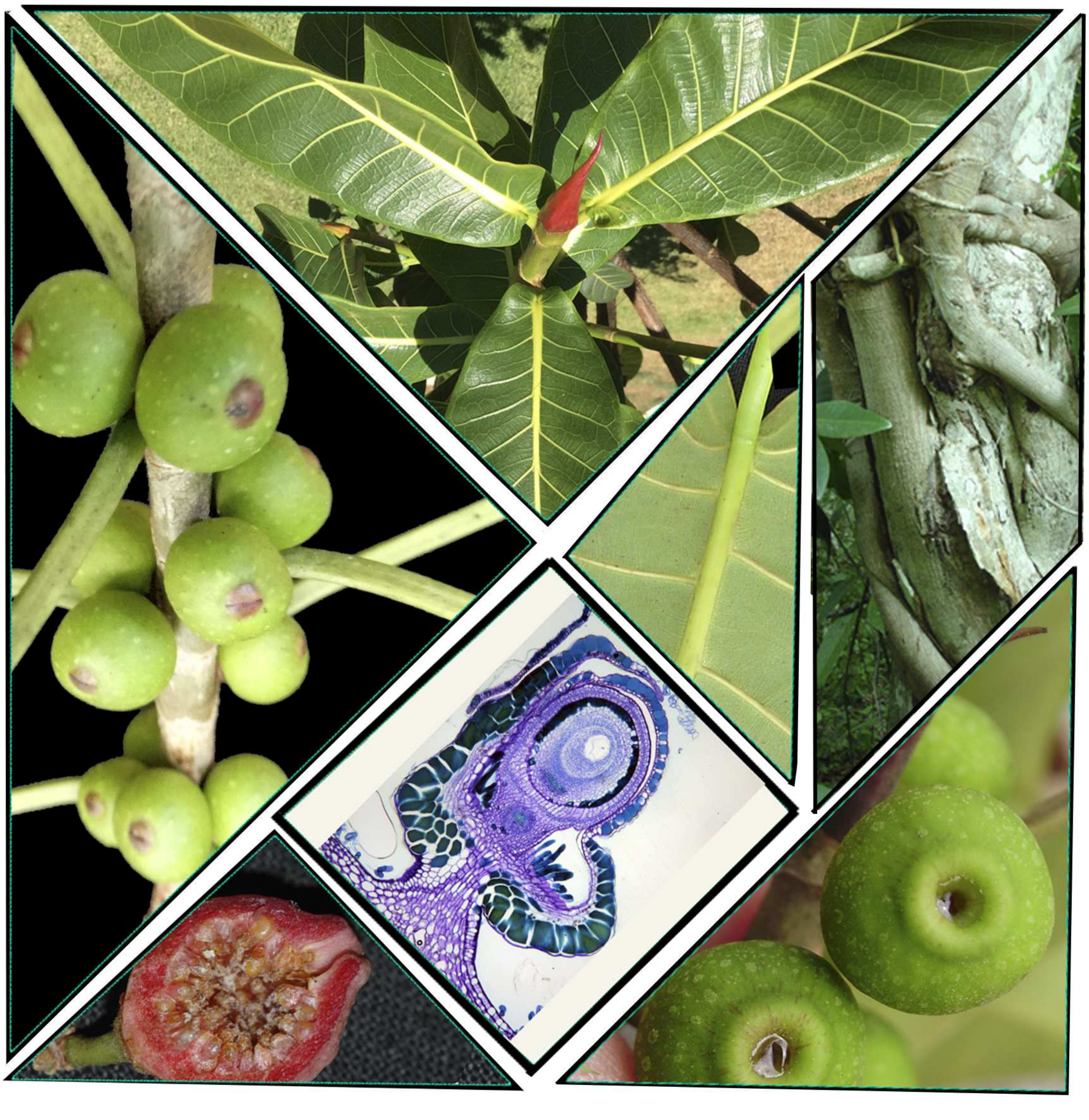
Universidade Estadual de Feira de Santana
Programa de Pós-Graduação em Botânica

Sistemática e Biogeografia de *Ficus* (Moraceae) na região Neotropical



Anderson F. P. Machado
2017

Anderson Ferreira Pinto Machado

Sistemática e Biogeografia de *Ficus* (Moraceae) na região Neotropical

FEIRA DE SANTANA – BAHIA
2017

UNIVERSIDADE ESTADUAL DE FEIRA DE SANTANA
DEPARTAMENTO DE CIÊNCIAS BIOLÓGICAS
PROGRAMA DE PÓS-GRADUAÇÃO EM BOTÂNICA

Sistemática e Biogeografia de *Ficus* (Moraceae) na região Neotropical

Anderson Ferreira Pinto Machado
Tese apresentada ao Programa de
Pós-Graduação em Botânica da
Universidade Estadual de Feira de Santana
como parte dos requisitos para a obtenção
do título de *Doutor em Botânica*.

ORIENTADOR: PROF. DR. Luciano Paganucci de Queiroz (UEFS)
FEIRA DE SANTANA – BA
2017

Ficha Catalográfica – Biblioteca Central Julieta Carteado

Machado, Anderson Ferreira Pinto
M129s Sistemática e Biogeografia de Ficus (Moraceae) na região Neotropical./ Anderson Ferreira Pinto Machado. Feira de Santana, 2017.
128f.: il.

Orientador: Luciano Paganucci de Queiroz
Tese (doutorado) – Universidade Estadual de Feira de Santana, Departamento de Ciências Biológicas, Programa de Pós-Graduação em Botânica, 2017.

1.Sistemática. 2.Biogeografia. 3.Ficus (Moraceae). I.Queiroz, Luciano Paganucci de, (orient.). II.Universidade Estadual de Feira de Santana. III. Título.

CDU : 582.635.3

ANDERSON FERREIRA PINTO MACHADO

SISTEMÁTICA E BIOGEOGRAFIA DE *FICUS* (MORACEAE) NA REGIÃO NEOTROPICAL

Tese de doutorado submetida ao Programa de Pós-Graduação em Botânica da Universidade Estadual de Feira de Santana – UEFS, como parte dos requisitos necessários à obtenção do título de Doutor em Botânica.

Feira de Santana, 27 de julho de 2017.

BANCA EXAMINADORA

Prof(a). Dr(a). Alessandra Selbach Schnadelbach

Prof(a). Dr(a). André Márcio Araújo Amorim

Prof(a). Dr(a). Charles Eugene Zartman (INPA)

Prof(a). Dr(a). Lidyanne Yuriko Saleme Aona (UFRB)

Prof. Dr. Luciano Paganucci de Queiroz (UEFS)

Orientador e Presidente da Banca

Feira de Santana – BA
2017

O único homem que eu conheço que se comporta de maneira sensata é o meu alfaiate. Cada vez que o visito ele me toma novamente as medidas. O resto das pessoas continua com suas velhas medidas e espera que eu me encaixe nelas.

George Bernard Shaw (1856-1950)

Sou um homem comum
brasileiro, maior, casado, reservista,
e não vejo na vida, amigo,
nenhum sentido, senão
lutarmos juntos por um mundo melhor.
(...)
Mas somos muitos milhões de homens comuns
e podemos formar uma muralha
com nossos corpos de sonho e margaridas.

Ferreira Gullar (1930-2016)

Dedico este trabalho aos meus filhos **Mel** e **Tomás** e minha Esposa **Andrea Karla** por serem a razão, a direção e a força que me fizeram seguir adiante. Ofereço também a minha Avó **Maria Ferreira** por ter me ensinado a Amar as plantas e ao meu Pai Botânico **Pedro Carauta** (1930-2013) por me ajudar a compreender as coisas deste mundo; as do alto e sobre as plantas.

AGRADECIMENTOS

Aos meus filhos **Mel & Tomás** por me receberem com imenso carinho cada vez que eu regressava a casa. No meu entendimento vocês me deram o maior título que um homem pode ter no mundo o de **Pai**. Obrigado.

A minha esposa **Andrea Karla** por todo seu carinho, dedicação, preocupação e presença. Por "segurar as pontas" com as crianças quando eu precisava me ausentar e pelo equilíbrio e Luz que seu Amor me trouxe desde que decidimos andar juntos.

A minha Avó, **Maria Ferreira**, que me ensinou primeiro sobre as plantas e a quem eu devo muito por ter me permitido e ajudado a estudar para que eu chegasse até aqui. A escolha da minha profissão e muitas das lentes com as quais eu enxergo a vida foram influência direta dela.

A toda a **minha família baiana** que me recebeu maravilhosamente e que me apoiou. Aos parentes em Cruz das Almas aqui representados por Sra. **Francisca** e Sr. **Matias**, meus sogros. Eles são exemplos de Pais, de casal e de vida, para mim. E aos de Feira de Santana: **Silvia, Cláudio** e meu afilhado **Heitor** que me receberam em sua ("nossa") casa de Feira de Santana.

Ao **Jorge Pedro Pereira Carauta** (1930-2013), Amigo querido, Pai Botânico que, além de muito do que aprendi na *Scientia Amabilis*, reforçou e ensinou-me valores eternos e indeléveis como o desprendimento, a disponibilidade, a cordialidade, a fé e a humildade. Tudo o que eu fiz e fizer em Botânica é e será fruto da base que ele me ajudou a construir.

Ao Dr. **Luciano Paganucci de Queiroz**, que sempre esteve preocupado com a minha formação e que confiou em minhas potencialidades e dando o necessário para que eu pudesse fazer o meu trabalho com dignidade. Sou lhe grato também por todas as chances que me deu.

Ao Dr. **Carlos André Espolador Leitão** por sua generosidade e auxílio, por me receber bem na Universidade Estadual do Sudoeste da Bahia e por sempre ser solícito com alguma dúvida pelo simples prazer de discutir Botânica e de ajudar.

Ao Dr. **Rodrigo Augusto S. Pereira** por ser uma referência em ecologia de *Ficus* e de seus polinizadores que me brindou com boas dicas e com uma conversa franca. Por sua participação na tese fornecendo materiais importantes para a amostragem.

A Drª. **Nina Rønsted** por ser extremamente proativa e animada com o trabalho participando de todas as etapas da coleta de dados à discussão. Suas mensagens eram sempre um ânimo e brindavam cada descoberta.

Ao pessoal da Universidade de Copenhagen em especial ao **Gary I. Stanford** e ao **Sam Brun-Lund** pela recepção, ensinamentos e conversas agradáveis.

Ao Dr. **Cornelis Christian Berg** (1934-2012) por ter participado ativamente das discussões quando eu ainda estava pensando no projeto. Por enviar bibliografias e por me dar a honra de participar de uma pequena publicação com ele.

A **Silvana da Costa Ferreira, María Cristina Lopez Roberts e Ariane Raquel** que muito me ensinaram sobre a rotina do laboratório de Biologia molecular.

Às Amigas **Alessandra S. Schnadelbach** e **Maria Luiza Silveira de Carvalho** (Tutti) pelas boas conversas, pelo empenho e desejo de justiça, pela ajuda e carinho de sempre.

Aos Amigos **Marcus Fellipe Oliveira da Silva**, **Marcelo D. M. Vianna Filho** e ao **Ricardo Lacerda** pela força e vontade de recomeçar e pelas discussões e revisões nos artigos.

Aos colegas **Eva María Piedra Malagón, Leandro Pederneiras e Otilene Matos** pelas discussões sobre a Taxonomia de *Ficus*.

Ao Amigo **Lizandro Peraza** por auxiliar consideravelmente na parte de Biogeografia aprendendo comigo as análises, me ensinando e tirando dúvidas. Uma parte considerável desta tese não seria possível sem a ajuda dele.

Ao Amigo **Lucas Marinho** por todas as dicas sobre revistas legais; por todos os auxílios com as imagens e por todas as conversas estimulantes sobre Botânica. É bonito ver o "menino" que eu conheci ainda na graduação crescer tanto em sabedoria mantendo a humildade e generosidade.

À Amiga **Aline de Souza** pelo carinho de sempre; pelo auxílio luxuoso no artigo de Anatomia e por me dar a honra de dizer que, de certa forma, influenciei sua escolha pela Taxonomia.

À Amiga **Maria Aparecida** (Cidinha) por ser este exemplo de dedicação ao trabalho e à pesquisa com competência e responsabilidade. Por todas as nossas conversas e pelo carinho e respeito que devotamos um ao outro.

Às Amigas **Juliana Freitas** e **Michella Del Rei** por todo o companheirismo, pelo cuscuz, pelo café, por todas as alegres conversas e pelos auxílios enormes com meus artigos.

À Amiga **Uiara Catharina** e ao **Rafael Almeida** pela ajuda no processo de Qualificação e por todas as dicas de "sobrevivência" além das conversas sobre Filogenia e Taxonomia.

Aos membros do Colegiado do PPGBot-UEFS em especial a coordenadora Prof. **R. Patrícia Oliveira** pelo auxílio e compreensão nas questões burocráticas.

Ao pessoal da Secretaria do PPGBot-UEFS pela presteza e educação **Gardênia** e **Daniela**. Mas também aos que por lá passaram e me foram igualmente solícitos como **Adriana Estrela** e **Fredson**.

Ao pessoal do Lamol que muito me auxiliou em especial ao **Ricardo Villas Bôas**, **Dissinho Almeida** e ao **Evandro Ancelmo**.

Ao pessoal do HUEFS **Téo, Elaine, Ítala, Maurício, Zezé** e vários outros que por lá passaram e que foram fundamentais neste trabalho.

Aos **Professores dos componentes curriculares** que cursei dentre eles **Alessandra Schnadelbach, Alessandro Rapini, Ana Maria Giulietti Harley, André Amorim, Cássio Van den Berg, Carlos W. N. Moura, Daniela Torres, Reyjane Patrícia** e também ao

Luciano e suas aulas que foram das melhores que tive até hoje. Agradeço também a aqueles que, mesmo sem eu ter participado de aulas formais, me auxiliaram com suas vivências e sua inteligência nominalmente os Professores **Abel A. Conceição; Domingos Cardoso; Efigênia M.; Flávio França; Francisco de Assis; Lígia S. Funch; Luís Gusmão** e **Patrícia Luz**.

Aos colegas e aos meus ex-alunos da UESB, onde fui Professor substituto, e tive uma experiência muito agradável. Em especial aos Professores **Carlos André**, **Cecília Azevedo**, **Claudenir Caires**, **Emília Valente** e **Débora Leonardo**. Que me trataram com respeito e generosidade quando dividimos os componentes curriculares.

Aos colegas da UFRB que me receberam com muito respeito e gentileza. Agradeço ao **Grênivel Mota, Márcio Lacerda L. Martins, Lidyanne Aona e a Patrícia Luz.**

A **FAPESB** e a **CAPES**, pelas bolsas concedidas, viabilizando a realização deste trabalho.

E a todos que contribuíram não somente para este trabalho ou para meu crescimento profissional, mas para minha formação como ser humano.

Muito obrigado, *Gracias*, *Thanks*, *Tak*.

SUMÁRIO

RESUMO

Ficus L. (Moraceae), com aproximadamente 750 espécies, caracteriza-se por seu tipo de inflorescência, o sicônio ou figo, um receptáculo encerrado por brácteas em uma região denominada ostíolo. Duas linhagens do gênero ocorrem na Região Neotropical, *Ficus* sect. *Americanae* (~100 species) e *Ficus* sect. *Pharmacosycea* (~20 species). A grande diversificação das figueiras nas florestas úmidas ao redor do globo e a ocorrência de espécies em todos os biomas neotropicais fazem de *Ficus* um modelo interessante para auxiliar na compreensão dos mecanismos associados à diversificação de espécies na região Neotropical. Este trabalho visou contribuir para a solução de problemas taxonômicos em *Ficus* sect. *Americanae*; apontar caracteres potencialmente importantes para a taxonomia do grupo e entender o processo de diversificação das espécies nos Neotrópicos auxiliando na compreensão da história da diversidade nesta região. Para tais fins, utilizou-se a metodologia da taxonomia clássica com análise das obras originais e das coleções tipo, trabalho de campo e estudos morfológicos; abordagem anatomia vegetal bem como análises filogenéticas e biogeográficas. Os resultados aqui apresentados incluem a descrição de duas novas espécies, o estabelecimento de dois nomes novos e o restabelecimento de uma espécie antes considerada sinônimo. Ainda na parte taxonômica é apresentada uma chave para as espécies de *Ficus* sect. *Americanae* no Domínio da Mata Atlântica. No que se refere ao estudo de caracteres micromorfológicos aqui é reportada, pela primeira vez, uma especialização das brácteas que encerram o sicônio, bem como dos coléteres nas inflorescências do gênero. A abordagem biogeográfica mostrou que a diversificação das figueiras neotropicais iniciou-se entre o Oligoceno e o Mioceno e que o gênero passou por dois momentos de maior diversificação, no Mioceno Médio e no Plioceno. Nossos resultados também evidenciaram que o hábito hemiepífito e o tamanho reduzido dos propágulos de *Ficus* sect. *Americanae* possibilitaram uma maior diversificação desta linhagem nos Neotrópicos se comparada a *Ficus* sect. *Pharmacosycea*.

Palavras chave: Amazônia, Biogeografia, *Ficus* sect. *Americanae*, *Ficus* sect. *Pharmacosycea*, Filogenia, Mata Atlântica.

ABSTRACT

Ficus L. (Moraceae), with approximately 750 species, is characterized by its typical inflorescence, the syconium or fig, a receptacle enclosed by bracts in a region called ostiole. Two lineages of the genus occur in the Neotropical Region, *Ficus* sect. *Americanae* (~ 100 species) and *Ficus* sect. *Pharmacosycea* (~ 20 species). The great diversity of the fig trees in the wet forests worldwide and the occurrence of species in all the Neotropical biomes make *Ficus* an interesting model to study the processes associated with diversification species in the Neotropical region. This work aimed to: contribute to the solution of taxonomic problems in *Ficus* sect. *Americanae*; to discover characters potentially relevant in taxonomy; to understand the process of species diversification in the Neotropics, helping to understand the history of diversity in this region. To accomplish to these goals, we use classical taxonomic procedures with analysis of the protologues and type collections, field work, morphological and anatomical studies as well as phylogenetic and biogeographical analyses. The results presented here are taxonomic novelties with the description of two new species, the establishment of two new names and the reestablishment of a species previously considered as a synonym. It is also is presented a key for species of *Ficus* sect. *Americanae* in the Mata Atlântica Domain. It is reported for the first time a specialization of the bracts surrounding the ostiole, as well as of the colleters in the inflorescences of the genus. The biogeographic approach showed that the diversification of the Neotropical fig trees began between the Oligocene and the Miocene and that the genus went through two bursts of diversification (in the Middle Miocene and Pliocene). Our results also showed that the hemiepiphyte habit and the reduced size of *Ficus* sect. *Americanae* allowed a greater diversification of this lineage in the Neotropics when compared to *Ficus* sect. *Pharmacosycea*.

Keywords: Amazon, Biogeography, *Ficus* sect. *Americanae*, *Ficus* sect. *Pharmacosycea*, Phylogeny, Atlantic Forest.

INTRODUÇÃO GERAL

Ficus L., as figueiras e gameleiras, compreende cerca de 750 espécies subordinadas a seis subgêneros e dezenove seções com distribuição nas regiões tropicais e subtropicais (Berg & Corner 2005, Pederneiras et al. 2015). São plantas latescentes com folhas alternas e com uma estípula terminal cônica (Carauta & Diaz 2002). Sua principal sinapomorfia é a presença do sicônio, uma inflorescência em forma de urna com uma abertura apical (ostíolo) encerrada por brácteas (Berg & Villavicencio 2004). O gênero é um dos elementos mais importantes em florestas tropicais úmidas (Harrison 2005).

As espécies de figueiras neotropicais incluem duas seções *Ficus* sect. *Pharmacosycea* (Miq.) Benth. & Hooker (ca. 20 spp.) e *Ficus* sect. *Americanae* Miq. (ca. 100 spp.), estas as figueiras estrangulantes ou “mata-paus” (Berg & Simonis 1981, Berg 1989, Berg e Villavicencio 2004, Carauta 1989). Algumas contribuições para o conhecimento destas espécies podem ser encontradas em Berg (2009; Flora do Equador); Berg (2012; Flora Mesoamericana); Berg & Dewolf (1975; Moraceae do Suriname); Berg e Simonis (2000; Moraceae da Venezuela); Berg et al. (1984; novas espécies de *Ficus* para Amazonia e Guianas); Berg e Villavicencio (2004; Estudos taxonômicos em *Ficus*); Burger (1977; Flora da Costa Rica); Carauta (1989; *Ficus* do Brasil); Carvajal (2012; Moraceae do México); Dugand (1942, 1943, 1944a, 1944b, 1944c, 1946, 1956); Ibarra-Manríquez et al. (2012; *Ficus* do México); Pittier (1937; *Ficus* da Venezuela); Standley (1917; *Ficus* do México e America Central); Standley (1937; Flora da Costa Rica) e Vázquez-Ávila (1981; *Ficus* da Argentina).

No Brasil, *Ficus* apresenta cerca de 80 espécies (BFG 2015) das quais pouco mais da metade ocorre na Mata Atlântica. Os mais relevantes tratamentos taxonômicos incluindo espécies com ocorrência no Brasil foram a Flora brasiliensis (Miquel 1853); a tese de J.P.P. Carauta sobre as figueiras no Brasil (1989) e a obra de Berg & Villavicencio (2004). No que se refere a estudos filogenéticos, duas teses foram defendidas com importantes contribuições para os *Ficus* dos Neotrópicos. Santos (2009) trabalhou com as figueiras ocorrentes no domínio Amazônico e Pederneiras (Pederneiras et al. 2015b) estudou as espécies neotropicais de *Ficus* sect. *Pharmacosycea.*

A despeito do grande número de obras focadas na taxonomia de figueiras neotropicais inúmeros problemas de delimitação específica ainda encontram-se irresolutos em especial em *Ficus* sect. *Americanae* onde foram reconhecidos vários complexos de espécies dentre eles: Complexo *F. americana*; *F. aurea*; *F. citrifolia; F. obtusifolia*; *F. pertusa* e *F. trigonata* (Berg & Simonis 1981, Berg 1989, Berg 2007). Contudo, as abordagens filogenéticas incluindo espécies destes complexos mostraram que os mesmos não são monofiléticos (ver Capítulo 6; Santos 2009; Cruaud et al. 2012). A grande variação morfológica, a sua maior diversificação na região neotropical e o fato de não haver uma abordagem filogenética e biogeográfica recente fazem de *Ficus* sect. *Americanae* um grupo de interesse para tais investigações.

A despeito da diversidade e importância dos *Ficus* nos neotrópicos nenhuma pesquisa abordou a filogenia e diversificação de *Ficus* sect. *Americanae*. Consequentemente pouco se sabe sobre a origem e diversificação do gênero nas Américas. Uma análise biogeográfica em contexto filogenético fornece a oportunidade de testar os padrões de diversificação nas florestas úmidas neotropicais. Mais especificamente correlacionando estes padrões com os eventos biogeográficos que influenciaram na diversificação de vários grupos taxonômicos nesta região. No capítulo 6 apresenta-se a mais abrangente filogenia datada para as *Ficus* dos neotrópicos na intenção de se testar hipóteses biogeográficas correntes. Adicionalmente apresentamos uma análise de evolução de caracteres que mostra como determinadas *inovações chave* podem ter influenciado e promovido a maior diversificação do grupo.

Na intenção de preencher a lacuna acerca do conhecimento das figueiras neotropicais, esta tese está estruturada da seguinte forma: **Parte I: Novidades Taxonômicas e Nomenclaturais em *Ficus* (Moraceae)**, onde realizamos abordagens taxonômicas com novidades nomenclaturais e descrição de novos táxons. Compreende, esta parte, dois artigos (Capítulos 1 e 2) e duas notas científicas (Capítulos 3 e 4).

O **Capítulo 1** trata das espécies de *Ficus* sect. *Americanae* no Domínio da Mata Atlântica. Neste apresenta-se a descrição de uma nova espécie e o restabelecimento de outra antes considerada como sinônimo nomenclatural. O artigo inclui ainda uma chave para as espécies de *Ficus* no domínio da Mata Atlântica (a ser submetido à *Systematic Botany*).

O **Capítulo 2** compreende a descrição de uma nova espécie até o momento conhecida apenas de duas localidades em regiões de campos rupestres no Nordeste do Brasil (Submetido à Phytotaxa).

O **Capítulo 3** (publicado na Phytotaxa) trata de um novo nome para *Ficus rupicola* C.C. Berg e Carauta. Enquanto que o **Capítulo 4**, também uma nota, trata de um nome novo para um fóssil que é homônimo posterior de uma espécie de *Ficus* bastante comum em Floresta Atlântica (*Ficus clusiifolia* Schott) (publicado na Phytotaxa).

A abordagem em Anatomia Vegetal apresentada no **Capítulo 5** (publicado na Revista Flora Jena) mostra, pela primeira vez, que há uma especialização estrutural entre as brácteas ostiolares que encerram a inflorescência. Além disso, também foi a primeira observação da evidência de coléteres em espécies de *Ficus*.

Finalmente o **Capítulo 6** (submetido na revista Molecular Phylogenetics and Evolution) trata da história Biogeográfica das figueiras neotropicais. Com especial foco nas espécies da seção *Americanae*. Os resultados desta abordagem Biogeográfica em *Ficus* sect. *Americanae* sugerem que o gênero passou por dois momentos de grande diversificação nos ambientes neotropicais (no Mioceno Médio e no Plioceno). Os resultados apontam para uma complexa diversificação marcada por dispersão à longa distância e influenciada por certas características morfológicas peculiares do grupo. Ainda neste capítulo nós utilizamos Binary State Speciation and Extinction Analysis (Bisse) para avaliar se o hábito hemiepífito e características dos propágulos influenciaram na maior diversificação de *F.* sec. *Americanae* se comparada a *F.* sect. *Pharmacosycea*, concluindo que o hemiepifitismo e que propágulos de tamanhos variados foram sim importantes para a diversificação nos biomas Neotropicais em especial das florestas úmidas onde a origem da diversidade foi marcada por um passado de grande instabilidade e por plantas que dispersaram a longa distância.

REFERÊNCIAS

Anjos, O. dos Santos. 2009. Taxonomia e Hipótese Filogenética da seção Americana, subgênero Urostigma, gênero *Ficus* F. (Moraceae). Tese de Doutorado. Instituto Nacional de Pesquisas da Amazônia, INPA, Brasil.

Berg, C.C. & DeWolf, G.P. 1975. Moraceae. *In:* Lanjouw, J. & Lanjouw, A.L. (Eds.) *Flora of Suriname.* E.J.Brill, Leiden, pp. 173–267.

Berg, C.C. & E. Simonis. 1981. The *Ficus* flora of Venezuela: Five species complexes discussed and two new species described. Ernstia 6: 1–12.

Berg, C.C. & Simonis, J.E. 2000. Moraceae. *In:* R. Riina (Ed.). *Flora de Venezuela.* Refolit C.A., Caracas, pp. 5–189.

Berg, C.C. & Villavicencio, X. 2004. Taxonomic studies on *Ficus* (Moraceae) in the West Indies, extra-Amazonian Brazil and Bolivia. *Ilicifolia* 5: 1–173.

Berg, C.C. 2009. Moraceae (*Ficus*). *In:* Harling, G. & Persson, C. (Eds.). *Flora of Ecuador, vol. 85.* University of Gothenburg, Göteborg, pp. 7–48.

Berg, C.C. 2012. Moraceae. *Flora Mesoamericana* 2: 1–91.

Berg, C.C., 2007. Proposals for Treating four species complexes in *Ficus* subgenus *Urostigma* section *Americanae* (Moraceae). Blumea. 52, 295–312.

Berg, C.C., Corner, E.J.H. 2005. Moraceae – *Ficus*, in: Nooteboom, H.P. (Ed.). Flora Malesiana Series I – Seed Plants Vol. 17/Part 2. National Herbarium of the Netherlands, Leiden, pp. 152.

Berg, C.C., Vázquez-Ávila, M. & Kooy, F. 1984. *Ficus* species of Brazilian Amazonia and the Guianas. *Acta Amazonica* 14(1/2) Suplemento:159–194.

Burger, W.C. 1977. Flora Costaricenses. Moraceae. *Fieldiana Botany* 40: 94–215.

Carauta, J.P.P. 1989. *Ficus* (Moraceae) no Brasil: conservação e taxonomia. *Albertoa* 2: 1–365.

Carvajal, S. 2012. Sistema para la familia Moraceae en México. *Ibugana* 3: 3–103.

Chantarasuwan, B., Rønsted, N., Kjellberg, F., Sungkaew, S., Welzen, P., 2015. Palaeotropical intercontinental disjunctions revisited using a dated phylogenetic hypothesis with nearly complete species level sampling of *Ficus* subsect. *Urostigma* (Moraceae). Journal of Biogeography. 43, 384–397.

Cruaud, A., Rønsted, N., Chantarasuwan, B., Chou, L.S., Clement, W.L., Couloux, A., Cousins, B., Genson, G., Harrison, R.D., Hanson, P.E., Hossaert-McKey, M., Jabbour-Zahab, R., Jousselin, E., Kerdelhué, C., Kjellberg, F., Lopez-Vaamonde, C., Peebles, J., Peng, Y.-Q.Q., Pereira, R.A., Schramm, T., Ubaidillah, R., Noort,

S. van, Weiblen, G.D., Yang, D.-R.R., Yodpinyanee, A., Libeskind-Hadas, R., Cook, J.M., Rasplus, J.-Y.Y., Savolainen, V., 2012. An extreme case of plant-insect codiversification: figs and fig-pollinating wasps. Syst. Biol. 61, 1029–1047.

Dugand, A. 1942. Nuevas especies colombianas de género *Ficus*. *Caldasia* 1: 25–74.

Dugand, A. 1943. Nuevas nociones sobre el género *Ficus* en Colombia. *Caldasia* 2: 265–283.

Dugand, A. 1944a. Nuevas nociones sobre el género *Ficus* en Colombia II. *Caldasia* 2: 375–386.

Dugand, A. 1944b. Nuevas nociones sobre el género *Ficus* en Colombia III. *Caldasia* 2: 439–442.

Dugand, A. 1944c. Nuevas nociones sobre el género *Ficus* en Colombia IV. *Caldasia* 3: 133–148.

Dugand, A. 1946. Nuevas nociones sobre el género *Ficus* en Colombia V. *Caldasia* 4: 113–120.

Dugand, A. 1956. Nuevas nociones sobre el género *Ficus* en Colombia VII. *Caldasia* 7: 213–246.

Harrison, R.D., 2005. Figs and the diversity of tropical rainforests. Bioscience. 55, 1053–1064.

Herre, E.A., Machado, C.A., Bermingham, E., Nason, J.D., Windsor, D.M., McCafferty, S., Van Houten, W., Bachmann, K., 1996. Molecular phylogenies of figs and their pollinator wasps. J. Biogeogr. 23, 521–530.

Ibarra-Manríquez, G., Cornejo-Tenorio, G., González-Castañeda, N., Piedra-Malagón, E.M. & Luna, A. (2012). El género *Ficus* L. (Moraceae) en México. *Botanical Sciences* 90: 389–452.

Jackson, A. P., Machado, C.A., Robbins, N., Herre E.A. 2008 Multi-locus phylogenetic analysis of neotropical figs does not support co-speciation with the pollinators: the importance of systematic scale in fig/wasp cophylogenetic studies. Symbiosis 45, 57–72.

Jousselin, E., Rasplus, J.Y., Kjellberg, F., 2003. Convergence and Coevolution in a mutualism: evidence from a molecular phylogeny of *Ficus*. Evolution. 57, 1255–1272.

Miquel, F.A.G. 1853. Urticinae. in C.F.P. Martius (ed.) Flora brasiliensis. Frid. Fleischer. Leipzig, vol. 4, pars 1, p. 77–218, tab. 25-70.

Pederneiras, L. C.; Carauta, J. P. P. ; Romaniuc-Neto, S. ; Mansano, V. F. 2015. An overview of the infrageneric nomenclature of Ficus (Moraceae). Taxon, v. 64, p. 589-594.

Pederneiras, L. C.; Romaniuc-Neto, S. ; Mansano, V. de F. 2015b. . Molecular Phylogenetics of Ficus Section Pharmacosycea and the Description of Ficus Subsection Carautaea (Moraceae). Systematic Botany, v. 40, p. 504-509.

Piedra-Malagón, E.M., Sosa, V. e Ibarra-Manríquez, G. 2011. Clinal variation and species boundaries in the Ficus petiolaris complex (Moraceae). Systematic Botany 36:80–87.

Pittier, H.F. 1937. Ensayo sobre la classificación de las espécies venezolanas del género *Ficus*. *Boletin de la sociedad venezolana de ciencias naturales* 4: 44–80.

Rønsted, N., Salvo, G., Savolainen, V., 2007. Biogeographical and phylogenetic origins of African fig species (*Ficus* section *Galoglychia*). Mol. Phylogenet. Evol. 43, 190–201.

Rønsted, N., Weiblen, G.D., Clement, W.L., Zerega, N.J.C., Savolainen, V., 2008. Reconstructing the phylogeny of figs (*Ficus*, Moraceae) to reveal the history of the fig pollination mutualism. Symbiosis. 45, 45–55.

Rønsted, N., Weiblen, G.D., Cook, J.M., Salamin, N., Machado, C.A., Savolainen, P., 2005. 60 million years of co-divergence in the fig-wasp symbiosis. Proc. R. Soc. Biol. Sci. Ser. B. 272, 2593–2599.

Rønsted, N., Weiblen, G.D., Savolainen, V., Cook, J.M., 2008b. Phylogeny, biogeography, and ecology of *Ficus* section *Malvanthera* (Moraceae). Mol. Phylogenet. Evol. 48, 12–22.

Standley, P.C. 1917. The Mexican and central American species of *Ficus*. *Contributions from the United States National Herbarium* 20: 1–35.

Standley, P.C. 1937. *Flora of Costa Rica* 18, part 1: 384–388.

Vázquez-Ávila, M.D. 1981. El gênero *Ficus* (Moraceae) en la Republica Argentina. *Darwiniana* 23: 605–636.

Weiblen, G.D. 2000. Phylogenetic relationships of functionally dioecious *Ficus* (Moraceae) based on ribosomal DNA sequences and morphology. Am. J. Bot. 87:1342–1357.

Zerega, N., Clement, W., Datwyler, S., Weiblen, G., 2005. Biogeography and divergence times in the mulberry family (Moraceae). Mol Phylogenet Evol. 37, 402–416.

CAPÍTULO 1

Synopsis of the strangler figs (*Ficus* sect. *Americanae* - Moraceae) in the Atlantic Forest, with a new species and a reinstatement

Anderson F. P. Machado,[1,3] and Luciano P. de Queiroz[1]

[1]Programa de Pós–Graduação em Botânica, Universidade Estadual de Feira de Santana,
Av. Transnordestina, Novo Horizonte, 44036–900, Feira de Santana, Bahia, Brazil.
[2]Author for correspondence (machadoafp@gmail.com)

Abstract— The strangler figs of *Ficus* sect. *Americanae* comprise one of most diversified groups of fig trees. They are characterized by the initial hemiepiphytic habit, by a single waxy gland at the base of the midvein and by the syconia with 2 basal bracts, ostiole enclosed by 2-3 external bracts and staminate flowers with one stamen. As part of the ongoing revision of *Ficus* from the Brazilian flora, a review of the protologues, types and names was carried out. We focused on the Atlantic forest because species from this area are not correctly recognized and there are certain contrasting taxonomic divergences between the older treatments that include species from this area. We conclude that twenty-nine species of strangler figs should be recognized for the Atlantic Forest. One of these is a new species described here (*Ficus sp. nov.*), and one which must be re-instated, *F. tweediana*. Furthermore, we present the most relevant synonyms, taxonomic notes and an identification key for the species in *Ficus* sect. *Americanae* from the Atlantic Forest domain.

Keywords—Fig tree, Moraceae, Neotropics, Rosales, wet forest.

Ficus L. in the Moraceae, is a pantropical tree genus mostly found in rainforests, with approximately 750 species in six subgenera and nineteen sections (Berg and Corner 2005; Pederneiras et al. 2015). Species of *Ficus* in the Neotropics are all restricted to *Ficus* sect. *Pharmacosycea* (Miq.) Miq. (ca. 20 spp.) and *Ficus* sect. *Americanae* (Miq.) Corner (ca. 100 spp.).

In Brazil there are 80 species of fig trees (Romaniuc Neto et al. 2015) and the most important taxonomic treatments for/or including brazilian *Ficus* were the Flora Brasiliensis Miquel (1853), the Carauta's PhD thesis (1989) and Berg & Villavicencio (2004).

The Mata Atlântica domain is a complex of ecosystems with high levels of richness and endemism and is one of the World hotspots of diversity (Mittermeier et al. 2004). The major part of Atlantic forest is in Brazil (95 %) and the other in Argentina and Paraguay. The principal region of the domain comprises ecosystems continuous among Brazilian costal (Stehmann 2009). This domain is an area with high level of species, endemism and threatened species (Morellato & Haddad, 2000; Myers et al., 2000). The coastal forests and woodlands (these locally known as Restingas) are the place of endemic fig species in the Neotropics (Berg & Villavicencio 2004). Some taxa in this area have overlapping morphological characters and problems in species circumscription. (Carauta, 1989 and Berg & Villavicencio, 2004).

The Neotropical species of *Ficus* needed some attention and taxonomic positions in face of the circumscriptions of some species adopted by Carauta (1989) and the divergences with the taxonomic positions published by Berg & Villavicencio (2004). We focused our paper in the strangler figs (*Ficus* sect. *Americanae*) in the Mata Atlântica because similar treatments were made for Amazonian species of *Ficus* (Santos et al. in prep.) and for sect. *Pharmacosycea* in Brazil (Pederneiras et al. in prep.). There is also a list of Brazilian species of *Ficus* in the Mata Atlântica (Romaniuc et al. 2009). However, this list includes outdated names and propagates divergent taxonomic positions as presented by previous authors as Carauta (1989) and Berg & Villavicencio (2004). Besides, some cited names are known as not occurrying in the Mata Atlântica.

The main goal of this study was revising the taxonomy of *Ficus* in the Mata Atlântica domain were: (1) to recognize and use correctly the names for *Ficus* species of the Atlantic Forest. (2) Make taxonomic decisions in order to reduce the dichotomy caused by different taxonomic placements in previous treatments. (3) Present a Taxonomic Key from the species.

MATERIALS AND METHODS

The morphological analyses were based in observation of plants in fieldworks and Herbaria. The expeditions were in São Paulo, Rio de Janeiro, Espírito Santo, Minas Gerais and Bahia states and the voucher are housed in HUEFS, MBML, SPFR and R herbaria. (Acronyms according to Thiers 2015, continuously updated). We also examined the protologues, type collections of the species recorded for this domain, including the study of approximately 9000 specimens from the following herbaria: ALCB, ASE, B, BHCB, BOTU, C, CEPEC, CESJ, CGMS, CVRD, EAC, ESA, FLOR, FUEL, FURB, GUA, HB, HRB, HUEFS, HUESB, HUFU, HURB, IAC, IAN, IAL, K, MBM, MBML, NX, PACA, PAMG, R, RB, SP, SPF, SPFR, UEC, VIC and VIES. Some collections were online consulted (BR, MO, NY, S, TO, U) (acronyms according to Thiers 2015.). The identification key was based on the morphological variation in herbaria and field material.

TAXONOMIC TREATMENT

Ficus* sect. *Americanae (Miq.) Corner, Gard. Bull. Singapore 17: 375. 1960. —TYPE: *F. nymphaeifolia* Mill., Gard. Dict. Ed. 8. no. 9. 1768.

Trees or shrubs hemiepiphytic (sometimes rupiculuous) at the initial phase of development, sometimes with aerial adventitious roots. Leaves alternate; lamina with 1 waxy gland at the base of midvein near the basal pair of lateral veins. Syconia mostly in pairs, axillary or rarely on brachyblasts; basal bracts 2; ostiole closed by 2–3 external bracts. Staminate flowers 1-staminated. Pistillate flowers with 1 stigmatic arm (not bifurcated).

Notes:—*Ficus* sect. *Americanae* is the most diverse group of *Ficus* in Americas, comprising ca. 100 species distributed in all biomes of the Neotropics (Berg & Villavicencio 2004). The hemiepiphyte (strangler) initial habit and the size of propagules are important taxonomic traits in the section. These features could have contributed with the expansion and diversification of this section (Machado et al. in prep.) In the Mata Atlântica, the strangler figs occurring in ombrophilous, semideciduous forest and restingas (Carauta 1989, Carauta et al. 1996, Romaniuc Neto et al. 2009).

KEY TO FICUS SECT. AMERICANAE IN MATA ATLÂNTICA

1. Leaves 4–10 × 1–5 cm, syconia small (4–10 mm diam.), yellow to red at maturity 2

2. Ostiole crateriform or depressed 3

3. Shrubs or trees with adventitious roots; syconia (4–6 mm diam.), receptacle umbilicate at apex, ostiole crateriform ***F. pertusa***

3. Shrubs or trees without adventitious roots, syconia (7–10 mm diam.), receptacle concave at apex, ostiole depressed ***F. laureola***

2. Ostiole flat, umbonate, or slightly prominent 4

4. Leaves elliptic, 6.5–10 × 2.5–5 cm 5

5. Branches, leaves and syconia with white hairs; syconia initially enclosed in a calyptrate bud ***F. lagoensis***

5. Branches, leaves and syconia glabrous or glabrescent; syconia not enclosed in a calyptrate bud 6

6. Young branches reddish with epidermis flaking off. Lamina with tector and glandular trichomes on abaxial surface. Syconia subsessile ***Ficus diamantina***

6. Young branches greyish to white without epidermis flaking off. Lamina glabrous on adaxial surface. Syconia pedicelate 7

7. Leaf apex shortly acuminate, tertiary venation parallel to lateral veins, waxy gland at top of petiole or 3 mm above, evident *in sicco*; ostiole umbonate; syconia basal bracts 3–5 mm; brachyblasts absent ***F. bahiensis***

7. Leaf apex rounded, tertiary venation reticulate, waxy gland not evident in sicco, ostiole flat; syconia basal bracts 6–8 mm; brachyblasts present ***F. clusiifolia***

4. Leaves oblong, ovate or lanceolate, 4–6 × 1–2 cm 8

8. Leaves sparsely puberulous to hirsute, 4–6 pairs of lateral veins, the basal pair with a divergence angle >60º; syconia rounded, turbinate or elliptical, ostiolar region slightly prominent 9

9. Leaves hirsute on both surfaces with sparse trichomes, tertiary venation finely reticulate, leaf base rounded to cuneate; syconia rounded, ostiolar region umbonate ***F. hirsuta***

9. Leaves glabrous on both surfaces or with sparse trichomes on abaxial surface, tertiary venation reticulate, leaf base subcordate to truncate; syconia turbinate, ostiolar region conical ***F. tweediana***

8. Leaves glabrous, 7–12 pairs of lateral veins, the basal pair of lateral veins with a divergence angle <60º; syconia rounded, ostiolar region flat 10

10. Leaves elliptical to oblong, apex rounded, 7–10 pairs lateral veins, prominent above; syconia 0.7–1.0 cm diam ***F. cestrifolia***

11. Leaves lanceolate, apex acute, 11–16 pairs lateral veins, impressed above; syconia 0.4–0.6 cm diam ***F. sp. nov.***

12. Leaves 6–24 × 5–12 cm, syconia medium (1–2.4 cm diam.) to large (≥ 2.5 cm diam.), green, vinaceous or purple at maturity 11

11. Leaves and branches glabrous 12

12. Petiole 0.8–2.5 cm long 13

13. Branches 10–20 mm thick; stipules persistent; syconia 20–30 mm diam., basal bracts to 1/2 of inflorescence, lobes acute, ostiolar bracts raised, conical ***F. cyclophylla***

13. Branches 4–10 mm thick; stipules deciduous or subpersistent; syconia 10–20 mm diam.; basal bracts only at the base of inflorescence, rounded lobes, ostiolar bracts flat, rounded 14

14. Leaves oblanceolate, 14–16 pairs of lateral veins, margin revolute; stipules subpersistent ***F. mexiae***

14. Leaves oblong to obovate, 10–12 pairs of lateral veins, margin not revolute; stipules deciduous ***F. enormis***

12. Petiole 3–12 cm long 15

15. Ostiolar region shortly raised, ostiole sunken in the crateriform apex 16

16. Leaves coriaceous, 15–16 × 6–7 cm ***F. arpazusa***

16. Leaves chartaceous, 6–9 cm × 3.5–4.5 cm ***F. broadwayi***

15. Ostiolar region flat or depressed, ostiole superficial, flat or raised 17

17. Leaves with 9–17 pairs of veins; syconia 15–25 mm diam 18

18. Petioles 0.5–2.5 cm long, 13–17 pairs of veins, tertiary venation parallel to secondary veins ***F. duartei***

18. Petioles 3–12 cm long, 6–12 pairs of veins, tertiary venation reticulate 19

19. Leaves oblong, ovate, subovate, rounded, basal pair of lateral veins up to 1/3 of the lamina; syconia sessile, elliptical, ostiolar bracts slightly prominent, brown to red ***F. luschnathiana***

19. Leaves elliptic or cordiform, basal pair of lateral veins up to 1/10 of the lamina; syconia short–pedunculate or pedunculate, elliptical, ostiolar bracts flat, strongly prominent, light green 20

20. Leaves dark green or black *in sicco*; syconia rounded to elliptical, initially enclosed by (1 cm long) calyptrate bud covers; ostiolar bracts strongly raised as a cone ***F. eximia***

20. Leaves brown *in sicco*; syconia pyriform, not enclosed in a calyptrate bud; ostiolar bracts flat 20

21. Peduncle 15–25 mm long; syconia pyriform, ostiolar region depressed, ostiole 4–5 mm diam ***F. guaranitica***

21. Peduncle 4–14 mm long, syconia rounded, ostiolar region flat, ostiole 2–3 mm diam ***F. citrifolia***

17. Leaves with 5–9 pairs of veins; syconia 25–35 mm diam 22

22. Leaves ovate or obovate, the basal pair of veins with a divergence angle <90º; syconia oblong to elliptic, pedunculate with verrucose surface ***F. obtusifolia***

22. Leaves cordiform, the basal pair of veins with a divergence angle >90º; syconia rounded, sometimes flattened in the ostiolar region, subsessile with smooth surface ***F. nymphaeifolia***

11. Leaves and branches with various types of trichomes and indumenta 23

23. Leaf glabrous on adaxial surface, abaxial puberulous or pulverulent; ostiolar region prominent, conical 24

24. Leaves cordiform to ovate, pale green on adaxial surface, lateral veins 6–10; young branches, terminal stipule, leaf twigs and adaxial surface puberulous covered by white trichomes. Syconia sessile, rounded, sometimes compressed, whitish and initially enclosed in a calyptrate bu ***F. calyptroceras***

24. Leaves oblong, dark green on adaxial surface, lateral veins 10–15; young branches, terminal stipule, leaf twigs and adaxial surface covered by brown to red pulverulent indument; syconia pedunculate, conical, dark green and without calyptrate bud ***F. castellviana***

23. Leaf with indument on adaxial surface presence of dense trichomes or only sparse trichomes near the midrib and lateral veins, abaxial strigose or densely pilosous; ostiolar region depressed; umbonated, flated with a ring or raised with a ring 25

25. Adaxial surface with sparse trichomes mainly near the midrib and lateral veins; ostiolar region depressed or with a 3-lobed ring 26

26. Petiole and midrib and lateral veins with appressed trichome; petiole epiderm persistent; tertiary venation reticulate; ostiole sunken in the depressed ostiolar region ***F. mariae***

26. Petiole, midrib and lateral veins with erect hairs, petiole epiderm flaking off; tertiary venation scalariform; ostiole surrounded by a 3–lobed ring ***F. trigona***

25. Adaxial surface with dense trichomes; ostiolar region umbonated, flated with a rounded ring or raised with a rounded ring 26

27. Leaves with 6–8 lateral veins, base cordate, apex short-acuminate; stipules persistent; syconia elliptic, covered by dense white indument, subssesile, with 10 mm diam; ostiolar region umbonate, not forming a ring ***F. holosericea***

27. Leaves with 8–15 lateral veins, base subcordate to truncate, apex acute to rounded; stipules deciduous; syconia rounded or pyriform, covered by sparse or dense brown indument, pedunculate, 15–25 mm diam; ostiolar region flat, with a raised ring 28

28. Leaves sparsely covered by white trichomes, mainly on abaxial surface; syconia pyriform, basal bracts deflexed ***F. crocata***

28. Leaves densely covered by brown to red trichomes, mainly in abaxial surface; syconia rounded, basal bracts not deflexed ***F. gomelleira***

1. ***Ficus arpazusa*** Casar., Nov. Stirp. Bras. 15. 1842 . — TYPE: BRAZIL. Rio de Janeiro, s.d., *Casaretto 1234* (Holotype: TO!) (Fig. 1C–D)

Specimens selected: — BRAZIL. Bahia Una 27 September 2011, *Melito, M* 2 (CEPEC, RB); Espírito Santo, Santa Teresa, 26 July 1986, *Marta Leitman* 143 (RB); Minas Gerais 24 May 2007, *L.F.M. Coelho* 8 (RB); Rio de Janeiro Paraty, 7 December 1993, *A.C.B. Rémon* 7 (RB).

Notes:— According to Berg and Villavicencio (2004), this species is a synonym of *Ficus pertusa* L.f.; however, there are significant differences between both taxa (see the key). This species is endemic to Brazil mostly in Atlantic Forest, but also occurs in Cerrado and Caatinga (BFG 2015).

2. ***Ficus bahiensis*** C.C.Berg & Carauta, Brittonia 54 (4): 238. 2002. —TYPE: BRAZIL. Bahia, Reserva Florestal de Porto Seguro, CVRD-BA, 6 November 1989, *Farias 320* (RB!; isotypes CVRD! 2418, BG, GUA!) (Fig. 1E–F)

Specimens selected: — BRAZIL. Bahia, Itacaré, 3 December 2011, *R.C.A. Pereira* 26 (RB); Bahia, Salvador, Arredores da Lagoa do Abaeté, 31 July 2010, *Machado, A.F.P.* 977 (HUEFS); Espírito Santo, 13 July 1991, *P.C. Vinha* 1257 (CEPEC, RB); Sergipe, Santa Luzia do Itanhy11 November 2011, *L.A. Gomes* 256 (RB).

Notes:— Endemic to Brazil, this species occurs only in Atlantic Forest to the north of Espírito Santo State, from Bahia and other littoral parts of the Northeast. The species is an element of coastal or restinga forest (Berg and Carauta 2002), frequently in sandy soil.

3. ***Ficus broadwayi*** Urb., Repert. Spec. Nov. Regni Veg 15: 110. 1917. — TYPE: TOBAGO. Near Lambeau, 12 November 1912, *Broadway 4382* (B!; isotypes G!, GH, K!, US). (Fig. 1G)

Ficus savannarum Standl., Bull. Torrey Bot. Club 75: 298. 1948. —Type: GUYANA. Kaieteur Plateau, 8 May 1994, *Maguire & Fanshawe 23292* (F!; isotypes A, K!, MO, NY, P, US).

Specimens selected: — BRAZIL. Bahia, Itagibá, 12 July 2009, *Guedes et al. 16293* (ALCB), Bahia, Jiquiriçá, 29 may 2014, Ramos et al. 59. (HUEFS).

Notes:— This species is most common in the Antillean region, Colombia and Venezuela. Its occurrence in Brazil is reported for AM, BA, CE, DF, GO, MT, MS RO, RR (Carauta 1989; BFG 2015). Berg (2007) included *F. broadwayi* in *F. pertusa* L.f.

based on the umbilicate ostiolar region. This inclusion is inconsistent in both vegetative and reproductive characters.

4. ***Ficus calyptroceras*** (Miq.) Miq., Ann. Mus. Bot. Lugduno-Batavi 3: 297. 1867.≡ *Urostigma calyptroceras* Miq., London J. Bot. 6: 527. 1847. —TYPE: BRAZIL. Piauí, banks of the lake at Paranagoa, August 1939, *Gardner 2729* (K!). (Fig. 1H)

= *Ficus rojasii* Hassler, Annuaire Conserv. Jard. Bot. Genève 21: 125. 1919. —TYPE: PARAGUAY. Lake Ypararay, November 1913, *Hassler 12367* (G!; isotypes A, B, C, K, NY, US)

Specimens selected: — BRAZIL. Bahia, Itatim, 19 February 2005, *R. M. Castro* 1101 (RB); Minas Gerais, Matozinhos, 31 October 1996, *J.A. Lombardi* 1425 (RB); Minas Gerais, 3 May 1963, *A.P.P.Duarte* 7824 (RB).

Notes:—*Ficus calyptroceras* is a typical fig tree from Caatinga. Nevertheless, the occurrence of this species in Atlantic Forest is reported for mostly semideciduous forest (Romaniuc-Neto et al. 2009), but also occurs in ombrophilous forest. Berg and Villavicencio (2004) included in its synonymy *F. elliotiana* S. Moore. However, both are distinct species (Carauta 1989) recognized by vegetative and reproductive characters and should not be treated as synonyms.

5. ***Ficus castellviana*** Dugand, Caldasia 1 (4): 33. 1942. —TYPE: COLOMBIA. Comisaria del Putumayo, Mocoa, resíduos de selva higrófila hacia Pueblo Viejo, 580-600 msm, 28 December 1940, *Cuatrecasas 11386* (COL; isotypes F, US). (Fig. 1I–J)

Specimens selected: — BRAZIL. Bahia, Ilhéus, 19 September 1973, *Salmon Soares dos Santos* 2684 (RB); Espírito Santo, Linhares, 29 September 2009, *Siqueira, G.S* 488 (RB); Espírito Santo, Santa Teresa, Estrada da Pedra da Onça P/ Praça Oito, 10 November 1998, *L. Kollmann* 962 (MBML).

Notes:— This species has a disjunct distribution between the Atlantic Forest and the Amazon. In the Atlantic Forest it occurs in Bahia, Espírito Santo, Rio de Janeiro and Minas Gerais states (Berg and Villavicencio 2004). It is a unique fig species in Atlantic Forest, with powdery brown indumentum on the abaxial surface of leaves and in young shoots.

6. ***Ficus cestrifolia*** Schott *in* Spreng., Syst. Veg. 4: 409. 1827. —TYPE: BRAZIL. Without locality, s.d., *Schott s.n* (B!). (Fig. 1K–L)

= *Ficus organensis* (Miq.) Miq., Ann. Mus. Bot. Lugduno-Batavi 3: 299. 1867. ≡ *Urostigma organense* Miq., London J. Bot. 6: 542. 1847. — TYPE: BRAZIL. Rio de Janeiro, Organ Mountains, 1837, *Gardner 620* (K!; isotypes G, NY, P)

= *Ficus pohliana* (Miq.) Miq., Ann. Mus. Bot. Lugduno-Batavi 3: 298. 1867. ≡ *Urostigma pohlianum* Miq. in Mart., Fl. Bras. 4(1): 100. 1853. — TYPE: BRAZIL. Rio de Janeiro, Mangaratiba, s.d., *Pohl s.n.* (U!; isotypes BR)

Specimens selected: — BRAZIL. Rio de Janeiro, Itatiaia, 23 April 2001, *H.C. de Lima* 5767 (RB); Rio de Janeiro, Teresópolis, 23 October 1999, *B. ernani Diaz* 168 (RB); Rio de Janeiro, Teresópolis, Parque Nacional da Serra dos Órgãos, 25 March 2010, *Machado, A.F.P.* 935 (HUEFS).

Notes:— *Ficus cestrifolia* is endemic to the Brazilian Atlantic Forest (BFG 2015) and is characterized by the small leaves and syconia. Carauta (1989) included it in the synonymy of *F. pertusa* L.f. The name *F. cestrifolia* Schott does not appear in subsequent papers by Carauta on *Ficus* (Carauta et al. 1996; Carauta and Diaz 2002). However, the author cited above identified certain exsiccatae recognized now as *F. cestrifolia* under the name *F. organensis* (Miq.) Miq. After analysis of the type collection and protologues, we are in agreement with Berg and Villavicencio (2004), and include *F. organensis* in the synonymy of *F. cestrifolia* Schott.

7. ***Ficus citrifolia*** Mill., Gard. Dict., Ed. 8. Ficus n. 10. 1768. —TYPE: West Indies: Antillas(?), s.d. Herb. Miller s.n.; (BM!). (Fig. 2A)

= *Ficus populnea* Willd., Sp. Pl. 4: 1141. 1806. —TYPE: ex Hort. Paris in herb., *Willdenow s.n.* (B)

Specimen selected: — BRAZIL. Minas Gerais, Barroso, Mata do Baú, 15 December 2001, *Assis 412* (CESJ).

Notes:—This species is widespread in Tropical America and is therefore very morphologically variable (Berg and Villavicencio 2004). The *F. citrifolia* Complex is one of most difficult to resolve among the complexes in *Ficus* due to the broad distribution of some species and the overlapping morphological characters among species (see Berg 2007).

8. ***Ficus clusiifolia*** Schott, Sist. Veg., Ed. 16, 4 (2): 409. 1827. —TYPE: BRAZIL. Without locality, s.d., *Schott s.n.* (B!). (Fig. 2B–C)

Specimens selected: — BRAZIL. Bahia, Ilhéus, 17 December 1970, *J.L.Hage* 41 (RB); Bahia, Porto Seguro, 9 July 2010, *G. M. Carvalho* 391 (RB); Bahia, Salvador, Arredores da Lagoa do Abaeté, 31 July 2010, *Machado, A.F.P.* 976 (HUEFS); Espírito Santo, Santa Leopoldina, 21 January 2006, *M.O.S. Crepaldi* 73 (RB); Rio de Janeiro, Cabo Frio, 21 February 2006, *Michel Barros* 7 (RB); Rio de Janeiro, Rio de Janeiro, 8 October 2001, *A. Oliveira* 327 (RB).

Notes:— This is a widespread species in Atlantic Forest (Berg and Villavicencio 2004). It occurs in Restinga, semideciduous and ombrophilous forests (BFG 2015). The most relevant traits are its leaves that resemble those of *Clusia* (Clusiaceae) and the red syconia at maturity, born on spurs, that make this species an important food resource for birds (Carauta and Diaz 2002).

9. ***Ficus crocata*** (Miq.) Miq., Ann. Mus. Bot. Lugduno-Batavi 3 (10): 297. 1867. ≡ *Urostigma crocatum* Miq., London J. Bot. 6: 531–532. 1847. —TYPE: BRAZIL. Pará, Santa Maria de Belém. *Martius s.n.* (M!, Isotype B). (Fig. 2D)

= *Ficus maximiliana* (Miq.) Miq., Ann. Mus. Bot. Lugduno-Batavi 3: 297. 1867. ≡ *Urostigma maximilianum* Miq., London J. Bot. 6: 529. 1847. — TYPE: BRAZIL. Rio de Janeiro, Between Cabo Frio and Campos Novo, s.d., *Pr. Maximilian s.n. in herb Mart* (U!; isotype BR)

= *Ficus tomentella* (Miq.) Miq., Ann. Mus. Bot. Lugduno-Batavi 3: 297. 1867. ≡ *Urostigma tomentellum* Miq., London J. Bot. 6: 531. 1847. — TYPE: BRAZIL. Pará, Without locality, s.d., *Martius s.n.* (M!; isotype U)

Specimens selected: — BRAZIL. Espírito Santo, Linhares, 7 November 2012, *G.S. Siqueira* 820 (RB); Paraná, Santo Inácio, 5 May 2008, *L. F. M. Coelho et. al.;* 27 (RB); Rio de Janeiro, 23 September 1980, *M. Vazquez Avila* 260 (RB); Rio de Janeiro, Cabo Frio, 14 September 1968, *D. Sucre* 3634 (RB); Rio de Janeiro, Rio de Janeiro, Quinta da Boa Vista, January 2010, *Machado, A.F.P.* 911 (HUEFS).

Notes:— *F. crocata* is an element of the "*Ficus trigonata* Complex" (Berg and Simonis 1981), which is characterized by the median to large leaves with thick secondary veins and pedunculate syconia with a ring in the ostiolar region. In Atlantic Forest *F. crocata* should be found in Restingas and ombrophilous forest at low altitudes (Berg and Villavicencio 2004).

10. ***Ficus cyclophylla*** (Miq.) Miq., Ann. Mus. Bot. Lugduno-Batavi 3: 297. 1867. ≡*Urostigma cyclophyllum* Miq. in Martius, Fl. Bras. 4(1): 91. 1853. —TYPE: BRAZIL. Pernambuco, Without locality, 1839, *Schornbaum* s.n. (U!; Isotypes B, BR). (Fig. 2E–F)

= *Ficus noronhae* Oliv., Hooker's Icon. Pl. 13: t. 1222. 1877. —TYPE: BRAZIL. Pernambuco, Fernando de Noronha, September 1873, *Mosely s.n.* (K!)

Specimens selected: — BRAZIL. Bahia, Vitória da Conquista, Poço Escuro, 29 May 2010, *Machado, A.F.P.* 960 (HUEFS); Bahia, Boa Nova, Mata de Cipó, 23 March 2013, *Machado, A.F.P.* 1227 (HUEFS); Espírito Santo, Linhares, 7 November 2012, *G.S. Siqueira* 816 (RB); Rio de Janeiro, Rio de Janeiro, 31 October 2011, *G. Pelissari et. al.* 156 (RB).

Notes:— This species is common in restingas, but also occurs in the Atlantic Forest in ES and BA (BFG 2015). It could be recognized by the dark purple figs with long basal bracts and ostiolar raised bracts, as well as by the conspicuous persistent stipules among the branches. C.C. Berg identified certain specimens of this taxon under the binomial *F. longifolia* Schott. After analyzing the type collection and protologues we are in agreement with Carauta (1989) and consider the type insufficient to characterize the taxon. The type of *F. longifolia* has only fallen leaves and very distinctive veins from the collections of *F. cyclophylla* analyzed throughout its distribution. Therefore, we consider *F. longifolia* a *nomen dubium.*

11. ***Ficus diamantina*** A.F.P.Machado & L.P.Queiroz, Phytotaxa *in press*. —TYPE: BRAZIL. Bahia, Mucugê, Capão do Correia, 11 July 2009, *M.M. Saavedra et al. 969* (HUEFS!, isotype RB!).

Specimen selected: — BRAZIL. Bahia, Rio do Pires, Serra Itubira, Mata do Cigano, 13°15'50"S, 41°55'04"W, 1750 m, November 2008, *F.H.F. Nascimento 621* (Paratype HUEFS!, Isoparatype RB!); BRAZIL. Bahia: Mucugê, Capão do Correia, 13°6 36.9"S, 41°22' 37.9"W, 1231 m, A.F.P.Machado & J.O Cruz. 1231 *st.*; L.c., A.F.P.Machado & J.O.Cruz 1232. *st.*

Notes:—The species is known only from a few collections and is endemic to Bahia state. (See chapter 5)

12. ***Ficus duartei*** C.C.Berg & Carauta, Brittonia 54 (4): 240–241. 2002. —TYPE: BRAZIL. Rio de Janeiro, Rio de Janeiro, Mundo Novo, Botafogo, 11 October 1960, *Duarte 5419* (HB; isotypes C!, G, NY, RB!, MBM!).

Specimen selected: — BRAZIL. Rio de Janeiro, Rio de Janeiro, Mata da Lagoinha, perto do Horto Florestal, 13 January 1928, *Pessoal do Horto Florestal* (RB).

Notes:—A rare species known only from a few collections, and most probably extinct in its type locality (Berg and Villavicencio 2004).

13. ***Ficus enormis*** Mart. *ex* Miq., Ann. Mus. Bot. Lugduno-Batavi 3: 298. 1867. ≡*Urostigma enorme* Miq., London J. Bot. 6: 544. 1847. —TYPE: BRAZIL. Minas Gerais, near Parapitinga, *Martius s.n.* (M, Isotype: U) (Fig. 2G)

Specimens selected: — BRAZIL. Espírito Santo, Linhares, 25 July 2012, *D.A. Folli* 6882 (RB); Rio de Janeiro, Petrópolis 4 February 1974, *G. Martinelli* 208 (RB); Rio de Janeiro, Rio de Janeiro, Fortaleza de São João, Morro Cara de Cão, 04 November 2004, *Machado, A.F.P.* 366 (HUEFS); Rio de Janeiro, Teresópolis, Parque Nacional da Serra dos Órgãos, 25 March 2010, *Machado, A.F.P.* 940 (HUEFS).

Notes:— *Ficus enormis* is closely related to *F. caatingae* R.M. Castro, *F. luschnathiana* (Miq.) Miq., and *F. mexiae* Standl. This species is endemic to Brazil and distributed in Caatinga, Cerrado and Atlantic Forest (BFG 2015). The characteristics used by Carauta (1989) to separate *F. enormis* and *F. luschnathiana* are overlapping and/or present variation in their range of distribution (see Piedra-Malagón et al. 2011). Probably for this reason several collections of *F. luschnathiana* in some Brazilian herbaria are identified under the name *F. enormis*.

14. ***Ficus eximia*** Schott in Spreng, Sys. Veg., ed. 16: 410. 1827. —TYPE: BRAZIL. Without locality, s.d., *Schott sn* (B). (Fig. 2H)

= *Ficus glabra* Vell., Fl. Flumin. 11: t. 50. 1829. —TYPE: Fl. Flum. 11: t.50. 1831.

Specimens selected: — BRAZIL. Espírito Santo, Santa Teresa, Escola Agrotécnica Federal de Santa Teresa, 23 August 2007, *Machado, A.F.P.* 645 (HUEFS); Espírito Santo, Nova Venécia, Serra de Baixo, Santuário Mãe Peregrina, 9 May 2008, *R. Goldenberg* 1135 (RB); Minas Gerais, Carangola, 1 April 2000, *E.A.Costa* 51 (RB); Minas Gerais, Alfenas, 30 April 2007, *M.C. Weyland Vieira* 2203 (RB); Minas Gerais, Alfenas, 30 April 2007, *M.C. Weyland Vieira* 2210 (RB); Paraná, Ribeirão do Pinhal, 12 November 2000, *J. Carneiro* 806 (RB); Paraná, Guaratuba, 27 July 1960, *A.P Duarte* 5346 (RB); Santa Catarina, Indaial, l3 July 2009, *L. F. M. Coelho* 77 (RB); São Paulo, Ribeirão Preto, 3 February 2006, *R.A.S. Pereira* 144 (RB).

Notes:—In spite of the papers published by Carauta (1973) on the effective date of publication for Fl. Fluminensis, he still used the name *F. glabra* Vell. for the taxon *F. eximia*. Carauta (1989) argues that the type of *F. eximia* is sterile. However, it is possible to identify the taxon from the available material and protologue. For this reason we adopted the name *F. eximia* Schott, as did Berg and Villavicencio (2004).

15. ***Ficus gomelleira*** Kunth, Index Seminum 18. 1847. —TYPE: BRAZIL. Without locality, s.d., *Hort. Berol. sn* (B, Isotype U). (Fig. 2I–J)

= *Ficus doliaria* (Miq.) Miq., Ann. Mus. Bot. Lugduno-Batavi 3: 297. 1867. ≡ *Urostigma doliarium* Miq., London J. Bot. 6: 527. 1847. —TYPE: Hort. Bot. München. (M!)

= *Ficus rufa* Schott in Spreng., Syst. Veg. 4: 410. 1827. —TYPE: BRAZIL. Without locality, s.d., *Schott* s.n. (B!).

Specimens selected: — BRAZIL. Bahia, Mucugê, Parque Municipal de Mucugê, November 2010, *Machado, A.F.P.* 992 (HUEFS); Bahia, Feira de Santana, Campus da UEFS, November 2010, *Machado, A.F.P.* 1026 (HUEFS); Espírito Santo, Linhares 7 February 2010, *Geovane S. Siqueira* 522 (RB); Minas Gerais, Joanésia15 September 2009, *T. Mansur* 34 (RB); Rio de Janeiro, Rio das Ostras 5 June 2001, *E.Erbedobler* 13 (RB); Rio de Janeiro, Paraty, 6 July 1912, *Lützelberg* 1707 (RB); Santa Catarina, Indaial, 30 June 2009, *L.F.M. Coelho* 71 (RB).

Notes:— This species can be recognized by its ferrugineous trichomes on young branches and abaxial surface of the leaf, and occurs in Caatinga, Cerrado, Amazon and Atlantic Forest. It appears in old publications under the name of *F. doliaria* (Miq.) Miq. but this is a well known synonym (Carauta 1989). *Ficus rufa* Schott in Spreng. is also a synonym of *F. gomelleira*. This last name was treated by Berg and Villavicencio (2004) as a synonym of *Ficus holosericea* Schott; however, analysis of the Schott type leaves no doubt about the identity of this taxon.

16. ***Ficus guaranitica*** Chodat, Bull. Soc. Bot. Genève 2 (11): 254. 1920. —TYPE: PARAGUAY. Near Asuncíon, June 1874, *Balansa 1986* (Lectotype: G; Isolectotype P). (Fig. 2K)

Specimens selected: — BRAZIL. Minas Gerais, Araxá, 18 May 2000, *B. Ernani Diaz* 293 (RB); São Paulo, Botucatu, 14 July 2009, *L.B. Santos* 302 (RB); Paraná, Foz do Iguaçu18 August 2001, *B. Ernani Diaz* 533 (RB); Minas Gerais, Alfenas 30 April 2007, *M. C. Weyland Vieira* 2203 (RB); Paraná, Fênix, 30 June 2005, *O.S. Ribas et. al.;* 6903 (RB); Minas Gerais, Araxá, 17 April 2001, *J. P. P. Carauta* 7137 (RB).

Notes:— According to Berg and Villavicencio (2004), this is a synonym of *F. citrifolia* Mill. However, analysis of exsiccatae, especially in southern Brazil, shows a consistent morphological variation and the validity of the name. *Ficus guaranitica* is similar to *F. eximia* Schott, which differs by the characteristics of the syconium and petioles. In Atlantic Forest it is more common in southern Rio de Janeiro state, São Paulo and in the states of the brazilian South region. It also occurs in Paraguay and Uruguay (Carauta 1989).

17. ***Ficus hirsuta*** Schott, Syst. Veg. 4 (2): 410. 1827. —TYPE: BRAZIL. Without locality, s.d., *Schott* s.n. (B). (Fig. 2L)

= *Ficus hirsuta* Vell. (1831: t.49). TYPE: Fl. Flum. 11: t. 49. 1831.

= *Ficus lanuginosa* Casar., Nov. Stirp. Bras. 48. 1843. —TYPE: BRAZIL. Rio de Janeiro, Taypú, s.d., *Casaretto s.n.* (TO!)

= *Ficus salzmanniana* (Miq.) Miq., Ann. Mus. Bot. Lugduno-Batavi 3: 299. 1867. ≡ *Urostigma salzmannianum* Miq., London J. Bot. 6: 547. 1847. —TYPE: BRAZIL. Bahia, Without locality, s.d., *Salzmann s.n. (521?)*(K!, Isotypes G .H. LE, MO, MPU, P).

Specimens selected: — BRAZIL. Bahia, Almadina, 19 March 2006, *J.L. Paixão* 862 (CEPEC, RB); Bahia, Salvador,18 February 1992, *M.L. Guedes et. al.;* 2569 (RB); Espírito Santo, Itapemirim, 7 April 1993, *Souza, V.D* 487 (RB); Espírito Santo, Santa Leopoldina, Colina Verde (Morro do Agudo), propr.: Israel Elias Ramos (trilha acima do bananal), 30 May 2007, *V. Demuner* 4123 (MBML); Rio de Janeiro, Saquarema, 27 April 1996, *A.Q. Lobão* 135 (RB); Rio de Janeiro, Armação dos Búzios, 12 November 1998, *D. Fernandes* 168 (RB).

Notes:— This species is endemic to Brazil (BFG 2015) and occurs in rainforests and restingas. Its distribution extends from Rio de Janeiro to the states of the Northeast. In this region *F. hirsuta* is variable in the amount of trichomes that appear almost glabrous, in contradiction to its specific epithet. This glabrous form of the species was proposed as *F. salzmanniana* (Miq.) Miq. However, experience with other species of *Ficus* clearly confirms that variation in indumentum is common within the same taxa (e.g. *F. crocata*, *F. gomelleira*). After analysis of material of *F. hirsuta* from its range of distribution we observed this as the only variation. Therefore, we are in agreement with Berg and Villavicencio (2004) who considered *F. salzmanniana* as a synonym of *F. hirsuta.*

18. ***Ficus holosericea*** Schott, Syst. Veg. 4: 410. 1827. —TYPE: BRAZIL. Without locality, s.d., *Schott s.n.* (B!). (Fig. 2M)

Specimens selected: — BRAZIL. Espírito Santo, Linhares, 30 September 2009, *Machado, A.F.P.* 826 (RB); Espírito Santo, Linhares, Reserva da Vale, 30 January 2009, *Machado, A.F.P.* 828 (HUEFS); Espírito Santo, Santa Teresa, Valão de São Brás, 02 January 2009, *Machado, A.F.P.* 832 (HUEFS); Minas Gerais, Aimorés, 3 January 2001, *D.A. Folli* 3797 (RB).

Notes:— A relatively rare species occurring in the Atlantic Forest (associated with rocks) and extending as far as the Caatinga. It has also been reported to Acre (BFG 2015), but the identification of this material was incorrect. Endemic to Brazil, this species occurs in Bahia, Espírito Santo, Minas Gerais and Rio de Janeiro States (BFG 2015).

19. ***Ficus lagoensis*** C.C.Berg & Carauta, Brittonia 54 (4): 243–246, f. 6. 2002. — TYPE: BRAZIL. Minas Gerais, Monte Belo, Fazenda Lagoa, 12 March 1989, *Carauta & Vieira 5795* (GUA; Isotype R). (Fig. 2N)

Specimens selected: — BRAZIL. Minas Gerais, Monte Belo, 3 April 1987, *M.C. Weyland Vieira* 1 (RB); Minas Gerais, São João del Rei, 6 April 2010, *M.Sobral* 13144 (RB); Paraná, Sertanópolis, 29 September 1995, *B.P. Carelli* 23 (RB); São Paulo, Campinas, 23 November 1979, *D. Sucre* 212 (RB); São Paulo, Ribeirão Preto, Fazenda Pau Alto, 14 December 2011, *Machado, A.F.P.* 1070 (HUEFS).

Notes:— Endemic to Brazil; occurs in Minas Gerais, São Paulo and Paraná States in semideciduous forest (BFG 2015). It species is misidentified as *F. hirsuta* Schott due to its indumentum. The populations are small and the species is apparently rare.

20. ***Ficus laureola*** Warb. ex C.C.Berg & Carauta, Brittonia 54 (4): 246, f. 7. 2002. — TYPE: BRAZIL. Minas Gerais, Ouro Preto, Serra do Ouro Preto, Cachoeira das Andorinhas, 1250 msm, 6 March 1982, *Grandi 900* (BHCB; isotypes R, RB, BG). (Fig. 2O)

Specimens selected: — BRAZIL. Espírito Santo, Pancas, Lajinha, propriedade de Vidal Krause, 5 August 2006, *A.P. Fontana* 2342 (RB); Espírito Santo, Venda Nova do Imigrante, 3 February 1995, *D.A. Folli* 2565 (RB); Minas Gerais, Ouro Preto, 25 July 1992, *J.R. Stehmann* 1104 (RB); Minas Gerais, Santa Bárbara, 30 August 1997, *J.R. Stehmann* 2285 (RB); Minas Gerais, Pedra Dourada, August 1997, *L.S. Leoni* 3702 (RB); Minas Gerais, Conceição do Mato Dentro, 16 August 2012, *E. Tameirão Neto* 5146 (RB); Minas Gerais, Santana do Riacho, 8 October 1981, *J.R. Pirani* CFSC 7597 (RB).

Notes:— Endemic to Brazil; occurs in Bahia, Espírito Santo and Minas Gerais States (BFG 2015). It holds similarities with *F. cestrifolia* Schott, but differs by the veins and the ostiolar region of the syconium.

21. ***Ficus luschnathiana*** (Miq.) Miq., Ann. Mus. Bot. Lugduno-Batavi 3: 298. 1867. ≡ *Urostigma luschnathianum* Miq., Fl. Bras. 4(1): 101. 1853. —TYPE: PARAGUAY. In regione lacus Ypacaray, October 1913, *Hassler, 12311* (?; isotype MO-204192). (Fig. 3A)

= *Ficus diabolica* Herter, Revista Sudamer. Bot. 6: 150. 1940. —TYPE: URUGUAY. Cerro Largo, Sierra de Ríos, 7 February 1937, *Herter 1356b* (B, Isotypes NY, SI).

= *Ficus monckii* Hassl., Annuaire Conserv. Jard. Bot. Genève 21: 127. 1919. —TYPE: PARAGUAY. Cerros de Tobaty, September 1900, *Hassler 6096* (Lectotype G, Isolectotypes MICH, MPU, NY, P, S).

Specimens selected: — BRAZIL. Bahia, Teodoro Sampaio, 22 September 2009, *L.F.M. Coelho* 80 (RB); Minas Gerais, Caxambu, 26 February 1987, *Senna* 2 (RB); Minas Gerais, Caxambu 24 November 2005, *R.A.S. Pereira* 142 (RB); Minas Gerais, Caldas, 24 October 2011, *G. Pelissari et. al.* 210 (RB); Paraná, Rolândia 27 January 1937, *G. Lessinam* 22 (RB); Paraná, Curitiba, 12 January 2010, *Machado, A.F.P.* 910 (HUEFS); Pernambuco, Inajá 20 July 1995, *M.F. Sales* 649 (RB); Rio de Janeiro, Nova Friburgo, 3 April 1989, *C.M. Vieira* 19 (RB); Rio de Janeiro, Teresópolis, 3 February 1983, *J.E. Simons* 33 (RB).

Notes:—This is the most common fig tree in the southern portion of the Atlantic Forest. It occurs in all forest physiognomies in the Mata Atlântica domain (BFG 2015) and their populations are frequently large (pers. obs.).

22. ***Ficus mariae*** C.C.Berg, Emygdio & Carauta, Bradea 8 (20): 112. 1999. —TYPE: BRAZIL. Espírito Santo, Reserva Florestal de Linhares, Estrada Cinco Folhas, km 0,71, 28 February 1996, *Folli 2693* (CVRD!; isotypes BG, GUA, RB!, U) (Fig. 3B)

Specimens selected: — BRAZIL. Minas Gerais, Caratinga, 9 January 1980, *A. Nishimura* 28 (RB); Espírito Santo, Sooretama, 1 November 2012, *P.C. Costa* 47 (RB); Espírito Santo, Linhares, 2 December 1981, *I.A. Silva* 276 (RB); Minas Gerais, Carangola, perto da margem do Rio Carangola, 20 August 1989, *Leoni, L.S.* 834 (RB); Espírito Santo, Conceição da Barra, Comunidade de Lajinha, Fazenda Rancho Tropical

II, Mata de Restinga, 5 July 2007, *C.Farney* 4760 (RB); Minas Gerais, Faria Lemos, 7 December 2007, *L.S. Leoni* 7067 (RB).

Notes:— This is a rare species with a disjunct distribution between the Atlantic Forest and Amazon. It occurs in Espírito Santo, Minas Gerais, Bahia and Rio de Janeiro States (BFG 2015).

23. ***Ficus mexiae*** Standl., Publ. Field Mus. Nat. Hist., Bot. Ser 17 (2): 173. 1937. — TYPE: BRAZIL. Minas Gerais, Fazenda de Aguada, Viçosa, on stream bank, 24 December 1930, *Mexia 5447* (F, Isotypes A, B, G, GH, MICH, MO, NY, S, U, US). (Fig. 3C)

Specimens selected: — BRAZIL. Bahia, Vitória da Conquista, 13 February 2010, *Machado, A.F.P.* 914 (HUEFS); Minas Gerais, Viçosa, 23 May 2007, *P.P.de Souza* 178 (RB); Minas Gerais, Carangola, 14 February 1993, *L.S. Leoni* 2107 (RB).

Notes:— Resembles *F. enormis* and *F. caatingae* R.M. Castro. After analyses of the protologues, type collections, and exsiccatae of these species we consider that there is sufficient morphological variation to support both species. The main differences between *F. enormis* and *F. mexiae* are presented in the key.

24. ***Ficus sp. nov.*** A.F.P.Machado & L.P. de Queiroz, *sp. nov.* (sect. ***Americanae***) Figs. 3E, F; 4.

—**TYPE:** BRAZIL. Espírito Santo: Santa Teresa, Estação Biológica Santa Lúcia, trilha que leva ao Túmulo de Augusto Ruschi, 29 March 2007, *Machado 595* (holotype R!).

Diagnosis: — *Ficus sp. nov. resembles* Ficus cestrifolia *Schott by the dimensions of the leaves but differs by the strictly lanceolate leaves (vs. elliptic to oblong in* F. cestrifolia*), by the greater number of lateral veins (9–13 pairs vs. 6–8 in* F. cestrifolia*), also by the lateral veins impressed above (vs. lateral veins prominent above in* F. cestrifolia*) and by the smaller syconia. Ficus sp. nov. also resembles* F. pallida *Vahl by the dimensions of leaves and lateral veins impressed above but presents some differences such as the more developed basal pair of lateral veins up to 1/6 of the length of lamina (vs. up to 1/10-1/20 of the length of lamina in* F. pallida*); by the midrib flat and green (vs. prominent and yellowish in* F. pallida*), and by the tertiary veins finely reticulate (vs parallel in* F. pallida*).*

Shrubs up to 2 m or trees up to 10 m tall, branches whitish, slender 3–7 mm diam., glabrous, juvenile branches with epidermis persistent; terminal stipule short, 0.4–0.8 cm long, conical, green to red, glabrate, deciduous. Internodes (0.7–) 0.9–1.2(–1.5) cm long; petiole not canaliculate 0.6–1.2 cm long, slender, 2–4 mm in diameter, glabrous, epidermis persistent; Leafy twigs 3–5 mm; leaf blades lanceolate 3.5–7.5 cm long × 0.9–2.1 cm wide, chartaceous, adaxial surface dark green, abaxial light green; base acute to cuneate; margin flat; apex acuminate to acute; both surfaces glabrous; lateral veins 9–14 pairs; impressed and distinctly slender; the basal pair up to 1/6 the length of the lamina, unbranched; forming an angle of 65º–85º; tertiary venation finely reticulate; waxy gland at the base of the midrib beneath, not evident *in sicco*; figs axillary or also just below leaves, solitary or in pairs, subsessile; peduncle 1–2 mm long, glabrous; basal bracts 1–2.5 mm wide, greenish, rounded; persistent; syconia glabrate, receptacle globose, 4–6(–8) mm diam., smooth, glabrous, maculate or not, probably yellowish at maturity, ostiole 2–4 mm diam., slightly prominent; enclosed by 3 ostiolar external bracts, red. Staminate flowers not seen. Pistillate flowers 1.0–1.5 mm, pedicellate, style 1.0–2.0 mm long; stigma ca. 0.2 mm long, ovary 0.9–1.1 mm long, asymmetrically reniform; interfloral bracts 1.8–2 mm; Fruit not seen.

Comments:— *Ficus sp. nov.* resembles and is sympatric with *Ficus cestrifolia* Schott; for this reason part of the specimens were identified under this name. In the comments on *F. cestrifolia* Schott, Berg and Villavicencio (2004) wrote about a form with lanceolate leaves that occurs at the northern distribution range of this species. A few years ago, in a letter sent to the first author, Berg suggested paying attention to a possible new species among the collections made by Domingos A. Folli, in Espírito Santo State. J.P.P. Carauta (pers. com.) was also in agreement after seeing my own collections made in Santa Teresa Municipality, Espírito Santo State.

After careful revision of the protologues, type collections and morphological studies we found similarities with *F. cestrifolia*, *F. leiophylla* and *F. pallida*. The main differences are consistent in all specimens studied.

Distribution, habitat, and conservation:— The new species occurs in Espírito Santo and Minas Gerais States, Brazil, in areas of 48 to 1200 m alt. *Ficus sp. nov.* is presently known from only three municipalities with an Extent of occurrence (EOO) of 4.812.595 Km² and Area of occupancy (AOO) of 12.000 Km² (EOO and AOO estimated in

GeoCat tool see Bachman et al. 2011). That suggests the Endangered (EN) conservation category (IUCN 2017).

Additional specimens examined (paratypes):— BRAZIL. Espírito Santo: Santa Teresa, Estação Ecológica Santa Lúcia, 19° 56' 08"S, 40° 36' 01"W, 655 m, s.d., *J. Rossini 735* (HUEFS!). BRAZIL. Espírito Santo: Santa Teresa, Estação Ecológica Santa Lúcia, 10 July 2001., L Kollmann 4110 (MBML!, R!). BRAZIL. Espírito Santo: Linhares, Reserva Natural Vale. Estrada Flamengo, 19º 23' 28"S, 40º 04' 20"W, 15 February 2006, *G.S. Siqueira* 208 (CRVD!, HUEFS!). BRAZIL. Espírito Santo: Linhares Reserva Natural Vale. Estrada Flamengo, 19º 23' 28"S, 40º 04' 20"W, 48 m, 18 May 2009, *D.A.Folli* 6352 (CRVD!, HUEFS!). BRAZIL. Minas Gerais: Rio Preto, Serra Negra, Vilarejo do Funil, Sumidouro, 22º 05' 21"S, 43º49' 40"W, 1100 m, 10 April 2004, *K.A. Antunes* 78 *et al.* (CESJ!, HUEFS!).

25. ***Ficus nymphaeifolia*** Mill., Gard. Dict. (ed. 8) no. 9.. —TYPE: Antilles(?), s.d., *Miller s.n.* (BM). (Fig. 3G)

Specimens selected: — BRAZIL. Bahia, Salvador, Arredores da Lagoa do Abaeté, 31 July 2010, *Machado, A.F.P.* 980 (HUEFS); Espírito Santo, Linhares, 30 September 2009, *Machado, A.F.P.* 825 (RB).

Notes:— Occurs in the Amazon and Atlantic Forest in the states of northeastern Brazil and down towards Espírito Santo, Minas Gerais and Rio de Janeiro States (BFG 2015). Its occurrence in the Atlantic Forest is scattered, forming small populations (Berg and Villavicencio, 2004). It can be confused with *F. elliotiana* S. Moore, which occurs in the Pantanal, but differs from it by foliar characters and the syconium (Carauta and Diaz 2002).

26. ***Ficus obtusifolia*** Kunth, Nov. Gen. Sp. 2: 49. 1817. —TYPE: MEXICO, Acapulco, April, *Humboldt & Bonpland 3884* (P, Isotype B). (Fig. 3H–I)

= *Ficus gardneriana* (Miq.) Miq. Ann. Mus. Bot. Lugduno-Batavi 3: 297. 1867 . ≡ *Urostigma gardnerianum* Miq., London J. Bot. 6: 30. 1847. —TYPE: BRAZIL. Piauí, Paranagoa 1839, *Gardner 2728* (Lectotype: K; isolectotype G, NY, US)

= *Ficus mattogrossensis* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22 (1): 16. 1940. —TYPE: BRAZIL. Mato Grosso, Road to Capão Bonito, September 1936, *Archer & Gerht 61* (US, Isotype F).

Specimens selected: — BRAZIL. Espírito Santo, Linhares, 27 December 2000, *Domingos A. Folli* 3790 (RB);
São Paulo, Gália, 28 September 2007, *R. A. S. Pereira* 158 (RB).

Notes:— A species with a wide distribution in the Americas, occurring from Mexico to Brazil (in Caatinga, Cerrado and Atlantic Forest) (Carauta 1989; BFG 2015).

27. ***Ficus pertusa*** L.f., Suppl. Pl. 442. 1782. —TYPE: SURINAM. Without locality, s.d., *Dahlberg s.n.* LINN.1240.09). (Fig. 3J–K)

= *Ficus gemina* (Miq.) Miq., Ann. Mus. Bot. Lugduno-Batavi 3: 298. 1867. ≡ *Urostigma geminum* Miq., London J. Bot. 6: 547. 1847. —TYPE: PERU. Pozuzo, *Ruiz s.n.* (U; isotypes U, BR, G, P)

= *Ficus subtriplinervia* Mart., Flora 24 (2): 67. 1841 (1841: 67). —TYPE: BRAZIL. Mato Grosso, Cuiabá, September, *Martius 584* (M, Isotypes B, G, K, LE, NY, P).

Specimens selected: — BRAZIL. Rio de Janeiro, Rio de Janeiro, Aeroporto Santos Dumont, January 2010, *Machado, A.F.P.* 913 (HUEFS); São Paulo, Ribeirão Preto30 August 2005, *R.A.S. Pereira* 127 (RB).

Notes:— This species can be recognized by its small leaves and syconia, and the ostiolar crateriform region (from latin = pertusus: bored, open) (Carauta 1989). It occurs in Central America and in all regions of Brazil (Carauta 1989; BFG 2015). Berg (2007) re-circumscribed the "*Ficus pertusa* Complex" considering all Neotropical fig species with a crateriform (or umbilicate) ostiolar region would be synonymous with *F. pertusa* L. f. In the universe of Atlantic Forest species, for example, according to Berg (2007) the following would be synonymized: *F. arpazusa* and *Ficus broadwayi*. However, both species are clearly distinct in vegetative and reproductive traits. For this reason we have decided to adopt the circumscription of Carauta (1989).

28. ***Ficus trigona*** L.f., Suppl. Pl. 441. 1782. —TYPE: SURINAM. Without locality, s.d., *Dahlberg s.n.* LINN.1240.12). (Fig. 3L–M)

Specimens selected: — BRAZIL. Espírito Santo, Dores do Rio Preto, 12 October 2000, *E. A. Costa* 81 (RB); Rio de Janeiro, Guapimirim, Estação Ecológica Estadual de Paraíso, 18 February 1992, *C.M.Vieira* 184 (RB); São Paulo, Gália, 15 October 2008, *L.F.M. Coelho* 37 (RB).

Notes:— This species can be recognized by the indumentum on the abaxial leaf surface and by the typical ostiolar region presenting a triangular ring (Berg and Villavicencio 2004). It occurs in Bolivia, Peru, Colombia, the Guianas and Venezuela (Berg and

Villavicencio 2004). In Brazil it is found in all regions, in gallery forest and in Atlantic Forest at low altitudes (BFG 2015; Berg and Villavicencio 2004).

29. ***Ficus tweediana*** (Miq.) Miq., Ann. Mus. Bot. Lugduno-Batavi 3: 299. 1867. ≡ *Urostigma tweedianum* Miq., London J. Bot. 6: 547. 1847. —TYPE: BRAZIL. Rio Grande do Sul, West of Lagoa dos Patos, s.d., *Tweedie 32* (K!).

(Fig. 3N–O)

Specimen selected: — BRAZIL. Rio Grande do Sul, Terra de Areia, s.d., *Gonçalves 602* (HUEFS)

Notes:— In the course of analyzing specimens determined as *F. cestrifolia* Schott from southern Brazil (mainly Rio Grande do Sul and Santa Catarina States), we found significant morphological differences between them and with the populations growing in southeastern Brazil. The main differences are: the orbicular oval shape of leaves and their coriaceous consistency, the base almost always cordate, the short petiole, the reduced number of lateral veins, the angle of divergence for the first pair of lateral veins, and the turbinate syconia. Such traits would be sufficient to consider that the specimens in question comprised a distinct taxon. After reviewing the names in the synonymy of *F. cestrifolia* we concluded that the original description and the type of *F. tweediana* (Miq.) Miq. fit perfectly with these specimens from southern Brazil. For this reason we have decided to reinstate this name.

ACKNOWLEDGEMENTS. The authors thank the Fundação de Amparo à Pesquisa do Estado da Bahia (FAPESB) for awarding a Doctoral Fellowship to AFPM (grant # BOL0563/2014). Michella Del Rei for line drawings and comments in Taxonomy; Geovane Siqueira, Eloína Matos, Andrea Santos, Luci Conchou, Rodrigo Pereira and Ricardo Lacerda by the photos; Lucas C. Marinho for the help with images; and Marcus Fellipe O. da Silva for the comments in the first version.

LITERATURE CITED

Bachman, S., Moat, J., Hill, A., de la Torre, J. & Scott, B. 2011. Supporting Red List threat assessments with GeoCAT: Geospatial Conservation Assessment Tool. *Zookeys* 150:117–126

Berg, C. C. 2007. Proposals for treating four species complexes in *Ficus* subgenus *Urostigma* section *Americanae* (Moraceae). *Blumea* 52: 295–312.

Berg, C. C. and Carauta, J. P. P. 2002. New species of Ficus (Moraceae) from Brazil. *Brittonia* 54: 236–250.

Berg, C. C. and Corner, E. J. H., 2005. Moraceae – *Ficus*. Pp. 1–152 in Flora Malesiana Series I – Seed Plants Vol. 17/Part 2. Nooteboom, H. P. (Ed.). National Herbarium of the Netherlands, Leiden.

Berg, C. C. and Simonis, J. E. 1981. The *Ficus* flora of Venezuela: five species complexes discussed and two news species described. *Ernestia* 6: 1–16.

Berg, C. C. and Villavicencio, X. 2004. Taxonomic studies on *Ficus* (Moraceae) in the West Indies, extra-Amazonian Brazil, and Bolivia. *Ilicifolia* 5, 1–132.

BFG –The Brazilian Flora Group. 2015. Growing knowledge: an overview of Seed Plant diversity in Brazil. *Rodriguésia* 66 (4): 1085–1113.

Carauta, J. P. P. 1973. The Text of Vellozo's Flora Fluminensis and Its Effective Date of Publication. *Taxon* 22: 281–284.

Carauta, J. P. P. 1989. *Ficus* (Moraceae) no Brasil: conservação e taxonomia. *Albertoa* 2: 1–365.

Carauta, J. P. P. and Diaz, B. E. 2002. Figueiras no Brasil. Rio de Janeiro, RJ: Editora UFRJ.

Carauta, J. P. P., Romaniuc Neto, S. and Sastre, C. 1996. Índice das espécies de Moráceas do Brasil. *Abertoa* 4: 77–93.

Corner, E. J. H. 1960. Taxonomic notes on *Ficus* Linn., Asia and Australasia. *Gard. Bull. Singapore* 17: 368–485.

IUCN Standards and Petitions Subcommittee. 2017. Guidelines for Using the IUCN Red List Categories and Criteria. Version 13. Prepared by the Standards and Petitions Subcommittee. IUCN, Gland, Switzerland, and Cambridge, United Kingdom. *http://www.iucnredlist.org/documents/RedListGuidelines.pdf*

Mittermeier, R. A., Gil, P. R., Hoffmann, M., Pilgrim, J., Brooks, T., Mittermeier, C. G., Lamourex, J. and Fonseca, G. A. B. 2004. Hotspots revisited. CEMEX, Mexico City, 392p.

Miquel, F. A. G. 1853. Urticineae. Pp. 78–218 in *Flora brasiliensis*, vol. 4, pars 1, ed. C. F. P. Martius. Leipzig: P. Oldenburg.

Morellato, L. P. C. and Haddad, C. F. B. 2000. Introduction: The Brazilian Atlantic Forest. *Biotropica* 32: 786-792.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Fonseca, G. A. B. and Kent, J., 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.

Pederneiras, L. C., Carauta, J. P. P., Neto, S. R. and Mansano, V. F., 2015. An overview of the infrageneric nomenclature of *Ficus* (Moraceae). *Taxon* 64: 589–594.

Pederneiras, L. C., Coelho, V. P. M. and Romaniuc-Neto, S. (in prep.). Ficus subg. Pharmacosycea sect. Pharmacosycea (Moraceae) do Brasil. *Rodriguesia.*

Piedra-Malagón, E. M., Sosa, V. and Ibarra-Manríquez, G. 2011. Clinal variation and species boundaries in the *Ficus* petiolaris complex (Moraceae). *Systematic Botany* 36: 80–87.

Romaniuc-Neto, S., Pelissari, G., Santos, A. dos. and São José, P. A. 2009. Moraceae in *Plantas de Floresta Atlântica*. Stehmann, J. R. Forzza, R. C., Salino, A., Sobral, M. Costa, D. P. da and Kamino, L. H. Y. (Eds.). Rio de Janeiro, Jardim Botânico do Rio de Janeiro. 519 p.

Santos, O. dos A., Absy, M. L. and Ribeiro, J. E. L. da S. (in prep.) Estudo taxonômico do gênero *Ficus* L. (Moraceae) na Amazônia Brasileira.

Stehmann, J. R. Forzza, R. C., Salino, A., Sobral, M. Costa, D. P. da and Kamino, L. H. Y. 2009. Diversidade taxonômica na Floresta Atlântica, in *Plantas da Floresta Atlântica* Stehmann, J. R. Forzza, R. C., Salino, A., Sobral, M. Costa, D. P. da and Kamino, L. H. Y. (Eds.). Rio de Janeiro, Jardim Botânico do Rio de Janeiro. 519 p.

Thiers, B. [continuously updated]. Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. http://sweetgum.nybg.org/science/ih/.

LEGENDS:

FIGURE 1. A–B: Habit diversity. A. Hemiepiphytous, B. Figtree. growing in rocks, C–D: *F. arpazusa.* C. Branches with syconia, D. Detail of syconia and ostiolar region; E–F. *F. bahiensis.* E. Branches with syconia, F. Detail of terminal stiple and syconia. G. *F. broadwayi* branches. H. F. calyptroceras branches. I–J. *F. castellviana.* I. Detail of young branches and terminal stipule, J. Syconia showing the format and ostiolar region. K–L. *F. cestrifolia.* K. Branches with syconya, L. Detail os terminal stipule and syconia. Photos: A by G. Siqueira; B and H by E. Matos; C, D, I, J by R. Lacerda; E, F, K L by A. Machado; G. by L. Conchou

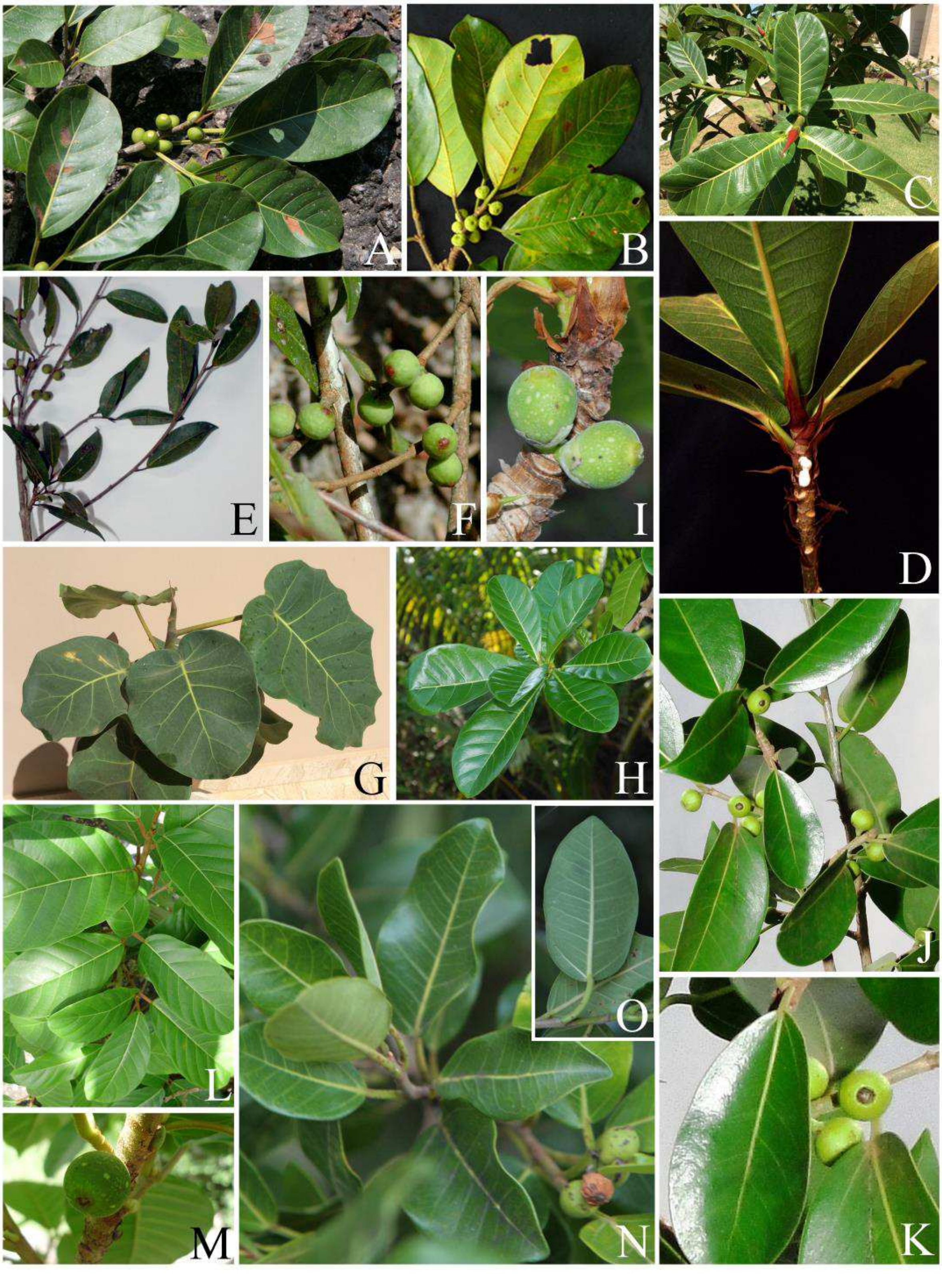
FIGURE 2. A. *F. citrifolia* detail of syconia, B–C. *F. clusiifolia.* B. Detail of leaves, C. Detail of syconyum and ostiolar region. D. *F. crocata* detail of sycony showing the ostiolar region with an elevated ring. E–F. *F. cyclophylla.* E. Detail of branches showing the persistent stipules, F. Detail of syconia showing the basal bracts and elevated ostiolar bracts. G. *F. enormis* branch with syconia, H. *F. eximia.* Branch with syconia. I–J. *F. gomelleira.* I. Leaves, J. Reproductive branch showing syconia and the terminal stipule. K. *Ficus guaratitica.*, L. *F. hirsuta.* M. *F. holosericea.* N. *F. lagoensis.* O. *F. laureola.* Photos: A by G. Siqueira; D, L, I, J by R. Lacerda and the others by A.F.P.Machado.

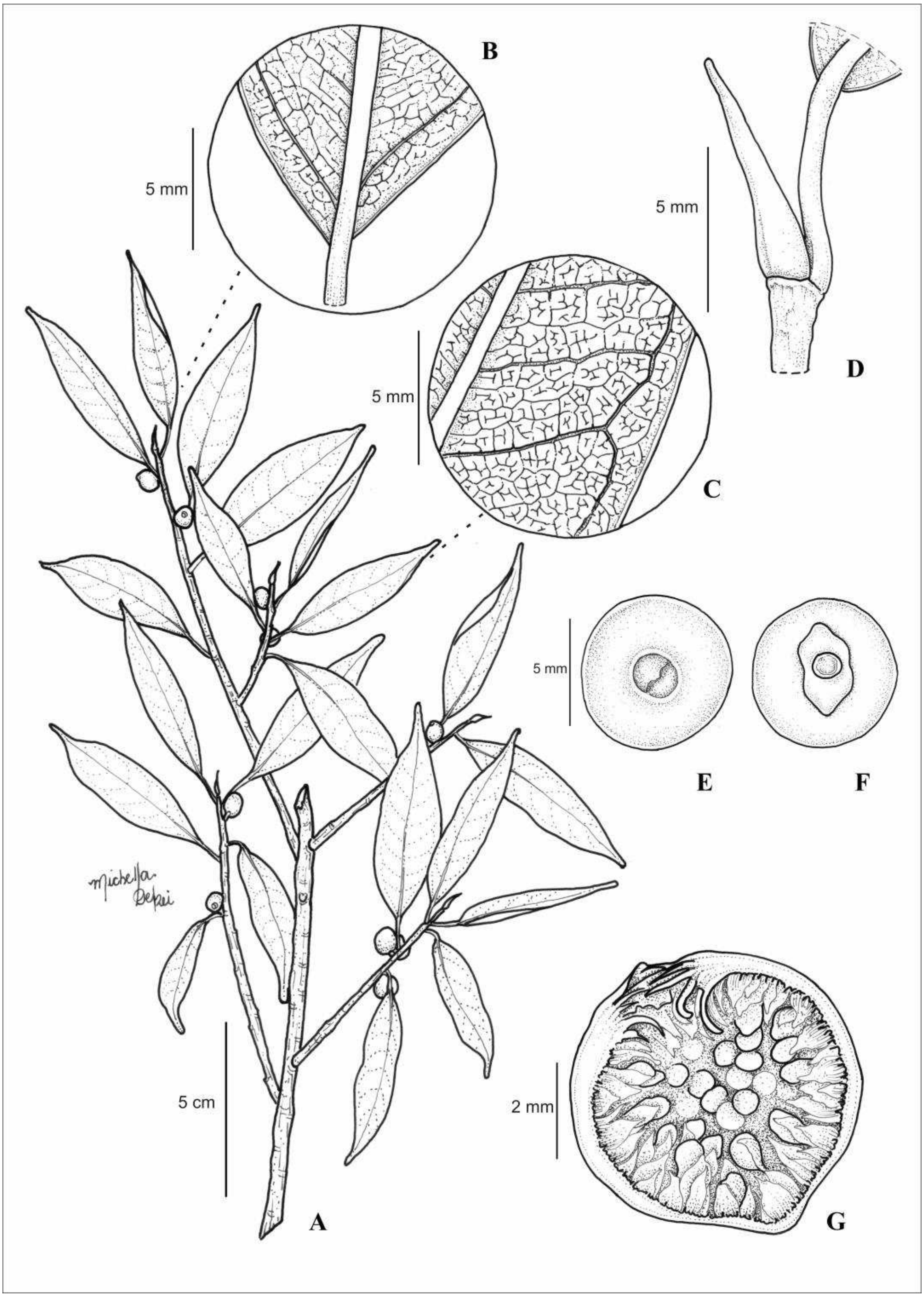
FIGURE 3. A–B: *F. luschnathiana.* C–D: *F. mexiae.* E–F. *F. sp.nov* G. *F. nymphaeifolia*, H–I. *F. obtusifolia.* H. Leaves, I. Detail of syconia. J–K. *F. pertusa.* J. Reproductive branch, K. Detail of syconium.. L–M. *F. trigona.*L. Reproductive branch, M. Detail of syconium showing ostiolar region. N–O. *F. tweediana* . N. Brach with figs. O. Abaxial of leaf showing the major veins. Photos A, B, H, I. by R. Pereira; C, D, E, F, J, K by A. Machado; L–M. by A. K. Santos. N, O by Amaury Jr.

FIGURE 4. *Ficus sp..nov.* A– Floriferous branch; B– Adaxial surface of the leaf showing the petiole and basal pair of secondary veins; C– Detail of tertiary nervation; D– Terminal stipule; E– Syconium superior view showing the ostiole and external ostiolar bracts; F– Syconium inferior view showing the basal bracts; G–Cross section of syconium showing flowers and ostiolar bracts. Ilustration from A.F.P. Machado 595. M. Del Rey *del.*


A
B
C
E
D
F
G
K
H
I
J
L


A
B
D
C
G
H
E
I
F
J
M
K
L
N
O


A
B
C
D
E
F
I
G
H
J
L
O
N
M
K


B
5 mm
D
5 mm
5 mm
C
5 mm
E
F
A
5 cm
2 mm
G

CAPÍTULO 2

A new species of *Ficus* (Moraceae) endemic from northeastern Brazil

ANDERSON F. P. MACHADO[1] & LUCIANO P. DE QUEIROZ[1]

[1] Programa de Pós–Graduação em Botânica, Universidade Estadual de Feira de Santana, Av. Transnordestina, Novo Horizonte, 44036–900, Feira de Santana, Bahia, Brazil. E–mail: machadoafp@gmail.com

Abstract

A new species of fig tree, endemic to the Chapada Diamanatina in the northeastern Brazilian state of Bahia, is described and illustrated. *Ficus diamantina* belongs to the *Ficus* sect. *Americanae*. The new species shows affinities with *Ficus bahiensis* and *F. clusiifolia* from which it is differentiated by the young branches reddish with epidermis flaking off; the lamina abaxial surface with tector and glandular trichomes; the number of lateral veins, the divergence angle of basal pair of veins and the subsessile syconia. It occurs in *Campos Rupestres* (rupestrian grasslands) and wet forests at altitudes up to 800 m.

Key words: sect. *Americanae*, Chapada Diamantina, fig tree, Rosales, Bahia, Northeast Brazil.

Introduction

Ficus L. (1753:1059) is a pantropical genus with approximately 750 species mostly found in moist rainforests. The species of *Ficus* in the Neotropics are subordinated to the subgenus *Pharmacosycea* (Miq.) Miq. (1847:525) (ca. 20 spp.) and *Urostigma* sect. Americanae Miq. (1847:525) (ca. 100 spp.). In Brazil, there are 80 species of fig trees (BFG 2015) and the most important taxonomic treatments for brazilian species of *Ficus* were published by Miquel (1853), Carauta (1989) and Berg & Villavicencio (2004).

Some species of *Ficus* in Brazil are associated with calcareous outcrops as *Ficus bonijesulapensis* R.M. Castro (2006: 14), *Ficus calyptroceras* (Miq.) Miq. (1867: 297), *Ficus mexiae* Standl. (1937: 173), *Ficus goiana* C.C.Berg et al. (2013: 54) and *Ficus laureola* Berg & Carauta (2002: 246). The last one occurs in areas of *Campos Rupestres* at Minas Gerais States but also in Atlantic Rainforest of Espírito Santo state, Brazil.

During the revision of Brazilian species of *Ficus* sect. *Americanae* by the first author, field trips were conducted around the country and the collections of principal herbaria from Brazil were examined. We collected a new species, which is described below it belongs to *Ficus* sect. Americanae and is known for two collections at the Chapada Diamantina region on Bahia State, northeast Brazil.

Taxonomy

Ficus diamantina A.F.P. Machado & L.P. Queiroz, *sp. nov.* (sect. ***Americanae***) Figs. 1, 2, 3.

Type:— BRAZIL. Bahia: Mucugê, Capão do Correia, estrada vicinal saindo de Caraíba a 7.5 Km da BA–142. Base de campo rupestre com solo pedregoso, antropizado, com *Pteridium.* Beira de estrada. 13°6 36.9"S, 41°22' 37.9"W, 1218 m, 11 July 2009, *M.M. Saavedra et al. 969* (holotype HUEFS!, isotype RB!).

Diagnosis: — *Ficus diamantina resembles Ficus bahiensis by the consistency, dimensions of the leaves and by the dimensions of syconia, but differs by the juvenile branches with epidermis flaking off; by the petiole with white elongated trichomes* (vs. *juvenile branches greyish without epidermis flaking off and petiole glabrous); acropeciolar waxy gland not evident in sicco* (vs. *waxy gland evident in sicco.); the basal pair of veins forming an angle 65º–85º and reaching 1/4 of the blade* (vs. *basal pair of veins forming an angle 95º–120º and reaching 1/8 – 1/10 of the blade); the presence of tector and glandular trichomes at the abaxial side of leaf blade* (vs. *adaxial surface glabrous) and the syconia elliptic and sessile* (vs. *syconia rounded and pedicelate).*

Trees up to 6 m tall, sympodial without aerial roots; bark fissured, greyish to reddish; branches reddish, slender 0.5–0.8 diam, pubescent, juvenile branches with epidermis flaking off. Terminal stipule short (1.0–) 1.2–1.5 (–1.7) cm long, conical, green to red, brown at the maturity, glabrate, deciduous. Internodes (0.4–) 1.2–1.5 (–2.0) cm long. Petiole canaliculate (1.2–) 2.5–9 (–12) cm long, slender, 3–4 mm diam., with sparse simple trichomes, epidermis persistent; leaf blades 8–15 × 5–8 cm, usually ovate-deltoid, coriaceous, base cuneate to rounded, margin slightly revolute towards the apex, apex acute, adaxial surface dark green, glabrous, abaxial surface light green, pubescent to glabrous with erect trichomes at the lamina and near to the veins, capitate glandular trichomes at the limb, lateral veins 7–9 (10) pairs, prominent on abaxial side, the basal pair up to 1/4 the length of the lamina, unbranched, forming an angle of 65º–85º, tertiary venation reticulate; waxy gland at the base of the midrib beneath, not evident *in sicco*. Syconia axillary or also just below the leaves, solitary or in pairs, green to pale green, subsessile, 8–13 mm in diameter when dry; peduncle 0.1 cm long, glabrous or sparsely minutely puberulous; basal bracts 0.3–0.5 cm wide, greenish and brownish in herbarium specimens, rounded, persistent, glabrescent to, glabrous to pubescent, persistent; receptacle subglobose, 0.6–1(–1.2) cm diam. (when dry), smooth or wrinkled when dry, glabrous or sparsely minutely puberulous, maculate, greenish to yellowish at maturity; ostiole 0.3–0.4 cm diameter; slightly prominent, closed by 3 external bracts, puberulous; interfloral bracts 1.8–2 mm long. Staminate flowers: pedicel 0.4–0.8 mm long; tepals 3, 0.5–0.8 mm long; stamen 1, anthers ca. 0.9 mm long, not apiculate. Pistillate flowers: pedicel 1.0–1.5 mm long; tepals 2-3; ovary 0.9–1.1 mm long, asymmetrically reniform, style 10–20 mm long, stigma ca. 0.2 mm long, bifid. Fruit not seen.

Comparison: *Ficus diamantina* was assigned to the section *Americanae* (1860: 319) as proposed by Miquel. This section comprises around to 100 species, occurring in Neotropics and is characterized by the initial hemiepiphytic habit, a single waxy gland in the petiole, the syconia with 2 basal bracts, ostiole enclosed by 2-3 external bracts and staminate flowers with one stamen.

Ficus diamantina occurs sympatrically with *Ficus clusiifolia* Schott (1931: 403), but they can be easily distinguished by the young branches reddish (*vs.* young branches greyish to white in *F. clusiifolia*), by the basal pair of veins up to 1/4 of the blade. Forming an angle 65º–85º. (*vs.*the basal pair of veins up to 1/10 of the blade. Forming an angle 120º–140º. in *F. clusiifolia*), by the indument of abaxial surface with tector and glandular trichomes (vs. adaxial surface glabrous in *F. clusiifolia*) and by the subsessile syconia with smaller (0.3-0.5 cm long) basal bracts (vs. 0.6–0.8 cm long).

Etymology:— The epithet *diamantina* from Chapada Diamantina, the major mountain range in Bahia State, northeastern Brazil, where the new species occur.

Distribution, habitat, and conservation:— *Ficus diamantina* occurs in Bahia State, Brazil, in areas of Campos rupestres a brazilian peculiar vegetation type formed by a mosaic of rocky outcrops and quartz and sandstone soils occurring mostly above 900 m. These areas are marked by the high rate of endemism (Conceição and Pirani 2005). *Ficus diamantina* is presently known from two municipalities with an Extent of occurrence (EOO) of 2.433 Km² (EOO estimated in GeoCat tool see Bachman et al. 2011). That suggests the Endangered (EN) conservation category (IUCN 2017).

Additional specimen examined (paratypes):— BRAZIL. Bahia: Rio do Pires, Serra Itubira, Mata do Cigano, 13°15'50"S, 41°55'04"W, 1750 m, November 2008, *F.H.F. Nascimento 621* (HUEFS!, RB!); BRAZIL. Bahia: Mucugê, Capão do Correia, 13°6 36.9"S, 41°22' 37.9"W, 1231 m, A.F.P.Machado & J.O Cruz. 1231 *st.*; L.c., A.F.P.Machado & J.O.Cruz 1232. *st.*

Acknowledgements

The authors would like to thank to Abel A. Conceição and Mariana M. Saavedra for the valuable help about the type locality.; to Francisco H. F. do Nascimento for information about the plants in the field and for the photos of the type specimen; to Carlos André E. Leitão for the advice with the description of the trichomes; to Joelma Cruz for the companionship in fieldtrip; to Michella del Rei for the line drawings and to Lucas C. Marinho for the suggestions, the map drawing and the help with the images. AFPM was supported by FAPESB Doctoral Fellowship (grant # BOL0563/2014).

References

Bachman, S., Moat, J., Hill, A., de la Torre, J. & Scott, B. (2011) Supporting Red List threat assessments with GeoCAT: Geospatial Conservation Assessment Tool. *Zookeys* 150:117–126

Berg, C.C. (2007) Proposals for treating four species complexes in *Ficus* subgenus *Urostigma* section *Americanae* (Moraceae). *Blumea* 52: 295–312.

Berg, C.C. & Carauta, J.P.P. (2002). New species of Ficus (Moraceae) from Brazil. *Brittonia* 54: 236–250.

Berg, C.C., Carauta, J.P.P. & Machado, A.F.P. (2013) *Ficus goiana*, a replacement name for a Brazilian species of fig (Moraceae). *Phytotaxa* 108: 54–56.

Berg, C.C. & Simonis, J.E. (1981) The *Ficus* flora of Venezuela: five species complexes discussed and two news species described. *Ernestia* 6: 1–16.

BFG –The Brazilian Flora Group. (2015) Growing knowledge: an overview of Seed Plant diversity in Brazil. *Rodriguésia* 66(4): 1085–1113.

Carauta, J.P.P. (1989) *Ficus* (Moraceae) no Brasil: conservação e taxonomia. *Albertoa* 2: 1–365.

Castro, R.M. & Rapini, A. (2006) Four new species of Moraceae from Bahia, Brazil. *Neodiversity* 1: 13–20.

Conceição, A., & Pirani, J. (2005) Delimitação de habitats em Campos rupestres na Chapada Diamantina, Bahia: substratos, composição florística e aspectos estruturais. *Bol. Bot. Univ. São Paulo* 23(1): 85–111.

IUCN Standards and Petitions Subcommittee. (2017) Guidelines for Using the IUCN Red List Categories and Criteria. Version 13. Prepared by the Standards and Petitions Subcommittee. IUCN, Gland, Switzerland, and Cambridge, United Kingdom. *http://www.iucnredlist.org/documents/RedListGuidelines.pdf*

Miquel, F.A.G. (1847) Prodromus monographiae Ficuum. *London J. Bot.* 6: 514–588, t. 21–22.

Miquel, F.A.G. (1853) Urticineae. In C.F.P. von Martius, *Fl. Bras.* 4(1):77–218, t.25–70. Leipzig.

Miquel, F.A.G. (1867) Annotationes de Ficus speciebus. In F.A.G. Miquel, *Ann. Mus. Lugd. Bat.* 3: 260–300.

Standley, P.C. (1937) Ficus. In J.F.Macbride, Flora of Peru, Part VII. *Publ. Field Mus Nat. Hist. Ser.* 17: 155–224.

Legends:

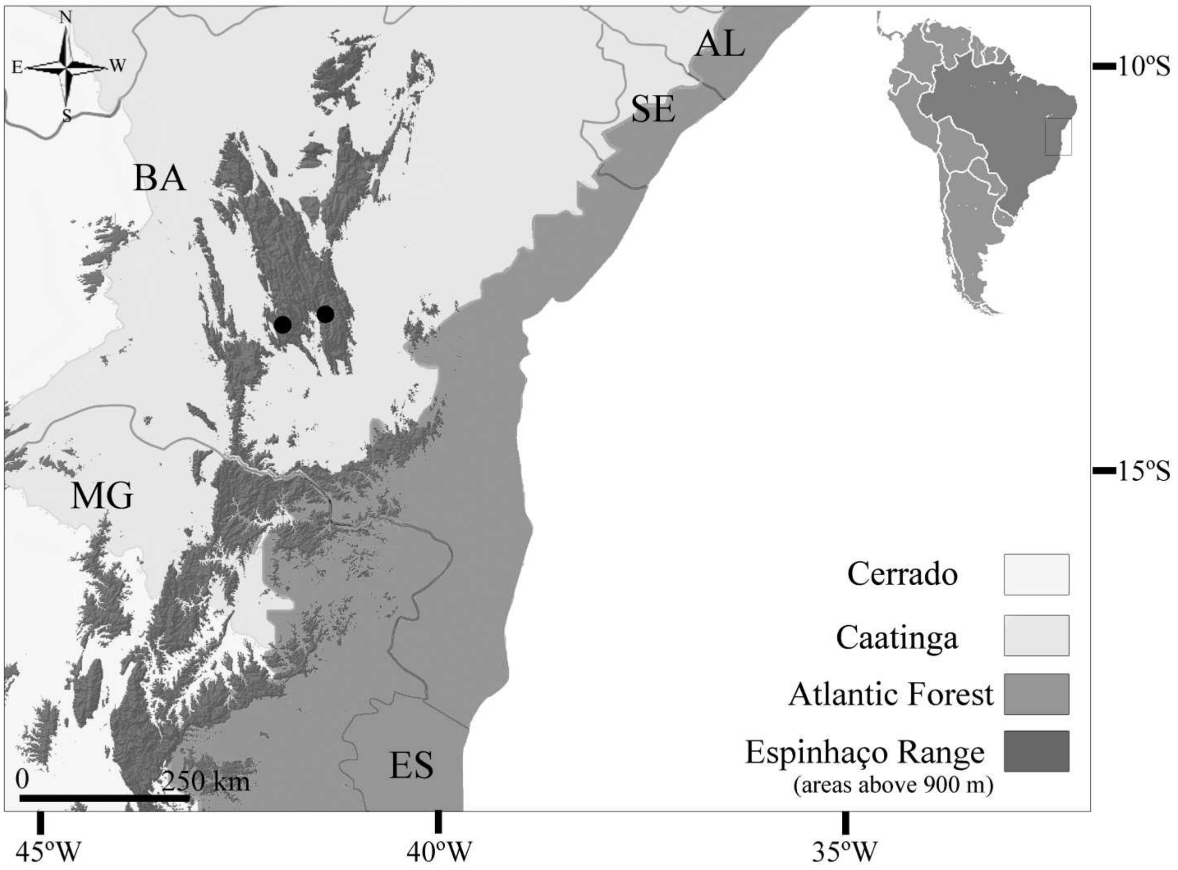
FIGURE 1. Map showing the geographic distribution of *Ficus diamantina* (black circle).

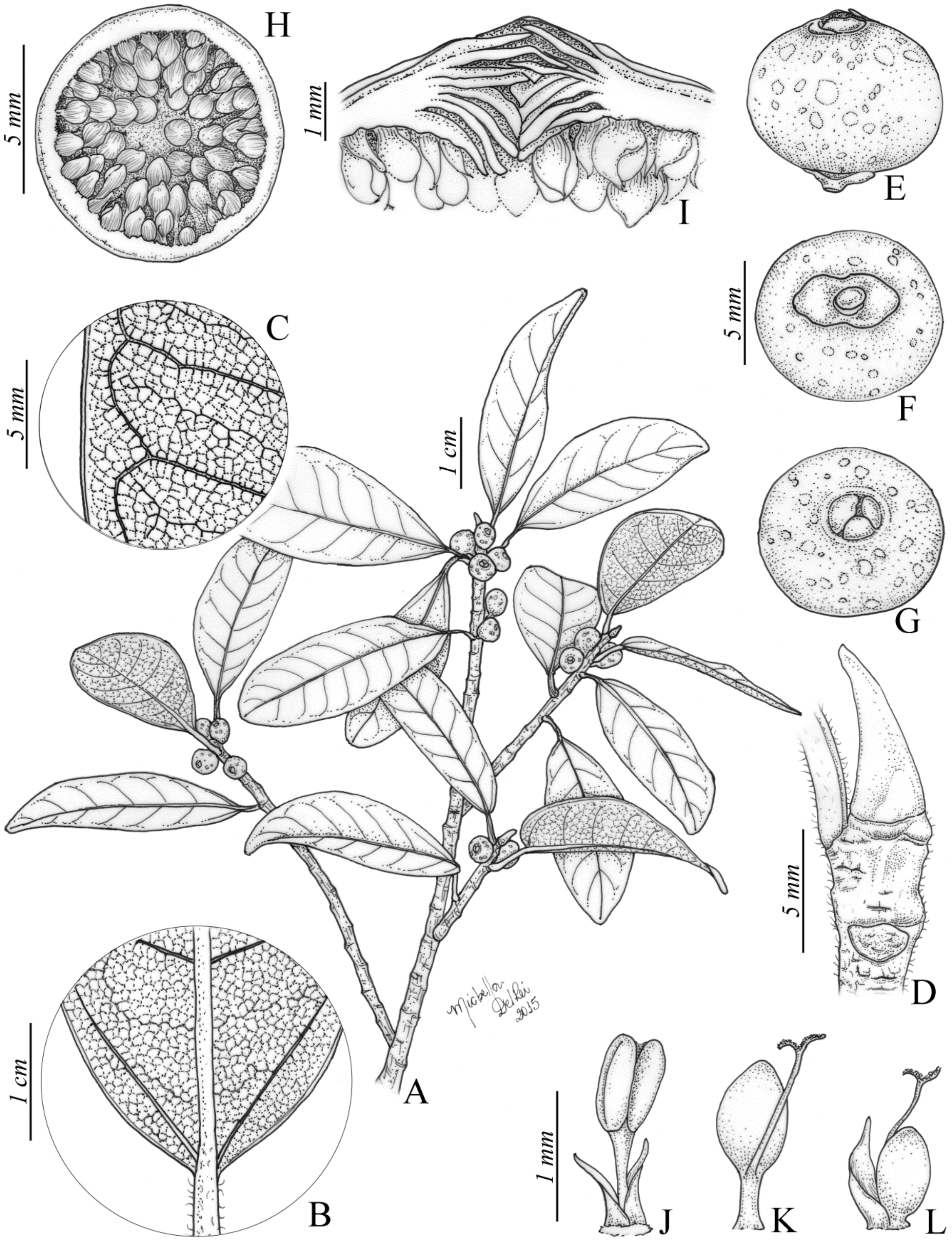
FIGURE 2. *Ficus diamantina.* A– Habit; B– Adaxial surface of the leaf showing the petiole and basal pair of secondary veins (*A.F.P.Machado 1032*); C– Detail of tertiary nervation; D– Terminal stipule (*A.F.P.Machado 1032*); E– Syconium in frontal view; F– Syconium inferior view showing the basal bracts; G– Syconium superior view showing the ostiole and external ostiolar bracts; H–Cross section of syconium; I– Cross section of ostiolar bracts; J– Staminate flower; K-L– Pistilate flowers. Ilustration from M. Saavedra 969 except B–D from paratype. M. Del Rei *del.*

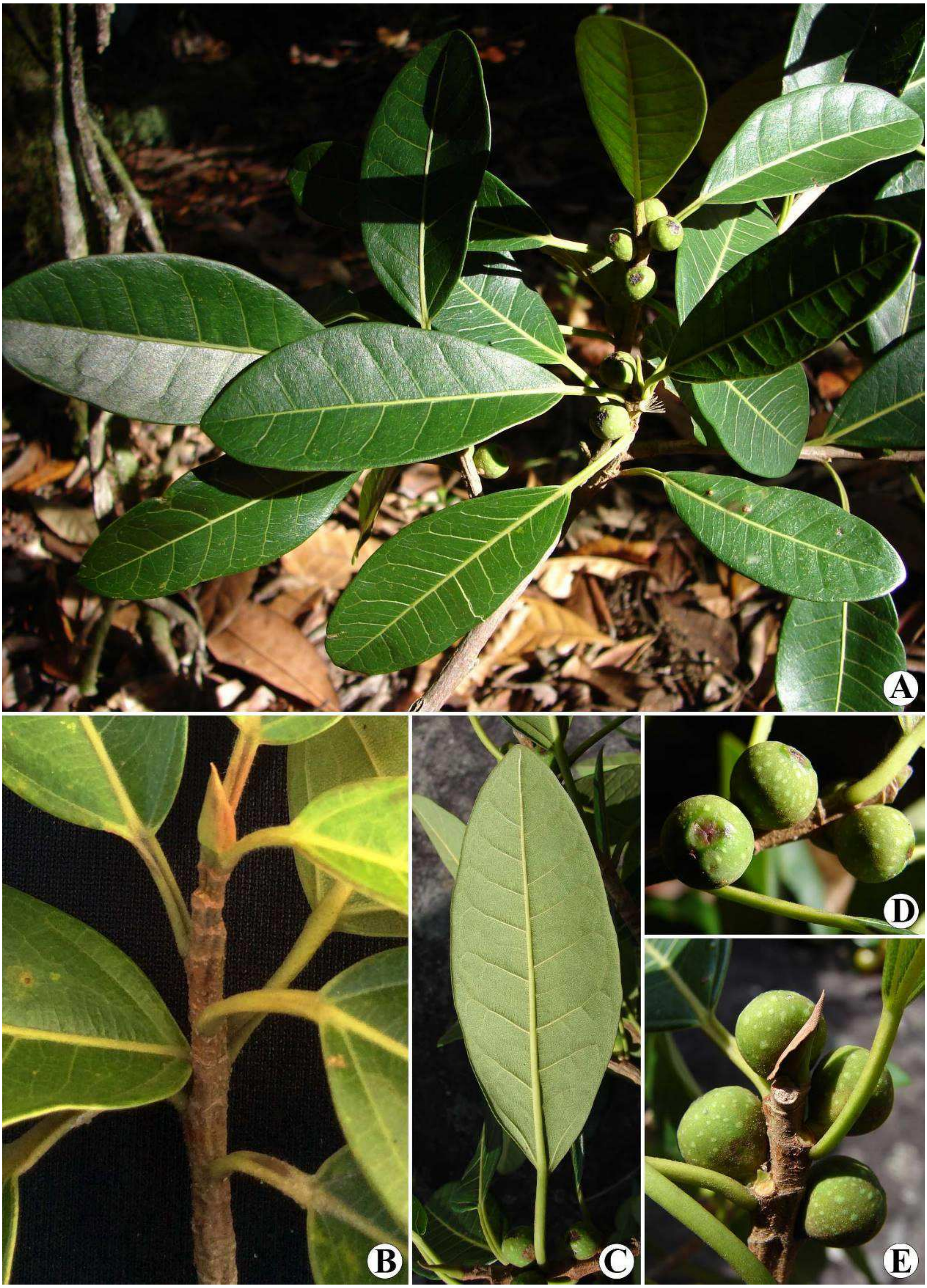
FIGURE 3. *Ficus diamantina.* A– Stem with syconia; B– Terminal stipule (A.F.P.Machado 1032); C– Leaf in abaxial view; D– Syconia showing the ostiole; E– Terminal stipule and syconia. A–C–D–E: F.H.F. Nascimento 621. Photos: A–C–D–E, by F.H.F. Nascimento; B. by A.F.P.Machado.

TABLE 1. Main characters distinguishing *Ficus diamantina* from *F. bahiensis, and F. clusiifolia.*

Character/Species	*F. bahiensis*	*F. clusiifolia*	*F. diamantina*
Branch indumentum	Young branches greyish without epidermis flaking off	Young branches greyish to white without epidermis flaking off	Young branches reddish with epidermis flaking off
shape of the apex of lamina	Obtuse rare sub acuminate.	Obtuse	Acute
Lamina indumentum (abaxial surface)	glabrous	glabrous	Tector trichomes and glandular capitate trichomes.
Number of lateral veins	8–10 pairs	10-14 pairs	7–9 pairs mm
Basal pair of veins	Up to 1/8 – 1/10 of the blade. Forming an angle 95º–120º.	Up to 1/10 of the blade. Forming an angle 120º–140º.	Up to 1/4 of the blade. Forming an angle 65º–85º.
Waxy gland	At the top of petiole or 0.2–0.3 cm above. Evident *in sicco.*	At the top of petiole. Not evident *in sicco.*	At the top of petiole. Not evident *in sicco.*
Syconium	Pedicelate. Peduncle 0.4–0.6 cm, basal bracts 0.3–0.5 cm.	Pedicelate. Peduncle 0.3–0.5 cm, basal bracts 0.6–0.8 cm.	Subsessile. Peduncle until 0.1 cm, basal bracts 0.3–0.5 cm.


N
E
W
S
BA
AL
SE
MG
ES
0
250 km
10ºS
15ºS
45ºW
40ºW
35ºW
Cerrado
Caatinga
Atlantic Forest
Espinhaço Range
(areas above 900 m)


H
5 mm
1 mm
I
E
C
5 mm
F
5 mm
1 cm
G
D
5 mm
Michellon Delkei 2015
1 cm
A
1 mm
J
K
L
B


A
B
C
D
E

Ficus goiana a replacement name for a Brazilian species of fig (Moraceae)

C. C. BERG[1†], J. PEDRO P. CARAUTA[2] & ANDERSON F. P. MACHADO[3]

[1.] *Netherlands Centre for Biodiversity - Naturalis, Section National Herbarium of the Netherlands, Leiden University, P.O. Box 9514, 2300 RA Leiden, the Netherlands.*
[2] *Departamento de Botânica, Museu Nacional, Universidade Federal do Rio de Janeiro, Quinta da Boa Vista s/n, São Cristóvão, 20940-040, Rio de Janeiro, RJ, Brazil.*
[3] *Programa de Pós-graduação em Botânica, Universidade Estadual de Feira de Santana, Av. Transnordestina, s.n., 44036-900, Feira de Santana, BA, Brazil, e-mail: afpmbot@gmail.com*

Ficus Linnaeus (1753: 1059). is the largest genus of Moraceae with ca. 750 species occurring mostly in the tropical and subtropical regions (Rønsted *et al.* 2008). The taxon known as *F. rupicola* Berg & Carauta (2002: 249) is endemic to Brazil and has been collected in the states of Bahia, Minas Gerais and Goiás as well as the Distrito Federal. The preparation of a worldwide list of published *Ficus* names revealed that the name *Ficus rupicola* had previously been used by Lebrun & Toussaint (1948: 43) for a species based on African material. This makes it necessary to provide a new name for *F. rupicola* Berg & Carauta (2002: 249). We propose the new name *Ficus goiana* C.C. Berg, Carauta & A.F.P. Machado.

The specific epithet refers to Goiás, the state where the type was collected. This region presents mainly the typical vegetation of the Cerrado a biome recognized as a global biodiversity hotspot.

Ficus goiana C.C.Berg, Carauta & A.F.P. Machado, *nom. nov.* (Fig. 1)

Replaced name: *Ficus rupicola* Berg & Carauta (2002: 249, fig. 8: 248), *nom. illeg.* (non Lebrun & Toussaint 1948: 43)

Type:—BRAZIL. Goiás: Mun. São Domingos, rd. Guaraní de Goiás-Terra Ronca, November 1996, *B.A.S. Pereira & D. Alvarenga 3291* (holotype IBGE!; isotypes BG!, HB!, SI).

This species of deciduous trees is distinct in its small, usually (sub)ovate leaf blades (2–5 × 1.5–2.2 cm) with a relatively long and slender petiole (1–3.5 cm). It probably belongs to the *Ficus cestrifolia* group, a group of small-leaved species found in extra-Amazonian Brazil (Berg & Villavicencio 2004), comprising, in addition *Ficus cestrifolia* Schott ex Sprengel (1827: 409), *F. bahiensis* Berg & Carauta (2002: 238), *F. carautana* Neves & Mello-Filho (1992: 37), *Ficus hatschbachii* Berg & Carauta (2002: 243), *F. hirsuta* Schott in Sprengel (1827: 410), *F. lagoensis* Berg & Carauta (2002: 243), and *F. laureola* Warb. ex Berg & Carauta (2002: 246). This species has also been treated in a study on extra-Amazonian Brazilian *Ficus* species by Berg & Villavicencio (2004).

The original publication of *F. rupicola* place this species as related to *Ficus citrifolia* Miller (1768: 10). However, this species cannot be placed in the *F. cestrifolia* group. The species of this complex have smaller leaves and inflorescences and a distinctive geographical distributional pattern restricted at Atlantic Rainforest east coast of Brazil.

Acknowledgements

The authors are thankful to the editors of Phytotaxa and to the anonymous reviewers for critical comments of the manuscript. This paper was carried out as part of the preparation of a list of published worldwide *Ficus* by the first authors and is part of Doctoral thesis of the last author at the Universidade Estadual de Feira de Santana. Anderson Machado is supported by a CAPES fellowship.

References

Berg, C.C. & Carauta, J.P.P. (2002) New species of *Ficus* (Moraceae) from Brazil. *Brittonia* 54: 236–250.

Berg, C.C. & Villavicencio, X. (2004) Taxonomic studies on *Ficus* (Moraceae) in the West Indies, extra-Amazonian Brazil, and Bolivia. *Ilicifolia*: 1–129.

Lebrun, J. & Toussaint, L. (1948) *Ficus*. *In*: Lebrun, J., Taton, A. & Toussaint, L. *Exploration du Parc National de La Kagera, Mission J. Lebrun (1937–1938).* Institut des parcs nationaux du Congo belge, Bruxelles, 99 pp.

Linnaeus, C. von (1753) *Species plantarum.* Laurentius Salvius, Stockholm, 1200 pp.

Miller, P. (1768) *Gardeners Dictionary (ed.8).* Printed for the author and sold by John and Francis Rivington, London, 1386 pp.

Neves, L.J. & Mello-Filho, L.E. (1992) Sobre uma nova espécie matogrossense de *Ficus* L. *Bradea* 6(5): 36–37.

Rønsted, N., Weiblen, G.D., Clement, W., Zerega, N. & Savolainen, V. (2008) Reconstructing the phylogeny of figs (*Ficus*, Moraceae) to unravel the origin of fig-wasp mutualisms. *Symbiosis* 45: 45–56.

Sprengel, C.P.J. (1827) *Systema Vegetabilium, editio decima sexta*, 4(2). L. Dieterich, Göttingen, 410 pp. mutualisms. *Symbiosis* 45: 45–56.

Sprengel, C.P.J. (1827) *Systema Vegetabilium, editio decima sexta*, 4(2). L. Dieterich, Göttingen,. 410 pp.

FIGURE 1. *Ficus goiana*. **A)** Leafy twig with figs; **B)** Long-styled pistillate flower and interfloral bract; **C)** Short-styled pistillate fower and interfloral bract; **D)** Staminate flower, interfloral bract, and stamen (*from Pereira et al. 3291*). Reprinted from Berg & Carauta (2002) as *Ficus rupicola* C.C.Berg & Carauta.

Herbarium BG - University of Bergen
Ficus rupicola C.C. Berg & Carauta

Det. C.C. Berg 2001 24/10 Isotype !

1961

PLANTAS DO BRASIL

IBGE

Goiás

Moraceae

Ficus maroma Castellanos

Det. C.C. Berg 10/5.97

Município de São Domingos. Altitude aprox.: 600 m. Coord. aprox. 13° 40' S & 46° 20' WGr. Km 34 da estrada Guaraní de Goiás/Terra Ronca.
Árvore cerca de 12 m de altura. Casca amarelada, praticamente lisa. Fruto imaturo de cor verde. Remanescente de mata estacional.

3291 23.xi.1996
Leg.: B. A. S. Pereira & D. Alvarenga.

HERBÁRIO IBGE - Reserva Ecológica do IBGE

EX

G

Herbarium BG

CAPÍTULO 4

Ficus bilinaensis (Moraceae), a replacement name for a fossil fig tree of the Czech Republic

ANDERSON F. P. MACHADO[1] * & LUCIANO P. DE QUEIROZ[1]

[1] *Programa de Pós–Graduação em Botânica, Universidade Estadual de Feira de Santana, Av. Transnordestina, Novo Horizonte, 44036–900, Feira de Santana, Bahia, Brazil. E–mail: machadoafp@gmail.com*

*Author for correspondence.

During a revision of fossils of *Ficus* Linnaeus (1753: 1059) (Moraceae) we consulted the International Fossil Plant Names Index (IFPNI) see (Doweld 2016) and found a name which is a later homonym of a living Neotropical species of fig tree.

Ficus clusiifolia Ettingshausen (1866: 63) is a fossil described from the Kučlín village at the south of Bílina town, Czech Republic. The Kučlín region represents a stratigraphically important locality of the North Bohemian Tertiary (Kvaček and Teodoridis 2011).

However this binomial was previously used by Heinrich Wilhelm Schott (1794-1865) for the neotropical species *Ficus clusiifolia* Schott (1827:409). Both names are validly published and currently accepted. For this reason the plant fossil name is illegitimate under the article 53.1 from ICN (McNeill & al. 2012) and a replacement name is proposed here.

Ficus bilinaensis A.F.P. Machado, **nom. nov**.

Replaced name: *Ficus clusiifolia* Ettingsh. (1866: 63). Die fossile Flora des Tertiärbeckens von Bilin I. 68-69. Tab. XXI. Fig. 4. 1866. *nom. illeg*.

Type: —*Ficus clusiifolia* Ettingsh. Die fossile Flora des Tertiärbeckens von Bilin I. 68-69. Tab. XXI. Fig. 4. 1866.

Acknowledgements

The authors would like to thank to Dr. Nicholas Turland (Freie Universität Berlin); Dr. Ruy Alves (Museu Nacional-UFRJ); Ricardo Lacerda and Michella Del Rei for their suggestions. AFPM was supported by Fundação de Amparo à Pesquisa do Estado da Bahia (FAPESB) Doctoral Fellowship (grant # BOL0563/2014).

References

Doweld, A. B. (2016). The International Fossil Plant Names Index (IFPNI): A global registry of scientific names of fossil organisms started. *Palaeobotanist* 65: 203–208.

Ettingshausen, C. V. (1866). *Die fossile Flora des Tertiärbeckens von Bilin I.* Denkschriften Öesterreichische Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Klasse, Wien, 98 pp.

McNeill, J., Barrie, F. R., Buck, W. R., Demoulin, V., Greuter, W., Hawksworth, D. L., Herendeen, P.S., Knapp, S., Marhold, K., Prado, J., Prud'Homme van Reine, W.F., Smith, G.F., Wiersema, J.H. & Turland, N.J. (eds.). (2012). *International Code of Nomenclature for the algae, fungi, and plants (Melbourne Code)* adopted by the Eighteen International Botanical Congress Melbourne, Australia, July 2011. Koeltz Scientific Books, Königstein, 240 pp.

Kvaček, Z. & Teodoridis, V. (2011). The Late Eocene flora of Kučlín near Bílina in North Bohemia revisited. *Acta. Mus. Nat. Pragae*, Ser. B, Hist. Nat. 67. 3–4.

Schott, H. (1827) Fasciculus plantarum brasiliensium. *In:* Sprengel, C.P.J. *Systema Vegetabilium.* 16 ed. Sumtibus Librariae Dieterichianae, Gottingae, Vol. 4, Pt. 2.: pp. 409–410.

CAPÍTULO 5

Secretory structures at syconia and flowers of *Ficus enormis* (Moraceae): a specialization at ostiolar bracts and the first report of inflorescence colleters

Anderson Ferreira Pinto Machado[1], Aline Matos de Souza[2] & Carlos André Espolador Leitão[2]

1. Programa de Pós-graduação em Botânica, Universidade Estadual de Feira de Santana, Av. Transnordestina s/n, Novo Horizonte, 44.036-900, Feira de Santana, BA, Brazil. (machadoafp@gmail.com)
2. Departamento de Ciências Naturais, Universidade Estadual do Sudoeste da Bahia, 45.083-900, Vitória da Conquista, BA, Brazil. (candreel@gmail.com)

Part of the doc. thesis of first author.

Keywords: Anatomy, Histochemistry, Urostigma sect. Americana, fig tree, pollination, fig-fig wasp.

Abstract:

The fig (*Ficus* L.) infrutescence, called syconium, is a receptacle with an apical opening, the ostiole, closed by bracts. The ostiolar bracts produce an exudate, which is rather conspicuous in some species. It has not been histochemically analysed yet, and the structures responsible for its production are still unknown. Some wild growing species of *Ficus* from Brazil produce high amounts of this ostiolar exudate. *Ficus enormis* (Mart. ex Miq.) Miq. grows as trees or shrubs in the Atlantic rainforest. Our goal was to identify the secretory structures present in the inflorescence and, to characterize histochemically the ostiolar tissues and exudates. Syconia samples of *F. enormis* were processed and stained according to the usual techniques in plant anatomy. The morphological analysis revealed different types of bracts, one type specialized in secretion, another showing transitional characteristics between secretory and non-secreting bracts, and a third one being non-secreting. They are designated as secretory ostiolar bracts, transitional bracts and wall bracts. The floral bracteoles, digital-shaped colleters present in the ostiole, at the syconium axis and the flower receptacle, were also analyzed. All have similar structure, like digital shaped secretory trichomes. The colleters present among ostiolar bracts may contribute to production and composition of the ostiole exudate.

Introduction

The inflorescence of *Ficus* L. (*Moraceae*), the fig or syconium, consists of a receptacle with an apical opening, closed by intercalary bracts, designated as an ostiole (Berg & Villavicencio 2004). Such ostiolar bracts are in parallel alignment, whereas in the innermost part of the ostiole, the bracts (wall bracts) are deflexed with the apex of which is directed towards the center of the syconium.

The ostiole is a key structure in the reproductive biology of the *Ficus* because it is the access entry of pollinating agents (*Hymenoptera Agaonidae* subfamily) of flowers. In addition, it traps the wasp in the inflorescence until the moment the larvae are hatching. Such wasps depend on figs for the reproduction and development of their progeny (Pereira et al., 2000).

The morphology of the ostiole is related to that of the pollinating agent (Verkerke 1989). There are also some variations of the circumference of such apertures, as well as of the position of ostiolar bracts, which generate a selective permeability synchronized with the lifecycle of pollinating agents and the stage of development of the inflorescence (Verkerke 1986, 1987, 1988; Hao-Yuan et al. 2010).

The inflorescence of some species of *Ficus* was anatomically analyzed by Verkerke (1986, 1987, 1988, 1989) and Kravtsova & Carvajal (1955). Papers on *F. ottoniifolia* (Miq.) Miq. (Verkerke 1986) and *F. asperfolia* Miq. (Verkerke 1987) discuss the importance of the syconium structures of these species in the symbiosis between figs and fig-wasps, giving special attention to the floral structures. Verkerke (1988) discusses the relation between flower morphology and the structure of ostiolar bracts in *F. sur* Forssk. A revision of the functional anatomy of *Ficus* was done by the same author (Verkerke 1989). Although interaction between fig and fig-wasp has been well-studied, these studies do not emphasize the morphology and histochemistry of secretory structures found within the syconium.

Kravtsova & Carvajal (1995) verified that the syconium wall structure varied considerably. Based upon the degree of development and distribution of parenchyma and sclerenchyma, five different types of anatomical structure were distinguished by these authors in two sections of such genus.

Brawn & Walsingham (1917 *apud* Janzen 1979) reported that, upon the entry by a pollinating agent to the African species *F. sycomorus*, the syconium began to secrete a liquid, through the ostiole, which eventually closed up the cavity; Janzen observed the same phenomenon in two Costa Rican species, and reported that such secretion contained “antibiotic compounds” (Janzen 1979). Some species of *Ficus subg. Urostigma sect. Americana* found in Brazil show such ostiolar secretion. However, it has not yet been analyzed chemically and histochemically, and the structures responsible for its production remain unknown.

F. enormis (Mart. ex Miq.) Miq. consists of trees or shrubs mainly growing in the Atlantic Forest. Syconia are sessil and subsessil, with a pair of rounded and persistent basal bracts, a globous to elliptical green receptacle (1 or 2 cm diameter) with white spots and an ostiole with 2-3 mm diameter (Berg & Villavicencio, 2004), that is closed by three visible ostiolar bracts. It releases a pale yellow, transparent secretion. (fig. 1a).

In view of the superficial knowledge of syconium anatomy and our lack of information about both the ostiolar secretion and the histochemical aspects of the syconium, this work aims to identify these superficial secretory structures present in the inflorescence and characterize histochemically the ostiolar exudate.

Materials and methods

The study material was collected at Rio de Janeiro and Bahia States, Brazil, and identified by the senior author. Voucher specimens are deposited in the Herbarium of the Universidade Estadual de Feira de Santana (HUEFS).

Syconia samples were fixed in FAA50 for 24 h, stored in 70% ethanol (Johansen 1940), dehydrated in ethanol series, embedded in Leica Historesin (Heraeus Kulzer GmbH & Co. KG, Hanau, Wehrheim, Germany) and sectioned with steel knives at 3 µm on a Leitz 1212 rotary microtome. The sections were stained with Toluidine Blue 0.025% in McIlvaine buffer at pH 4.0 (Vidal 1977).

Histochemical tests were performed to detect the presence of mucilage using 5% tannic acid and 3% ferric chloride (Pizzolato & Lillie 1973), total proteins using 0.1% Xylidine Ponceau at pH 2.5 (Vidal 1970), lipophilic compounds using Sudan IV (Jensen 1962) and total polysaccharides, using PAS reaction (Maia 1979). Measurements and photomicrographs were obtained by use of an Olympus CX 21 light microscope (Olympus America Inc., Centre Valley, PA, USA) with digital image acquisition system.

Results

The ostiole of *F. enormis* produces a yellowish crystalline secretion that may be found in a solid state, covering said structure, in herbalized matter or in the field (Figure 1a). The three most external pairs of ostiolar bracts are positioned parallel to each other, whereas the most internal ones are progressively inclined towards the center of the syconium in a cone shaped arrangement, following the curve of the surface they are inserted in. They are elongated, "V" shaped in transversal section, and with the abaxial surface directed to the interior of the syconium (fig. 1b).

The anatomical structure of the bracts varies according to their position in the syconium ostiole. This permitted the classification of *F. enormis* bracts into three groups: Three pairs of bracts, forming the most external ones, are herein designated ‘secretory ostiolar bracts’, the following two pairs are named ‘transitional bracts’. Ostiolar and transitional secretory bracts are in parallel arrangement. The third group, composed of the ‘wall bracts’, is organized in a conical pattern. Besides these bracts, flower bracteoles were also analyzed. We observed a structural and functional gradient between internal non-secretory bracts and external secretory bracts (figs. 1b, h).

Secretory ostiolar bracts – The secretory ostiolar bracts have an abaxial epidermis formed by one to three anticlinally elongated cell layers, giving a palisade aspect. Such units will be called ‘trichomoids’ here~~;~~ they make up almost half the thickness of the bracts (fig. 1c, d). The internal periclinal wall and the anticlinal walls at the base of the trichomoids are relatively thin and are stained by the PAS test. However, in the middle portion of trichomoids anticlinal walls are thickened, contiguous to the cuticle, impregnated with matter that becomes intensely stained with Sudan IV (fig. 1g), and there may also be birefringent matter (figs. 1d, e). Several plasmodesmata occur in this area, interconnecting adjacent trichomoid cells (fig. 1f). The external periclinal wall is similar to the thickened anticlinal walls and even has small canals, similar to plasmodesmata, but these latter are directed towards the surface (figs. 1d, g, k). On such walls there is birefringent matter that did not stain upon any of the tests applied (figs. 1e). The cells have several vacuoles, a relatively large nucleus and cytoplasm, which becomes intensely stained with Xylidine Ponceau. Such staining is progressively more intense in the trichomoid base (fig. 1h). Approximately half of the epidermic cells contain matter that reacts positively to potassium dichromate (fig. 1i).

The mesophyll has approximately six cell layers in the thicker area of the bract and is vascularized by xylem and phloem (fig. 1c). Towards the margins, the mesophyll becomes progressively thinner and does not exist at all on the margins (figs. 1c, i). The prevailing parenchyma consists of cells containing monocrystals or druse bundles, cells containing phenolic substances, and lacticiferous cells as well (fig. 1c). Underlying both layers of epidermis, differentiated phenolic cells prevail, with phenols in peripheral position, apparently in a large colorless central vacuole. The adaxial epidermis consists of cubic cells, approx. half of which contain phenolic compounds, according to the staining reactions (figs. 1c, i). The cuticle of such cells is fine and appears solely on the external periclinal wall (fig. 1j).

Transitional ostiolar bracts – Transitional ostiolar bracts, which are more internal and also oriented parallel to each other, have a thickness similar to secretory bracts, but their trichomoids are progressively shorter and more filled with phenolic substances (fig. 1i). Small canals the external periclinal wall, containing PAS positive matter, are numerous and have a reticulate form (fig. 1k). A birefringent secretion is not noticeable on such walls. Phenolic cells underlying the epidermis are less frequent. The mesophyll and the adaxial epidermis are somewhat thicker than the respective tissues of the external bracts, but with the same number of layers. Small groups of fibers start to occur in the mesophyll (Fig. 1l).

Between the ostiolar bracts in the syconium receptacle trichomes occur that secrete heterogeneous matter, consisting of a matrix that becomes faintly stained greenish-bluish by Toluidine Blue. It contains metachromatic globular corpuscles. Trichomes are long and formed by a basal cell, a neck cell with thickened anticlinal walls and a biserial head, constituted by phenolic cells (fig. 2a).

Wall bracts – The wall bracts of the syconium are located in the internal wall of the ostiole. They have a characteristic conical arrangement; a "V" shape in the cross section and their abaxial epidermis is not constituted by trichomoids (fig. 2b, c). This epidermis is, therefore, formed by large slightly anticlinally elongated cells which are staining phenolic-positive (fig. 2b). The external periclinal wall is thick, with birefringent (fig. 2d) and stratified aspect, being strongly PAS positive (fig. 2c), and metachromatic with Toluidine Blue (fig. 2b). Differing from parallel bracts, there are no canals in this wall. Anticlinal and internal periclinal walls are thin (fig. 2c).

The mesophyll consists almost entirely of fibers, with a few parenchymatic cells containing prismatic crystals or cluster crystals (fig. 2d). It is vascularized by collateral vascular bundles, with the central ones being thicker (fig. 2c).

The adaxial epidermis cells have an isodiametric shape in cross section. They are smaller than those of the abaxial epidermis, and very few are staining phenolics-positive (figs. 2b, c). Cell walls follow the same pattern described with regard to the abaxial epidermis, where internal periclinal and anticlinal ones are thin, and the external periclinal one is thicker, but not as much as in the case of the abaxial epidermis (fig. 2c). Both epidermis have thin cuticles, restricted to the surface of periclinal walls.

Floral bracteoles – Floral bracteoles (fig. 2e), as well as sepals (fig. 2f) are anatomically similar to wall bracts, but smaller, with the external periclinal wall of the phenolic epidermis being less thick and the mesophyll less fibrous. The sepals have no fibers.

Among the flowers, trichomatous colleters, consisting of a basal cell, a neck cell, narrower than the head, with thickened anticlinal walls, and a head with one to eight cells in two series, are inserted in the inflorescence wall (figs. 2g-h), as well as in the floral receptacle (figs. 2f, i-k). It has four to eight phenolic cells (fig. 2i). Only one of the samples analysed had such trichomes covered with secretion. As they were found on the inflorescence wall, the secretion was heterogeneous (fig. 2i), similar to that seen near the trichomes found among the ostiolar bracts (fig. 2a). Staining with Toluidine Blue showed the spherical droplets present in the secretion to be metachromatic, amalgamated by a homogeneous fraction faintly colored light blue (fig. 2g). Such droplets give a positive result when PAS-stained (fig. 2h).

The secretion produced by floral colleters fills the hypsophyll-subtended internal space of the inflorescence buds (figs. 2j, k). It has a relatively homogenous aspect and became intensely stained with Toluidine Blue, but without any metachromasia, changing to a color similar to the content of trichome heads and phenolic cells of sepals. The secretion also reacted positively to PAS (fig. 2j) and potassium dichromate staining (fig. 2k).

Discussion

Organization and specialization of ostiolar bracts – The structural analysis of *F. enormis* ostiole revealed a complex structure with three different types of bracts, one specialized in secretion, the other apparently specialized in mechanical functions. Among these types there are bracts with transitional characteristics. Presence of a glandular epidermis at the ostiolar bracts was also reported in *F. ottoniifolia* (Verkerke 1986) and compared with extrafloral nectaries of *Aphelandra* (Acanthaceae) (Verkerke 1989). However, in *F. asperifolia* (Verkerke 1987) and *F. sur* (Verkerke 1988) bracts were considered to have no indication of secretion activity.

The *F. enormis* secretory ostiolar bracts are characterized by an abaxial epidermis, one to three cells thick, the cell content of which stains intensely with Xylidine Ponceau, a dye used for detecting proteins (Cortelazzo & Vidal 1991). This indicates high metabolic activity. Therefore, one may infer that these cells are the greatest source of the ostiolar secretion.

The position of secretory epidermis cells in anticlinal series of one to three, but not constituting continuous strata with adjacent epidermal cell series, in addition to the fact that they are separated by a cuticle deeply extending into anticlinal direction, gives a first impression that theses series are uniseriate glandular trichomes. Consequently, we named them trichomoids. Such structures are morphologically similar to the illustration presented by Verkerke (1986) with regard to the secretory epidermis on the border of the ostiole (ostiolar lip) of *F. ottonifolia*, but being absent in the ostiolar bracts there. A net comprised of long ramified plasmodesmata connects the adjacent trichomoid cells across the cuticle barriers, and there are similar structures on the terminal periclinal wall towards the periphery, which are probably ectodesmata. However, a safe assertion about this would need investigations of trichomoids at the ultrastructural level.

Among exogenous secretory structures, there are some in which the epidermis is the main secretory tissue, which may or may not be subtended by a modified subsecretory parenchyma (Fahn 1979). This is the case in osmophores (Ascensão et al., 2005), elaiophores (Pansarin et al. 2009), several extra-floral nectaries (Lersten & Brubaker 1987; Subramanian & Inamdar 1989; Delgado et al. 2011) and in some floral nectaries (Leitão et al. 2005), in colleters (Thomas 1991), salt glands (Barhoumi: et al. 2008) digestive glands (Robins& Juniper 1980) and secretory trichomes in general (Fahn 1988, Ascensão et al. 1999).

The secretory epidermis of the above-mentioned structures rather often has the form of papillae (Ascensão et al. 2005) trichomes (Leitão & Cortelazzo 2008) or modifications of them, originating in more complex protodermal structures (Thomas & Dave 1992). A very common condition of the non-trichomatous secretory epidermis is that cells are elongated in the anticlinal direction, arranged as a kind of palisade parenchyma (Wilkinson 2007; Pansarin et al. 2009). Some of which may lack periclinal divisions (Thomas et al. 1989). The abaxial epidermis of secretory bracts of *F. enormis* would fit the latter case, with the particularity of organizing itself as structures herein designated as trichomoids. These bracts are vascularized with phloem and xylem, situated few cells below the secretory epithelium. This indicates the supply of precursors of the secreted matter.

Composition of the secretion – In this study it was not possible to identify, by histochemical methods, the matter secreted by bracts. However, translucent and birefringent substances were visualized on the surface of secretory bracts and among the trichomoids. During processing of the samples, some ethanol-soluble matter was probably removed. The remaining matter did not react positively to PAS, demonstrating that it was not a polysaccharide. Neither did it become colored with Toluidine Blue at pH4.0, showing that it did not have significant amounts of anionic components (sulphates, nitrates, carbonates, carboxyl) under such a low pH. In view of its aspects and insolubility in water and alcohol, it may be a resin (Ramaya & Bahadur, 1968), but one cannot be certain about this, merely based on the data obtained here.

Wall bracts – The wall bracts following in proximal direction the secretory and transitional bracts are characterized by an abaxial epidermis consisting of large phenolic cells, i.e., positively staining upon a test with potassium dichromate. Their mesophyll, consisting almost entirely of lignified cells, provides rigidity and, consequently, a mechanical role with regard to permeability phenomena and ostiole selectivity can be suggested.

Verkerke (1987) reported bract movements caused by loss of turgescence in the *F. asperifolia* ostiole. In *F. enormis*, the wall bracts are very asymmetrical in the dorsiventral cross section, due to the large abaxial epidermis cells. Bulliform cells, responsible for the rolling and the opening of the foliar blade, due to the differences in turgor pressure are common in many plants (Dickison 2000). As bract movements also occur in *F. enormis*, as reported with regard to *F. asperifolia*, it is probable that the large epidermis cells of *F. enormis* syconium wall bracts act similarly to bulliform cells.

The external periclinal wall of these cells, although thick, seems to be able to bending. The mesophyll, on the other hand, seems to be more rigid, albeit malleable to a certain extent.

Floral colleters – Colleters are structures that secrete a sticky matter (Thomas 1991) that may contain carbohydrates (Thomas & Dave, 1989), and proteins (Klein et al. 2004); Gonzalez & Tarragó 2009), and among those, enzymes (Vieira et al. 2006) and fatty matter. The secretion is, therefore, mucilaginous or resiniferous (Thomas 1991). They are associated with the protection of young organs, maintaining hydrated meristem (Thomas 1991) and may also act against pathogenic attacks (Klein et al. 2006). Colleter secretion may function as lubricant~~s~~ (Leitão & Cortelazzo 2008) and can in some cases establish a symbiotic relation with bacteria (Lersten 1974).

Although also may designate trichomes (Esau 1977), the word colleter is generally applied to such secretory emergences found in several families of dicotyledons (Thomas 1991). In an increasing number of recent studies (Paiva & Machado 2006; Leitão & Cortelazzo 2008; Paiva 2009, Mayer et al. 2011) more specifically in view of the occurrence of colleters in young structures and the function of protecting such organs, the word colleter has also been applied to structures of protodermal origin.

The secretory trichomes described in this work are another example of trichomatous colleters with a mucilaginous secretion, indicated by their positive reaction to PAS and their sticky aspect. They are all morphologically similar to each other, having the form of capitate trichomes with a bi-seriated head and containing phenolic compounds. Trichomes similar to those described herein were reported in various locations of *F. ottonifolia* syconium (Verkerke 1986), but their functional aspect was not emphasized there. The presence of abundant secretion between the sepals of flower buds suggests that their function is to protect these latter against desiccation. The secretion may even act as a lubricant facilitating sliding of floral segments against each other during the expansion growth of the sycomium.

Colleters on the inner wall of the syconium, occurring among the flower buds may have a similar function. Verkerke (1986) reported pluricellular hairs inside the syconial wall of *F. ottonifolia*, related to the secretion of latex-like fluid, which fills the syconium cavity. Although trichomes have not been illustrated in that study, we believe they are structures homologous to the *Ficus enormis* wall colleters. The colleters present among ostiolar bracts may contribute to the final composition of the ostiole secretion, which could be a mixture of the matter produced by bracts and that produced by colleters. They could also lubricate ostiolar bracts during opening and closing of the ostiole.

The data obtained in this study, compared to data in the literature, show the complexity of a mechanical and secretory system not very well known up until now. Further detailed studies are needed on the ontogenesis, nature and secretion mechanism of the cells and tissues of the fig syconium as well of the movements of ostiolar structures.

Fig. 1. Syconia ostiole of *Ficus enormis* in a surface view (*a*), paradermal (*f*) and longitudinal sections (*b-e, g-l*). (*a*) A general view of the syconia showing the secretion over ostiole (arrows). (*b*) General view of the bract organization in the ostiole. PAS. (*c*) Detail of the superficial bract. Toluidine Blue. (*d*) Detail of the trichomoids in the superficial bract, showing canals (arrows) in the cuticle. PAS. (*e*) Like (*d*), but under polarization, showing birefringent material between and over trichomoids (arrows). (*f*) Trichomoids in transversal section in a superficial bract, with numerous plasmodesmata connecting them (arrows). A fungus hypha (asterisk) occurs over the bract. PAS. (*g*) Trichomoids of a secretory bract (not the superficial one), showing canals (arrows) in the cuticle. PAS/Sudan IV. (*h*) General view of parallel bracts. Xylidine Ponceau. (*i*) General view of ostiole bracts. Potassium dichromate. (*j*) Detail of adaxial epidermis of superficial bract, showing thin cuticle (arrow). Sudan IV. (*k*) Detail of apices of abaxial epidermal cells in a transitional bract, showing numerous canals in reticulate aspect (arrows) in the cuticle. Toluidine Blue. (*l*) General view of the bract in (*k*), with some fibers in the mesophyll (arrows). Toluidine Blue. Legends: ae - adaxial epidermis; fb- floral bud; lt- laticifer; sb- secretory bracts; tb- transitional bracts; vb- vascular bundle; wb- wall bracts. Scale bars are in micrometers.

Fig. 2. Internal bracts and colleters in ostiole syconia of *Ficus enormis*. (*a*) Trichomatous colleters inserted at the ostiole between the parallel bracts, partially embedded in the secretion. Toluidine Blue. (*b*) Transversal section of a funnel bract. Toludine Blue. (*c*) Detail of transversal section of a funnel bract. PAS. (*d*) Like (*c*), but under polarization, showing a cluster cristal (arrow) and birefringence in external wall of abaxial epidermis (asterisk). (*e*) Longitudinal section of a bracteole. PAS. (*f*) Longitudinal section of a floral bud showing colleters (arrow). Toluidine Blue. (*g*) Detail of basis of receptacular colleters embedded in secretion. Toluidine Blue. (*h*) Neck cell and basal half of trichomatous colleter at receptacle, with globular fraction of secretion positive to PAS. (*i*) Detail of colleters in (*f*), without secretion. (*j*) Longitudinal section of a floral bud with copious secretion (asterisk) cumulated inside calice, showing colleter parts (arrows). PAS. (*k*) Detail of floral colleter region with copious secretion (asterisk). Potassium Dichromate. Legends: pb- parallel bract; se- sepal. Scale bars are in micrometers.

Acknowledgements

We acknowledge the Dra. Bárbara Sá Haiad (MN-UFRJ) for his valuable assistance with literature and suggestions to improve the manuscript. We also greatly appreciate critical comments from Dr. Luciano Paganucci de Queiroz (UEFS), Dr. Pedro Carauta (MN-UFRJ) and Dra. Simone de Pádua Teixeira (FCFRP - USP). A.F.P.M. was supported by the CAPES fellowship.

References

Ascensão, L; Mota, L. and Castro, M. M. 1999 Glandular trichomes on the leaves and flowers of *Plectranthus ornatus*: morphology, distribution and histochemistry. Ann. Bot. 84: 437-447.

Ascensão, L., Francisco, A., Cotrim, H. & Pais, M.S. 2005 Comparative structure of the labellum in *Ophrys fusca* and *O. lutea* (Orchidaceae). Amer. J. Bot. 92: 1059-1067.

Barhoumi, Z.; Djebali, W.; Abdelly, C.; Chaïbi, W. and Smaoui, A. 2008 Ultrastructure of *Aleuropus littoralis* leaf salt glands under NaCl stress. Protoplasma 233: 195-202.

Benes, K. 1964 Detection of lipids in plant meristematic cell with aid of Sudan black staining. Biol. Plant. 6: 142–151.

Berg, C.C., Vilaviccencio, X. 2004 Taxonomic studies on *Ficus* (Moraceae) in the West Indies, extra-Amazonian Brazil, and Bolivia. Ilicifolia 5: 1-177.

Brundret,t M.C., Kendrick, B., Peterson, C.A. 1991 Efficient lipid staining in plant material with Sudan Red 7B or Fluoral Yellow 088 in polyethylene glycol-glycerol. Biotech. Histochem. 66: 111-116.

Cain, A.J. 1947 The use of Nile blue in the examination of lipids. Quart. J. Miscroscop. Sci. 88: 383-392.

Carauta, J.P.P. 1989 Ficus (Moraceae) no Brasil: Conservação e Taxonomia. Albertoa 2: 1-365.

Cortelazzo, A. L. and Vidal, B. C. 1991 Soybean seed proteins: detecton *in situ* and mobilization during germination. Rev. Bras. Bot. 14: 27-33.

David, R., Carde, J.P. 1964 Coloration différentielle dês inclusions lipidique et terpeniques dês pseudophylles du Pin maritime au moyen du reactif Nadi. C. R. Acad. Sci. Paris 258: 1338-1340.

Delgado, M. N.; Silva, L. C.; Báo, S. N.; Morais, H. C. and Azevedo, A. A. 2011 Distribution, strucutural and ecological aspects of the unusual leaf nectaries of *Calolisianthus* species (Gentianaceae). Flora 206: 676-683.

Dickison, W. C. 2000 Integrative plant anatomy. Academic Press, San Diego.

Esau, K. 1977 Anatomy of seed plants. John Wiley & Sons, New York.

Fahn, A. 1979 Secretory tissues in plants. Academic Press, London.

Fahn, A. 1988 Secretory tissues in vascular plants. New Phytol. 108: 229-257.

Galil, J., Eisikowitch, D. 1968 On the pollination of Ficus sycomorus in East Africa. Ecology 49: 259-269.

Gonzalez, A.M.,Tarragó, J.R. 2009 Anatomical structure and secretion compounds of colleters in nene *Ilex* species (Aquifoliaceae) from southern South America. Bot. J. Linn. Soc. 160: 197-210.

Hao-Yuan, H.; Li-Ming, N.; Guang-Chang, M.; Yue-Guan, F.; Zheng-qiang, P. and Da-Wei, H. 2010 Permeability of receptive fig fruits and its effects on the re-emergence behaviour of pollinators. Ecological Entomology 35: 115-125.

Janzen, D.H. 1979 How to be a Fig. Annu. Rev. Ecol. Syst. 10: 13-51.

Klein, D. E.; Gomes, V. M.; Silva-Neto, S. J. and Cunha, M. (2004 The structure of colleters in several species of *Smira* (Rubiaceae). Ann. Bot. 94: 733-740.

Kravtsova, T.I., Carvajal, S. 1995 Syconium wall structure in mexican species of genus *Ficus* (Moraceae) Bot. Zh. 80: 42-55.

Leitão, C. A. E. and Cortelazzo, A. L. 2008 Structural and histochemical characterisation of the colleters of *Rodriguezia venusta* (Orchidaceae). Austral. J. Bot. 56: 161-165.

Leitão, C. A. E.; Meira, R. M. S. A.; Azevedo, A. A.; Araújo, J. M.; Silva, K. L. F. and Collevatti, R. G. 2005 Anatomy of the floral, bract, and foliar nectaries of *Triumfetta semitriloba* (Tiliaceae). Canad. J. Bot. 83: 279-286.

Lersten, N. R. 1974 Morphology and distribution of colleters and crystals in relation to the taxonomy and bacterial leaf nodule symbiosis of *Psichotria* (Rubiaceae). Amer. J. Bot. 61: 973-981.

Lersten, N. R. and Brubaker, C. L. 1987 Extrafloral nectaries in Leguminosae: review and original observations in *Erythrina* and *Mucuna* (Papilionoideae; Phaseoleae). Bull. Torrey Bot. Club 114: 437-447.

Machado, A.F.P., Carrijo, T.T., Vianna Filho, M.D.M., Santos. O. A. 2007 *Ficus* (Moraceae): Caracteres de importância taxonômica e guia para coleta. Albertoa 30: 225-228.

Maia, V. 1979 Técnica histológica. Atheneu, São Paulo.

Mayer, J. L. S.; Cardoso-Gustavson, P. and Appezzato-da-Glória, B. 2011 Colleters in monocots: new record for Orchidaceae. Flora 206: 185-190.

Mello-Filho, L.E., Neves, L.J., Carauta, J.P.P., Diaz, B.E. 2001 Morfologia de certos sicônios de *Ficus* (Moraceae). Albertoa 3, 17-18.

Paiva, E. A. 2009 Occurrence, structure and functional aspects of the colleters of *Copaifera langsdorffii* Desf. (Fabaceae, Caesalpinioideae). C. R. Biologies 332, 1078-1084.

Paiva, E. A. S and Machado, S. R. 2006 Ontogenesis, structure and ultrastructure of *Hymenaea stigonocarpa* (Fabaceae: Caesalpinioideae) colleters. Rev. Biol. Trop. 54, 943-950.

Pansarin, L. M.; Castro, M. M. and Sazima, M. 2009 Osmophore and elaiophores of *Grobya amherstiae* (Catasetinae, Orchidaceae) and their relation to pollination. Bot. J. Linn. Soc. 159, 408-415.

Pereira, R.A.S., Semir, J., Menezes-Junior, A.O. 2000 Pollination and other biotic interactions in figs of *Ficus eximia* Schott (Moraceae) Revista Brasil. Bot. 23: 2, 217-224.

Pizzolato, T.D., Lillie, R.D. 1973 Mayer's tannic acid-ferric chloride stain for mucins J. Histochem. Cytochem. 21, 56–64.

Ramaya, N. and Bahadur, B 1968 Morphology of the "squamellae" in the light of their ontogeny. Curr. Sci. 37, 520-522.

Robins, R. and Juniper, B. E, 1980 The secretory cycle of *Dionaea muscipula* Ellis. New Phytol. 86, 279-296.

Subramanian, R. B. and Inamdar, J. A. 1989 The structure, secretion and biology of nectaries in *Tecomaria capensis* Thunb (Bignoniaceae). Phytomorphology 39, 69-74.

Thadeo, M., Meira, R.M.S.A., Azevedo, A.A., Araújo, J.M. 2009 Anatomia e histoquímica das estruturas secretoras da folha de *Casearia decandra* Jacq. (Salicaceae) Revista Brasil. Bot. 32:2, 329-338.

Thomas, V. 1991 Structural, functional and phylogentic aspects of the colleter. Ann. Bot. 68, 287-305.

Thomas, V. and Dave, Y. 1989 Histochemistry and senescence of colleters of *Allamanda cathartica* (Apocynaceae). Ann. Bot. 64, 201-203.

Thomas, V. and Dave, Y. 1992 Structure and biology of nectaries in *Tabebuia serratifolia* Nichols (Bignoniaceae). Bot. J. Linn. Soc. 109, 395-400.

Thomas, V., Dave, Y. and Menon, A. R. S. 1989 Anatomy and histochemistry of colleters in *Roupelia grata* (Apocynaceae). Nord. J. Bot. 8, 493-496.

Verkeke, W. 1987 Syconial anatomy of *Ficus asperifolia* (Moraceae), a gynodioecious tropical fig. Proc. K. ned. Akad. Wet. C 90, 461-492.

Verkeke, W. 1986 Anatomy of *Ficus ottoniifolia* (Moraceae) syconia and its role in the fig-fig wasp symbiosis. Proc. K. ned. Akad. Wet. C 89, 443-469.

Verkeke, W. 1988 Sycone morphology and its influence on the flower structure of *Ficus sur* (Moraceae). Proc. K. ned. Akad. Wet. C 91, 320-344.

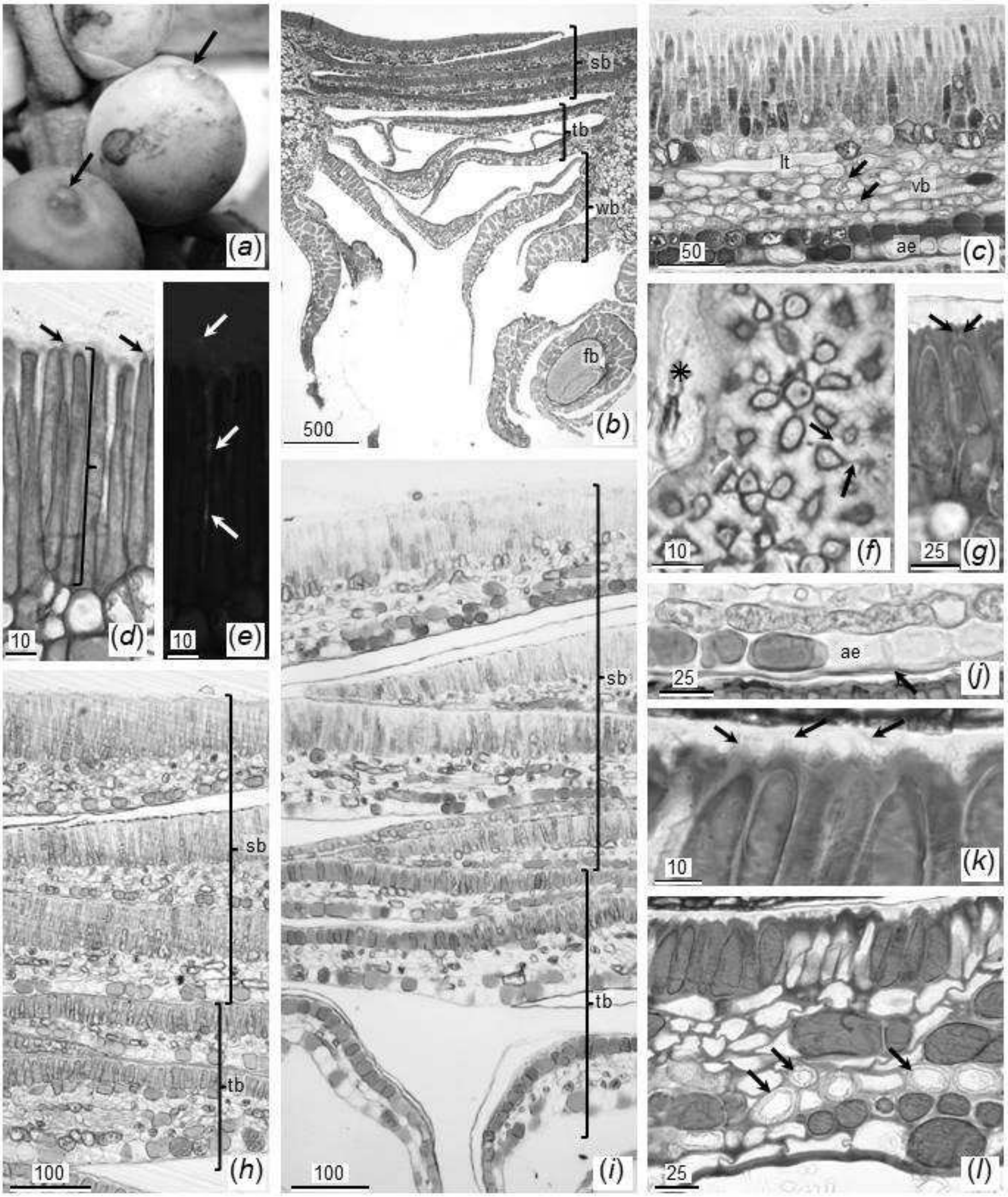
Verkeke, W. 1989 Structure and function of the fig. Experientia 45, 612-622.

Vidal, B.C. 1970 Dichroism in collagen bundles stained with xylidine ponceau 2R. *Ann. Histoch.* 15, 289–296.

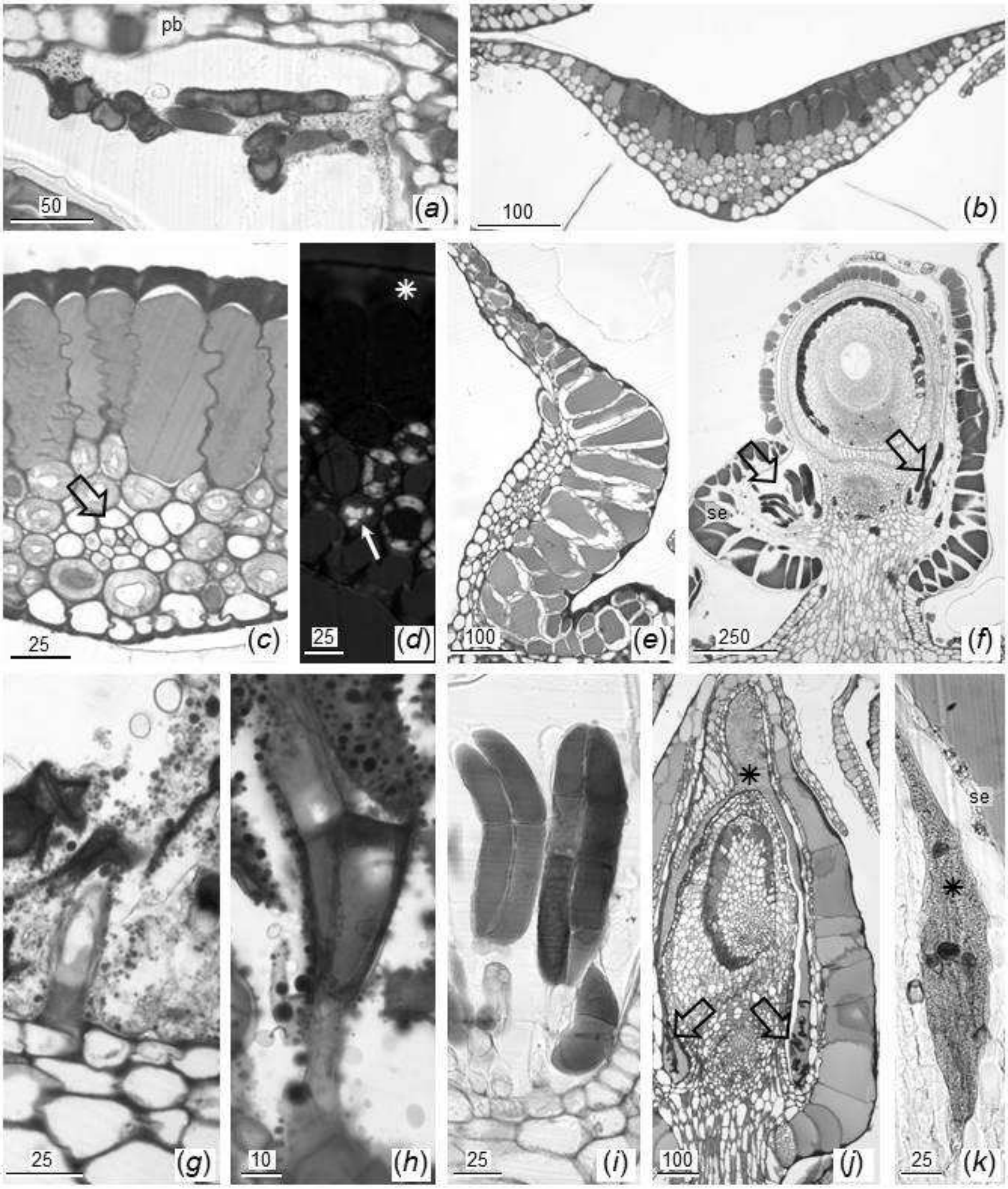
Vidal, B.C. 1977 Acid glycosaminoglycans and endochondral ossification: microespectrophotometric evaluation and macromolecular orientation. Cell. Molecular Biology 22, 45–64.

Vieira, F. A., Cunha, M., Klein, D. E., Carvalho, A. O. and Gomes, V. M. 2006 Purification and characterization of β-1, 3-Glucanase from the secretion of *Smira glaziovii* colleters (Rubiaceae). Braz. Arch. Biol. Technol. 49, 881-888.

Wilkinson, H. P. 2007 Leaf teeth in certain Salicaceae and 'Flacourtiaceae'. Bot. J. Linn. Soc. 155, 241-256.


(a)
sb
tb
wb
fb
500
(b)
lt
vb
ae
50
(c)
10
(d)
10
(e)
10
(f)
25
(g)
ae
25
(j)
10
(k)
sb
tb
100
(h)
sb
tb
100
(i)
25
(l)

1



2

CAPÍTULO 6

From Atlantic forest to the all Americas: Biogeographical history and divergence times of Neotropical *Ficus* (Moraceae)

Anderson Ferreira Pinto Machado[1*] Nina Rønsted[2] Sam Bruun-Lund[2] Rodrigo Augusto Santinelo Pereira[3], Luciano Paganucci de Queiroz[1].

[1]Programa de Pós-graduação em Botânica, Universidade Estadual de Feira de Santana, Av. Transnordestina s/n, Novo Horizonte, 44.036-900, Feira de Santana, BA, Brazil.
[2]Natural History Museum of Denmark, University of Copenhagen, Sølvgade 83S. DK-1307 Copenhagen K, Denmark.
[3]Departamento de Biologia/FFCLRP-Universidade de São Paulo, Av. Bandeirantes, 3900. 14040-901 - Ribeirão Preto, SP.
*Corresponding author.
E-mail address: machadoafp@gmail.com (Anderson F. P. Machado)

ABSTRACT

Ficus (Moraceae) is well diversified in the Neotropics with two lineages inhabiting the wet forests of this region. The hemiepiphytes of section *Americanae* are the most diversified with c. 120 species, whereas section *Pharmacosycea* includes about 20 species mostly with a terrestrial habit. To reconstruct the biogeographical history and diversification of *Ficus* in the Americas, we produced a dated Bayesian phylogenetic hypothesis of Neotropical *Ficus* including two thirds of the species sequenced for five nuclear regions (At103, ETS, G3pdh, ITS/5.8S and tpi). Ancestral range was estimated using all models available in Biogeobears and Binary State Speciation and Extinction analysis was used to evaluate the role of the initial habit and propagule size in diversification. The phylogenetic analyses resolved both Neotropical sections as monophyletic but the internal relationships between species in section *Americanae* remain unclear. *Ficus* started their diversification in the Neotropics between the Oligocene and Miocene. The genus experienced two bursts of diversification: in the middle Miocene and the Pliocene. Colonization events from the Amazon to adjacent areas coincide with the end of the Pebas system (10 Mya) and the connection of landmasses. Divergence of endemic species in the Atlantic forest is inferred to have happened after its isolation and the opening and consolidation of the Cerrado. Our results suggest a complex diversification in the Atlantic forest differing between postulated refuges and more instable areas in the South distribution of the forest. Finally the selection for initial hemiepiphytic habit and small to medium propagule size influenced the diversification and current distribution of the species at Neotropical forests marked by the historical instability and long-distance dispersal.

Keywords: *Americanae*; Ancestral range estimation; Biogeography; character evolution; Neotropics; *Pharmacosycea*.

1. Introduction

Neotropical rainforests are characterized by a dense canopy mainly consisting of angiosperm trees and lianas, mostly presenting entire-margined and large leaves, high abundance of leaf drip tips, large fruit and seed size, and abundant epiphytes. They occur in areas with high rainfall and temperatures and low seasonality (Gentry, 1992; Burnham & Johnson, 2004) and present higher biodiversity compared to African and Asian rainforests (Koenen et al. 2015). Explanations for the high diversity in rainforests have been subject to debate as to whether they are old or recent radiations (*e.g.* Pennington et al., 2006; Moritz et al., 2001; Antonelli and Sanmartín, 2011; Hughes et al., 2013; Hughes et al., 2015). The "museum model" of diversification (Stebbins, 1974) explains their hyper diversity as old and evolving by constant rates of diversification and low rates of extinction with relative ecological stability over a long time. Another hypothesis considers rainforest as cradles of diversification with recent and elevated speciation rates and this so-called "cradle model" gained further support with the "refuge theory" suggesting that drier climates during glacial periods caused speciation by vicariance in rainforest species (Haffer, 1969; Prance, 1982; Carnaval & Moritz, 2008).

Recent literature provides examples of old radiations in rainforests such as the Malpighiales (Davis et al. 2005), which diversified at 112-94 Mya followed by adaptations of wet forests. Ancient diversification and lineage accumulation are also found in Annonaceae (Couvreur et al., 2011; Chatrou et al., 2012; Pirie & Doyle, 2012), Arecaceae (Couvreur et al., 2011), and Menispermaceae (Wang et al., 2012).

On the other hand, examples of species-rich clades in rainforests lending support to the cradle model with young radiations in rainforests are well documented in rainforest specialist taxa such as *Inga* (Richardson et al., 2001), *Guatteria* (Annonaceae, Erkens et al. 2007), Gesneriaceae (Perret et al., 2013), *Astrocaryum* (Arecaceae, Roncal et al., 2013), *Attalea* (Arecaceae, Freitas et al., 2016), and *Philodendron* (Araceae, Loss-Oliveira et al., 2016). The accumulation of examples of rainforests groups supporting both the museum and the cradle models suggests the models are not mutually exclusive (Pennington et al., 2015) and consequently a recent hypothesis suggests that the diversity of rainforests is a result of recent radiations from a large stock of higher-level taxa (Koenen et al., 2015).

In addition to the complex diversification of both ancient and recent groups, the wet forest lineages present other characteristics such as lack of geographic structure (Gustaffson and Bittrich, 2003; Erkens et al., 2007; Richardson et al., 2001; Torke and Schaal, 2008) reflecting the composition of these communities having been shaped through long-distance dispersal (Pennington and Dick, 2004; Hughes et al., 2013). In some cases, specific "key innovations" triggering speciation can be identified as for example in ferns, where the diversification in the Cenozoic was apparently linked to evolution of epiphytism (Schuettpelz & Pryer, 2009)

Ficus L. with approximately 750 species distributed in tropical and subtropical regions worldwide is one of the most important plant genera in lowland tropical rainforests with high alpha-diversity (Harrison, 2005). Neotropical *Ficus* appear clearly separated into a speciose section *Americanae* (Miq.) Corner (~ 120 spp.) consisting of hemi-epiphytic stranglers and section *Pharmacosycea* (Miq.) Benth. & Hook f. (~ 20 spp.) including mostly large free-standing trees (Berg and Simonis, 1981; Berg, 1989). According to previous studies (Rønsted et al., 2005; Rønsted et al., 2007; Rønsted et al., 2008; Cruaud et al., 2012), both Netropical sections are monophyletic. Whereas section *Pharmacosycea* is thought to be sister to the remainder of *Ficus* (Herre et al., 1996; Rønsted et al., 2005; 2008; Cruaud et al., 2012; Bruun-Lund, et al. 2017), section *Americanae* is closely related to the African section *Galoglychia* (Gasp.) Endl. and other primarily Asian and Australasian monoecious hemiepithytes of sections *Conosycea* (Miq.) Corner and *Malvanthera* Corner.

The morphological variation, complexity, and the massive diversification of *Ficus* in the Neotropics make this genus an important element for understanding diversification in species rich biomes such as the South American rainforests. Geological and paleoclimatic events in South America resulted in different responses in Amazonia (AM) and Atlantic forests (AF) and the characterization of the biogeographical patterns of a diverse and ecologically important group like *Ficus* could shed light on the complex diversification in the two major blocks of wet forests in the Neotropics forest.

Amazonian *Ficus* show great morphological diversity compared to Atlantic forest elements. The Amazonian figs comprises about 50 species of large and small trees with a great variety of leaves and syconia (propagule) sizes, but endemism in this area is low and most Amazonian species are also found in the Antilles, Mesoamerica and North

America. Some taxa present a disjunct distribution with the Atlantic rainforest (e.g. *F. castellviana* Dugand, *F. mariae* C.C.Berg et al., *F. pulchella* Schott, *F. trigona* L.f.) another ones are widely distributed in the Americas (e.g. *F. gomelleira* Kunth, *F. obtusiuscula* (Miq.) Miq., *F. obtusifolia* Kunth. *F. pertusa* L.f. and *F. citrifolia* Mill.).

With about 35 *Ficus* species (Carauta, 1989; BFG, 2015) the Atlantic forest constitute a center of endemic *Ficus* species (e.g. *F. bahiensis* C.C.Berg & Carauta, *F. cestrifolia* Schott, *F. hirsuta* Schott, *F. enormis* Mart. ex Miq., *F. luschnathiana* (Miq.) Miq., and *F. guaranitica* Chodat) in the Neotropics (Carauta, 1989; Berg and Villavicencio, 2004). Some species with records in the Atlantic forest also occur in adjacent areas as for example *F. holosericea* Schott, occurring in Caatinga, and *F. lagoensis* C.C.Berg & Carauta present also in Cerrado.

Many studies of *Ficus* on a more global scale have focused on breeding system evolution (Weiblen 2000); infrageneric classification (Rønsted et al. 2008; Xu et al. 2011), or elucidation of the mutualism and coevolution between figs and fig-pollinating wasps (Herre el al., 1996; Jousselin et al. 2003; Weiblen, 2004; Rønsted et al., 2005; Jackson et al., 2008; Cruaud et al., 2012). Some studies have also attempted to elucidate the biogeographical origins of the family Moraceae (Zerega et al., 2005); or particular sections in Africa [sect. *Galoglychia* (Gasp.) Endl. (Rønsted et al., 2007)]; Australia and New Guinea [sect. *Malvanthera* Corner (Rønsted et al., 2008b)], and subsect. *Urostigma* (Gasp.) Berg in Africa, Asia, and Australia (Chantarasuwan et al., 2015).

In spite of the diversity and importance of *Ficus* in the Neotropics, only one study has recently attemped to clarify the phylogeny of the smaller section *Pharmacosycea* (Pederneiras et al., 2015b), but no published study to date has focused on the phylogeny and diversification of the megadiverse section *Americanae*. Consequently, little is known about the origin and diversification of Neotropical *Ficus* in general and this could improve our understanding of diversification patterns and processes in the tropical forests. About a half of the fig species are hemiepiphytic woody plants (Berg and Corner, 2005; Harrison 2005), a growth habit that could have evolved independently three times in *Ficus* (Jousselin et al., 2003), and which may have influenced the ability to diversify and colonize new areas in neotropical rainforests.

Likewise, the dispersal ability of propagules may have influenced the diversification of *Ficus* in the Neotropics. Long distance dispersal occurred in many groups of plants especially in South America (Renner, 2004) and probably resulted in an increase the number of species on the continent despite the competition between immigrants and autochthonous species (Antonelli and Sanmartín, 2011). Two major morphofunctional propagule types are found in Neotropical *Ficus*. The mostly bat-dispersed type is characterised by larger, green or yellow syconia, which provide little color contrast against the background, but instead produce many volatile compounds and large peduncles evident among the leaves (Lomáscolo et al. 2008; Lomáscolo et al. 2010). In contrast, the mostly bird-dispersed figs are small syconia with bright colors (red, orange or purple, never green) at maturity, growing between the foliage and procucing few volatile compounds (Lomáscolo et al., 2010). Figs with intermediate traits may be dispersed both by bats and birds (Lomáscolo et al., 2010). Species with small and intermediate propagules are expected to have higher dispersal range/efficiency due the bird dispersal effectiveness (Traveset, 1998; Jacomassa and Pizo, 2010; Lomáscolo et al., 2008; 2010).

A biogeographical analysis of *Ficus* in a phylogenetic context provides the opportunity to test the diversification patterns of the South American rainforests. More specifically, correlation with the main biogeographical events that might have influenced the diversification of Neotropical *Ficus* can be tested including: (1) Orogeny: the uplift of the northern part of the Andes; Neotectonic changes in the Atlantic forest; (2) Hydrological changes such as the Pebas System (24-10 mya) and the change of flow in the Amazon River; (3) The closure of the Panama Isthmus; (4) The Plio-Pleistocene refuges; (5) The formation of open and/or dry vegetation across South America isolating Amazon and Atlantic forest (Antonelli et al. 2009; Antonelli and Sanmartín, 2011; Bacon et al., 2015; Hoorn et al., 2010; Hughes et al. 2013; Pennington et al. 2004). Accordingly, the aim of this study were to obtain a dated phylogenetic hypothesis for Neotropical *Ficus* based on comprehensive sampling in order to test phylogenetic and biogeographical hypotheses. Specifically, we ask: (1) What is the most likely biogeographical hypothesis of evolution of *Ficus* in Neotropics? (2) When and where did the most recent common ancestor (MRCA) of both sections of Neotropical figs originate? (3) How did Amazonian geological events influence the divergence history of *Ficus*? (4) Can Atlantic forest biogeographical scenarios explain the divergence history of *Ficus*? (5) Could the initial growth habit and the propagule traits have influenced diversification rates?

2. Material and methods

2.1. Sampling

To assess the biogeographical history and diversification of *Ficus* in the Neotropics we assembled the largest and most representative data matrix to date including 66 species of section *Americanae* and 11 species of section *Pharmacosycea* (more than 65% of the Neotropical *Ficus*). Sampless were collected in the field or from herbarium specimens and a list of material and vouchers is included in Appendix A. We produced 178 new sequences for *Ficus* (39 of At103, 40 of ETS, 31 of G3pdh, 34 of ITS, and 34 of tpi) expanding the sampling of Neotropical species available in GenBank for phylogenetic studies considerably from 31 species included in Cruaud et al. (2012) to 77 species (65%) included in the present study. Our sampling comprises species from all areas of the Americas including 28 of approximately 50 species found in Amazonia and 30 of 35 species of the Atlantic Rainforest (see Carauta, 1989; BFG, 2015; Berg and Villavicencio, 2004). *Antiaropsis decipiens, Castilla elastica* and *Sparratosyce dioica* representing Castilleae, the sister tribe of *Ficus*, were used as outgroups following previous studies (Rønsted et al., 2005; Zerega et al., 2005).

2.2. DNA extraction, amplification, and sequencing

Total genomic DNA was extracted using the CTAB protocol of Doyle and Doyle (1987) from 15-30 mg of silica dried leaf-fragments or herbarium material. Since plastid regions provide little phylogenetic information within *Ficus* (Rønsted et al., 2008a), phylogenetic studies of *Ficus* have focused on the more informative single- or low copy nuclear regions. For the present study, we sequenced five nuclear markers: the Internal Transcribed Spacer including the coding (ITS) region, the External Transcribed Spacer (ETS) region, the Glycerol-3-phosphate dehydrogenase gene (*G3pdh*), the Magnesium-protoporphyrin IX monomethyl ester cyclase (*At103*) and the Triosephosphate isomerase gene (*Tpi*).

We chose the ITS, ETS and the G3pdh regions because they have provided good resolution of *Ficus* in previous studies (Rønsted et al. 2008). Additionally, At103 and Tpi were selected because they have provided both good amplification and resolution in other studies (Strand et al., 1997; Li et al., 2008).

Amplification of ITS, ETS and *G3pdh* followed Rønsted et al. (2008). Amplification of *At103* followed Li et al. (2008) except that 1 uL each of DMSO and BSA were added to all reactions. Amplification of *Tpi* was performed in 25 uL reactions adding 0.5 uL DNA to a reaction mixture of 1x Buffer, 1.5 mM $MgCl_2$, 0.2 mM of each dNTP, 0.5 mM of each primer, 1U of Taq polymerase (VWR international, Haasrode, Belgium), 1 uL of BSA and DMSO. The PCR protocol for *Tpi* consisted of 2 min at 95 °C, followed by 35 cycles of 1 min at 95 °C, 1.30 min at 46.5 °C, 2 min at 72 °C and a final extension for 9 min at 72 °C. PCR products were purified using a Qiagen PCR purification kit (Qiagen Inc., Valencia, California, USA) except for PCR products of *Tpi* which were purified using ExoSAP-IT® (Affymetrix UK Ltdn, High Wycombe, UK), following the manufacturers protocols.

PCR products were sequenced using Big Dye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems, Austin, Texas, USA) and purified sequencing products were run on an AB3130x1 Genetic Analyzer (Applied Biosystems/HITACHI, Tokyo, Japan) at the Laboratório de Sistemática Molecular de Plantas of the Universidade Estadual de Feira de Santana (LAMOL/UEFS) or at the National Sequencing Centre, Natural History Museum of Denmark. Forward and reverse sequences were edited and assembled in Geneious V. 7 to V. 8 (http://www.biomatters.com) or with Sequencer 4.8^{TM} software (Gene Codes, Ann Arbor, MI, USA). Alignments were conducted using MUSCLE (Edgar, 2004) with default settings and were inspected in Mesquite (Maddison and Maddison, 2015).

2.3 Phylogenetic analyses

Despite some missing data all major clades are represented by all DNA regions sampled. Prior to analysis, the best fitting model of sequence evolution was determined using jModeltest v. 2.1.7. (Darriba et al. 2012) following the AIC criterion (Posada and Buckley, 2004). The HKY+G model of sequence evolution was selected for At103, ETS, G3pdh and Tpi; and GTR+G was selected for ITS.

Maximum-likelihood (ML) analysis was performed in RAxML v. 8 (Stamatakis, 2014) in the CIPRES Science Gateway v.3.3 (Miller et al., 2010). We executed 1000 rapid bootstrap inferences and, thereafter, a thorough ML search following Stamatakis (2014).

Bayesian analyses were conduced in MrBayes v.3.2.5 (Ronquist and Huelsenbeck, 2003) in the CIPRES Science Gateway v.3.3 (Miller et al., 2010). Two separate MCMC runs each initiated with a randon tree and eight simultaneous chains set at default temperatures (Ronquist and Huelsenbeck, 2003). Markov chains were run for 2×10^7 generations sampling every 1000th generation. Convergence of runs was tested by inspecting whether the standard deviation of split frequencies of the runs was <0.01 and by using the effective sample sizes (ESS) > 200 in Tracer v.1.6 (Rambaut and Drummond, 2013). We then used MrBayes command “sumt” to summarize 75% of the trees sampled from post burn-in generations into a 50% majority rule consensus tree that included posterior probabilities (PP) as branch support estimates. The trees were annotated for presentation using FigTree v.1.4.2 (Rambaut, 2014).

2.4. Divergence time estimation

To obtain the chronograms we used the uncorrelated log-normal relaxed clock implemented in the BEAST package v.1.8.0 (Drummond et al., 2012) in the CIPRES Science Gateway v.3.3 (Miller et al., 2010) with a null tree prior (Yule speciation), and a random starting tree. A XML file was generated in BEAUti v.1.8.0 (Drummond et al., 2012). We conducted 2 runs of 60×10^6 generations, sampling trees every 6×10^3 generations. The output files were examined in Tracer v.1.6 (Rambaut and Drummond, 2013) to assess convergence of the runs and that the ESS values were > 200 for all parameters. The runs were combined using LogCombiner v.1.8.2 (Drummond et al., 2012). Following the removal of 10% burn-in, the sampled posterior trees were summarized using TreeAnnotator v.1.8.2 (Drummond et al., 2012) to generate a maximum clade credibility tree and calculate the mean ages, 95% highest posterior density intervals (95% HPD) and PP. The chronogram was visualized and annotated using FigTree v.1.4.2 (Rambaut, 2009).

For the molecular dating, calibration points were selected based on sampling of lineages and the ages derived from the most comprehensive analyses of *Ficus* (Cruaud et al., 2012). We adopted the dates from Cruaud et al. (2012) for the Most Recent Common Ancestor (MRCA) of the genus *Ficus*; the MRCA of section *Americanae*; section *Conosycea*; section *Galoglychia*; section *Malvanthera*; section *Pharmacosycea* and section *Sycomorus* using a normal prior for each node.

2.5. Biogeographical analyses

For biogeographical analyses we defined nine areas based on the current species distribution (Table 3) and the biogeographical regions of the neotropics defined by Morrone (2014). Species occurrence data were compiled from the literature including taxonomic revisions, floras and checklists (Berg and Villavicencio, 2004, Carauta, 1989; BFG, 2015) as well as from inspections of scientific collections of plants of Neotropical area mainly in Brazilian herbaria: ALCB, ASE, B, BHCB, BOTU, C, CEPEC, CESJ, CGMS, CVRD, EAC, ESA, FLOR, FUEL, FURB, GUA, HB, HRB, HUEFS, HUESB, HUFU, IAC, IAN, IAL, K, MBM, MBML, NX, NY, PACA, PAMG, R, RB, SP, SPF, SPFR, UEC, VIC and VIES. Herbarium acronyms follow Thiers (continuously updated). Reconstructions were inferred using the MCC tree obtained in BEAST. The maximum number of areas was restricted to the maximum number of regions observed among extant taxa (five) and dispersion probabilities among areas were equally weighted (unconstrained model).

The analyses were conducted in the package BioGeoBEARS 0.2.1 (Matzke, 2013) implemented in R 3.1.2 (R Core Team, 2014), which allows comparison of different models of ancestral range estimation (ARE). We used six different models, namely DEC, DEC+J, DIVA, DIVA+J, BayArea, BayArea+J (J models include a j parameter controlling founder event speciation). Massana et al. (2015) suggest the DEC model underestimates local extinction because the model allows observed species to transition into being present in no areas (i.e., null range). Consequently, we also accounted for the impact of the null range for each tested model to improve inference of local extinction (Massana et al. 2015, Matzke 2013). These modified models are identified with an asterisk (*) in Table 3. Fit of the models was compared using AIC values in BioGeoBEARS.

2.5.1 Diversification through time.

The temporal accumulation of lineages was assessed with a lineage-through-time plot (LTT) using the R package phytools 0.4-45 (Revell, 2012). We use the MCC tree and 1000 ultrametric trees randomly sampled from the posterior distribution of trees obtained in the BEAST analyses to obtain the 95% confidence interval (CI).

2.5.2 Diversification and evolution of life-history traits and propagule (syconia) size in Neotropical figs.

Neotropical figs are composed of two distinct lineages, sections *Americanae* and *Pharmacosycea* (Herre el al., 1996; Jousselin et al. 2003; Weiblen, 2004; Rønsted et al., 2005; Jackson et al., 2008; Cruaud et al., 2012), which both present different life forms in the initial phase of development.

To explore the importance of the initial life-history traits to the diversification of Neotropical *Ficus*, we reconstructed the evolution of habit (terrestrial vs hemiepiphyte). We also evaluate propagule traits and their association with diversification patterns. A matrix was constructed scoring syconia as small (0.5-1 cm diam.) or medium (1-2.4 cm diam.) yellow, orange or purple at maturity vs. large syconia (> 2.5 cm diam.) usually green at maturity. Data for life histories and syconia size were obtained from taxonomic literature (Berg and Villavicencio, 2004; Carauta, 1989) supplemented by measurements made by the authors.

We tested the hypothesis that small and medium syconia being yellow, red or purplish at maturity (state 1) have allowed for greater diversification compared to larger syconia green at maturity (state 2). To test whether life history or propagule characteristics are associated with differential rates of diversification, ancestral-state reconstruction on the MCC tree and the 1000 subsampled posterior trees was assessed in phytools 0.4.98 using stochastic character mapping (Huelsenbeck et al. 2003). We also implemented the Binary State Speciation and Extinction model (BiSSE) (Maddison et al., 2007) using the R package Diversitree 0.9-7 (FitzJohn, 2012). BiSSE estimates speciation and extinction rates among lineages with different states of a binary trait. We compared eight models: full; equal.l (lambda0=lambda1); equal.m (mu0=mu1); equal.q (q01=q10); equal.lm; equal.lq; equal.mq; equal.lmq. Fit of alternative models were evaluated using LnL and AIC scores. The median of AIC are plotted using a R Package plot3D (Soetaert 2013). All analyses were run on the 1000 random trees as well as on the maximum credibility tree.

3. Results

Both Neotropical *Ficus* sections *Americanae* and *Pharmacosycea* were supported as monophyletic and with sect. *Pharmacosycea* sister to all other sampled sections (Fig. 1). Most speciation events yielding the current diversity of these sections occurred between 15.0 and 2.0 Mya and the greater diversification was observed from the middle Miocene (Fig. 1).

Ancestral range estimation recovered the BayArea*+J (Landis et al. 2013) as the best-fit model for our data set (lnL = -369.2, AIC = 744.3) followed by the BayArea* (Table 4, fig. 2). The use of parameter j (founder-event speciation) and the impact of the null range (Massana et al. 2015) both significantly improved the fit of all models tested (Table 4).

Both molecular dating analysis and ancestral range estimation indicate that Neotropical *Ficus* sections arrived in eastern Brazilian Atlantic Forest from Old World ancestors between the late Oligocene and earlier Miocene (Fig. 2; Table 2). *Pharmacosycea* diverged in the Paleogene 58.1 Mya (95% HPD 34.6 – 60.8) from an Asian ancestor (clade I in Fig. 2) and the MRCA of section *Pharmacosycea* was dated to the early Miocene (19.9 Mya; 95% HPD: 26.6−13.6 Mya). The divergence of section *Americana*e is dated to around 31.4 Mya (95% HPD 23.6 – 40.5) (Fig. 1). Atlantic Forest is the most probable ancestral area of this clade in the Oligocene (Fig. 2. II) and the MRCA of *Americanae* was dated to the Oligocene (25.9 Mya; 95% HPD: 32.5−20.3 Mya) suggesting that both lineages of Neotropical *Ficus* arrived on the continent between the later Oligocene and the early Miocene (Fig. 2). We detected a first diversification event resulting in *F. bonijesulapensis* a species endemic to Seasonally Tropical Dry Forests (STDF) of Brazil. A second lineage consisting of all other *Americanae* species diverged in the early Miocene with inferred origin in both rainforests (Atlantic Forest, Amazonia, Central America).

At the end of the early Miocene there was a split resulting in the origin of a group with Atlantic rainforest species (Fig. 2. IV). In the middle Miocene we detected a divergence between lineages of *Ficus* in the Atlantic Forest and the Amazon or Central America (Fig. 2. III). In the late Miocene (11.6-5.3 mya) our analysis (Fig. 2) identified colonization events from Amazonia to Antillean, Central American and Andes.

Neotropical figs experienced expansion to other American rain forests by the early to middle Miocene, evidenced by the reconstruction of a composed BCG area for the MRCA (Fig. 2) of the most speciose clades in both sections. The sections also had an increase in diversification rate between 16–5 Mya (Fig. 1 B). From the middle Miocene, diversification rate increases in both sections and remained high until the Pleistocene (2.6-0.0 mya), which was marked by a slightly smaller *Ficus* diversification in rainforests (Fig. 2B). However, there has been diversification to adjacent biomes e.g. *F. lagoensis* (Cerrado and Atlantic Forest) and *F. caatingae* (endemic to Caatinga). (Fig. 2).

Endemic species of the Atlantic Forest and Amazonia started diversification in the late Miocene (Fig. 2). We also detected dispersal events between Amazonia and Atlantic Forest and diversification in a group of endemic species to Central and North America at this time. At the end of the Miocene and Pliocene, dispersal and diversification of *Ficus* was inferred from rain forests to seasonally dry forests, and savannas on the continent. In the Pliocene (5.3-2.6 mya) we detected the first occurrence of species in the Antillean and the Andes region (Fig. 2). The analysis detects an expansion of Amazonian and Atlantic species to the Cerrado and Caatinga and intensification of floristic exchanges between the Amazon and the Atlantic Forest in this period.

We detected two transitions between the different initial habits (terrestrial vs. hemiepiphyte) in Neotropical *Ficus* (Fig. 3A, B). Only one species in section *Pharmacosycea* (*F. crassivenosa*, not sampled here), initially presents the hemiepiphytic habit. DAIC scores from BiSSE analyses recovered equal.l (lambda1=lambda0) as the best-fit model (Fig. 5 B-C; Table 5). We did not find evidence for different rates of speciation associated with the hemiepiphytic habit. However, posterior density of the parameters q (transitions) and mu (extinction) were differentiated (Fig. 5 B-C) suggesting lower extinction associated with the hemiepiphytic habit.

Eleven transitions among syconia size were inferred in Neotropical *Ficus*. The best-fit model was equal.lq (lambda1 = lambda0; q01 = q10) (Fig. 5 E-G; Tab. 7) meaning that the speciation and transitions between traits are equal. However, we found lower extinction rates associated with small or medium and coloured syconia (mu0) compared to large green syconia (mu1).

4. Discussion

4.1. Phylogeny, divergence times and diversification of Neotropical figs

In agreement with previous molecular studies including Neotropical samples (Rønsted et al., 2005; Rønsted et al., 2007; Rønsted et al., 2008; Cruaud et al., 2012) we found a strong statistical support for monophyly of sections *Americanae* and *Pharmacosycea*. However the internal relationships among the species, mainly in section *Americanae*, are not strongly supported. This lack of phylogenetic resolution with the short branch lengths is probably a consequence of recent diversification observed in Neotropical *Ficus*. This pattern is also found in other species-rich lineages in Neotropical rainforests [e.g. *Inga* (Richardson et al., 2001); Gesneriaceae (Perret et al., 2013); *Astrocaryum* (Arecaceae, Roncal et al., 2013); *Attalea* (Arecaceae, Freitas et al. 2016); *Philodendron* (Araceae, Loss-Oliveira et al. 2016)] and have been interpreted as a consequence of incomplete lineage sorting due to their recent diversification since the late Miocene (Hughes et al. 2013), as we found here in *Ficus*.

Most of the divergence in Neotropical *Ficus* took place in rainforests and happened in the last 16 Mya. In fact, high levels of rainfall, temperature, and habitat heterogeneity have been correlated with high species richness in general (Kreft and Jetz, 2007) and were the prevalent conditions by the middle Miocene climatic optimum, allowing the expansion of rainforests in America (Morley, 2000; Zachos, et al. 2001). All idiosyncratic geographical and climatic events in the Neotropical region probably variously influenced the diversification of *Ficus* in different domains of the region.

4.2. Diversification of Ficus *in Amazonia*

Amazonian species of *Ficus* appeared scattered across the phylogeny (Fig. 3). The lack of geographic structure was observed in other Amazonian groups (Hughes et al., 2013) such as *Clusia* (Gustaffson and Bittrich, 2003), *Guatteria* (Erkens et al., 2007), *Inga* (Richardson et al., 2001) and *Swartzia* (Torke and Schaal 2008). This pattern suggests that vicariance events (e.g. the Pebas System) were not the major driver of speciation in this region (Hughes et al., 2013) and that these communities were assembled mostly by dispersal. The importance of immigrants in the composition of the Amazonian flora has already been suggested (Pennington et al., 2004; Pennington and Dick, 2010).

We found species endemic to the Amazon diversifying only in the last 10 Mya (late Miocene), which coincides with the end of the Pebas system and the establishment of the current course of the Amazon River (Hoorn et al., 2010). Biotic interchange between South America, the Antilles and Central America occurred mainly at 23-20 and 8-6 mya (Bacon et al., 2015). Events of colonization of adjacent areas from Amazonian taxa were inferred at this time. Diversification in Mesoamerica is detected for a clade of endemic species diverging from 10 Mya. *Ficus* reached the Antillean region around 8-5 Mya, coinciding with the closure of the Isthmus of Panama connecting these areas.

Species shared between the Amazon and the South American Transition Zone (*sensu* Morrone, 2014) are rare and probably colonized the latter area around 10 Mya coinciding with the end of the Pebas System (Hoorn et al., 2010) as a potential barrier to colonization of these areas. Other colonization events between these areas were detected in the Pliocene, which were probably due to the final phase of the Andes uplift creating new niches. Despite the biotic interchange between Amazonia, the Antilles and the South American Transition zone we did not find an increase in diversification rates in these areas as reported for Arecaceae (Roncal et al., 2013; Freitas et al., 2016).

4.3. Diversification of Ficus *in the Atlantic Forest*

Neotropical *Ficus* of both sections diversified first in Atlantic Forest and expanded to other areas during the Oligocene and Miocene in accordance with favorable climatic conditions and the continuity of Neotropical wet forests during this time (Morley, 2000; Zachos et al., 2001). Thenceforth *Ficus* in the Atlantic Forest experienced two bursts of diversification in the middle Miocene (16.0-11.6 mya) and in the Pliocene (5-3 mya), respectively. We compared the patterns observed in *Ficus* with the different available hypotheses of diversification in this area reflecting the complexity and different histories of Atlantic Forest areas.

Situated in an area with less drastic tectonic and hydrological changes the Atlantic Forest is considered more stable than Amazonia. The first burst of *Ficus* in the middle Miocene (16.0-11.6 mya) is chronologically coherent with the Miocene climatic optimum (Morley, 2000; Zachos, et al. 2001) and continuous rainforests in the Americas. Examples of wet forest Neotropical taxa originating in the Miocene are well documented: *Inga* (Richardson et al., 2001) Gesneriaceae (Perret et al., 2013), *Astrocaryum* (Arecaceae, Roncal et al., 2013); *Attalea* (Arecaceae, Freitas et al. 2016);

Philodendron (Araceae, Loss-Oliveira et al. 2016) and the Miocene favorable climatic conditions also appears to have driven the diversification of *Myrcia* (Lucas et al. 2011) in AF and Amazonia.

The Pliocene was characterized by a gradual decrease in temperature and humidity resulting in contraction of wet forests and expansion of dry forests (Zachos et al. 2001). Some AF areas served as *refugia* during this time (Thomé et al., 2010; Carnaval and Moritz, 2008). As an effect of these fluctuations, *Ficus* experienced a second burst of diversification in the Pliocene (5-3 Mya) resulting in the majority of species endemic to the Atlantic Forest and the southern part of the domain. Besides identifying an increase in diversification, our analyses also detected evidence of colonization of the new opened formations followed by *in situ* diversification. Dispersal events from Atlantic Forest to adjacent areas and Amazonia are common (DaSilva and Pinto-da-Rocha, 2013) and were reported in *Attalea* (Freitas et al., 2016) and other genera occurring in dry forests (Pennington et al., 2004).

The distinct histories between the south and north part of AF generated different patterns in species distribution in the AF. The existence of a more stable area in the northern part of the AF, the Bahian refugium (Carnaval and Moritz, 2008), is supported by recent studies (e.g. Martins, 2011; Staggemeier et al., 2015). The occurrence of endemic species of *Ficus* is coherent with *in situ* speciation into refuges (Staggemeier et al., 2015). The shared species between Amazonia and the northern part of AF could be resulted from past forest connections between Amazonia and AF in climatically favorable times at the Neogene and Quaternary (Santos et al. 2007).

In contrast, the southern part of the AF was more unstable due to neotectonic events in the Pliocene. These were followed by a decrease in rainfall and a fragmentation of the southern parts (Ricommini and Assumpção, 1999), a scenario, which would have prevailed until the end of the Pliocene (Grazziotin et al., 2006). A recent hypothesis suggests that the southern part of the AF would have expanded (not contracted) during the last glacial maximum (21 kya) (Leite et al., 2016). In spite of the unfavorable climatic conditions in the south there were probably more terrestrial habitats in areas at lower elevation and an expansion of the forest would have promoted immigration between areas of the Atlantic Forest. This hypotheis is partially corroborated by a palynological study (Freitas et al., 2013), which supports the occurrence of a tropical forest in a region of the Brazilian continental shelf during this epoch. Furthermore, we detected a decrease in speciation in the Pleistocene but extant species can be experiencing an increase in population size taking advantage of the exposure of new areas on the Brazilian continental shelf (Leite et al., 2016). Similar patterns have been reported for snakes experiencing a population size increase in the Pliocene (Grazziotin et al., 2006).

4.4. Evolution of traits: the importance of being hemiepiphyte

Hemiepiphytism in *Ficus* is thought to be an adaptation to avoid deep shade in the forest understory (Ramirez, 1977; Harrison, 2005). This trait enables greater initial access to light in the canopy and the hemiepiphytic woody species are adapted to adverse water conditions, which possibly could have been an advantage in colonizing unstable areas and dry regions. We hypothesize that the hemiepiphytic habit provides the species of section *Americanae* with greater ability for establishment under adverse lighting conditions and water stress (Hao et al., 2012).

According to our results hemiepiphytism reduces the extinction rates (Fig. 4. A-D) if compared with primarily terrestrial lineages. The hemiepihiphytic habit can reduce risks related to terrestrial growth such as high competition, flooding, and terrestrial herbivores, which are common in tropical rainforests (Hao et al., 2012). This could have been particularly important for the diversification of *Ficus* in highly unstable and newer habitats such as the Amazonia.

In addition, all Neotropical *Ficus* species occurring in drier regions today are hemiepiphytes or hemiepilithics/lithophytes ("rock splitters"), as has also been found in a lineage of Australian and Australasian *Ficus* (Rønsted et al., 2008b). Hao et al. (2012) suggest that an important characteristic related to drought resistance is the loss and regeneration of the canopy. In the Neotropics several of the section *Americanae* are deciduous (e.g., *F. bahiensis*, *F. bonijesulapensis*, *F. caatingae, F. enormis*, *F. eximia*, *F. gomelleira, F. hirsuta*, *F. holosericea* and *F. mexiae*; AFPM, pers. obs.; Pereira et al. 2007; Bianchini et al. 2015). However, it is not known if all Neotropical hemiepiphytic species present this characteristic.

4.5. Evolution of traits: the importance of having small (and more) propagules for dispersal ability

Ficus shows traits typical of pioneer species such as small seeds, high fecundity, flexible rooting habits and high growth rates (Harrison, 2005). However, the obligatory pollination mutualism between Agaonidae wasps and *Ficus* is a limiting factor for reproduction (Janzen, 1979; Ramírez, 1970; Wiebes, 1979).

Our results indicate that occurrence of small and medium propagules reduce extinction rates (Fig. 5. E-G). This may be related with the fact that species with small figs having red shades or yellow ones are likely dispersed by birds and figs with intermediate characteristics are probably dispersed both by bats and birds (Lomáscolo et al., 2008; 2010). Species with small syconia present more infructescenses along the branches and higher reproductive success compared to species with large, bat-dispersed syconia (Lomáscolo et al., 2008; 2010). While small syconia can be swallowed whole and dispersed over long distances, larger syconia are dispersed by larger animals over a shorter distance. It also seems to be an advantage to have the seeds in many infructescences instead of having seeds concentrated in few infructescences.

In addition, larger syconia generally have far less inflorescences per individual compared to species with smaller syconia. Large figs are also more susceptible to attacks by non-pollinating wasps. Aditionally, large figs tend to be dispersed by bats, which are less effective dispersers compared to birds. Bats also eat immature fruits ones as well (Jacomasa and Pizo 2010). Finally, many seeds lose viability when passing through the digestive tract of bats, which happens at a much lower rate when passing through birds (Traveset 1998).

5. Conclusions and perspectives

The first biogeographic approach focused in Neotropical *Ficus* is presented here. This study provides a phylogenetic background, which allows for addressing questions about the history of diversification and the importance of traits of *Ficus* in this process.

Despite the inclusion of both more species and more DNA regions, the internal relationships between the species of section *Americanae* are still not completely resolved. Future studies should preferably include several terminals per taxa and use a high-throughput NGS approach to fully resolve the phylogeny and clarify the relationship of most of its species. Despite uncertainty in some of the species relationships, the present study showed that the two lineages of *Ficus* with different traits arrived in the Americas at the Atlantic Forest, began to diversify in the Miocene, and expanded to other regions of the continent.

The Amazonian *Ficus* species diversity is a result of immigrations to this region occurring during unstable periods. Our results are consistent with well-documented events that influenced the history of these forests (the Andean uplifts, the end of Pebas system, and the closure of the Panama Isthmus). Dispersal events from the Amazon to the Andes, Antilles and Central America after the end of the Pebas system supports the hypothesis of colonization of new habitats in the Andes after the end of this barrier. The diversification of *Ficus* in Atlantic Forest was significantly different, being marked by endemisms related to its isolation after the separation of two blocks of Neotropical wet forests. Our results point to a complex diversification in the Atlantic Forest during two periods in the middle Miocene and the Pliocene as a result of neotectonic events in the southern and southeastern distribution and a more stable area in the northern distribution of this forest.

Finally our BiSSE analysis of specific traits in Neotropical *Ficus* suggests that some traits may also have influenced the diversification and current distribution of the species. The hemiepiphytic habit of section *Americanae* and the adaptation to adverse water conditions (*i.e.*, apparently common feature of losing and regenerating the canopy during the dry season) allowed further expansion of this lineage in the Neotropical biomes. Additionally small and medium sized propagules were possibly selected in Neotropical forests marked by long-distance dispersal allowing greater success and reducing risk of extinction.

The successful diversification of Neotropical *Ficus* was likely the result of a complex and different history in each Neotropical area. This study provides new insights into the biogeographical history of *Ficus* in the Neotropical region and to the broader understanding of diversification of large genera. Future studies in *Ficus* or other megadiverse genera should include phylogeography and species distribution modelling approaches to better understand diversification in tropical forest communities.

Acknowledgements

We thank Alessandra Schnadelbach, Ariane Barbosa, Cassio Van den Berg and Lizandro Perazza for the help with analysis; to Bruno Ferraz by the help in the Graphical abstract; to Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) for issuing collecting permits. Fieldwork and DNA sequencing were partly sponsored by the PRONEX (FAPESB PNX0014/2009), PROTAX (CNPq 562354/2010-7). This study is part of the first author's PhD thesis developed in the Programa de Pós-Graduação em Botânica (UEFS) and supported by PhD fellowship grants from FAPESB (No. BOL0563/2014) and CAPES. The work was also supported by an International Network Grant from the Danish Ministry of Science, Innovation and Education, 2012 to NR, AFPM, RASP and LPQ. RASP was funded by CNPq (grant # 306078/2014-7) and FAPESP (grant #2004/10299-4).

References

Antonelli, A., Nylander, J.A.A., Persson, C., Sanmartín, I., 2009. Tracing the impact of the Andean uplift on Neotropical plant evolution. Proc. Natl. Acad. Sci. U.S.A. 106, 9749–9754.

Antonelli, A. and Sanmartín, I. 2011. Why are there so many plant species in the Neotropics? Taxon 60 (2): 403–414

Bacon, C.D., Silvestro, D., Jaramillo, C., Smith, B.T., Chakrabarty, P., Antonelli, A., 2015. Biological evidence supports an early and complex emergence of the Isthmus of Panama. Proc. Natl. Acad. Sci. U.S.A. 112, 6110–6115.

Baldwin, B.G., Markos, S., 1998. Phylogenetic utility of the external transcribed spacers (ETS) of 18S–26S rDNA: congruence of ETS and ITS trees of *Calycadenia* (Compositae). Mol. Phylogenet. Evol. 10, 449–463.

Berg, C.C., 1989. Classification and distribution of *Ficus*. Experientia. 45, 605–611.

Berg, C.C., 2003. Flora Malesiana precursor for the treatment of Moraceae 1: The main subdivision of *Ficus* the subgenera. Blumea 48, 167–178.

Berg, C.C., Corner, E.J.H., 2005. Moraceae – *Ficus*, in: Nooteboom, H.P. (Ed.). Flora Malesiana Series I – Seed Plants Vol. 17/Part 2. National Herbarium of the Netherlands, Leiden, pp. 1–152.

Berg, C.C., Simonis, E., 1981. The *Ficus* flora of Venezuela: Five species complexes discussed and two new species described. Ernstia 6, 1–12.

Berg, C.C., Villavicencio, X., 2004. Taxonomic studies on *Ficus* (Moraceae) in the West Indies, extra-Amazonian Brazil, and Bolivia. Ilicifolia 5, 1–132.

Bianchini, E., Emmerick, J., Messetti, A., Pimenta, J., 2015. Phenology of two Ficus species in seasonal semi-deciduous forest in Southern Brazil. Braz J Biol 75, 206–214.

BFG –The Brazilian Flora Group. 2015. Growing knowledge: an overview of seed plant diversity in Brazil. Rodriguésia 66, 1085–1113.

Bruun-Lund, S., Clement, W.L., Kjellberg, F., Rønsted, N. 2017. First plastid phylogenomic study reveals potential cyto-nuclear discordance in the evolutionary history of *Ficus* L. (Moraceae). Mol. Phylogen. Evol. 109, 93-104.

Carauta, J.P.P., 1989. *Ficus* (Moraceae) no Brasil: Conservação e Taxonomia. Albertoa 2, 1–365.

Carnaval, A.C., Moritz, C. 2008. Historical climate modelling predicts patterns of current biodiversity in the Brazilian Atlantic forest. J. Biogeograp. 35, 1187–1201.

Chantarasuwan, B., Rønsted, N., Kjellberg, F., Sungkaew, S., Welzen, P., 2015. Palaeotropical intercontinental disjunctions revisited using a dated phylogenetic hypothesis with nearly complete species level sampling of *Ficus* subsect. *Urostigma* (Moraceae). J. Biogeograph. 43, 384–397.

Core Team, R., 2015. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.r- project.org

Cruaud, A., Rønsted, N., Chantarasuwan, B., Chou, L.S., Clement, W.L., Couloux, A., Cousins, B., Genson, G., Harrison, R.D., Hanson, P.E., Hossaert-McKey, M., Jabbour-Zahab, R., Jousselin, E., Kerdelhué, C., Kjellberg, F., Lopez-Vaamonde, C., Peebles, J., Peng, Y.-Q.Q., Pereira, R.A., Schramm, T., Ubaidillah, R., Noort, S. van, Weiblen, G.D., Yang, D.-R.R., Yodpinyanee, A., Libeskind-Hadas, R., Cook, J.M., Rasplus, J.-Y.Y., Savolainen, V., 2012. An extreme case of plant-insect codiversification: figs and fig-pollinating wasps. Syst. Biol. 61, 1029–1047.

Darriba, D., Taboada, G.L., Doallo, R., Posada, D., 2012. jModelTest 2: more models, new heuristics and parallel computing. Nature Methods 9, 772–772.

DaSilva, M.B., Pinto-da-Rocha, R., 2011. História biogeográfica da Mata Atlântica: opiliões (Arachnida) como modelo para sua inferência, in: Carvalho, C.J.B., Almeida, E.A.B. (Orgs.). Biogeografia da América do Sul - Padrões e Processos Roca, São Paulo, pp. 221–238.

Doyle, J.J., Doyle, J.L., 1987. A rapid DNA isolation method for small quantities of fresh tissues. Phytochem. Bull. 19, 11–15.

Drummond, A.J., Suchard, M.A., Xie, D., Rambaut, A., 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. Mol. Biol. Evol. 29, 1969–1973.

Edgar, R.C., 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucl. Acids Res. 32, 1792–1797.

Erkens, R.H.J., Chatrou, L.W., Maas, J.W., Van-der-Niet, T., Savolainen, V., 2007. A rapid diversification of rainforest trees (*Guatteria*: Annonaceae) following dispersal from Central into South America. Mol. Phylogenet. Evol. 44, 399–411.

Freitas, A.G., Carvalho M.A.de, Mendonça, C.B.F., Gonçalves-Esteves, V., 2013. Pollen grains in quaternary sediments from the Campos Basin, state of Rio de Janeiro, Brazil: Core BU-91-GL-05. Acta Bot. Bras., 27, 761–772.

Freitas, C., Meerow, A., Pintaud, J., Henderson, A., Noblick, L., Costa, F., Barbosa, C., Barrington, D., 2016. Phylogenetic analysis of *Attalea* (Arecaceae): insights into the historical biogeography of a recently diversified Neotropical plant group. Bot. J. Linn. Soc. 2, 1–16.

FitzJohn, R.G., 2012. Diversitree: comparative phylogenetic analyses of diversification, in R. Methods Ecol. Evol. 3, 1084–1092.

Gentry A. 1992. Tropical forest biodiversity: distributional patterns and their conservational significance. Oikos, 63:19–28.

Grazziotin, F.G., Monzel, M., Echeverrigaray, S., Bonatto, S.L., 2006. Phylogeography of the Bothrops jararaca complex (Serpentes: Viperidae): past fragmentation and island colonization in the Brazilian Atlantic forest. Mol. Ecol. 15, 3969–3982.

Gustafsson, M, Bittrich, V. 2003. Evolution of morphological diversity and resin secretion in flowers of Clusia L. (Clusiaceae): insights from ITS sequence variation. Nord. J. Bot. 22. 183–203.

Haffer, J., 1969. Speciation in Amazonian forest birds. Science, 165, 131–137.

Hao, G.Y., Wang, A.Y., Sack, L., Goldstein, G., Cao, K.F., 2012. Is hemiepiphytism an adaptation to high irradiance? Testing seedling responses to light levels and drought in hemiepiphytic and non-hemiepiphytic *Ficus*. Physiol. Plantarum. 148, 74–86.

Harrison, R.D., 2005. Figs and the diversity of tropical rainforests. Bioscience 55, 1053–1064.

Herre, E.A., Machado, C.A., Bermingham, E., Nason, J.D., Windsor, D.M., McCafferty, S., Van Houten, W., Bachmann, K., 1996. Molecular phylogenies of figs and their pollinator wasps. J. Biogeogr. 23, 521–530.

Hoorn, C., Flantua, S., 2015. An early start for the Panama land bridge. Science 348, 186–187.

Hoorn, C., Wesselingh, F.P., ter Steege, H., Bermudez, M.A., Mora, A., Sevink, J., Sanmartin, I., Sanchez-Meseguer, A., Anderson, C.L., Figueiredo, J.P., Jaramillo, C., Riff, D., Negri, F.R., Hooghiemstra, H., Lundberg, J., Stadler, T., Sarkinen, T., Antonelli, A., 2010. Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. Science 330, 927–931.

Huelsenbeck, J.P, Nielsen, R, Bollback, J.P., 2003. Stochastic mapping of morphological characters. Syst. Biol. 52, 131–158.

Hughes, C.E., Pennington, R.T., Antonelli, A., 2013. Neotropical plant evolution: assembling the big picture. Bot. J. Linn. Soc. 171, 1–18.

Jackson, A. P., Machado, C.A., Robbins, N., Herre E.A. 2008. Multi-locus phylogenetic analysis of neotropical figs does not support co-speciation with the pollinators: the importance of systematic scale in fig/wasp cophylogenetic studies. Symbiosis 45, 57–72.

Jacomassa, F.A.F. and Pizo, M.A. 2010. Birds and bats diverge in the qualitative and quantitative components of seed dispersal of a pioneer tree. Acta Oecol. 36, 493–496.

Janzen, D.H. 1979. How to be a fig. Annu. Rev. Ecol. Syst. 10: 13–51.

Jousselin, E., Rasplus, J.Y., Kjellberg, F., 2003. Convergence and Coevolution in a mutualism: evidence from a molecular phylogeny of *Ficus*. Evolution 57, 1255–1272.

Koenen, E.J.M., Clarkson, J.J., Pennington, T.D., Chatrou, L.W., 2015. Recently evolved diversity and convergent radiations of rainforest mahoganies (Meliaceae) shed new light on the origins of rainforest hyperdiversity. New Phytol. 207, 327–339.

Kreft, H., Jetz, W., 2007. Global patterns and determinants of vascular plant diversity. Proc. Natl. Acad. Sci. U.S.A. 104, 5925–5930.

Landis, M.J., Matzke, N.J., Moore, B.R., Huelsenbeck, J.P., 2013. Bayesian analysis of biogeography when the number of areas is large. Syst. Biol. 62, 789–804.

Leite, Y., Costa, L., Loss, A., Rocha, R., Batalha-Filho, H., Bastos, A., Quaresma, V., Fagundes, V., Paresque, R., Passamani, M., Pardini, R., 2016. Neotropical forest expansion during the last glacial period challenges refuge hypothesis. Proc. Natl. Acad. Sci. U.S.A. 113, 1008–1013.

Li, M., Wunder, J., Bissoli, G., Scarponi, E., Gazzani, S., Barbaro, E., Saedler, H., Varotto, C., 2008. Development of COS genes as universally amplifiable markers for phylogenetic reconstructions of closely related plant species. Cladistics 24, 727–745.

Lomáscolo, S.B., Levey, D.J., Kimball, R.T., Bolker, B.M., Alborn, H.T., 2010. Dispersers shape fruit diversity in *Ficus* (Moraceae). Proc. Natl. Acad. Sci. U.S.A. 107, 14668–14672.

Lomáscolo, S.B., Speranza, P., Kimball, R., 2008. Correlated evolution of fig size and color supports the dispersal syndromes hypothesis. Oecologia. 156, 783–796.

Loss-Oliveira, L., Sakuragui, C., Soares, M., Schrago, C., 2016. Evolution of *Philodendron* (Araceae) species in Neotropical biomes. PeerJ. 4, 1–18.

Lucas, E.J., Matsumoto, K., Harris, S.A., Nic Lughadha, E.M., Benardini, B., Chase. M.W., 2011. Phylogenetics, morphology, and evolution of the large genus *Myrcia* s.l. (Myrtaceae). Int. J. Pl. Sci. 172, 915–934.

Maddison, W.P., Maddison, D.R., 2015. Mesquite: a Modular System for Evolutionary Analysis. Version 3.02. <http://mesquiteproject.org>.

Maddison, W.P, Midford, P.E, Otto, S.P., 2007. Estimating a binary character's effect on speciation and extinction. Syst. Biol. 56, 701–710.

Martins, F.M. 2011. Historical biogeography of the Brazilian Atlantic forest and the Carnaval–Moritz model of Pleistocene refugia: what do phylogeographical studies tell us? Biol. J. Linn. Soc. 104, 499–509.

Massana, K.A., Beaulieu, J.M., Matzke, N.J., O'Meara, B.C. 2015. Non-null effects of the null range in biogeographic models: Exploring parameter estimation in the DEC model, bioRxiv. September 16, 2015. http://dx.doi.org/10.1101/026914 http://biorxiv.org/content/early/2015/09/16/026914.abstract

Matzke, N.J., 2013a. BioGeoBEARS: Biogeography with Bayesian (and likelihood) evolutionary analysis in R Scripts. CRAN: The Comprehensive R Archive Network. Vienna, Austria. http://cran.r-project.org/package=BioGeoBEARS.

Matzke N.J., 2013b. Probabilistic historical biogeography: new models for founder-event speciation, imperfect detection, and fossils allow improved accuracy and model-testing. Front. Biogeogr. 5, 242–248.

Miller, M.A., Pfeiffer, W., Schwartz, T., 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: Proceedings of the Gateway Computing Environments Workshop (GCE), November 2010, New Orleans, pp. 1–8.

Montes, C., Cardona, A., McFadden R.,, Morón, S.E., Silva, C.A., Restrepo-Moreno, S., Ramírez, D.A., Hoyos, N., Wilson, J., Farris, D., Bayona, G.A., Jaramillo, C.A., Valencia, V., Bryan, J., Flores, J.A., 2012. Evidence for middle Eocene and younger land emergence in central Panama: Implications for Isthmus closure. Geo. Soc. Am. Bull. 124, 780–799.

Morley, R.J., 2000. Origin and evolution of tropical rain forests. John Wiley & Sons Ltd., Chichester, England, pp. 1–362.

Morrone, J.J., 2014. Biogeographical regionalisation of the Neotropical region. Zootaxa 3782, 1–110.Myers, N., Mittermeier, R.A., Mittermeier, C.G., Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858.

Nylander, J.A.A., 2004. MrModeltest v. 2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University, Uppsala, Sweden. https://github.com/nylander/MrModeltest2

Pederneiras, L.C., Carauta, J.P.P., Neto, S.R., Mansano, V.F., 2015a. An overview of the infrageneric nomenclature of *Ficus* (Moraceae). Taxon 64, 589–594.

Pederneiras, L.C., Romaniuc-Neto, S., Mansano, V.F. 2015b. Molecular phylogenetics of *Ficus* section *Pharmacosycea* and the description of *Ficus* subsection *Carautaea* (Moraceae). Syst. Bot., 40, 504–509.

Pennington, R.T. and Dick, C.W. 2004. The role of immigrants in the assembly of the South American rainforest tree flora. Philos. Trans. R. Soc. Lond. B, Biol. Sci., 359, 1611–1622

Pennington, R.T., Dick, C.W., 2010. Diversification of the Amazonian flora and its relation to key geological and environmental events: a molecular perspective. In: Hoorn C, Wesselingh F (eds.). Amazonia, landscape and species evolution, 1st edition. Oxford: Blackwell Publishing, 373–385.

Pennington R., Cronk Q., Richardson J., 2004. Introduction and synthesis: plant phylogeny and the origin of major biomes. Phil. Trans. Roy. Soc. B. 359, 1455–1464.]

Pennington, R.T., Hughes, M., Moonlight, P.W., 2015. The origins of tropical rainforest hyperdiversity. Trends Plant Sci. 20, 693–5.

Pereira, R., Rodrigues, E., Menezes, A., 2007. Phenological patterns of Ficus citrifolia (Moraceae) in a seasonal humid-subtropical region in Southern Brazil. Plant Ecol 188, 265–275.

Perret, M., Chautems, A., Araujo, O.A., Salamin, N., 2013. Temporal and spatial origin of Gesneriaceae in the New World inferred from plastid DNA sequences. Bot. J. Linn. Soc. 171, 61–79.

Prance, G.T., 1982. Forest refuges: evidence from woody angiosperms, in: Prance, G.T. (ed.), Biological diversification in the tropics. Columbia University Press, New York, pp. 137–158.

Posada, D., Buckley, T.R., 2004. Model selection and model averaging in phylogenetics: advantages of Akaike information criterion and Bayesian approaches over likelihood ratio tests. Syst. Biol. 53, 793–808.

Queiroz, L.P. de; São-Mateus, W; Delgado-Salinas, A.; Torke, B. M.; Lewis, G. P.; Dorado, Ó.; Ardley, J. K.; Wojciechowski, M. F.; Cardoso, D. 2017. A molecular phylogeny reveals the Cuban enigmatic genus Behaimia as a new piece in the Brongniartieae puzzle of papilionoid legumes. Mol. Phylogen. and Evol. xxx xxx-xxx

R Core Team. 2016. R: A language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. URL http://www.R-project.org/.

Rambaut, A., 2014. FigTree version 1.4.2: tree figure drawing tool. Version 1.4.2. http://tree.bio.ed.ac.uk/software/figtree

Rambaut, A., Drummond, A.J., 2013. Tracer version 1.6. http://beast.bio.ed.ac.uk/Tracer

Ramírez, W.B. 1970. Host specificity of fig wasps (Agaonidae). Evolution 24, 680–691.

Ramirez, B.W., 1977. Evolution of the strangling habit in *Ficus* L. subgenus *Urostigma* (Moraceae). Brenesia 12, 11–19.

Renner, S., 2004. Plant dispersal across the Tropical Atlantic by wind and sea currents. Int. J. Plant Sci. 165, S23–S33.

Revell, L.J., 2012. Phytools: An R package for phylogenetic comparative biology (and other things). Methods Ecol. Evol. 3, 217–223.

Richardson, J.E., Pennington, R.T., Pennington, T.D., Hollingsworth, P.M., 2001. Rapid diversification of a species-rich genus of Neotropical rain forest trees. Science 293, 2242–2245.

Ricommini, C., Assumpção, M., 1999. Quaternary tectonics in Brazil. Episodes 22, 221–225.

Roncal, J., Kahn, F., Millan, B., Couvreur, T.L.P., Pintaud, J.-C., 2013. Cenozoic colonization and diversification patterns of tropical American palms: evidence from *Astrocaryum* (Arecaceae). Bot. J. Linn. Soc. 171, 120–139.

Ronquist, F., Huelsenbeck, J.P., 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19, 1572–1574.

Rønsted, N., Salvo, G., Savolainen, V., 2007. Biogeographical and phylogenetic origins of African fig species (*Ficus* section *Galoglychia*). Mol. Phylogenet. Evol. 43, 190–201.

Rønsted, N., Weiblen, G.D., Clement, W.L., Zerega, N.J.C., Savolainen, V., 2008a. Reconstructing the phylogeny of figs (*Ficus*, Moraceae) to reveal the history of the fig pollination mutualism. Symbiosis 45, 45–55.

Rønsted, N., Weiblen, G.D., Cook, J.M., Salamin, N., Machado, C.A., Savolainen, P., 2005. 60 million years of co-divergence in the fig-wasp symbiosis. Proc. R. Soc. B. 272, 2593–2599.

Rønsted, N., Weiblen, G.D., Savolainen, V., Cook, J.M., 2008b. Phylogeny, biogeography, and ecology of *Ficus* section *Malvanthera* (Moraceae). Mol. Phylogenet. Evol. 48, 12–22.

Salariato, D.L., Zuloaga, F.O., Franzke, A., Mummenhoff, K., Al-Shehbaz, I., 2016. Diversification patterns in the CES clade (Brassicaceae tribes Cremolobeae, Eudemeae, Schizopetaleae) in Andean South America. Bot. J. Linn. Soc. 181, 543–566.

Santos, A.M.M., Silva, J.M.C., Tabarelli, M., 2007. Biogeographical relationships among tropical forests in northeastern Brazil. J. Biogeograp. 34: 437–446.

Schuettpelz, E., Pryer, K., 2009. Evidence for a Cenozoic radiation of ferns in an angiosperm-dominated canopy. Proc Natl Acad Sci 106, 11200–11205.

Soetaert, K. 2013. plot3D: Plotting multi-dimensional data. R package version 1.0.

Staggemeier VG, Diniz-Filho JAF, Forest F, Lucas E, 2015. Phylogenetic analysis in

Myrcia section *Aulomyrcia* and inferences on plant diversity in the Atlantic rainforest. Ann. Bot. 115, 747–761.

Stamatakis, A., 2014. RAxML Version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30, 1312–1313.

Stebbins, G.L., 1974. Flowering plants: Evolution above the species level. Harvard University Press, Cambridge, MA. pp. 1–399.

Strand, A.E., Leebensmack, J., Milligan, B.H., 1997. Nuclear DNA-based markers for plant evolutionary biology. Mol. Ecol. 6, 113-118.

Thiers, B. [continuously updated]. Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. http://sweetgum.nybg.org/science/ih/Thomé, M.T.C., Zamudio, K.R., Giovanelli, J.G.R., Haddad, C.F.B., Baldissera, F.A. Jr, Alexandrino, J., 2010. Phylogeography of endemic toads and post-Pliocene persistence of the Brazilian Atlantic Forest. Mol. Phylogen. Evol. 55, 1018–1031.

Thomé MTC, Zamudio KR, Giovanelli JGR, Haddad CFB, Baldissera FA Jr, Alexandrino J. 2010. Phylogeography of endemic toads and post-Pliocene persistence of the Brazilian Atlantic Forest. MolecularPhylogenetics and Evolution 55: 1018–1031.

Torke, B.M., Schaal, B.A., 2008. Molecular phylogenetics of the species-rich Neotropical genus *Swartzia* (Leguminosae, Papilionoideae) and related genera of the swartzioid clade. Am. J. Bot. 95, 215–228.

Traveset, A., 1998. Effect of seed passage through vertebrate frugivores' guts on germination: a review. Persp. Plant Ecol. Evol. Syst. 1, 151–190.

Weiblen, G.D., 2000. Phylogenetic relationships of functionally dioecious *Ficus* (Moraceae) based on ribosomal DNA sequences and morphology. Am. J. Bot. 87, 1342–1357.

Weiblen, G.D., 2004. Correlated evolution in fig pollination. Syst. Biol. 128, 128-139.

Wiebes, J.T. 1979. Co-evolution of figs and their insect pollinators. Annu. Rev. Ecol. Syst. 10: 1–12.

Xu, L., Harrison, R.D., Yang, P., Yang, D.-R., 2011. New insight into the phylogenetic and biogeographic history of genus *Ficus*: Vicariance played a relatively minor role compared with ecological opportunity and dispersal. J. Syst. Evol. 49, 546-557.

Zachos, J., Pagani, M., Sloan, L., Thomas, E., Billups, K., 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292, 686–693.

Zerega, N., Clement, W., Datwyler, S., Weiblen, G., 2005. Biogeography and divergence times in the mulberry family (Moraceae). Mol. Phylogenet. Evol. 37, 402–416.

Figure 1. A. MCC tree of Neotropical *Ficus* derived from divergence time estimation in Beast. Black diamonds refer to the calibration points. Section *Americanae* is highlighted in blue and section *Pharmacosycea* in red. Shaded horizontal bars show the 95% highest posterior densities of divergence times. B. Log-lineages-through time-plot (LTT) following the same time scale as the chronogram.

Figure 2. Ancestral range estimations for the Neotropical *Ficus* using the BAYAREA*+j model in BioGeoBEARS -LnL = 369.2. States at nodes (squares) represent the most probable ancestral area before the speciation event. Squares with more than one letter refer to ancestral areas composed of more than one biogeographical area. Stratigraphical time in millions of years ago (Mya) is indicated on the time-scale.

Figure 3. A. Result from 10 000 stochastic character-mapping reconstructions of the life forms (terrestrial vs. hemiepiphyte) on the MCCT of the Neotropical *Ficus* using Phytools. Red indicates hemiepiphytic habit. **B.** Result from 10 000 stochastic character-mapping reconstructions of the life forms (terrestrial vs. hemiepiphyte) from 1000 subsampled posterior trees using Phytools. The colour of branches in the tree indicates the posterior probability along the branches. Red indicates high posterior probability of hemiepiphytic habit.

Figure 4. A. Result from 10 000 stochastic character-mapping reconstructions of the syconia size (small vs. medium and large) on the MCCT of the Neotropical *Ficus* using Phytools. Red indicates small size. **B.** Result from 10 000 stochastic character-mapping reconstructions of the syconia size (small vs. medium and large) from 1000 subsampled posterior trees using Phytools. The colour of branches in the tree gives the posterior probability of each size along the branches. Red indicates high posterior probability of small syconia.

Figure 5. Result of Binary State Speciation and Extinction (BiSSE analysis). **A-D:** Habit (0-Terrestrial, 1-Hemiepiphyte). **A.** Distributions of DAIC values to q01, *lambda*0 and *mu*0; **B.** Distributions of DAIC to q01, *lambda*0 and *mu*0; **C.** Posterior probability distributions of extinction (*mu*0 and *mu*1); **D.** Posterior probability distributions transition rates (q01, q10). **E-G:** Syconia traits (0-Large, green; 1-Medium to small, not green). **E.** Distributions of DAIC values to q01, *lambda*0 and *mu*0; **F.** Distributions of DAIC to q01, *lambda*0 and *mu*0; **G.** Posterior probability distributions of extinction (*mu*0 and *mu*1).

Figure 6. Habit, branches and syconia diversity in Neotropical figs. A–D: Habit diversity. A: *F. bonijesulapensis* growing on stones, B. *F. arpazusa* hemiepiphytous, C.

F. gomelleira hemiepiphytic; D. *F. cyclophylla* in an urban area. E–L: Branches. E: *F. castellviana*, F. *F. clusiifolia*, G. *F. holosericea*, H. *F. luschnathiana*, I. *F. cestrifolia*, J. *F. crocata*, K. *F. hirsuta*, L. *F. pulchella*, M–Y: Syconia diversity, M. *F. adhatodifolia* (Section *Pharmacosycea*), N. *F. arpazusa*, O. *F. bahiensis*, P. *F. cyclophylla*, Q. *F. eximia*, R. *F. guaranitica*, S. *F. gomelleira*, T. *F. hirsuta*, U. *F. lagoensis*, V. *F. mariae*, W. *F. mexiae*, X. *F. pertusa*, Y. *F. trigona*. Photos A, D, T by E. Matos; B–C, E–I, N–Q, U–X by A. Machado; J–K. by R. Lacerda; L, R, S, Y by R. Pereira and M, V. by G. Siqueira.

Figure 1

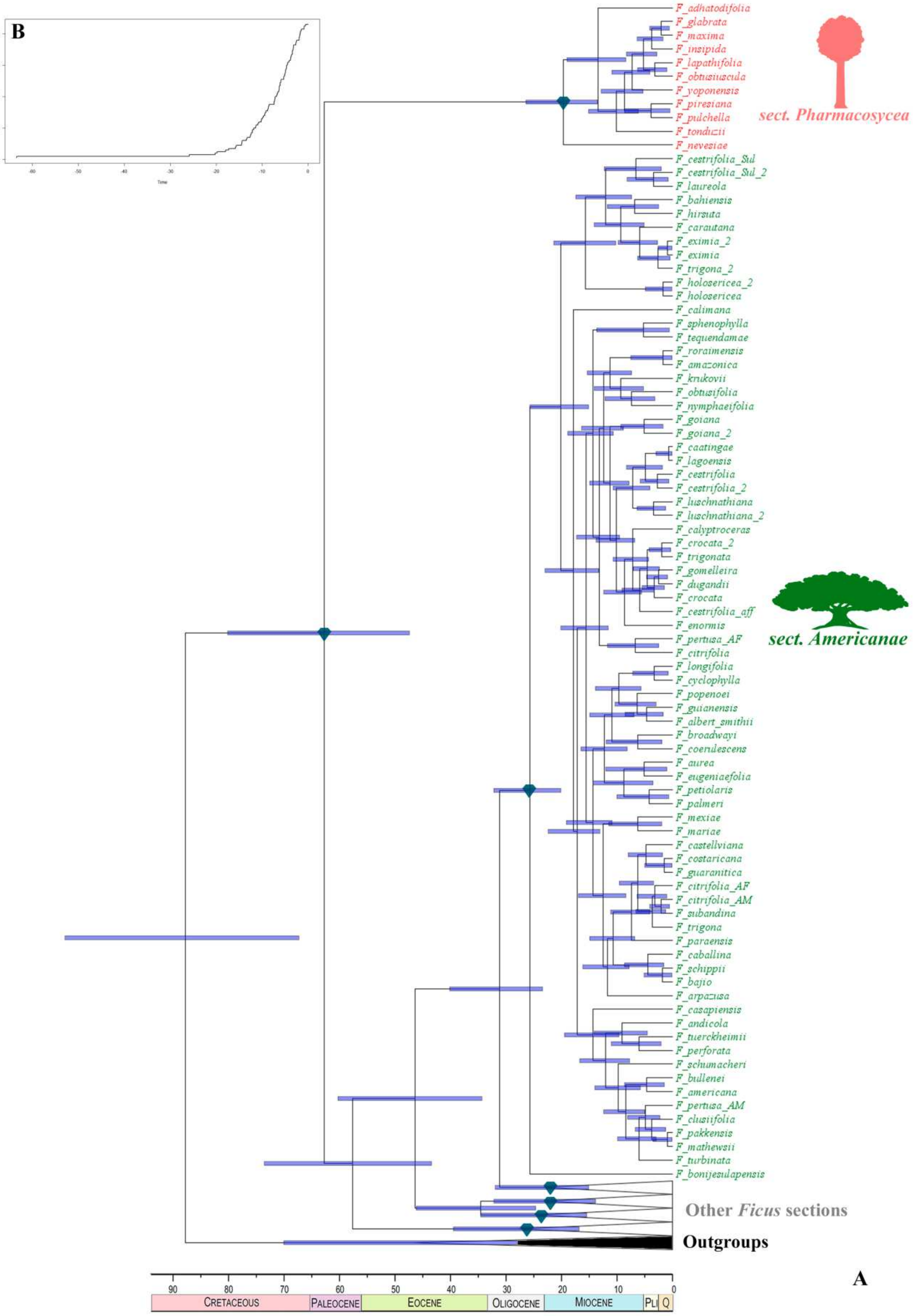

B
0
20
40
60
80
-60
-50
-40
-30
-20
-10
0
Time
F_adhatodifolia
F_glabrata
F_maxima
F_insipida
F_lapathifolia
F_obtusiuscula
F_yoponensis
F_piresiana
F_pulchella
F_tonduzii
F_nevesiae
sect. Pharmacosycea
F_cestrifolia_Sul
F_cestrifolia_Sul_2
F_laureola
F_bahiensis
F_hirsuta
F_carautana
F_eximia_2
F_eximia
F_trigona_2
F_holosericea_2
F_holosericea
F_calimana
F_sphenophylla
F_tequendamae
F_roraimensis
F_amazonica
F_krukovii
F_obtusifolia
F_nymphaeifolia
F_goiana
F_goiana_2
F_caatingae
F_lagoensis
F_cestrifolia
F_cestrifolia_2
F_luschnathiana
F_luschnathiana_2
F_calyptroceras
F_crocata_2
F_trigonata
F_gomelleira
F_dugandii
F_crocata
F_cestrifolia_aff
F_enormis
F_pertusa_AF
F_citrifolia
F_longifolia
F_cyclophylla
F_popenoei
F_guianensis
F_albert_smithii
F_broadwayi
F_coerulescens
F_aurea
F_eugeniaefolia
F_petiolaris
F_palmeri
F_mexiae
F_mariae
F_castellviana
F_costaricana
F_guaranitica
F_citrifolia_AF
F_citrifolia_AM
F_subandina
F_trigona
F_paraensis
F_caballina
F_schippii
F_bajio
F_arpazusa
F_casapiensis
F_andicola
F_tuerckheimii
F_perforata
F_schumacheri
F_bullenei
F_americana
F_pertusa_AM
F_clusiifolia
F_pakkensis
F_mathewsii
F_turbinata
F_bonijesulapensis
sect. Americanae
Other Ficus sections
Outgroups
90
80
70
60
50
40
30
20
10
0
CRETACEOUS
PALEOCENE
EOCENE
OLIGOCENE
MIOCENE
PLI
Q
A

Figure 2.

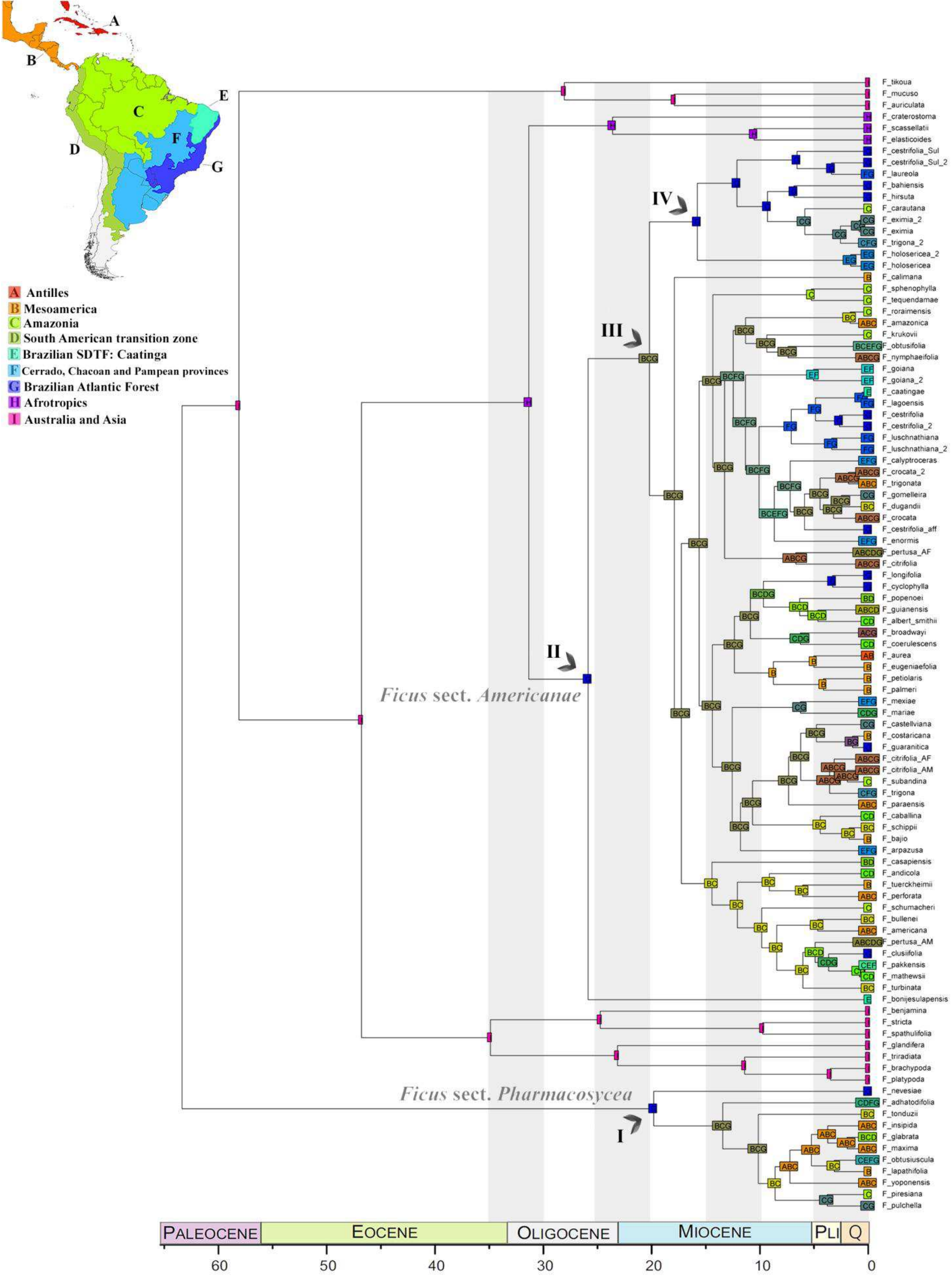

A
B
C
D
E
F
G
A Antilles
B Mesoamerica
C Amazonia
D South American transition zone
E Brazilian SDTF: Caatinga
F Cerrado, Chacoan and Pampean provinces
G Brazilian Atlantic Forest
H Afrotropics
I Australia and Asia
I
II
III
IV
Ficus sect. Americanae
Ficus sect. Pharmacosycea
F_tikoua
F_mucuso
F_auriculata
F_craterostoma
F_scassellatii
F_elasticoides
F_cestrifolia_Sul
F_cestrifolia_Sul_2
F_laureola
F_bahiensis
F_hirsuta
F_carautana
F_eximia_2
F_eximia
F_trigona_2
F_holosericea_2
F_holosericea
F_calimana
F_sphenophylla
F_tequendamae
F_roraimensis
F_amazonica
F_krukovii
F_obtusifolia
F_nymphaeifolia
F_goiana
F_goiana_2
F_caatingae
F_lagoensis
F_cestrifolia
F_cestrifolia_2
F_luschnathiana
F_luschnathiana_2
F_calyptroceras
F_crocata_2
F_trigonata
F_gomelleira
F_dugandii
F_crocata
F_cestrifolia_aff
F_enormis
F_pertusa_AF
F_citrifolia
F_longifolia
F_cyclophylla
F_popenoei
F_guianensis
F_albert_smithii
F_broadwayi
F_coerulescens
F_aurea
F_eugeniaefolia
F_petiolaris
F_palmeri
F_mexiae
F_mariae
F_castellviana
F_costaricana
F_guaranitica
F_citrifolia_AF
F_citrifolia_AM
F_subandina
F_trigona
F_paraensis
F_caballina
F_schippii
F_bajio
F_arpazusa
F_casapiensis
F_andicola
F_tuerckheimii
F_perforata
F_schumacheri
F_bullenei
F_americana
F_pertusa_AM
F_clusiifolia
F_pakkensis
F_mathewsii
F_turbinata
F_bonijesulapensis
F_benjamina
F_stricta
F_spathulifolia
F_glandifera
F_triradiata
F_brachypoda
F_platypoda
F_nevesiae
F_adhatodifolia
F_tonduzii
F_insipida
F_glabrata
F_maxima
F_obtusiuscula
F_lapathifolia
F_yoponensis
F_piresiana
F_pulchella
PALEOCENE
EOCENE
OLIGOCENE
MIOCENE
PLI
Q
60
50
40
30
20
10
0

Figure 3.

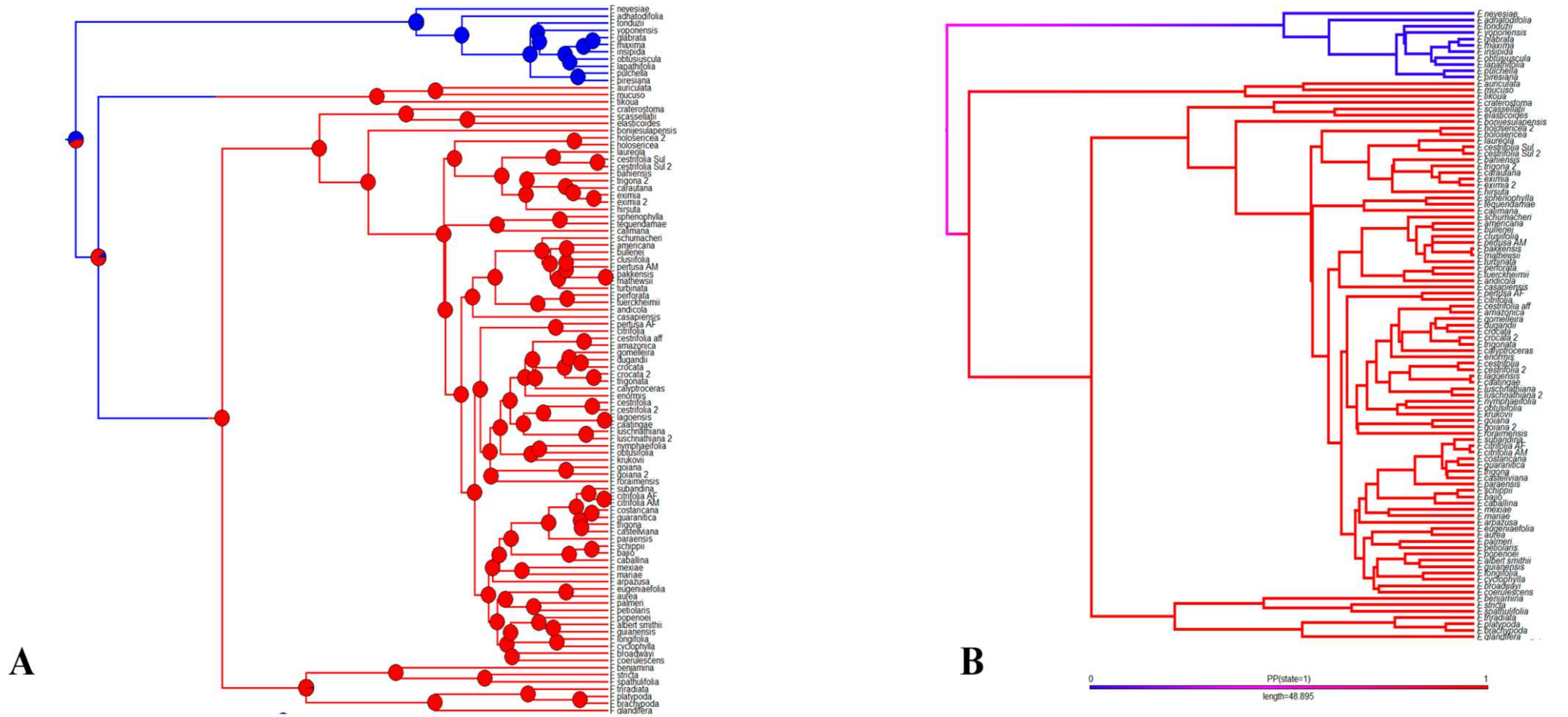

A
nevesiae
adhatodifolia
tonduzii
yoponensis
glabrata
maxima
insipida
obtusiuscula
lapathifolia
pulchella
piresiana
auriculata
mucuso
tikoua
craterostoma
scassellatii
elasticoides
bonijesulapensis
holosericea 2
holosericea
laureola
cestrifolia Sul
cestrifolia Sul 2
bahiensis
trigona 2
carautana
eximia
eximia 2
hirsuta
sphenophylla
tequendamae
calimana
schumacheri
americana
bullenei
clusiifolia
pertusa AM
pakkensis
mathewsii
turbinata
perforata
tuerckheimii
andicola
casapiensis
pertusa AF
citrifolia
cestrifolia aff
amazonica
gomelleira
dugandii
crocata
crocata 2
trigonata
calyptroceras
enormis
cestrifolia
cestrifolia 2
lagoensis
caatingae
luschnathiana
luschnathiana 2
nymphaeifolia
obtusifolia
krukovii
goiana
goiana 2
roraimensis
subandina
citrifolia AF
citrifolia AM
costaricana
guaranitica
trigona
castelviana
paraensis
schippii
bajio
caballina
mexiae
mariae
arpazusa
eugeniaefolia
aurea
palmeri
petiolaris
popenoei
albert smithii
guianensis
longifolia
cyclophylla
broadwayi
coerulescens
benjamina
stricta
spathulifolia
triradiata
platypoda
brachypoda
glandifera
B
0
PP(state=1)
1
length=48.895

Figure 4.

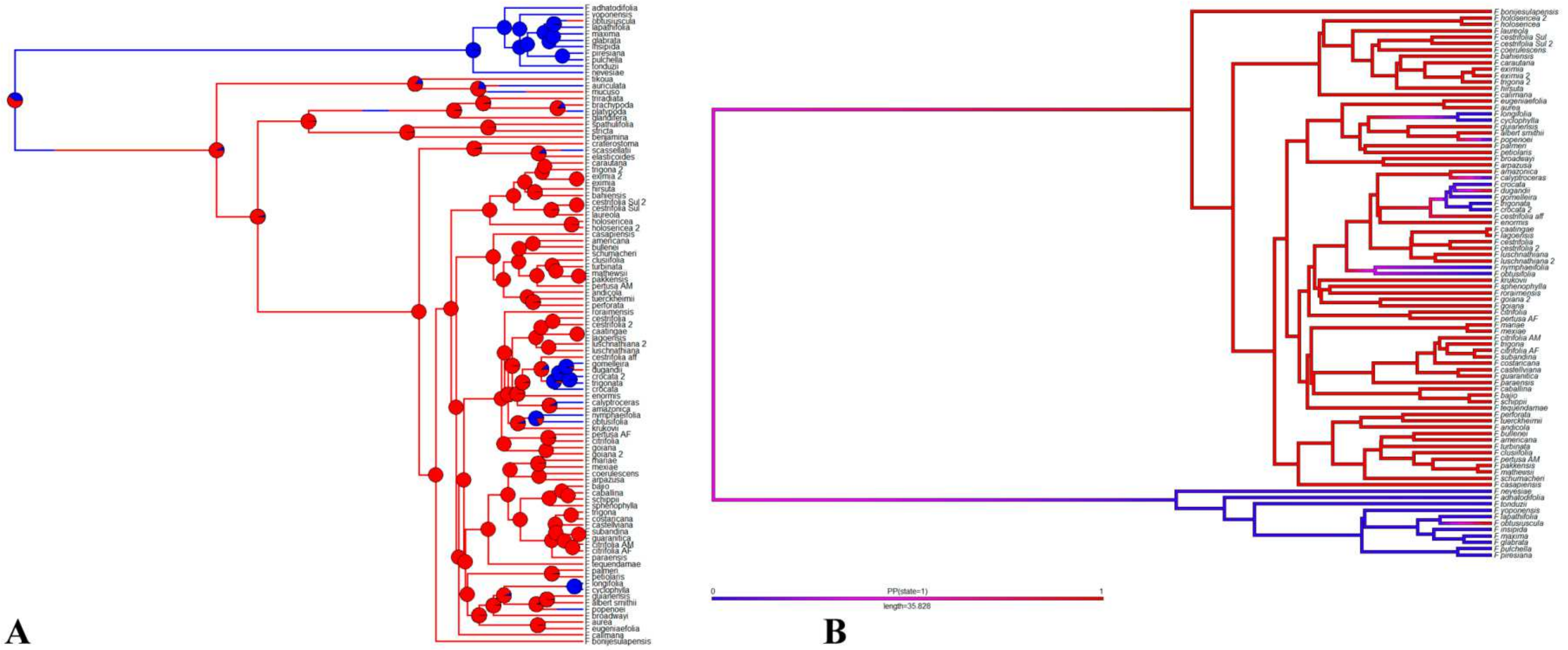

adhatodifolia
yoponensis
obtusiuscula
lapathifolia
maxima
glabrata
insipida
piresiana
pulchella
tonduzii
nevesiae
tikoua
auriculata
mucuso
triradiata
brachypoda
platypoda
glandifera
spathulifolia
stricta
benjamina
craterostoma
scassellatii
elasticoides
carautana
trigona 2
eximia 2
eximia
hirsuta
bahiensis
cestrifolia Sul 2
cestrifolia Sul
laureola
holosericea
holosericea 2
casapiensis
americana
bullenei
schumacheri
clusiifolia
turbinata
mathewsii
pakkensis
pertusa AM
andicola
tuerckheimii
perforata
roraimensis
cestrifolia
cestrifolia 2
caatingae
lagoensis
luschnathiana 2
luschnathiana
cestrifolia aff
gomelleira
dugandii
crocata 2
trigonata
crocata
enormis
calyptroceras
amazonica
nymphaeifolia
obtusifolia
krukovii
pertusa AF
citrifolia
goiana
goiana 2
mariae
mexiae
coerulescens
arpazusa
bajio
caballina
schippii
sphenophylla
trigona
costaricana
castellviana
subandina
guaranitica
citrifolia AM
citrifolia AF
paraensis
tequendamae
palmeri
petiolaris
longifolia
cyclophylla
guianensis
albert smithii
popenoei
broadwayi
aurea
eugeniaefolia
calimana
bonijesulapensis
A
F. bonijesulapensis
F. holosericea 2
F. holosericea
F. laureola
F. cestrifolia Sul
F. cestrifolia Sul 2
F. coerulescens
F. bahiensis
F. carautana
F. eximia
F. eximia 2
F. trigona 2
F. hirsuta
F. calimana
F. eugeniaefolia
F. aurea
F. longifolia
F. cyclophylla
F. guianensis
F. albert smithii
F. popenoei
F. palmeri
F. petiolaris
F. broadwayi
F. arpazusa
F. amazonica
F. calyptroceras
F. crocata
F. dugandii
F. gomelleira
F. trigonata
F. crocata 2
F. cestrifolia aff
F. enormis
F. caatingae
F. lagoensis
F. cestrifolia
F. cestrifolia 2
F. luschnathiana
F. luschnathiana 2
F. nymphaeifolia
F. obtusifolia
F. krukovii
F. sphenophylla
F. roraimensis
F. goiana 2
F. goiana
F. citrifolia
F. pertusa AF
F. mariae
F. mexiae
F. citrifolia AM
F. trigona
F. citrifolia AF
F. subandina
F. costaricana
F. castellviana
F. guaranitica
F. paraensis
F. caballina
F. bajio
F. schippii
F. tequendamae
F. perforata
F. tuerckheimii
F. andicola
F. bullenei
F. americana
F. turbinata
F. clusiifolia
F. pertusa AM
F. pakkensis
F. mathewsii
F. schumacheri
F. casapiensis
F. nevesiae
F. adhatodifolia
F. tonduzii
F. yoponensis
F. lapathifolia
F. obtusiuscula
F. insipida
F. maxima
F. glabrata
F. pulchella
F. piresiana
0
PP(state=1)
1
length=35.828
B

Figure 5.

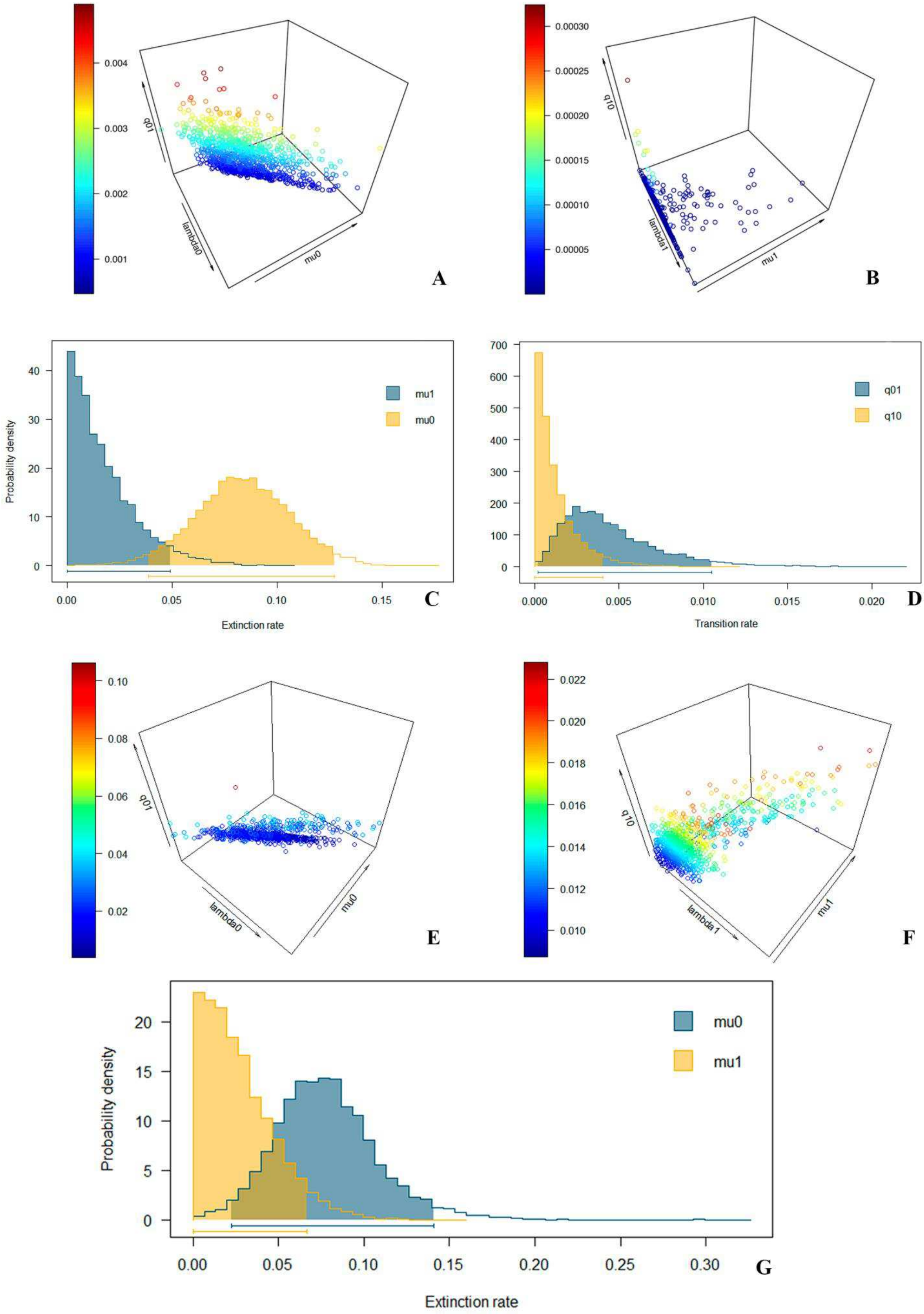

0.004
0.003
0.002
0.001
q01
lambda0
mu0
A
0.00030
0.00025
0.00020
0.00015
0.00010
0.00005
q10
lambda1
mu1
B
Probability density
40
30
20
10
0
mu1
mu0
0.00
0.05
0.10
0.15
Extinction rate
C
700
600
500
400
300
200
100
0
q01
q10
0.000
0.005
0.010
0.015
0.020
Transition rate
D
0.10
0.08
0.06
0.04
0.02
q01
lambda0
mu0
E
0.022
0.020
0.018
0.016
0.014
0.012
0.010
q10
lambda 1
mu1
F
Probability density
20
15
10
5
0
mu0
mu1
0.00
0.05
0.10
0.15
0.20
0.25
0.30
Extinction rate
G

Figure 6.

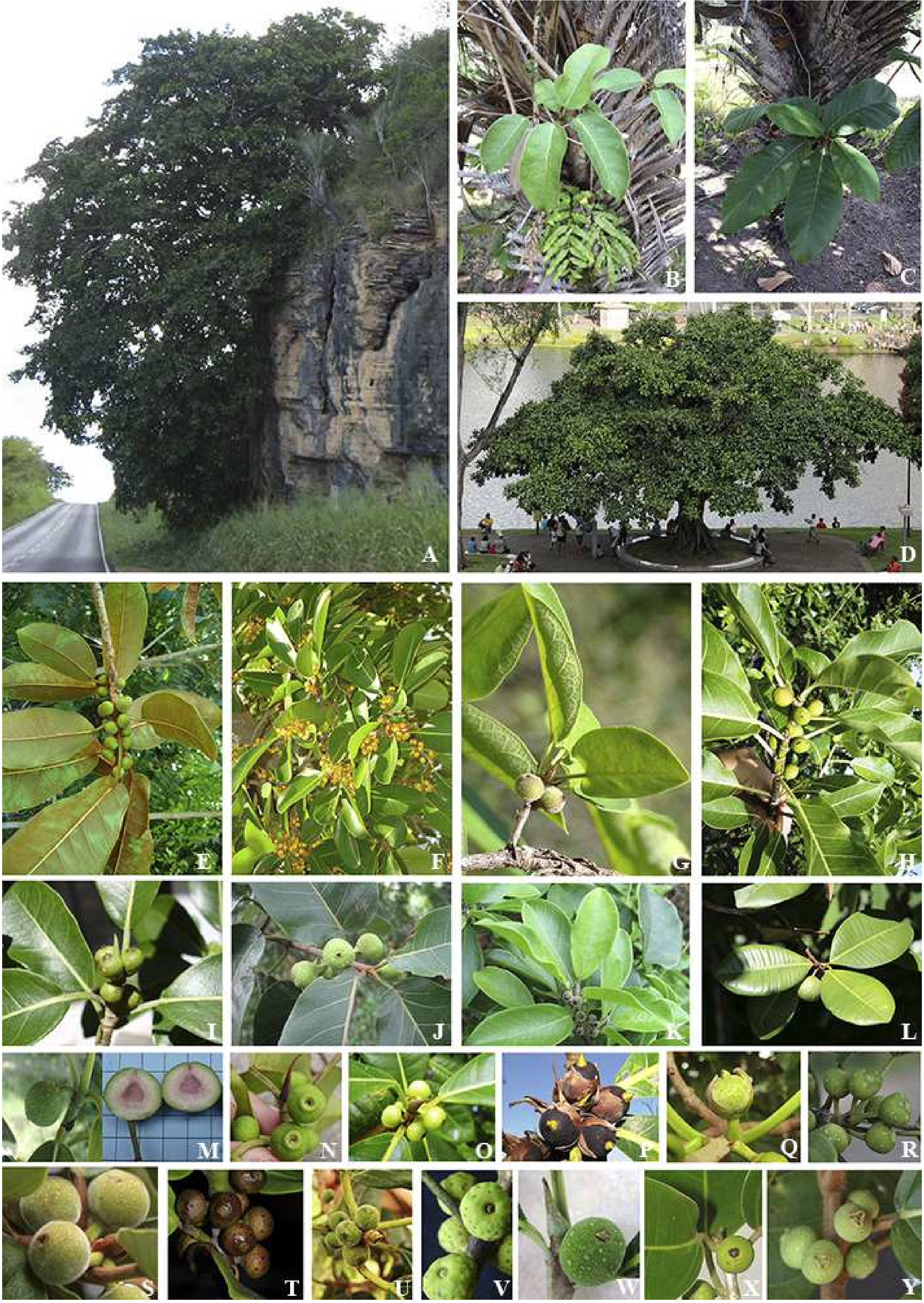


Table 1: Main differences between the two clades of Neotropical figs. *Ficus* section *Americanae* vs. *Ficus* section Pharmacosycea.

	Pharmacosycea	**Americanae**
Number of species	~20	~120
Distribution	Rainforests, rare in other biomes.	All biomes.
Initial habit / habit	Terrestrial (one case of hemi-epiphytic habit) / Tall trees.	Hemiepiphytic, hemiepilhitic, rupicolous, terrestrial. Shrubs, small trees or large “banyan trees”.
Glandular spot(s)	A pair in the axils of basal lateral veins.	One at the top of the petiole.
Syconia position	Axillary and generally solitary.	Axillary or along the branches. Generally in pairs or grouped.
Syconia size and color	Large (> 2.5 cm diam.) rare small. Often green.	Small (0.5-1 cm diam.); medium (1-2.4 cm diam.) or large (> 2.5 cm diam.). Yellow, red, purple.
Basal bracts	3 (three).	2 (two).
Male flowers	2-stamens.	1-stamen.

Table 2: Estimated ages (Mya; median and 95% HPD) for crown nodes of the main lineages for selected nodes and their corresponding support values (BS, maximum-likelihood bootstrap; PP, Bayesian posterior probability).

Node	**Cruaud *et al.* 2012 median ages Ma (95% HPD)**	**This study Calibration with crown ages**	**This study Calibration with crown and stem ages**	**Support (BS/PP)**
Crown *Ficus*	74.9(101.9−60.0)	63.4(80.8−47.8)	63.5(83.5−45.4)	100/1
Crown *Americanae*	20.5(29.3−13.1)	25.9(32.45−20.3)	26.7(33.2−20.5)	88/0.99
Stem *Americanae*	32.3(46.1−22.1)	31.36(40.5−23.6)	32.6(42.65−24.2)	-
Crown *Pharmacosycea*	16.2(25.7−8.2)	19.87(26.6−13.6)	20.1(27.0−13.9)	100/1
Stem *Pharmacosycea*	74.9(101.9−60.0)	63.37(80.8−47.8)	55.4(74.9−38.0)	-

Table 3: Geographical areas used in the Biogeographical analysis.

Code	Geographical Areas
A	Antilles
B	Mesoamerica
C	Amazonia
D	South American transition zone
E	Brazilian seasonally dry tropical forest: Caatinga
F	Brazilian Atlantic forest
G	Cerrado, Chacoan and Pampean provinces (*Sensu* Morrone 2014)
H	Afrotropics
I	Australia and Asia

Table 4. Likelihood (LnL) and Akaike information criterion (AIC) scores from each of the models tested in BioGeoBEARS. The best model is highlighted in bold.

	LnL	numparams	d	e	J	AIC
DEC	-459.3	2	0.010	0.0046	0	922.6
DEC+J	-458.1	3	0.0098	0.0032	0.0060	922.2
DIVALIKE	-478.8	2	0.012	0.0088	0	961.5
DIVALIKE+J	-477.8	3	0.010	1.0e-12	0.0071	961.5
BAYAREALIKE	-405	2	0.0059	0.054	0	814
BAYAREALIKE+J	-399.7	3	0.0056	0.050	0.0022	805.4
DEC*	-436.1	2	0.019	0.10	0	876.2
DEC*+J	-436.1	3	0.020	0.11	1.0e-05	878.2
DIVALIKE*	-445.1	2	0.024	0.15	0	894.2
DIVALIKE*+J	-436.1	3	0.020	0.11	1.0e-05	878.2
BAYAREALIKE*	-372.8	2	0.0063	0.080	0	749.7
BAYAREALIKE*+J	**-369.2**	**3**	**0.0060**	**0.076**	**0.0017**	**744.3**

Table 5: Likelihood ratio test and AIC of each tested model in BiSSE analyses of correlated diversification. Initial habit (terrestrial vs hemiepiphytic) of the Neotropical *Ficus*. The best model is highlighted in bold.

	Df	lnLik	AIC	ChiSq	Pr(>|Chi|)
full	6	-358.78	729.56		
equal.l	**5**	**-358.79**	**727.57**	**0.0113**	**0.91**
equal.m	5	-360.55	731.10	3.5383	0.059
equal.q	5	-360.13	730.26	2.698	0.10
equal.lm	4	-365.00	738.00	12.44	0.001
equal.lq	4	-360.20	728.40	2.835	0.24
equal.mq	4	-363.07	734.13	8.573	0.013
equal.lmq	3	-366.34	738.68	15.11	0.001

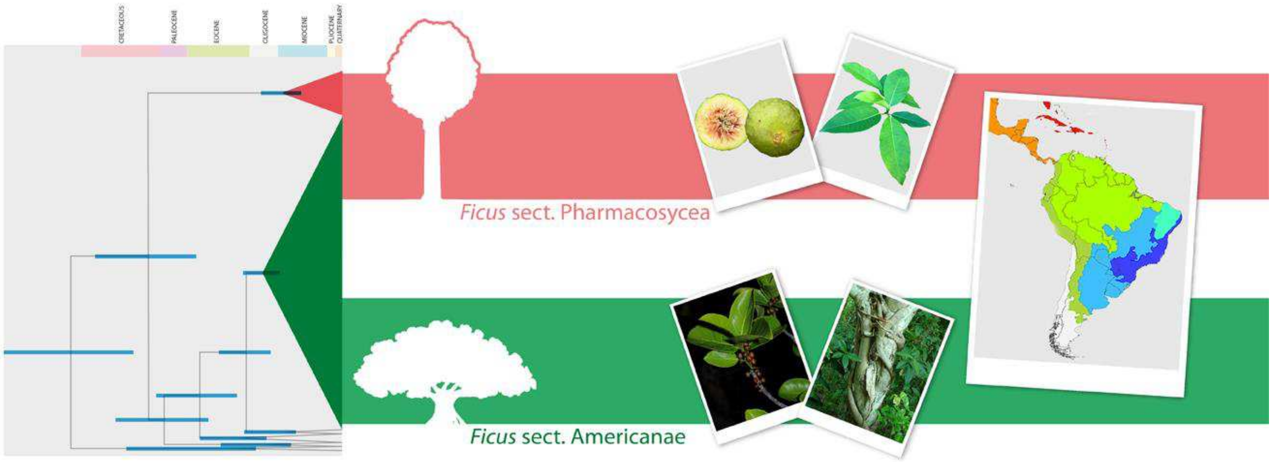
Table 6: Likelihood ratio test and AIC of each tested model in BiSSE analyses of correlated diversification. Syconia size (Large vs. Small) of the Neotropical *Ficus*. The best model is highlighted in bold.

	Df	lnLik	AIC	ChiSq	Pr(>|Chi|)
full	6	-395.75	803.51		
equal.l	5	-396.25	802.49	0.9876	0.3203
equal.m	5	-396.18	802.35	0.8478	0.3572
equal.q	5	-395.76	801.53	0.0195	0.8890
equal.lm	4	-397.33	802.66	3.1548	0.2065
equal.lq	**4**	**-396.38**	**800.76**	**1.2493**	**0.5354**
equal.mq	4	-396.42	800.84	1.3335	0.5134
equal.lmq	3	-398.65	803.30	5.7917	0.1222

Highlights

- Neotropical Ficus diversified in Atlantic Forest and expanded to other rainforests.
- Ficus experienced two bursts of diversification in the Neotropics.
- The diversity of Amazonian figs comes from immigrants and in situ diversification.
- Endemic species in the Atlantic forest diverged after the opening of Cerrado.
- The hemiepiphytic habit and small propagule size influenced the diversification.

Graphical abstract



Appendix A

Voucher information and GenBank accession numbers for each specimen includer in this study. Letters in parenthesis indicate herbarium where voucher is housed. Classification according Berg (2003).

Taxa	Origin	Voucher specimen	GenBank accession				
			At103	**ETS**	**G3pdh**	**ITS**	**Tpi**
Ficus sect.Pharmacosycea							
F. adhatodifolia Schott	Brazil, Santa Catarina.	L.Coelho 51 (HUEFS)	**Pending submission**	**Pending submission**	**Pending submission**	**Pending submission**	-
F. adhatodifolia Schott	Cultivated.	N.Rønsted 148 (K)	-	EU084404	EU087608	EU091563	-
F. glabrata Kunth.	Panama	Jousselin et al. 2003.	-	AY063550	AY967960	AY063593	-
F. insipida Willd.	Cultivated.	N.Rønsted 119 (K)	-	AY063549	AY967961	AY063592	-
F. lapathifolia (Liebm.) Miq.	Mexico, UNAM.	Oyama.	-	EU084405	EU087609	EU091564	-
F. maxima Mill.	Panama.	N.Rønsted 156 (K)	-	-	AY967958	AY063595	-
F. nevesiae Carauta	Brazil, Rio de Janeiro.	A.Machado 108 (HUEFS)	**Pending submission**	**Pending submission**	**Pending submission**	**Pending submission**	**Pending submission**
F. obtusiuscula (Miq.) Miq.	Brazil, Amazonas.	P.Costa AM (SPFR)	**Pending submission**	**Pending submission**	**Pending submission**	-	**Pending submission**
F. obtusiuscula (Miq.) Miq.	Brazil, São Paulo.	R.Pereira 120 (SPFR)	-	-	-	**Pending submission**	-
F. piresiana Vázq.Avila & C.C.Berg	Cultivated.	W.Clement 216 (MIN)	-	-	EU087610	KP406969	-
F. pulchella Schott	Brazil, Santa Catarina.	L. Coelho 64 (SPFR)	**Pending submission**	-	-	-	**Pending submission**
F. pulchella	Brazil,	A.Machad	-	**Pendin**	**Pendin**	-	-

Schott	Rio de Janeiro.	o 1039 (HUEFS)		**g submission**	**g submission**		
F. tonduzii Standl.	Cultivated.	FB/S3752 (BR)	-	AY730230	EU087611	AY730140	-
F. yoponensis Desvaux	Panama	FK2000-14	-	AY063552	AY967959	AY063594	-
Ficus* sect. *Americanae							
F. albert-smithii Standl.	Cultivated.	N.Rønsted 105 (K)	-	AY730157	EU087635	AY730069	-
F. amazonica (Miq.) Miq.	Brazil, Amazonas, São Paulo do Olivença.	L.Queiroz 15738 (HUEFS)	**Pending submission**	-	-	-	**Pending submission**
F. americana Aubl.	Cultivated.	N.Rønsted 154 (K)	-	AY730158	EF092339	AY730070	-
F. andicola Standl.	Cultivated.	N.Rønsted 145 (K)	-	AY730159	EF092340	AY730071	-
F. arpazusa Casar.	Brazil, Bahia, Lençóis.	A.Rapini 1908 (HUEFS)	-	**Pending submission**	**Pending submission**	**Pending submission**	-
F. aurea Nutt.	Cultivated.	N.Rønsted 130 (K)	-	EU084431	EU087636	EU091598	-
F. bahiensis C.C.Berg & Carauta	Brazil, Bahia, Santa Cruz Cabrália.	A.Machado 955 (HUEFS)	-	**Pending submission**	-	**Pending submission**	-
F. sp "bajio"	Cultivated.	Clement 184 (MIN)	-	EU084432	EU087637	EU091599	-
F. bonijesulapensis R.M.Castro	Brazil, Bahia, Carinhanha.	A.Rapini 1476 (HUEFS)	-	-	**Pending submission**	**Pending submission**	**Pending submission**
F. broadwayi Urb.	Cultivated.	N.Rønsted 121 (K)	-	AY730160	EF092341	AY730072	-
F. bullenei I.M.Johnst.	Cultivated.	Jackson et al. 2008.	-	-	EU089833	EU081758	-
F. caatingae R.M.Castro	Brazil, Bahia.	A.Conceição 3124 (HUEFS)	-	-	-	**Pending submission**	-
F. caatingae R.M.Castro	Brazil, Bahia, Santa	A.Machado 1067 (HUEFS)	**Pending submission**	**Pending submis**	-	-	**Pending submis**

	Cruz Cabrália.			**sion**			**sion**
F. caballina Standl.	Cultivated.	N.Rønsted 101 (K)	-	AY730161	-	AY730073	-
F. calimana Dugand	Cultivated.	N.Rønsted 108 (K)	-	AY730162	-	AY730074	-
F. calyptroceras (Miq.) Miq.	Brazil, Bahia, Maracás.	E.Melo et al. 10597 (HUEFS)	-	-	-	-	**Pending submission**
F. calyptroceras (Miq.) Miq.	Brazil, Mato Grosso do Sul, Miranda.	R.Pereira 179 (HUEFS)	**Pending submission**	-	**Pending submission**	**Pending submission**	**Pending submission**
F. carautana Emygdio	Brazil, Mato Grosso do Sul, Corumbá.	M.Bortolin s.n. (SPFR)	**Pending submission**	**Pending submission**	**Pending submission**	**Pending submission**	**Pending submission**
F. casapiensis (Miq.) Miq.	Cultivated.	N.Rønsted 149 (K)	-	AY730163	-	AY730075	-
F. castellviana Dugand	Brazil, ES, Linhares.	A.Machado 823 (HUEFS)	-	**Pending submission**	**Pending submission**	**Pending submission**	**Pending submission**
F. cestrifolia Schott.	Cultivated.	N.Rønsted 139 (K)	-	AY730164	EF092342	AY730076	-
F. cestrifolia Schott.	Brazil, RJ, Teresópolis.	A.Machado 932 (HUEFS)	**Pending submission**	**Pending submission**	EF092342	-	-
F. cestrifolia Schott.	Brazil, SC, Indaial.	L.Coelho 69 (HUEFS)	**Pending submission**	**Pending submission**	**Pending submission**	**Pending submission**	**Pending submission**
F. cestrifolia Schott.	Brazil, RS, Terra de Areia.	C.Gonçalves 602 (HUEFS)	**Pending submission**	**Pending submission**	-	-	-
F. citrifolia Mill.	Cultivated.	N.Rønsted 112 (K)	-	AY730165	AY967955	AY730077	-
F. citrifolia Mill.	Brazil, São Paulo.	R.Pereira 157 (SPFR)	**Pending submission**	-	-	-	-
F. citrifolia Mill.	Brazil, SP, Teodoro Sampaio	L.Coelho 21 (HUEFS)	-	**Pending submission**	**Pending submission**	-	**Pending submission**

	.						
F. citrifolia Mill.	Brazil, Amazonas.	P.Costa AM 58 (SPFR)	-	-	**Pending submission**	**Pending submission**	-
F. citrifolia Mill.	Brazil, Amazonas.	P.Costa 11 (SPFR)	**Pending submission**	-	-	-	**Pending submission**
F. clusiifolia Schott	Brazil, Rio de Janeiro.	A.Machado 917 (HUEFS)	**Pending submission**	**Pending submission**	**Pending submission**	**Pending submission**	**Pending submission**
F. coerulescens (Rusby) Rossberg	Cultivated.	N.Rønsted 122 (K)	-	EU084434	EU087638	EU091601	-
F. costaricana (Liebm.) Miq.	Mexico, UNAM.	Oyama.	-	EU084435	AY967952	EU091602	-
F. crocata (Miq.) Miq.	Brazil, Amazonas.	P.Costa 8 (SPFR)	**Pending submission**	**Pending submission**	**Pending submission**	**Pending submission**	**Pending submission**
F. crocata (Miq.) Miq.	Brazil, MS, Miranda.	R.Pereira 181 (HUEFS)	**Pending submission**	**Pending submission**	**Pending submission**	**Pending submission**	**Pending submission**
F. cyclophylla (Miq.) Miq	Brazil, Espírito Santo.	A.Machado 882 (HUEFS)	**Pending submission**	-	-	-	-
F. cyclophylla (Miq.) Miq	Brazil, São Paulo.	R.Pereira 111 (SPFR)	-	**Pending submission**	**Pending submission**	**Pending submission**	**Pending submission**
F. dugandii Standl.	Cultivated.	Jackson et al. 2008.	-	-	AY967957	EU081763	-
F. enormis Mart. ex Miq.	Brazil, Bahia.	A.Machado 966 (HUEFS)	-	**Pending submission**	**Pending submission**	**Pending submission**	-
F. eugeniifolia (Liebm.) Hemsl.	Mexico, UNAM.	Rønsted et al. 2005.	-	AY730166	-	AY730078	-
F. eximia Schott	Cultivated.	N.Rønsted 146 (K)	-	AY730167	EF092344	AY730079	-
F. eximia Schott	Brazil, Espírito Santo.	A.Machado 645 (HUEFS)	**Pending submission**	-	-	-	-
F. eximia	Brazil,	A.Machad	-	**Pendin**	**Pendin**	**Pendin**	**Pendin**

Schott	São Paulo.	o 1071 (HUEFS)		**g submission**	**g submission**	**g submission**	**g submission**
F. goiana C.C.Berg et al.	Brazil, Bahia.	L.Queiroz 12735 (HUEFS)	**Pending submission**	**Pending submission**	-	**Pending submission**	**Pending submission**
F. goiana C.C.Berg et al.	Brazil, Goiás.	B.Pereira 3597 (HUEFS)	**Pending submission**	**Pending submission**	-	**Pending submission**	**Pending submission**
F. gomelleira Kunth.	Brazil, Bahia.	A.Machado 967 (HUEFS)	**Pending submission**	**Pending submission**	**Pending submission**	**Pending submission**	**Pending submission**
F. guaranitica Chodat	Brazil, Paraná.	C.Snak 520 (HUEFS)	-	**Pending submission**	**Pending submission**	-	-
F. guianensis Desv.	Brazil, Amazonas.	P.Costa AM 20 (SPFR)	**Pending submission**	**Pending submission**	-	**Pending submission**	**Pending submission**
F. hirsuta Schott	Brazil, Espírito Santo.	V.Demuner, 3317	-	-	-	**Pending submission**	-
F. hirsuta Schott	Brazil, RJ, Maricá.	A.Machado 920 (HUEFS)	**Pending submission**	**Pending submission**	**Pending submission**	-	-
F. holosericea Schott	Brazil, ES, Linhares.	A.Machado 828 (HUEFS)	**Pending submission**	**Pending submission**	**Pending submission**	**Pending submission**	**Pending submission**
F. holosericea Schott	Brazil, ES, Santa Teresa.	A.Machado 832 (HUEFS)	**Pending submission**	**Pending submission**	**Pending submission**	-	**Pending submission**
F. krukovii Standl.	Cultivated.	N.Rønsted 107 (K)	-	EU084436	-	EU091603	-
F. lagoensis C.C.Berg & Carauta	Brazil, SP, Ribeirão Preto.	A.Machado 1070 (HUEFS)	**Pending submission**	**Pending submission**	-	**Pending submission**	-
F. lagoensis C.C.Berg & Carauta	Brazil, MS, Corumbá.	A.Silva 415 (MBM)	-	**Pending submission**	-	**Pending submission**	-
F. laureola	Brazil,	A.Machad	**Pending**	**Pendin**	-	**Pendin**	**Pendin**

C.C.Berg & Carauta	Espírito Santo, Linhares.	o et al. 829 (HUEFS)	**submission**	**g submission**		**g submission**	**g submission**
F. longifolia Schott	Cultivated.	N.Rønsted 140 (K)	-	-	-	EU091604	-
F. luschnathiana (Miq.) Miq.	Brazil, São Paulo.	L.Coelho 30 (SPFR)	-	-	**Pending submission**	-	-
F. luschnathiana (Miq.) Miq.	Brazil, RJ, Maricá.	A.Machado 916 (HUEFS)	**Pending submission**	**Pending submission**	-	**Pending submission**	**Pending submission**
F. luschnathiana 2 (Miq.) Miq.	Cultivated.	N.Rønsted 151 (K)	-	AY730170	EF092345	AY730082	-
F. enormis Mart. ex Miq.	Brazil, RJ, Teresópolis.	A.Machado 940 (HUEFS)	-	-	-	**Pending submission**	**Pending submission**
F. mariae C.C.Berg & al.	Brazil, ES, Linhares.	A.Machado 825 (HUEFS)	**Pending submission**	**Pending submission**	**Pending submission**	-	-
F. mathewsii (Miq.) Miq.	Brazil, Amazonas.	P.Costa AM 28 (SPFR)	-	**Pending submission**	-	**Pending submission**	-
F. mathewsii (Miq.) Miq.	Brazil, Amazonas.	P.Costa AM 18 (SPFR)	-	**Pending submission**	-	-	-
F. mathewsii (Miq.) Miq.	Brazil, Amazonas.	P.Costa AM 56 (SPFR)	**Pending submission**	-	-	-	**Pending submission**
F. mexiae Standl.	Brazil, Minas Gerais.	A.Machado 1089 (HUESBVC)	-	-	-	**Pending submission**	**Pending submission**
F. mexiae Standl.	Brazil, BA, Vitória da Conquista.	A.Machado 914 (HUEFS)	**Pending submission**	**Pending submission**	**Pending submission**	-	
F. nymphaeifolia Mill.	French Guyana	N.Rønsted 144 (K)	-	AY063527	EU089843	AY063566	-

F. obtusifolia Kunth.	Cultivated.	N.Rønsted 147 (K)	-	AY730172	AY967949	AY730084	-
F. obtusifolia2 Kunth.	Brazil, SC, Gurinhatã.	L.Coelho 10 (HUEFS)	**Pending submission**	-	**Pending submission**	-	**Pending submission**
F. pakkensis Standl.	Brazil, Amazonas.	P.Costa 30 (SPFR)	**Pending submission**	-	-	-	-
F. palmeri S. Watson	Rønsted et al. 2005.	N.Rønsted 93 (C)	-	AY730173	-	AY730085	-
F. paraensis Miq.	Cultivated.	N.Rønsted 107 (K)	-	AY730174	AY967954	AY730086	-
F. perforata L.	Cultivated.	Oyama	-	AY730175	AY967951	AY730087	-
F. pertusa3 L.	Brazil, RJ, Rio de Janeiro.	A.Machado 913 (HUEFS)	**Pending submission**	**Pending submission**	**Pending submission**	-	**Pending submission**
F. pertusa2 L.	Brazil, Amazonas.	P.Costa AM 60 (SPFR)	**Pending submission**	**Pending submission**	**Pending submission**	**Pending submission**	-
F. petiolaris Kunth.	Cultivated.	N.Rønsted 94 (K)	-	AY730177	-	AY730088	-
F. popenoei Standl.	Cultivated.	Jackson et al. 2008.	-	-	EU089842	EU081761	-
F. roraimensis C.C.Berg	Brazil, Amazonas.	P.Costa AM 9 (SPFR)	**Pending submission**	**Pending submission**	**Pending submission**	**Pending submission**	**Pending submission**
F. schippii Standl.	Cultivated.	N.Rønsted 120 (K)	-	AY730178	-	AY730089	-
F. schumacheri Griseb.	Cultivated.	N.Rønsted 123 (K)	-	-	EF092346	AY063567	-
F. sphenophylla Standl.	Cultivated.	N.Rønsted 98 (K)	-	-	-	EU091605	-
F. subandina Dugand	Cultivated.	N.Rønsted 104 (K)	-	DQ455687	EU087639	DQ455668	-
F. tequendamae Dugand	Cultivated.	FB/S3754 (BR)	-	EU084437	-	EU091606	-
F. trigona L.f.	BG 90-630	N.Rønsted 103 (K)	-	DQ455688	-	DQ455669	-
F. trigona L.f.	Brazil, ES, São Mateus.	A.Machado 822 (HUEFS)	**Pending submission**	**Pending submis**	-	-	-

				sion			
F. trigonata L.	Mexico, UNAM.	Oyama.	-	-	AY967956	EU091607	-
F. tuerckheimii Standl.	Mexico, UNAM.	Oyama.	-	EU084438	EU087640	EU091608	-
F. turbinata Willd.	Cultivated.	Jackson et al. 2008.	-	-	EU089832	EU081769	-
Ficus* sect. *Galoglychia							
Ficus craterostoma	Africa.	Forest 340 (NBG)		AY730186	EF092349	GQ504308	
F. elasticoides De Willd.	Africa.	N.Rønsted 128 (K)	-	AY730192	EF092354	AY730103	-
F. scassellatii Pamp.	Africa.	N.Rønsted 110 (K)	-	AY730196	EF092357	AY730107	-
Ficus* sect. *Malvanthera							
F. brachypoda (Miq.) Miq.	Australia.	Dixon s.n	-	-	EF538788	EF545652	-
F. glandifera Summerh.	Australia.	Wheatley 297 (K)	-	AY730202	EF092361	AY730113	-
F. platypoda A.Cunn. ex Miq.	Australia.	Jacobs/Wilson 5665 (K)	-	AY730206	EF538794	AY730116	-
F. triradiata Corner	Australia.	Hind & Herscovitch 6409 (K)	-	AY730207	EF092364	AY730117	-
Ficus* sect. *Sycomorus							
F. auriculata Loureiro	Asia.	N.Rønsted 264 (HITBC)	-	FJ812281	EU087653	KM234117	-
F. mucuso Welw. ex Ficalho	Cultivated.	N.Rønsted 129 (K)	-	AY730210	EF092372	AY730120	-
F. tikoua Bur.	Asia.	N.Rønsted 294 (HITBC)	-	EU084468	EU087673	EU091641	-
Ficus* sect. *Conosycea							
F. benjamina L.	C 1870-5193 / Thailand	N.Rønsted 81 (C) / N.Rønsted 179 (AAU/K),	-	AY063520	EF092333	AY063559	-
F. spathulifolia	Asia.	G.Weiblen 929	-	EU084428	EU087631	EU091594	-

Corner		(MIN)					
F. stricta (Miq.) Miq.	Asia.	N.Rønsted 288 (HITBC)	-	EU084429	EU087632	EU091595	-
Outgroup: Tribe Castillae							
Antiaropsis decipiens K.Schum.	PNG.	G.Weiblen 1706 (MIN)	**Pending submission**	**EU084403**	**Rønsted 08a**	**Rønsted 05**	-
Castilla elastica Sessé in Cerv.	Panama.	MWC 19850	**MWC19850**	**AY730232**	**AY730232**	**FJ916997**	-
Sparattosyce dioica Bur.	New Caledonia.	G.Weiblen 1223 (MIN)	**Pending submission**	**AY730231**	**EU087607**	**AY730141**	-

CONSIDERAÇÕES FINAIS

As duas seções de figueiras neotropicais, *Ficus* sect. *Americanae* (~120 spp.) e *Ficus* sect. *Pharmacosycea* (~20 spp.), apresentam taxonomia e biogeografia complexas. Por esta razão, as abordagens biogeográficas, filogenéticas, taxonômicas, nomenclaturais e morfológicas que compõem este trabalho mostraram-se importantes para a solução de alguns problemas taxonômicos e nomenclaturais bem como para a compreensão da história evolutiva e da diversificação das figueiras presentes na região.

As abordagens taxonômicas e nomenclaturais aqui apresentadas evidenciaram a ocorrência de dois novos táxons para a flora brasileira (*Ficus diamantina* sp. nov. e *Ficus ninae* sp. nov.) e a correta aplicação de nomes para outros táxons (*Ficus goiana* C.C.Berg et al. e *Ficus bilinaensis* nom. nov. este, um fóssil) bem como reestabelecimento de um binômio (*Ficus tweediana*) anteriormente incluído na sinonímia de *F. cestrifolia* Schott.

Também nesta tese é apresentada a primeira chave contemplando as espécies de *Ficus* sect. *Americanae* (figueiras estrangulantes ou mata-paus) para o Domínio da Mata Atlântica, preenchendo assim uma lacuna no que se refere ao conhecimento das espécies que ocorrem no Brasil. Nesta região ocorrem 28 espécies (dentre estas uma espécie nova e uma reestabelecida).

A existência de pesquisas recentes abordando as espécies amazônicas de *Ficus* e a seção *Pharmacosycea* para o Brasil e, agora, os resultados deste trabalho, fazem-nos crer que novas investigações devem focar no estudo das espécies ocorrentes no semiárido e sua relação com os inselbergs, bem como as espécies do Cerrado. C.C. Berg (1934-2012) & J.P.P. Carauta (1930-2013) apontaram a ocorrência de novas espécies no semiárido brasileiro e, possivelmente, de híbridos nestas regiões (com. pess). Apesar de ter me voltado mais especificamente para as florestas úmidas analisei a alguns materiais de florestas secas para os quais não pude chegar a um nome com precisão.

A taxonomia de *Ficus* apresenta alguns problemas no que se refere à utilização de caracteres para delimitação de espécies. Neste sentido, lançamos mão de caracteres anatômicos da inflorescência em um determinado grupo de espécies de *Ficus* na intenção de descrever estruturas florais com potencial valor taxonômico. Este esforço resultou em uma interessante observação da especialização estrutural das brácteas secretoras e da observância de coléteres. Sugere-se que espécies de seções diferentes e/ou complexos de espécies podem apresentar arranjos distintos das brácteas e caracteres microestruturais da inflorescência. Provavelmente a investigação de caracteres anatômicos das inflorescências, estes subutilizados na taxonomia de *Ficus*, poderá lançar luz sobre a classificação infragenérica do grupo uma vez que sabemos que a maior parte dos subgêneros reconhecidos até o momento não são monofiléticos.

Finalmente, a nossa abordagem filogenética e biogeográfica dos *Ficus* neotropicais apresenta uma hipótese, fortemente sustentada, de diversificação nas florestas úmidas da região a partir da Floresta Atlântica e expandindo-se para todo o continente Americano. O hábito hemiepífito inicial e os propágulos pequenos a medianos das espécies de *Ficus* sect. *Americanae* possibilitaram a sua maior diversificação nos Neotrópicos.

Em síntese, esta tese demonstrou a importância de múltiplas abordagens para a melhor compreensão da taxonomia e para a elucidação da história biogeográfica de grupos ricos em espécies. Estudar *Ficus*, com suas peculiaridades reprodutivas e morfológicas, na região Neotropical, com seus complexos eventos geológicos e hidrológicos, possibilitou a utilização de abordagens diversas na intenção de lançar luzes sobre os processos que geraram os padrões de riqueza e diversidade observados.