPEC, SP); *loc. cit.*, 20 July 2013, fr., *Lima* 7655 (HUEFS, RB); *loc. cit.*, 6 June 2006, fr., *Freire et al.* 44 (ESA, SP).

Distribution, habitat and phenology:—*Byrsonima fanshawei* was first described to Amazonian savanna from Kaieteur Plateau in Guyana. For almost two decades it was only known from the type collection (collected in 1944 and described in 1981), and just in 1998 two more collections were discovered from the Submontane Atlantic Forest of Bahia state in Brazil. Just recently, we were able to locate five new collections for *B. fanshawei* dating from 2006-2013 for the States of Amazonas and Espírito Santo (Fig. 3). About 8% of plant species found in Southern Bahia forests show a disjunct distribution between Amazon and Atlantic Forests (Mori *et al.* 1981; Amorim *et al.* 2008). The same pattern is recorded to *B. crispa* (1840: 335), *B. duckeana* (1995: 20) and *B. stipulacea* (1840: 332) (BFG 2015). Flowering from January to May, and fruiting from February to July.

Conservation status:—*Byrsonima fanshawei* should be regarded as Critically Endangered [categorie B2ab(ii)], due to its area of occupancy being <10 km² and continually declining in habitat quality. Fortunately, all seven specimens were located within conservation units in Brazil.

Etymology:—The epithet makes reference to one of the collectors of the type specimen, Denny Basil Fanshawe (b. 1915–).

Discussion:—*Byrsonima fanshawei* is characterized by its shorter, persistent stipules (sometime deciduous), sessile leaf-hairs (fig. 2) and by the small fruits. It is close related to *B. stipulacea*, but the latter has longer and deciduous stipules, stellate leaf-hairs and larger fruits (Anderson 1981). The connectives show an acute to acuminate apex, while in *B. stipulacea* it is only acute. The original description was based only on a single fruiting specimen, but the author had strong suspicious that the petals were yellow and the anthers sericeous, at least between the locules (Anderson 1981). The description of flower characters here provided corroborated his suspicious.

Acknowledgments

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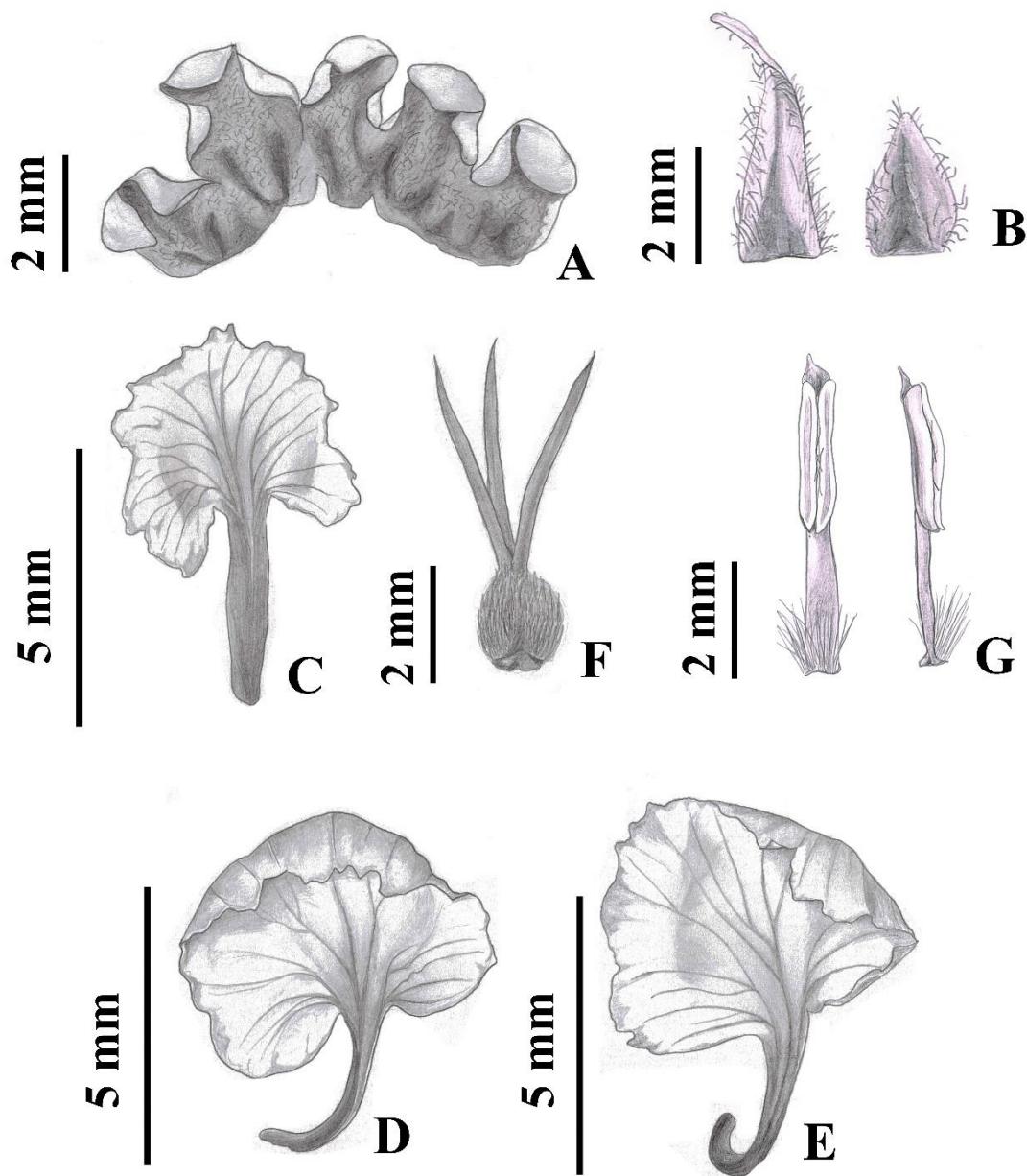


Figure 1 – *Byrsonima fanshawei*: A. E glandular sepals, B. Bracts and bracteoles in abaxial view, C. Posterior petal, D-E. Lateral petals, F. Sericeous ovary, G. Stamens, frontal and lateral view (*Carvalho et al. 6472*).

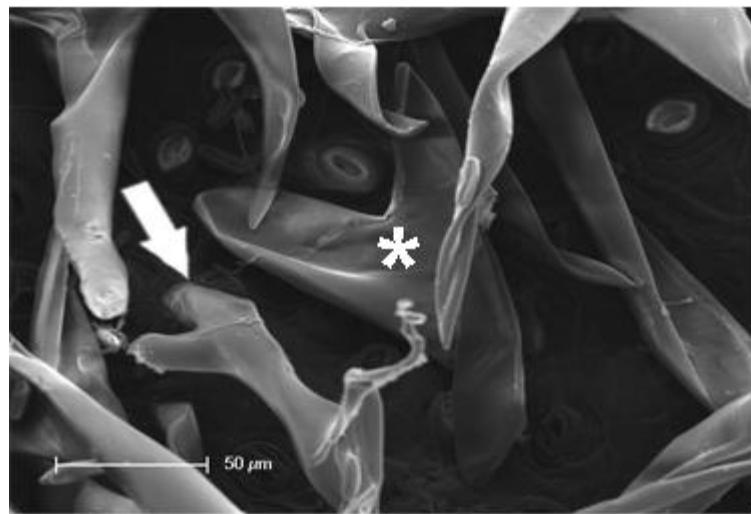


Figure 2 – *Byrsonima fanshawei*: Sessile hairs (asterisk) and subsessile hairs (arrow).

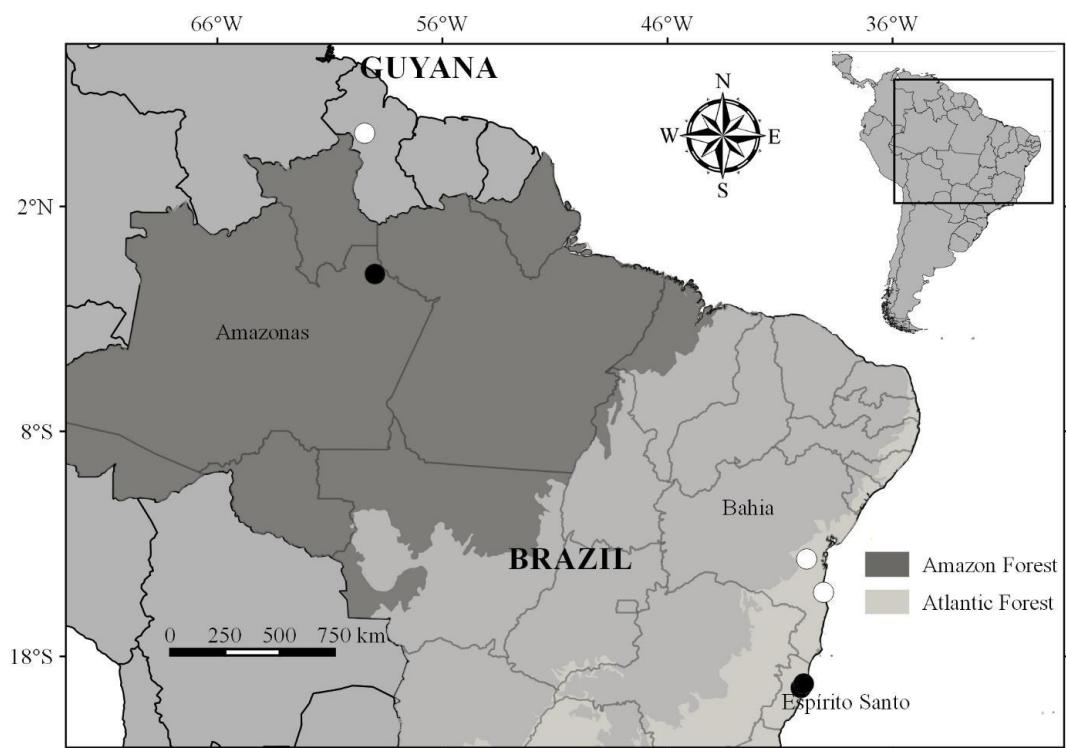


Figure 3 – Distribution of *Byrsonima fanshawei*: dark circle represents new records; white circle represents specimens previously cited in literature.

ANEXO 2

Guia de campo: Espécies brasileiras do gênero *Byrsonima* (Malpighiaceae)

Formatado de acordo com as normas do Field Museum

Brazilian species of the genus *Byrsonima* (Malpighiaceae)

Byrsonima of Brazil

1

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1 *Byrsonima affinis*



2 *Byrsonima affinis*



3 *Byrsonima affinis*



4 *Byrsonima arthropoda*



5 *Byrsonima arthropoda*



6 *Byrsonima arthropoda*



7 *Byrsonima basiloba*



8 *Byrsonima basiloba*



9 *Byrsonima basiloba*



10 *Byrsonima basiloba*



11 *Byrsonima brachybotrya*



12 *Byrsonima brachybotrya*



13 *Byrsonima cacaophila*

Photo: F. Flores



14 *Byrsonima cacaophila*

Photo: F. Flores



15 *Byrsonima cacaophila*

Photo: F. Flores



16 *Byrsonima chalcophylla*

Photo: M. Nadruz



17 *Byrsonima chalcophylla*

Photo: M. Nadruz



18 *Byrsonima chrysophylla*

Photo: F. Flores



19 *Byrsonima chrysophylla*

Photo: F. Flores



20 *Byrsonima chrysophylla*

Brazilian species of the genus *Byrsonima* (Malpighiaceae)

Byrsonima of Brazil

2

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21 *Byrsonima chrysophylla*



22 *Byrsonima cipoensis*



23 *Byrsonima cipoensis*



24 *Byrsonima clausseniana*



25 *Byrsonima clausseniana*

Photo: C. Silva



26 *Byrsonima clausseniana*

Photo: C. Silva



27 *Byrsonima cocolobifolia*

Photo: R.D.Sartor



28 *Byrsonima cocolobifolia*



29 *Byrsonima cocolobifolia*



30 *Byrsonima cocolobifolia*



31 *Byrsonima coniophylla*

Photo: L.O.A. Teixeira



32 *Byrsonima coniophylla*

Photo: L.O.A. Teixeira



33 *Byrsonima coniophylla*

Photo: L.O.A. Teixeira



34 *Byrsonima correifolia*

Photo: C.Silva



35 *Byrsonima correifolia*

Photo: C.Silva



36 *Byrsonima correifolia*

Photo: C.Silva



37 *Byrsonima crassifolia*



38 *Byrsonima crassifolia*



39 *Byrsonima crassifolia*



40 *Byrsonima crispa*

Brazilian species of the genus *Byrsonima* (Malpighiaceae)

Byrsonima of Brazil

3

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41 *Byrsonima crispa*



42 *Byrsonima crispa*



43 *Byrsonima crispa*



44 *Byrsonima cydoniifolia*

Photo: S.N. Moreira



45 *Byrsonima cydoniifolia*



46 *Byrsonima cydoniifolia*



47 *Byrsonima cydoniifolia*



48 *Byrsonima cydoniifolia*



49 *Byrsonima dealbata*

Photo: A.J.Fernandes-Júnior



50 *Byrsonima dealbata*

Photo: A.J.Fernandes-Júnior



51 *Byrsonima dealbata*

Photo: A.J.Fernandes-Júnior



52 *Byrsonima dealbata*

Photo: C.Silva



53 *Byrsonima gardneriana*



54 *Byrsonima gardneriana*



55 *Byrsonima incarnata*



56 *Byrsonima incarnata*



57 *Byrsonima incarnata*



58 *Byrsonima incarnata*



59 *Byrsonima intermedia*



60 *Byrsonima intermedia*

Brazilian species of the genus *Byrsonima* (Malpighiaceae)

Byrsonima of Brazil

4

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76 *Byrsonima linguifera*

77 *Byrsonima linguifera*

78 *Byrsonima linguifera*

Photo: C.Silva

80 *Byrsonima macrophylla*

Photo: L. Echternacht

Brazilian species of the genus *Byrsonima* (Malpighiaceae)

Byrsonima of Brazil

5

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Brazilian species of the genus *Byrsonima* (Malpighiaceae)

Byrsonima of Brazil

6

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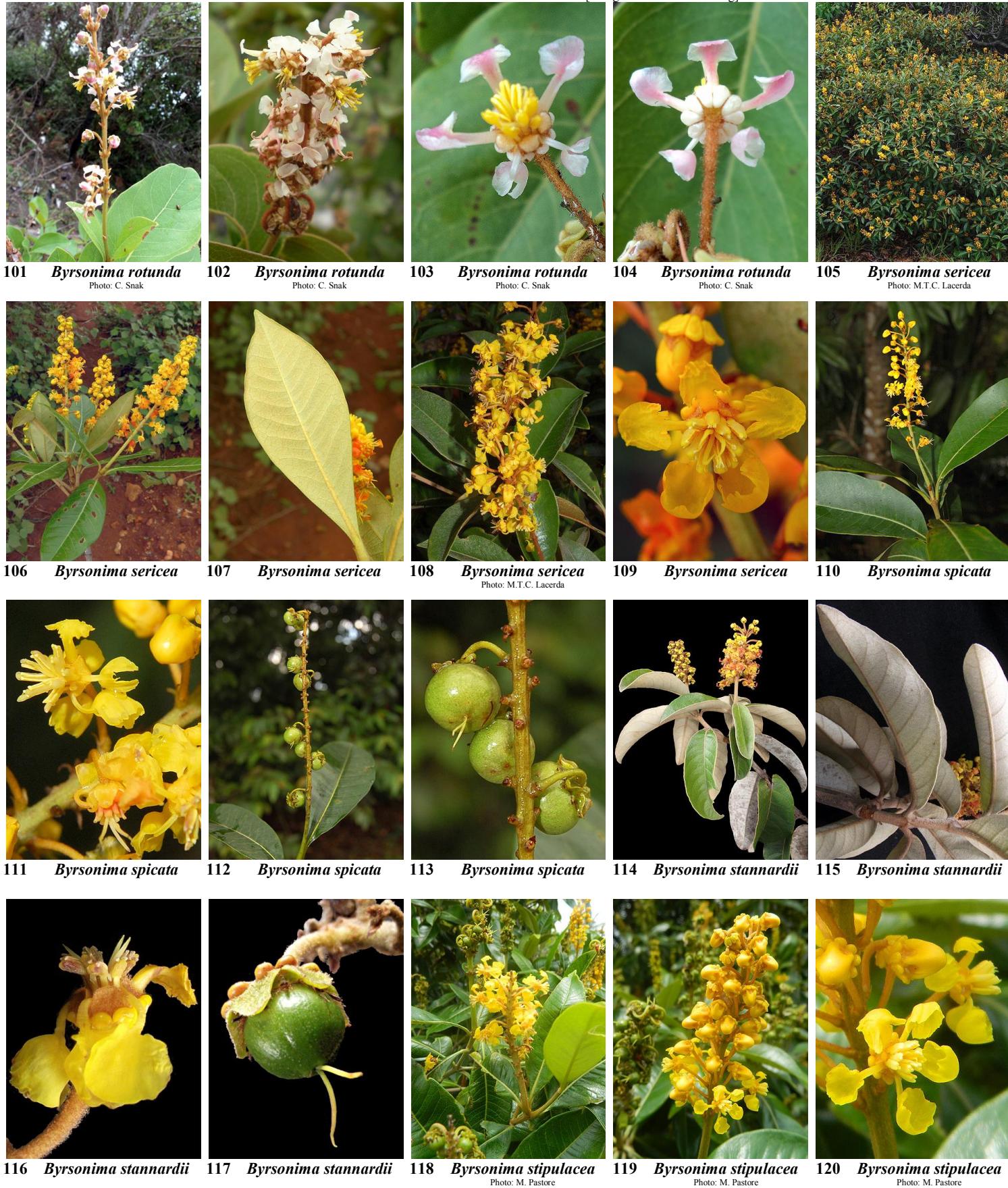
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Brazilian species of the genus *Byrsonima* (Malpighiaceae)

Byrsonima of Brazil

7

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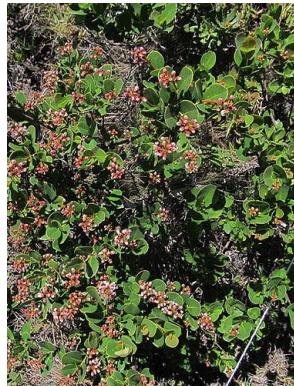
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121 *Byrsonima tripterifolia*

Photo: G. Almeida



122 *Byrsonima tripterifolia*

Photo: L. Marinho



123 *Byrsonima tripterifolia*

Photo: F. Flores



124 *Byrsonima tripterifolia*

Photo: F. Flores



125 *Byrsonima umbellata*



126 *Byrsonima umbellata*



127 *Byrsonima umbellata*



128 *Byrsonima vacciniifolia*



129 *Byrsonima vacciniifolia*



130 *Byrsonima vacciniifolia*



131 *Byrsonima variabilis*



132 *Byrsonima variabilis*



133 *Byrsonima variabilis*



134 *Byrsonima variabilis*



135 *Byrsonima variabilis*



136 *Byrsonima verbascifolia*

Photo: C. Silva



137 *Byrsonima verbascifolia*

Photo: C. Silva



138 *Byrsonima viminifolia*



139 *Byrsonima viminifolia*



140 *Byrsonima viminifolia*

Photo: C. Silva

CONSIDERAÇÕES FINAIS

O gênero *Byrsonima* apresenta grandes dificuldades para seu estudo, dentre as quais a grande quantidade de espécies descritas, a falta de revisões recentes e também a grande quantidade de material depositado nos herbários.

Diversos nomes foram propostos para *Byrsonima* mas apenas 135 representam espécies aceitas. O grupo com menos estudos taxonômicos é *Byrsonima* sect. *Eriolepis*, muito abundante no Cerrado brasileiro e também na área do Planalto das Guianas, exatamente nos dois centros de diversidade para Malpighiaceae e também para *Byrsonima*. Assim, foram realizadas visitas a um grande número de herbários brasileiros especialmente ricos em coletas do Cerrado, consultas às bases de dados de herbários estrangeiros, e uma grande quantidade de espécies foi identificada. Em muitos herbários, pelo menos a metade do material ali depositado se encontrava indeterminada, não apenas da seção *Eriolepis*, o que nos permitiu um conhecimento amplo da morfologia e distribuição do gênero em sua totalidade, principalmente das espécies ocorrentes no Brasil.

Vários nomes dentro da seção *Eriolepis* careciam de lectotipificações, inclusive a própria seção. Foi possível realizar uma busca aos tipos desses nomes, e então propor lectótipos para vários deles.

Foi realizado também um grande esforço de coleta de campo, que foi recompensado com a coleta de uma espécie nova no Parque Nacional das Emas, com um melhor conhecimento das espécies *in loco* e também para a coleta de amostras frescas em sílica-gel para a realização de análises moleculares, pois amostras contidas em herbários dificilmente eram amplificadas, e assim conseguiu-se uma amostragem de cerca de um terço das espécies de *Byrsonima*. Isso possibilitou-nos a realização da análise filogenética do gênero como um todo, com dados inéditos, além de prover o aumento no número de amostras sequenciadas no GenBank, ampliando de nove para 42 espécies depositadas. Inicialmente estava prevista uma amostragem de seis a sete marcadores moleculares, todavia várias regiões apresentaram problemas, mesmo após a amplificação, não permitindo um bom sequenciamento.

Da análise realizada, vários clados surgiram, muitos deles ainda sem uma sinapomorfia clara, sendo que, para a seção *Eriolepis* foi comprovado seu polifiletismo, com o surgimento de um clado monofilético (Clado *Byrsonima crassifolia*), cuja revisão taxonômica reconheceu oito espécies. São necessários futuros trabalhos para compreender melhor as prováveis sinapomorfias deste clado, além de um aumento no número de espécies amostradas, especialmente extra-brasileiras, mas também sendo necessária uma análise com a técnica de NGS (Next Generation Sequencing) para elucidar melhor alguns grupos.

A análise dos materiais depositados nos vários herbários visitados e daqueles recebidos por empréstimo, levou à descoberta de novidades taxonômicas, a localização novas populações de *B. fanshawei*, que permitiram a complementação de sua descrição original.

As viagens a campo também permitiram fotografar várias espécies de *Byrsonima*, o que, somado ao envio de fotos por diversas pessoas possibilitou a elaboração de um Guia de Campo para o gênero no Brasil.

Foi muito prazeroso trabalhar com o grupo, que quero continuar a estudar nos próximos anos, em diversas frentes de trabalho, continuando o trabalho taxonômico, participando da revisão do grupo para a Flora do Brasil, além de estudos de filogenia e de ecologia de suas espécies.