Sistemática e Biogeografia de *Parkia* (Leguminosae, Caesalpinioideae, clado mimosoide)

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Programa de Pós-Graduação em Botânica

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Manaus, AM
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Orientador: Dr. Michael John Gilbert Hopkins
Coorientadora: Dra. Doriane Picanço Rodrigues

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INPA INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA
DIVISÃO DO CURSO DE PÓS-GRADUAÇÃO EM BOTÂNICA

PÁTRIA AMADA BRASIL
GOVERNO FEDERAL

ATA DEFESA PÚBLICA DE TESE DE DOUTORADO DISCENTE DO PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS (BOTÂNICA) DO INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA.

Aos vinte e um dias do mês de agosto de 2020 às 14:00 horas, através da plataforma online Google Meets, reuniu-se a Comissão Examinadora da Defesa Pública, composta pelos seguintes membros: Dr. Leandro Lacerda Giacomin, da Universidade Federal do Oeste do Pará (UFOPA), Dr. Marcelo Fragomeni Simon, da Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA) e Dr. Domingos Benício Oliveira Silva Cardoso, da Universidade Federal da Bahia (UFBA), tendo como suplentes: Dra. Camila Cherem Ribas, do Instituto Nacional de Pesquisas da Amazônia (INPA) e Dr. Jadson José Souza de Oliveira, do Instituto Nacional de Pesquisas da Amazônia (INPA), sob a presidência do primeiro, a fim de proceder a arguição pública da defesa de **TESE DE DOUTORADO**, intitulada: **"Sistemática e Biogeografia de *Parkia* (Leguminosae, Caesalpinoideae, clado mimosoide)"** pela discente **Lorena Conceição Oliveira**, sob orientação do Dr. Michael John Gilbert Hopkins e coorientação da Dra. Doriane Picanço Rodrigues. Após a exposição, dentro do tempo regulamentar, a discente foi arguida oralmente pelos membros da Comissão Examinadora, tendo recebido o conceito final:

EXAMINADORES	PARECER		ASSINATURA
DOMINGOS BENÍCIO O. S. CARDOSO	(X) APROVADO	( ) REPROVADO	Domingos Benício Oliveira Silva Cardoso
LEANDRO LACERDA GIACOMIN	(X) APROVADO	( ) REPROVADO	Leandro L. Giacomin
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JADSON JOSÉ SOUZA DE OLIVEIRA	( ) APROVADO	( ) REPROVADO	

Manaus (AM), 21 de agosto de 2020.

OBS: A banca considerou a aluna aprovada por unanimidade e encaminha comentários e sugestões a serem consideradas pelo aluno e orientador.

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

Dr. Michael John Gilbert Hopkins
Coordenador do Programa de Pós-Graduação em Botânica
PO. 116/2017 - DIBOT/INPA

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Sinopse:

Foram inferidas as relações filogenéticas de 30 espécies de *Parkia* (Leguminosae, Caesalpinioideae, clado mimosoide) com base em dados do DNA cloroplastidial e nuclear, utilizando-se abordagens analíticas de máxima verossimilança e inferência bayesiana. Também foram estimados os tempos de divergência das linhagens por meio de uma filogenia datada por calibração fóssil e a reconstrução da biogeografia histórica. Investigamos ainda a evolução da morfologia floral, da quiropterofilia e entomofilia no gênero.

Palavras-chave: Fabaceae, filogenia molecular, sistemas de polinização

“Nothing in biology makes sense except in the light of evolution”

Theodosius Dobzhansky

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Ao Programa de Pós-Graduação em Botânica do INPA, que tornou possível a realização deste trabalho.

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Resumo

Parkia R.Br. (Leguminosae, Caesalpinioideae, mimosoid clade) é um gênero pantropical com aproximadamente 35 espécies reconhecidas em três seções taxonômicas (*Parkia*, *Platyparkia* e *Sphaeroparkia*), definidas com base no tipo e no arranjo das flores em suas inflorescências. Com alto grau de endemismo, as espécies do gênero tem se diversificado em florestas tropicais e savanas na América do Sul e Central, África, Madagascar e região Indo-Pacífico. Neste estudo, análises filogenéticas datadas por calibração fóssil (Máxima Verossimilhança e Inferência Bayesiana) e análises biogeográficas (BioGeoBEARS) foram realizadas usando dados de DNA cloroplastidial (*matK*, *trnL*, *psbA-trnH* e *rps16-trnQ*) e nuclear (ITS/18S/26S) com os objetivos de testar a monofilia de *Parkia* e seus três grupos infragenéricos; estimar os tempos de divergência de suas linhagens e quais fatores podem ter influenciado sua diversificação; inferir a origem geográfica e investigar a evolução de sua morfologia floral e de seus sistemas de polinização. Nossos resultados apoiam a monofilia do gênero, as seções *Sphaeroparkia* e *Platyparkia* são monofiléticas; a seção *Parkia* é recuperada como parafilética. As análises biogeográficas e bayesianas calibradas por fóssil estimam a origem de *Parkia* há aproximadamente 18,49 Ma na região Neotropical. A evolução do capítulo mostra uma transição de uma estrutura mais especializada para uma estrutura mais simples. A quiropterofilia é provavelmente ancestral e a entomofilia é derivada.

Palavras-chave: evolução floral, Fabaceae, filogenia molecular, reconstrução biogeográfica

Abstract

Parkia R.Br. (Leguminosae, Caesalpinioideae, mimosoid clade) is a pantropical genus with approximately 35 species recognized in three taxonomic sections (*Parkia*, *Platyparkia* and *Sphaeroparkia*), defined based on the type and arrangement of the flowers in their inflorescences. With a high degree of endemism, the species of the genus have diversified into tropical forests and savannas in South and Central America, Africa, Madagascar and the Indo-Pacific region. In this study, phylogenetic analyses dated by fossil calibration (Maximum Likelihood and Bayesian Inference) and biogeographic analyses (BioGeoBEARS) were performed using chloroplast DNA (*matK*, *trnL*, *psbA-trnH* and *rps16-trnQ*) and nuclear (ITS/18S/26S) data in order to test the monophyly of *Parkia* and its three infrageneric groups; estimate the times of divergence of their lineages and what factors may have influenced their diversification; infer the geographical origin and investigate the evolution of its floral morphology and its pollination systems. Our results support the monophyly of the genus, the sections *Sphaeroparkia* and *Platyparkia* are monophyletic; the section *Parkia* is recovered as paraphyletic. Fossil-calibrated biogeographic and bayesian analyses estimate *Parkia* origin approximately 18.49 Ma in the Neotropical region. Capitulum evolution shows a transition from a specialized structure to a simpler structure. Chiropterophily is probably ancestral and entomophily is derived.

Keywords: biogeographic reconstruction, floral evolution, Fabaceae, molecular phylogeny

Sumário

Lista de figuras

CAPÍTULO 1

CAPÍTULO 2

Apresentação

Leguminosae compreende aproximadamente 770 gêneros e 19.500 espécies, sendo a terceira maior família das angiospermas em número de espécies, depois de Orchidaceae e Asteraceae. As leguminosas são cosmopolitas e representam constituintes importantes em quase todos os biomas do globo, ocorrendo mesmo em ambientes mais extremos (Schrire *et al.*, 2005). A capacidade de fixar nitrogênio atmosférico através de simbiose com bactérias permitiu que alguns grupos de Leguminosae alcançassem um notável sucesso evolutivo em termos de diversificação, o que lhes conferiu grande importância econômica e ecológica (Lewis *et al*,. 2005, LPWG, 2013; 2017).

O monofiletismo da família tem sido sustentado, bem como o seu posicionamento em Fabales, juntamente com Polygalaceae, Quillajaceae e Surianaceae (APG IV, 2016).

A taxonomia de Leguminosae tem sido bem estudada (Polhill e Raven, 1981; Polhill 1994; Lewis *et al.*, 2005) e diversos são os estudos filogenéticos, baseados tanto em dados moleculares quanto morfológicos, realizados para a família (Doyle, 1995; Kass e Wink, 1995, 1996, 1997; Doyle *et al.*, 1997, 2000; Hu *et al.*, 2000; Bruneau *et al.*, 2001, 2008; Lavin *et al.*, 2001, 2003, 2005; Kajita *et al.*, 2001; Luckow *et al.*, 2003; Pennington *et al.*, 2001; Doyle e Luckow, 2003; Wojciechowski *et al.*, 2003, 2004; Judd e Olmstead, 2004; LPWG, 2013).

Esse notável desenvolvimento quanto à compreensão das relações filogenéticas indica que a tradicional e amplamente aceita classificação das Leguminosae em três subfamílias – Caesalpinioideae DC., Mimosoideae DC., Papilionoideae DC. – não reflete as relações filogenéticas da família. Baseado no padrão filogenético, consistentemente resolvido nesses vários estudos, foi proposta uma nova classificação para as leguminosas, e atualmente são reconhecidas seis subfamílias monofiléticas: Duparquetioideae LPWG, Cercidoideae LPWG, Detarioideae Burmeist., Caesalpinioideae DC. e Papilionoideae DC. (LPWG, 2017).

Mimosoideae, tradicionalmente reconhecida como uma das três subfamílias, atualmente é reconhecida como um clado (mimosoide) aninhado em Caesalpinioideae (LPWG, 2017).

Com cerca de 83 gêneros e 3.273 espécies (Lewis *et al.*, 2005, LPWG, 2017), morfologicamente, o clado mimosoide difere das demais linhagens de Leguminosae pelas folhas geralmente bipinadas (com exceção do gênero *Inga*), corola com prefloração valvar, flores actinomorfas, agrupadas em espigas, glomérulos, racemos e umbelas (LPWG, 2017).

Parkia R.Br. é um gênero da família Leguminosae com ca. de 35 espécies arbóreas distribuídas pelos trópicos do Novo e do Velho Mundo. Baseado no alto grau de simpatria das espécies; Luckow e Hopkins (1995) descreveram quatro áreas de endemismo para o gênero: (1) América do Sul, (2) África, (3) Madagascar e (4) região Indo-Pacífico. As espécies ocorrem em diferentes hábitats incluindo desde florestas e savanas da África, Madagascar e região Indo-Pacífico, até florestas de várzea, florestas periodicamente inundadas e florestas de areia branca pobre em nutrientes na bacia amazônica, que tem sido descrito como o principal centro de diversidade morfológica e taxonômica, com ca. de 56% das espécies reconhecidas do gênero (Hopkins, 1986; Luckow e Hopkins, 1995).

Brown (1826) descreveu o gênero pela presença de flores férteis de cálice cilíndrico com prefloração imbricada, dez estames férteis levemente conados até a base e pela presença de estaminódios em algumas espécies. Desde sua definição, o gênero vem sofrendo uma série de reorganizações em relação à sua classificação infragenérica. Bentham (1875) dividiu o gênero em duas seções *Euparkia* (espécies africanas, asiáticas e parte das espécies neotropicais) e *Paryphosphaera* (demais espécies neotropicais). Posteriormente, Ducke (1949) realizou um estudo com ênfase nas espécies neotropicais, onde descreveu cinco espécies novas, propôs a circunscrição do gênero em quatro seções, manteve parte das espécies neotropicais submetidas à seção *Paryphosphaera*, as espécies do Velho Mundo continuaram submetidas à *Euparkia*, e criou duas novas seções, *Platyparkia* e *Sphaeroparkia*, onde agrupou o restante das espécies neotropicais. Hopkins (1986) propôs uma nova circunscrição para o gênero, reconhecendo três seções com base nos tipos funcionais das flores e seus arranjos no capítulo. Na seção *Sphaeroparkia*, foram incluídas as espécies com capítulos formadas inteiramente por flores férteis; na seção *Platyparkia* foram reunidas as espécies que apresentam dois tipos de flores em seus capítulos, flores férteis e nectaríferas, e por fim, na seção *Parkia* agrupou as espécies com capítulos contendo três tipos de flores: férteis, nectaríferas e flores neutras formando estaminódios.

A presença de um cálice cilíndrico com lobos desiguais de prefloração imbricada tem sido a sinapomorfia morfológica que distingue *Parkia* dos demais gêneros em Leguminosae. Estudos filogenéticos recentes realizados para o clado mimosoide com base em dados de regiões de cloroplasto, suportam o monofiletismo do gênero, e recuperam *Parkia* como clado irmão do grupo Piptadenia (Lewis *et al.*, 2005; LPWG, 2013). O estudo filogenético mais abrangente que se concentrou em o grupo Piptadenia (Jobson e Luckow, 2007) apresentou uma contribuição substancial para a compreensão dos relacionamentos dentro do grupo. No entanto, ainda existem questões em aberto sobre as delimitações genéricas, principalmente por falta de resolução na filogenia e amostragem limitada de alguns táxons. Nesse sentido, são necessários mais filogenias de gêneros previamente subamostrados em estudos filogenéticos (Simon, 2016).

Oliveira (2015) inferiu as relações filogenéticas de 22 espécies de *Parkia* com base em dados de três regiões cloroplastidiais (*trnH-psbA*, *trnQ-rps16* e *trnL*). Corroborando estudos prévios, o monofiletismo do gênero foi sustentado por altos valores de bootstrap e probabilidade posterior (BS 99%, PP 1). Quanto à classificação infragenérica, as seções *Platyparkia* e *Sphaeroparkia* foram sustentadas como monofiléticas e a seção *Parkia* aparece como parafilética. Entretanto, tais relações fora estimadas apenas com dados do DNA de cloroplasto. Luckow e Hopkins (1995) também inferiram o monofiletismo do gênero com base em dados de 52 caracteres morfológicos, entretanto, discordando dos dados do DNA cloroplastidial, a seção *Sphaeroparkia* foi recuperada como parafilética, e as seções *Platyparkia* e a *Parkia* aparece como monofilética neste estudo.

Luckow e Hopkins (1995), em sua análise cladística, inferiram uma provável origem neotropical e, com base em seu padrão de disjunção continental, propuseram uma distribuição Gonduânica para *Parkia* durante o último cretáceo. No entanto, registros fósseis indicam que os primeiros representantes de Leguminosae surgiram entre 50-60 Ma na América do Norte, Europa e África (Herendeen e Dilcher, 1992; Herendeen *et al.*, 1992), excluindo uma origem Gonduânica para o gênero. Estudos filogenéticos recentes também indicam que a família foi rapidamente diversificada há aproximadamente 60 milhões de anos atrás, durante o terciário (Lavin *et al.*, 2005). As primeiras linhagens do clado mimosoide teriam diversificado ca. 50 Ma e clado formado pelos membros do Grupo Piptadenia, são datados aproximadamente. 45 Ma. Lavin et al. (2004) sugere que a dispersão a longas distâncias tem sido a força predominante que molda a distribuição de Leguminosae.

Entender as relações filogenéticas das espécies de gêneros geograficamente difundidos pode revelar se filogenias estão geograficamente estruturadas e quando esses gêneros estão distribuídos em mais de um continente, também oferecem oportunidades para testar a hipótese de dispersão de espécies à longa distância ou por vicariância (Renner, 2004; Schrire *et al.*, 2009; Simon *et at.*, 2011).

O advento de técnicas filogenéticas e métodos biogeográficos nas últimas décadas tem permitido inferir quais os padrões de diversificação das linhagens de plantas atuais e quais processos deram origem a estes padrões (Pennington *et al.*, 2006). Esta diversificação provavelmente está associada a processos ecológicos (Antonelli e SanMartín, 2011; Rull, 2011) e eventos geológicos complexos que agiram em conjunto ao longo do tempo (Graham, 2011; Hoorn *et al.*, 2010, 2011; Christenhusz e Chase, 2013).

Inferir a origem e compreender como ocorreu a dispersão das linhagens de *Parkia* auxiliará na compreensão da evolução das síndromes de polinização dentro do gênero. Em *Parkia* são registrados a quiropterofilia e a entomofilia. A entomofilia é exclusivamente Neotropical e ocorre nas três espécies descritas na seção *Sphaeroparkia*. A quiropterofilia ocorre nas espécies agrupadas nas seções *Parkia* (Pantropical) e *Platyparkia* (Neotropical). Nos Neotrópicos a polinização é feita por morcegos Phyllostomidae e nos Paleotrópicos por morcegos Pteropodidae (Baker e Harris, 1957; Hopkins, 1984). Tais morcegos são distantemente relacionados entre si, o que pode sugerir que a quiropterofilia teria evoluído de maneira independente nas linhagens neotropicais e paleotropicais do gênero.

A quiropterofilia é considerada um "beco sem saída" evolutivo, o que significa que raramente pode ser substituída por outro sistema de polinização (Tripp e Manos, 2008; Muchhala e Thomson, 2010; Gómez *et al.*, 2014). A rota de transição reversa entre entomofilia e quiropterofilia é um evento evolutivo mais comum (Tripp e Manos, 2008; Muchhala e Thomson, 2010), devido ao fato de muitas plantas polinizadas por morcegos terem um provável ancestral polinizado por abelhas (Rosas-Guerrero *et al.*, 2014). A presença dessas duas síndromes de polinização em *Parkia* permite examinar mudanças na morfologia floral e nos sistemas de polinizadores em um contexto filogenético e biogeográfico.

Neste contexto, este estudo visa inferir uma hipótese sobre as relações filogenéticas e a biogeografia histórica de *Parkia* através de uma filogenia molecular datada construída a partir de uma ampla amostragem em análises de sequências dos genes plastidiais *matK*, *trnL*, *rps16-trnQ* e *psbA-trnH* e do DNA nuclear ribossomal ITS/18S/26S. Além disso, o trabalho aqui proposto busca contribuir não somente para a sistemática filogenética e biogeografia de *Parkia*, mas também para futuros estudos sobre as relações genéricas no grupo Piptadenia e para a reconstrução da história biogeográfica da família Leguminosae.

OBJETIVOS

O presente trabalho foi conduzido com os objetivos de: (1) inferir uma hipótese de relação filogenética para *Parkia*; (2) estimar o tempo de divergência das espécies paleotropicais e neotropicais; (3) propor uma hipótese de distribuição ancestral das linhagens atuais de *Parkia*; (4) compreender quais processos originaram os padrões de diversificação e distribuição das espécies; (5) reconstruir os estados de caracteres morfológicos ancestrais dos capítulos de *Parkia*, e (6) investigar a evolução das síndromes de polinização do gênero.

Organização da Tese

A tese está organizada em 2 capítulos, onde são apresentados (1) as relações filogenéticas de 30 espécies de *Parkia* e a reconstrução da sua biogeografia histórica; e a (2) evolução de sua morfologia floral e dos sistemas de polinização do gênero. Os capítulos são manuscritos escritos em inglês, e seguem as normas de formatação da revista à qual o mesmo será submetido. Algumas modificações na formatação foram feitas com o intuito de facilitar a leitura.

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Capítulo 1

Phylogeny and historical biogeography of the pantropical genus *Parkia* (Leguminosae, Caesalpinioideae, mimosoid clade)

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ABSTRACT

Parkia R.Br. (Leguminosae, Caesalpinioideae, mimosoid clade) is a pantropical genus with approximately 35 recognized species in three taxonomic sections (*Parkia*, *Platyparkia* and *Sphaeroparkia*), distributed widely in tropical forests and savannas in South and Central America, Africa-Madagascar and the Indo-Pacific region. In this study, phylogenetic (Maximum Likelihood and Bayesian Inference) and biogeographic (BioGeoBEARS) analyses were performed using chloroplast (*matK*, *trnL*, *psbA-trnH* and *rps16-trnQ*) and nuclear (ITS/18S/26S) DNA sequences for the purpose of testing the monophyly of *Parkia* and its three infrageneric groups and inferring the geographic origin of the genus and times of divergence of the various lineages. This enabled investigation of factors that may have influenced its diversification in both hemispheres. Our results support the monophyly of the genus, and of sections *Sphaeroparkia* and *Platyparkia*, whereas section *Parkia* is paraphyletic in Bayesian analysis, and the species in this section are recovered in two geographically structured lineages (Neotropical and Paleotropical). A fossil-calibrated Bayesian analysis dated the *Parkia* crown node to the Miocene (at c. 18.49 Ma). Biogeographic analysis reconstructed an origin in Amazonia with subsequent radiation in the Neotropical region from the Miocene onwards, with dispersion events as far as Central America, and the Atlantic Forest and the *cerrado* of Brazil. A single dispersion from the Neotropics to the Paleotropics is hypothesised, with subsequent smaller radiations in Africa-Madagascar and the Indo-Pacific (crown ages 3.76 and 5.4 Ma respectively). Factors that may have influenced the radiation and speciation of *Parkia* include the elevation of the Andes (especially in the Miocene), and more recently the closing of the Panama gap in Neotropics, the climatic fluctuations of the Pleistocene influenced the diversification of species on both continents. The elevation of the Sunda Shelf in Indo-Pacific region during the last glacial maximum (LGM) appears to be the main driving force for speciation in that region. In Africa, the low number of species may be related to extinction processes.

Keywords: Fabaceae, divergence times, last glacial maximum, long-distance dispersal, molecular phylogeny

1. Introduction

Parkia R.Br. is a pantropical genus with approximately 35 species of trees distributed in South and Central America, Africa-Madagascar and the Indo-Pacific region (Luckow and Hopkins, 1995; Luckow, 2005). The species have a high degree of regional endemism. The Amazon basin is the main centre of taxonomic and morphological diversity with 17 of the 19 Neotropical species found there, of which 10 are restricted to the Amazonian biome. In the Neotropics, the genus extends beyond Amazonia to coastal, north-eastern and central Brazil, to the Guianas, Venezuela and the Pacific coast of Colombia, and northwards to Panama, Costa Rica and Nicaragua. In the Paleotropics, 12 species are endemic to the Indo-Pacific region, extending from north-eastern India to Ponape and Fiji, and four others are restricted to the African continent, including one endemic to northern Madagascar (Hopkins, 1983, 1986, 1994).

Most species of *Parkia* throughout its distribution occur in lowland rain forest (*terra firme* forest in Amazonia) (rarely above 1000 m) but the African, Malagasy and Indo-Pacific taxa occupy a more limited range of habitats than do the Neotropical ones (Hopkins, 1983, 1994, 2000). For instance, although *P. biglobosa* occurs in woodland, which is perhaps the African equivalent of Brazilian *cerrado* (occupied by *P. platycephala* and *P. cachimboensis*), and *P. leiophylla* and *P. sumatrana* are found in dry evergreen forest in Thailand (Nielsen, 1985), no species in the Paleotropics is a specialist in *kerangas* or heath forest, which is probably the closest equivalent to the forest on nutrient-poor white sands (*campinarana,* occupied by *P. igneiflora* in Amazonia), nor in the equivalent of *restinga* (occupied by *P.*

bahiae in coastal Brazil). Other habitats occupied by local endemics in the Neotropics for which no Paleotropical equivalent is known include dwarf forest on sandstone ridges (occupied by *P. nana* D.A. Neill in Peru; Neill, 2009) and granite inselbergs in Venezuela (*P. truncata* Cowan). However, in the Indo-Pacific, *P. paya* and *P. sherfeseei* Merr. occur in freshwater and coastal swamp forest respectively, and the Neotropics also have species in flooded forest, especially *P. discolor* (in *igapó*) and *P. barnebyana,* and *P. multijuga* also occurs in tidally flooded forest near Belém.

Amongst the characters given by Brown (1826) when establishing the genus are its cylindrical calyx with imbricate aestivation of the lobes, ten fertile stamens that are slightly connate at the base, and flower heads ("spikes") that are "axillary, pedunculate and clavate, with the inferior flowers often male (in a cylinder only half the width)" (translated).

Subsequent authors (Bentham, 1875; Ducke, 1932; Hopkins, 1986) based sectional classifications on the shape of the capitulum and arrangement of flowers of different functional types. The current infrageneric arrangement for *Parkia* divides the genus into 3 sections:

1) sect. *Parkia* is pantropical with flowers of three functional types: each capitulum has an apical ball of fertile flowers, below that a constricted region of nectar-secreting ones, and at the base, a variable number of sterile flowers. These sometimes have elongated staminodia, forming a fringe that when well developed, hangs down and conceals the nectar-secreting flowers. In shape, the capitula range from clavate (staminodial fringe absent, thin or short) to biglobose (staminodial fringe well-developed, Fig. 1A). Clavate capitula are either pyriform or sometimes have an almost spherical ball of fertile flowers with a depressed nectar-ring (e.g. *P. biglobosa*, *P. biglandulosa*).

2) sect. *Platyparkia* is entirely Neotropical with flowers of two types: the capitulum is oblate, with fertile flowers extending from the base to the middle, and the nectar-secreting

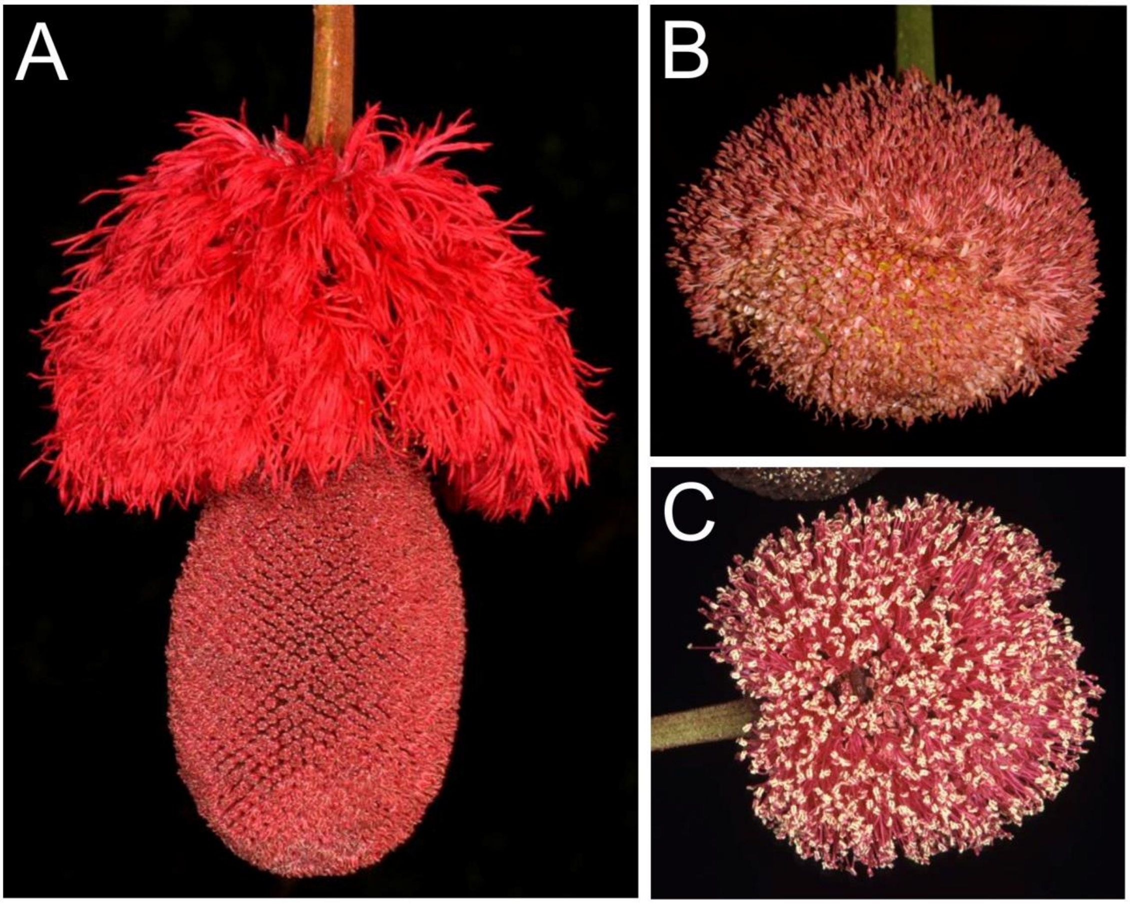

Figure 1. Morphology of capitula in *Parkia* (Leguminosae, Caesalpinioideae, mimosoid clade). (A) *Parkia igneiflora*, capitulum with fertile flowers forming a ball at the apex, nectar-secreting flowers in the middle portion (beneath the fringe and therefore not visible) and staminodial flowers at the base, their staminodes forming a fringe; (B) *P. pendula,* oblate capitulum with fertile flowers in the middle and basal portion and nectar-secreting flowers at the apex (note nectar droplets visible); (C) *P. velutina*, spherical capitulum comprised only of fertile flowers. Photographs: A & B by Francisco Farroñay; C by Michael Hopkins.

flowers are at and around the apex, their surface forming an almost flat disc (Fig. 1B).

3) sect. *Sphaeroparkia* is again entirely Neotropical but the capitula are composed of only a single functional floral type (fertile); no morphologically distinct nectar-secreting or sterile flowers are present. The capitulum is spherical or almost so (Fig. 1C).

In a cladistical analysis based on 54 morphological characters (Luckow and Hopkins, 1995), *Parkia* was shown to be monophyletic. Sections *Parkia* and *Platyparkia* were also resolved as monophyletic while *Sphaeroparkia* was paraphyletic. However, the authors demonstrated that the genus shows wide variation, making it difficult to resolve relationships among species in an analysis based only on morphological characters. Phylogenetic studies within the mimosoid clade using chloroplast and nuclear DNA regions have also indicated the monophyly of the genus (Luckow et al., 2003) but these have involved limited sampling within *Parkia*.

Luckow and Hopkins (1995) inferred a probable Neotropical origin for *Parkia* and discussed various theories that might account for its intercontinental disjunction, including the possibility of a Gondwanic distribution during the late Cretaceous. However, fossil records indicate that the first certain representatives of Leguminosae emerged between 50-60 Ma in North America, Europe and Africa (Herendeen and Dilcher, 1992; Herendeen et al., 1992), thus excluding a Gondwanic origin for the genus. Recent phylogenetic studies also indicate that the family underwent rapid diversification, approximately 60 Ma ago, during the Tertiary (Lavin et al., 2005). The first lineages of mimosoids would have diversified c. 50 Ma and the clade formed by members of the Piptadenia group, which comprises the genera most closely related to *Parkia*, is dated at approximately 45 Ma. Lavin et al. (2004) suggested that dispersion over long distances has been the predominant force that shaped the distribution of Leguminosae. In phylogenetic studies of similar pantropical genera (e.g., Simon et al., 2011), geographically structured phylogenies have been observed, with probable transoceanic dispersion between the Neotropical and Paleotropical regions.

Parkia has diversified in the tropics and several causes have been proposed to explain high biodiversity, including biotic factors such as adaptations to edaphic conditions, interactions with pollinators, dispersers and herbivores, niche conservatism and dispersal, as well as abiotic factors such as time, precipitation, temperature and area, mountain elevation and hydrological changes. Phylogenies, well sampled and dated, offer an excellent model for investigating which processes gave rise to the patterns of diversification of current plant lineages, and when in pantropical genera, such phylogenies allow comparison of processes in different continents (Pennington et al., 2006; Hoorn et al., 2010, 2011; Antonelli and Sanmartín, 2011).

In this context, this study provides the first molecular phylogenetic trees for the pantropical genus *Parkia*, with the objectives of (1) testing the monophyly of the genus and its three sections; (2) inferring its geographical origin; (3) estimating the divergence times of different lineages, and (4) investigating which factors (biotic and abiotic) may have influenced diversification.

2. Materials and methods

2.1. Taxon sampling

We sampled 30 of the 35 species currently recognised in the genus. Sections *Platyparkia* and *Sphaeroparkia* were 100% sampled; in section *Parkia* we sampled 17 of 19 Neotropical species; for the Paleotropics we sampled all four African species (including Madagascar), and nine of 12 species for the Indo-Pacific region. The outgroups were chosen on the basis of previous phylogenetic studies of the mimosoid clade (Luckow et al., 2003; Luckow, 2005) and included species of the genera placed in the Piptadenia group: *Anadenanthera* Speg., *Lachesiodendron* P.G.Ribeiro, L.P.Queiroz & Luckow, *Microlobius* (Jacq.) M.Sousa & G.Andrade, *Mimosa* L., *Parapiptadenia* Brenan, *Piptadenia* Benth., *Pityrocarpa* (Benth.) Britton & Rose, *Pseudopiptadenia* Rauschert and *Stryphnodendron* Mart.

2.2. DNA extraction, amplification and sequencing

We extracted total genomic DNA from silica-gel dried leaves or herbarium material using the 5% CTAB protocol described by Oliveira et al. (2017) in the Laboratório de Evolução Aplicada of the Universidade Federal do Amazonas (LEA-UFAM). Other samples were extracted using DNeasy Plant Mini Kit (QIAGEN, CA, USA) or 2% CTAB (Doyle and Doyle, 1987) in the Jodrell Laboratory, Royal Botanic Gardens, Kew (see www.kew.org/data/dnaBank/).

Polymerase chain reactions (PCR) were conducted for all samples on a total volume of 20 μl, containing the final concentration of ~ 10 ng of each DNA sample, 1X buffer, 1 mmol/L of $MgCl_2$, 10 mmol/L of dNTPs, 1 pmol/L of each primer and 1.5 U *Taq* polymerase (Kapa Biosystems, Wilmington, USA). We amplified four chloroplast regions (*matK*, *trnL*, *psbA-trnH* and *rps16-trnQ*) and the nuclear region ITS/18S/26S, listed in Table 1. The PCR cycling conditions for *matK*, *psbA-trnH* and *trnL* were an initial denaturation for 4 min at 95°C; followed by 35 cycles consisting of denaturation for 45 sec at 94°C, annealing for 1 min at 56°C (50°C for *trnL*), 1 min at 72°C; and finally 10 min at 72°C. For *rps16-trnQ*, the process was an initial denaturation at 80°C for 5 min followed by 30 cycles of denaturation at 95°C for 1 min, and annealing at 50°C for 1 min, followed by a ramp of 0.3°C/s to 65°C, and primer extension at 65°C for 4 min; followed by a final extension step of 5 min at 65°C (Shaw et al., 2007). For the ITS, the process was 4 min at 95°C; followed by 35 cycles consisting of denaturation for 45 sec at 94°C, annealing for 1 min at 56°C, 1 min at 72°C; and finally 10 min at 72°C. PCR products were purified by treatment with ExoSAP enzyme (Fermentas, St. Leon-Rot, Germany) and sequenced in an automatic sequencer ABI 3730 by capillary electrophoresis with ABI BigDye Terminator version 3.1 kit (Applied Biosystems Inc., Foster City, CA, USA).

The consensus sequences were assembled using the Sequencer v.4.1 (GeneCodes Corporation, Ann Arbor, MI, USA), the alignment was done using Mafft-win v.7.221 (Katoh and Standley, 2013). Estimation of variables and nucleotide composition sites were made

Table 1. Chloroplast and ribosomal regions used in this study.

Region	Primer sequence (5’– 3’)	Authors
matKM	TCGACTTTCTGGGCTATC	Tate and Simpson (2003)
trnK-2R	AACTAGTCGGATGGAGTAG	Johnson and Soltis (1994)
trnL A	CATTACAAATGCGATGCTCT	Taberlet et al. (1991)
trnL B	TCTACCGATTTCGCCATATC	Taberlet et al. (1991)
trnQ	GCG TGG CCA AGY GGT AAG GC	Shaw et al. (2007)
rsp16x1	GTTGCTTTYTACCACATCGTTT	Shaw et al. (2007)
psbA	GTTATGCATGAACGTAATGCTC	Sang et al. (1997)
trnH2	CGCGCATGGTGGATTCACAATCC	Tate and Simpson (2003)
ITS18	GTCCACTGAACCTTATCATTTAGAGG	Delgado-Salinas et al. (2006)
ITS26	GCCGTTACTAAGGGAATCCTTGTTAG	Delgado-Salinas et al. (2006)

using the program MEGA v.7.0.26 (Kumar et al., 2016). Some sequences used in the analysis were downloaded from GenBank from previous studies on the mimosoid clade (Luckow et al., 2003; Ribeiro et al., 2018; Simon et al., 2016; LPWG, 2017). Voucher information, taxon author, and GenBank accession numbers of all sequences used in this study are provided in Appendix A1.

2.3. Phylogenetic analyses

Analyses were performed with concatenated data (cpDNA and ITS). The best-fit substitution models selected for cpDNA dataset was GTR+I+Γ and K80 for ITS/18S/26S using the Akaike information criterion (AIC) implemented in jModeltest v.2.1.7 (Posada, 2008; Darriba et al., 2012). Bayesian inference (BI) was performed using MrBayes v.3.2.6 (Ronquist et al., 2012), with two simulations Monte Carlo Markov Chain (MCMC) independently run for 10,000,000, recording the tree parameters every 10000 generations. The results were assessed to have reached stationarity and convergence using the program Tracer v.1.6 (Rambaut and Drummond, 2009), and data from multiple runs were combined after exclusion of burn-in trees. The sample sizes and estimated values (ESS) were >200. The maximum clade credibility (MCC) tree with 95% highest posterior density (HPD) was prepared in FigTree v.1.4.2 (Rambaut, 2014). Maximum likelihood (ML) analyses were performed with PhyML v.3.1 (Guindon et al., 2010) using the bootstrap algorithm with 1000 replications to assess branch support, combined with a search of the best-scoring ML tree under default parameters. A full data set, containing the alignment matrix and all trees generated in the phylogenetic analysis is available in the TreeBase database (http://treebase.org, study accession number 25719).

2.4. Species tree and divergence time estimates

A species tree was reconstructed using the multilocus data set and the lineage divergence times of *Parkia* were estimated using the uncorrelated lognormal relaxed clock Bayesian method in BEAST v.2 (Bouckaert et al., 2014), assuming a general time-reversible model, with invariable sites and among-site rate heterogeneity (GTR+I+Γ). The Markov Chain Monte Carlo simulations (MCMC) were performed in two runs of 10,000,000 generations, recording the tree parameters every 1000th generation. Tracer v.1.6 (Rambaut and Drummond, 2009) was used to check if sample sizes and estimated values (ESS) were >200, and results were assessed to have reached stationarity and convergence. Data from multiple runs were combined after exclusion of burn-in trees. A maximum clade credibility (MCC) tree was calculated in TreeAnnotator v.1.8.0 (Drummond and Rambaut, 2010). The MCC tree with 95% highest posterior density (HPD) was visualized in FigTree v.1.4.2 (Rambaut, 2014).

The divergence between the lineages was estimated as the Middle Eocene using the crown node of the mimosoid legumes which was constrained to 45 Ma according to fossil pollen "Q" (Lavin et al., 2005; Bruneau et al., 2008; Simon et al., 2009).

2.5. Ancestral area reconstruction

The maximum clade credibility tree obtained in BEAST was used as the dated input tree for a biogeographical analysis. We performed likelihood-based dispersal-extinction-cladogenesis (DEC; Ree et al., 2005; Ree and Smith, 2008) analysis in RASP v.4.2 (Yu et al., 2015) using the package BioGeoBEARS (Matzke, 2013). Using information about the current distribution ranges of *Parkia* species, obtained from the Global Biodiversity Information Facility (GBIF online), three biogeographic regions were defined for the ancestral area analyses: (A) Tropical America, (B) Africa (including Madagascar) and (C) Indo-Pacific. The AIC was used to select the model that best fits our data among the six available BioGeoBEARS models: DEC, DEC+J, DIVALIKE, DIVALIKE+J, BAYAREALIKE, BAYAREALIKE+J (Ronquist, 1997; Ree and Smith, 2008; Landis et al., 2013; Matzke, 2014). DEC is the likelihood-based Dispersal-Extinction Cladogenesis model (Ree and Smith, 2008). DIVALIKE is a likelihood version of the parsimony-based Dispersal-Vicariance Analysis model (Ronquist, 1997). BAYAREALIKE is a likelihood version of the Bayesian BayArea model (Landis et al., 2013). The '+J' versions of these models include a founder-effect speciation parameter that allows a descendant to occupy a different area from its immediate ancestor (Matzke, 2013). Likelihood Ratio Tests were used to compare the three pairs of nested models (e.g., DEC vs. DEC+J). Biogeographical Stochastic Mapping (BSM; Dupin et al., 2016) is a simulation approach that estimates the probability of ancestral biogeographical character states for each node of a phylogeny. An analysis with 100 BSMs and using the best-fit model was carried out to estimate the relative numbers of different biogeographical events.

3. Results

3.1. Molecular data and phylogenetic inferences

Our data matrix for the phylogenetic analysis comprised 2453 characters, of which 550 are variable and 419 are parsimoniously informative (Table 2). Overall, the BI (Fig. 2) and ML (Fig. S1) of MrBayes and PhyML analyses resulted in similar topologies. In both analyses *Parkia* is monophyletic (PP = 1, BS = 87%) and sister to *Anadenanthera* (PP = 1, BS =100%). Both topologies recovered five main clades within *Parkia*, geographically structured. Bayesian analyses did not recover as monophyletic all the sections described by Hopkins (1986); however, the topology recovered by the ML analysis is in agreement with the sectional limits proposed by this author (sect. *Sphaeroparkia* = BS 76%; sect. *Platyparkia* = BS 50%; sect. *Parkia* = BS 49%). Here we use the topology from the BI for discussion.

Table 2. DNA sequence loci and best-fit substitution models analysed in this study

Characteristic	*matK*	*psbA-trnH*	*trnL*	*rps16-trnQ*	ITS/18S/26S
Sampling species	72	69	68	50	69
Aligned length (including gaps)	649	393	369	583	459
Variable sites	68	59	53	207	163
Parsimony informative sites	49	33	23	184	130
Best-fit substitution model	GTR+I+Γ	GTR+I+Γ	GTR+I+Γ	GTR+I+Γ	K80

Of the five clades recovered by our analyses, four were strongly supported, and only clade 1 was the least supported in the Bayesian analysis (PP = 0.54). However, it has high support in the analysis of Maximum Likelihood (BS = 76%). Clade 1 is composed of the three Neotropical species in sect. *Sphaeroparkia*: *Parkia multijuga* Benth., *P. ulei* (Harms) Kuhlm. and *P. velutina* Benoist. Clade 2 (PP = 1, BS = 98%) is composed of the three Neotropical species in *P.* sect. *Platyparkia*: *P. paraensis* Ducke, *P. pendula* (Willd.) Benth. ex Walp and *P. platycephala* Benth. Clade 3 (PP = 1, BS = 76%) is composed of the Neotropical species in *P.* sect. *Parkia*: *P. bahiae* H.C.Hopkins, *P. barnebyana* H.C.Hopkins, *P. cachimboensis* H.C.Hopkins, *P. decussata* Ducke, *P. discolor* Spruce ex Benth., *P. gigantocarpa* Ducke, *P.*

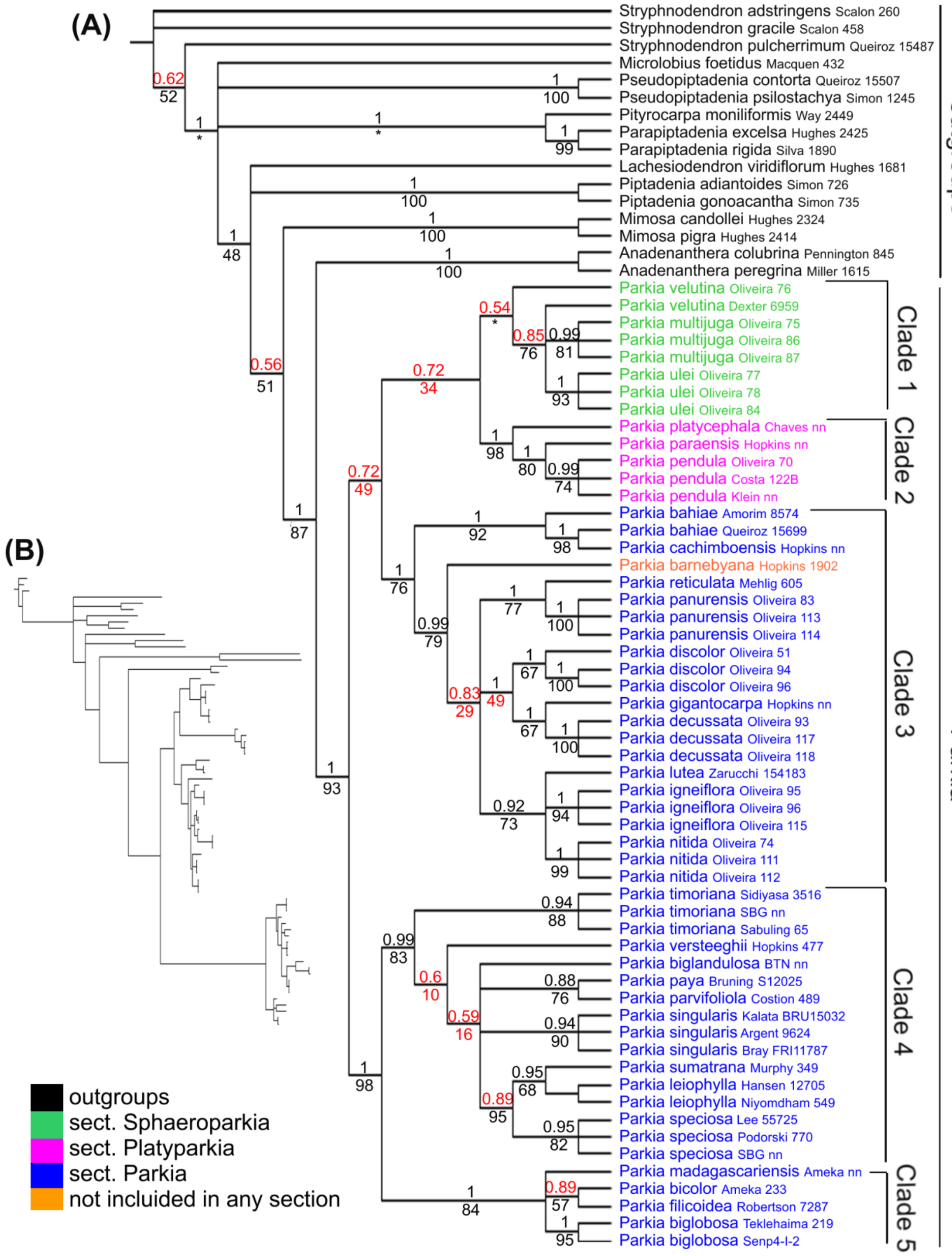

Figure 2. Majority-rule consensus tree (A) and phylogram (B) derived from the Bayesian analysis based on DNA sequences of the *matK*, *trnL*, *psbA*-*trnH* and *rps16*-*trnQ* noncoding plastid loci and ITS/18S/26S nuclear region, showing the relationships among 30 species of *Parkia* and 16 outgroups. Numbers are Bayesian posterior probability (PP) and bootstrap values (BS) from ML, respectively. Asterisks correspond to relationships for which BS values were not recovered.

igneiflora Ducke, *P. lutea* H.C.Hopkins, and *P. nitida* Miq, *P. panurensis* Benth. ex H.C.Hopkins and *P. reticulata* Ducke. Clade 4 (PP = 0.99, BS = 83%) comprised the Paleotropical species in sect. *Parkia* from the Indo-Pacific region: *P. biglandulosa* Wight & Arn., *P. leiophylla* Kurz, *P. parvifoliola* Hosok., *P. paya* H.C.Hopkins, *P. singularis* Miq., *P. speciosa* Hassk, *P. sumatrana* Miq., *P. timoriana* (DC.) Merr. and *P. versteeghii* Merr. & L.M.Perry. Clade 5 (PP = 1, BS = 84%) comprised the species in sect. *Parkia* from Africa: *P. bicolor* A.Chev., *P. biglobosa* (Jacq.) R.Br., *P. filicoidea* Oliv. plus the Malagasy endemic, *P. madagascariensis* R.Vig.

3.2. Divergence time estimation

Divergence time estimates for *Parkia* are shown in Fig. 3. Our analysis suggested that the most recent common ancestor (MRCA) of *Parkia* and the outgroups used here dates to the first half of the Eocene at 46.13 Ma (95% highest posterior density (HPD) 44.08–48.61 Ma). The Neotropical and Paleotropical clades diverged at around 18.49 Ma (95% HPD 11.95–26.17 Ma) in the first half of the Miocene, and so this is the likely date of dispersal from the Neotropics to the Paleotropics. The Neotropical clades subsequently split into clades (1 + 2) and clade 3 at 12.89 Ma (7.99–17.7 Ma), again in the Miocene. The split between clade 1 and clade 2 is estimated to have occurred at 9.79 Ma (95% HPD 5.66–14.39 Ma), and the divergence of extant lineages in clade 3 started at 7.22 Ma (95% HPD 4.41–10.45 Ma). In the Paleotropics, clades 4 and 5 diverged at around 8.28 Ma (95% HPD 4.74 –11.5 Ma), with the current diversification in clade 4 occurring around 5.4 Ma (95% HPD 3.26 –7.61 Ma) and in clade 5 at around 3.76 Ma (95% HPD 1.69–6.01 Ma).

3.3 Biogeographical reconstruction

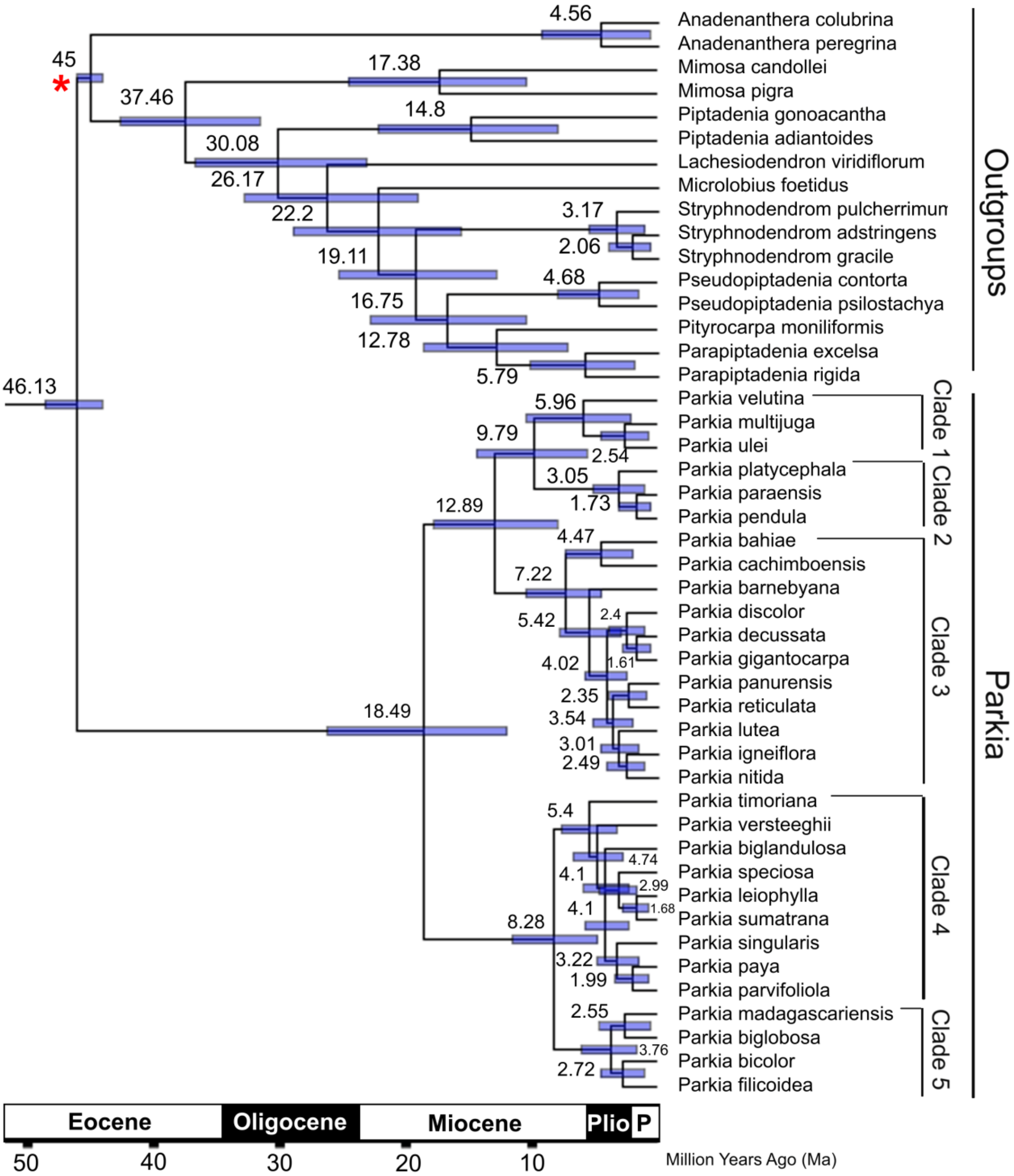

Figure 3. Chronogram of *Parkia* derived from a divergence time estimation in Beast. The asterisk refers to the calibration point. The shaded blue horizontal bars show the 95% highest posterior densities (HPD) for the divergence times. On the timescale, Plio = Pliocene; P = Pleistocene.

The ancestral area reconstructions are shown in Fig. 4. The best-fit model was DEC+J (Table 3). Biogeographic reconstruction using this model indicates that *Parkia* probably originated in Neotropics (area A) around the middle Miocene. The DEC analysis also inferred that *Parkia* colonized the Paleotropics from the Neotropics in the late Miocene. Founder event (j) speciation is particularly important in the historical biogeography of clades currently distributed on oceanic islands (Matzke, 2014).

Table 3. Biogeographic models and comparative statistics. Abbreviations: Par= Number of free parameters; LnL=log-likelihood; AICc=Akaike Information Criterion, corrected; AICc_wt=Akaike weights; DEC=Dispersal Extinction Cladogenesis model; DIVALIKE=BioGeoBEARS implementation of DIVA model; BAYAREALIKE=BioGeoBEARS implementation of BayArea model; J=founder-event speciation. The dispersal (d), extinction (e) and jump dispersal (j) values are available for each model. The best model is in bold.

Model	Par	LnL	d	e	j	AICc	AICc_wt
DEC	2	-17.04	5.60e-05	1.00e-12	0	38.36	0.3
DEC+J	**3**	**-17.04**	**5.60e-05**	**1.00e12**	**1.00e-05**	**40.65**	**0.094**
DIVALIKE	2	-16.64	6.60e-05	1.00e-12	0	37.55	0.45
DIVALIKE+J	3	-16.64	6.60e-05	1.00e-12	1.00e-05	39.84	0.14
BAYAREALIKE	2	-25.08	4.50e-05	5.70e-05	0	54.44	9.60e-05
BAYAREALIKE+J	3	-18.57	2.30e-05	1.00e-07	0.0036	43.72	0.02

4. Discussion

4.1. Monophyly of Parkia and its affinities in the mimosoid clade

For a relatively small genus, *Parkia* shows considerable variation, not only in the structure, shape and colour of the capitulum but also in its leaves (always bipinnate but variable in the size and shape of the leaflets) and in its fruits (see below). This degree of variability is probably greater than in other genera of similar size in the mimosoid clade. Nevertheless, *Parkia* is confirmed here as monophyletic, as previously suggested in studies using both morphological and molecular data (Luckow and Hopkins, 1995; Luckow et al., 2003).

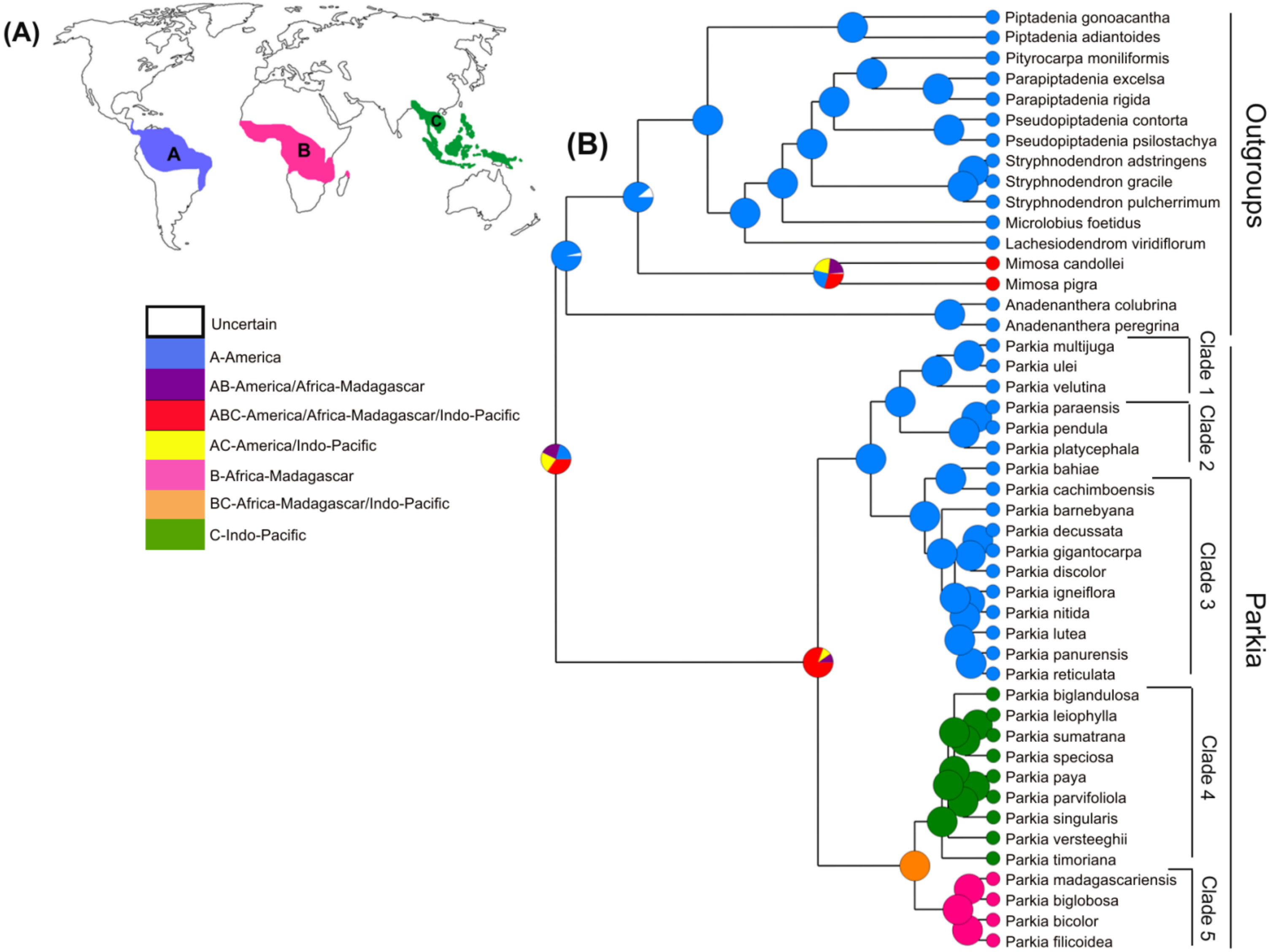
(A)
A
B
C
Uncertain
A-America
AB-America/Africa-Madagascar
ABC-America/Africa-Madagascar/Indo-Pacific
AC-America/Indo-Pacific
B-Africa-Madagascar
BC-Africa-Madagascar/Indo-Pacific
C-Indo-Pacific
(B)
Piptadenia gonoacantha
Piptadenia adiantoides
Pityrocarpa moniliformis
Parapiptadenia excelsa
Parapiptadenia rigida
Pseudopiptadenia contorta
Pseudopiptadenia psilostachya
Stryphnodendron adstringens
Stryphnodendron gracile
Stryphnodendron pulcherrimum
Microlobius foetidus
Lachesiodendrom viridiflorum
Mimosa candollei
Mimosa pigra
Anadenanthera colubrina
Anadenanthera peregrina
Parkia multijuga
Parkia ulei
Parkia velutina
Parkia paraensis
Parkia pendula
Parkia platycephala
Parkia bahiae
Parkia cachimboensis
Parkia barnebyana
Parkia decussata
Parkia gigantocarpa
Parkia discolor
Parkia igneiflora
Parkia nitida
Parkia lutea
Parkia panurensis
Parkia reticulata
Parkia biglandulosa
Parkia leiophylla
Parkia sumatrana
Parkia speciosa
Parkia paya
Parkia parvifoliola
Parkia singularis
Parkia versteeghii
Parkia timoriana
Parkia madagascariensis
Parkia biglobosa
Parkia bicolor
Parkia filicoidea
Outgroups
Clade 1
Clade 2
Clade 3
Clade 4
Clade 5
Parkia

Figure 4. Ancestral area reconstruction for *Parkia*. (A) Map illustrating the three biogeographic areas (A, B and C) considered in the analysis. (B) Tree in which pie-charts depict the ancestral geographic ranges of corresponding nodes inferred by the BioGeoBEARS analysis under the DEC model in RASP.

Within the mimosoid clade, *Parkia* is sister to *Anadenanthera* in this analysis, corroborating other studies of the Piptadenia group (Ribeiro et al., 2018; Simon et al., 2016; LPWG, 2017). For instance, Ribeiro et al. (2018) recovered *Anadenanthera*, *Mimosa* and *Piptadenia* as the genera most closely related to *Parkia*, though in a clade with poor support; our results concur, and offer better support for this relationship.

In terms of gross morphology and chemistry, *Parkia* and *Anadenanthera* have little in common. *Anadenanthera* is a small, tropical and subtropical American genus of two quite similar species with small spherical capitula and pods dehiscent along one suture (von Reis Altschul, 1964). The genus contains the hallucinogenic compound bufotenin, plus a range of other psychotropic substances, and is used in Amerindian rituals as a snuff (Torres and Repke, 2014); these compounds have not been reported from *Parkia*.

4.2. Clades, sections, and morphological characters

None of the various sectional classifications that have been proposed within *Parkia* is entirely supported by our Bayesian analysis. The Maximum Likelihood tree (Fig. S1) is congruent with the infrageneric classification proposed by Hopkins (1986).

Bentham (1875) divided the genus into two: sect. *Euparkia* (*nom. illeg.* = sect. *Parkia*) contained all the Paleotropical species and three from the Neotropics, now in *Platyparkia* (*P. pendula*, *P. platycephala*) and *Sphaeroparkia* (*P. multijuga*). He described *Euparkia* as having “clavate capitula with the inferior part sterile and much narrower than the fertile part (or perhaps more or less equal in the American species)”; in this, he misinterpreted the three

American species. His second section, *Paryphosphaera*, comprised the remaining Neotropical species then known, which all had a well-developed staminodial fringe ("capitula biglobose, superior part [sic] sterile, twice as wide as the fertile part on account of the elongated staminodia").

Ducke (1932, 1949) recognised four sections: *Parkia* (as *Euparkia*), contained all the species from the Paleotropics, which were described as having clavate capitula (i.e. corresponding to clades 4 and 5 plus the Amazonian *P. decussata* Ducke from clade 3); *Paryphosphaera*, from tropical America (species with biglobose capitula, closely equivalent to clade 3); *Sphaeroparkia* from tropical America (capitula spherical, clade 2); and *Platyparkia*, also from tropical America (capitula oblate, clade 1). However, using his sectional diagnoses, *P. bicolor* from Africa and *P. paya* from Borneo, which both have quite well developed staminodial fringes (see Hagos, 1962: Fig. 3, Hopkins, 2000a: Fig.1), would be included in sect. *Paryphosphera*, and *P. cachimboensis* and *P. barnebyana*, which were unknown to Ducke, would be included, with *P. decussata*, in the Paleotropical sect. *Parkia*. Several species from the Indo-Pacific have short staminodial fringes and are thus intermediate between sections.

Hopkins (1986) used the arrangement of flowers of different functional types, especially the relative position of the nectar-secreting flowers, when present, irrespective of the degree of development of the staminodial ones, to recognise three sections. Her arrangement differed from Ducke's only by combining sections *Parkia* and *Paryphosphaera*. She recognised that in the Neotropics, the presence of a staminodial fringe in sect. *Parkia* was related to whether the capitula were pendent or erect, and her arrangement also circumvented the problem of Paleotropical species in which the staminodia were intermediate in length, producing a short but distinct fringe.

Morphologically, the five clades recovered in *Parkia* can be characterised as follows:

Clade 1: Neotropical (sect. *Sphaeroparkia*); capitula spherical, composed of only fertile flowers, neither erect nor pendent, cream, yellow or red; pods dehiscent or indehiscent, with little or no gum and no pulp; seeds in 1 row. Although the three species within this clade are markedly distinct from one another, the relationships among them are not resolved.

Clade 2: Neotropical (sect. *Platyparkia*); capitula oblate, formed of fertile and nectar-secreting flowers, pendent, red to purplish red; pods tough-fleshy and indehiscent (*Parkia platycephala*), or dehiscent with the adaxial suture laterally expanded and secreting abundant gum; seeds in 1 or 2 rows. *Parkia platycephala* is sister to the other two species (*P. pendula*, *P. paraensis*), which have similar pods to each other. The capitular structure in this section appears to be unique among the mimosoid legumes.

Clade 3: Neotropical (sect. *Parkia*); capitula clavate, with three types of flower (fertile, nectar-secreting and staminodial), either erect and staminodes few or weakly developed or pendent and staminodial fringe well developed, red, yellow or a mixture of both in a single capitulum; pods leathery or woody, not or only slightly twisted, indehiscent or rarely dehiscent, without pulp but sometimes with small amounts of gum; seeds in 1 row. Within this clade, the subclade formed by *Parkia bahiae* (coastal Brazil; capitula pendent with a small fringe; pods indehiscent) plus *P. cachimboensis* (Serra do Cachimbo; capitula erect, no fringe and staminodia few; pods thin-leathery, dehiscent) is sister to the other species. *Parkia barnebyana* is then sister to the remaining species, which form the “nitida clade” of Luckow and Hopkins (1995). This fairly tight-knit group has many shared features and can be characterised by the pods, in which the funicular suture is narrower than the opposite one. Except for *P. decussata*, all species in the nitida clade have a well-developed staminodial fringe. Despite this general morphological similarity, variation occurs in flower colour (white to egg-yolk yellow, orange, pink, red or dark dull pink), and in the size of the capitula, the largest being those of *P. gigantocarpa* (15–21.5 cm long). Some sister groups are evident in Fig. 2 but overall relationships remain unresolved.

In the protologue, *Parkia barnebyana* was described from fruiting material and so was not assigned to a section (Hopkins, 2000b), although the vegetative characters suggested it might be related to the species in sect. *Sphaeroparkia*. A flowering specimen is now known, *Redden et al. 3651* (K) from Amazonas State, Venezuela, which has cream-yellow, clavate capitula with an apical ball of fertile flowers, a narrower collar of nectar-secreting ones towards the base and rather few sterile basal flowers with shortly projecting staminodes. It is unusual in having long, erect inflorescences axes that bear quite short erect peduncles from which the capitula project upwards; in this it somewhat resembles *P. decussata* and *P. cachimboensis*. Its morphology places it in sect. *Parkia* and this is confirmed by our results.

Clade 4: Indo-Pacific (sect. *Parkia*); capitula formed of fertile, nectar-secreting and staminodial flowers, clavate (with few basal flowers) or with exserted staminodia, pendent, cream to yellow; pods indehiscent, flat or sometimes spirally twisted, at least sometimes containing pulp, without gum; seeds in 1 row. Relationships among the species are not well resolved. In taxonomic studies, leaf characters were useful in the delimitation of species, especially the size and shape of the leaflets, sometimes in combination with other characters (Hopkins, 1994).

A general morphological similarity exists among the African, Malagasy and Indo-Pacific species that suggests they may be more closely related to one another than to the Neotropical species in sect. *Parkia* (see Hopkins, 1983, 1986, 1994), and our phylogenetic results confirm this. These paleotropical species exhibit a smaller range of variation in their capitula than seen in Neotropical sect. *Parkia*. However, we are not able at present to identify with certainty a synapomorphy for clades 4 + 5, although pod morphology appears potentially useful (presence of pulp, but not confirmed for all species; spiral twisting of sutures at maturity, but not present in all species).

Clade 5: Africa-Madagascar (sect. *Parkia*); capitula with fertile, nectar-secreting and staminodial flowers, clavate (with few basal flowers) or with exserted staminodia, pendent, red (including orange and purple-red) or cream-yellow (*P. madagascariensis*); pods indehiscent, flat or ± cylindrical, sometimes spirally twisted, at least sometimes containing mealy pulp, without gum; seeds in 1 row. *Parkia bicolor* and *P. filicoidea* are indicated as sister taxa in Fig. 2 but other relationships among the four species are largely unresolved.

4.3 Historical Biogeography

Origin of *Parkia*

We found a strong geographical structure in the phylogenetic relationships of *Parkia*, with the species in each clade occurring in the same biogeographic region (Fig. 4) and geography is generally considered an important predictor of phylogenetic structure (Schrire et al., 2005; Simon et al., 2011). This structure has been attributed to niche conservatism (Donoghue, 2008), limited dispersion and in situ speciation within individual geographic areas (Schrire et al., 2009; Pennington et al., 2006, 2009).

A Neotropical origin for *Parkia*, as found in our biogeographical reconstruction, was one of the hypotheses considered by Baker and Harris (1957) and Luckow and Hopkins (1995) when discussing the evolution of the genus in relation to its pollination. The African and Asian clades share an immediate common ancestor after their separation from the America lineage (at 18.49 Ma) and only a single dispersal event from the Neotropics to the Paleotropics seems likely.

The origin of *Parkia* coincided with the intensification of the elevation of the Andes (Hoorn et al., 2010). According to Hoorn et al. (2010), this Andean uplift caused the erosion of large amounts of sediments that resulted in the availability of nutrients that did not previously exist in the region, creating new habitats with relatively high soil fertility. With the drainage of swamps during the Late Miocene, vast areas of the upland habitat would be available for recolonization, presumably encouraging diversification.

Guinet and Salard-Cheboldaeff (1975) described fossil pollen from Cameroon in Africa, dating from the Lower Miocene (and/or upper Eocene, see Salard-Cheboldaeff 1978), as *Parkiidites microreticulatus*. They stated that it was most similar to the pollen of *Parkia ulei*. This same type of pollen was found by Lima et al. (1985) in São Paulo with an approximate age in the Oligocene. Recently, Leite et al. (2020) described fossil pollen in the Western Amazon, *Parkiidites marileae*, aged approximately 12–13 Ma. According to the authors, *Parkiidites marileae* may belong to the lineages of *Parkia cachimboensis*, *P. discolor*, *P. igneiflora*, *P. lutea*, *P. nitida* or *P. panurensis*. It does not appear to closely similar to any of the species in section *Sphaeroparkia* (*Parkia multijuga*, *P. ulei* and *P. velutina*) nor to either of the species in the section *Platyparkia* sampled by them (*P. pendula* and *P. platycephala*). Although not given a precise age with radiometric dating, it is dated by palynological biozones (Carlos D'Apolito, personal communication), and provides evidence of the presence of Neotropical lineages of *Parkia* during the Oligocene and Miocene, and African lineages in the Miocene, in agreement with the confidence intervals of the dates retrieved in our study.

Neotropical diversification

The Amazon basin is the region with the highest species richness and morphological diversity for *Parkia*, containing 54% of the currently known species. The genus has radiated into a variety of habitats where it is represented by trees or large shrubs ranging from 3–4 m (*P. nana*) to 45 m (*P. gigantocarpa*) and its biogeographic history suggests several dispersal events within Amazonia between the Middle Miocene and the Pleistocene (12.89–1.73 Ma). This is in agreement with phylogenetic studies of other Neotropical lineages that corroborate the "cradle model" for diversification, with recent and rapid accumulation of species through high speciation rates (Richardson et al., 2001; Erkens et al., 2007; Simon et al., 2009; Terra-Araujo et al., 2015; Vicentini, 2016), perhaps triggered by changes during the Pleistocene (Rull, 2011) or relatively recent tectonic events such as the final elevation of the Andes in the Pliocene (Gregory-Wodzicki, 2000; Hughes and Eastwood, 2006) or the rise of the Isthmus of Panama.

In the Amazon rainforest, the diversity of habitats available for occupation results from variation in total precipitation and its seasonal pattern, in temperature and in soil type. Many authors have documented turnover in species composition in habitats in Amazonia and other tropical forests (for example, Tuomisto et al., 2003a, 2003b; Fine et al., 2005, 2014) and conclude that habitat diversity contributes to the high richness of species.

Dispersion to Central America occurred around 2.49 Ma in the Late Pliocene, probably following the formation of the Isthmus of Panama (3.5 Ma), which connected South America with Central and North America, and thus established an important route of migration between these regions, that gave rise to the Great American Biotic Interchange (GABI) (Simpson, 1980; Hoorn et al., 2010).

During the evolutionary history of *Parkia*, there were at least two dispersion events to the Atlantic forest on the Brazilian coast involved or gave rise to *P. bahiae*, a species endemic to sand dunes, around 4.47 Ma (node 4; Fig. 3) and *P. pendula*, which extends from Central America to south-eastern Brazil, at 1.73 Ma. Currently, a climate barrier formed by the *cerrado* and *caatinga* biomes separates the Amazon rainforest from the Atlantic coast (Cheng et al., 2013). However, at least two connections between these two forests have been established at different times since the Tertiary, via riverine forests in Central Brazil and the

Paraná river basin, along the Atlantic coast (Costa, 2003; Batalha-Filho et al., 2012; Terra-Araujo et al., 2015; Vicentini, 2016). A similar pattern of disjunction has been found in other groups of plants (Givnish et al., 2004, 2011; Terra-Araujo et al., 2015; Vicentini, 2016; Ferreira, 2018; Silva et al., 2020) and animals (Costa, 2003; Pellegrino et al., 2011; Batalha-Filho et al., 2012; Fouquet et al., 2012). Dispersions to the *cerrado* in Central Brazil occurred at least twice, with *P. platycephala* at around 3.05 Ma and *P. cachimboensis* at 4.47 Ma (node 2 and node 3; Fig. 3).

Asia and Africa diversification

Divergence time estimates for the lineage that gave rise to the Paleotropical species indicate that *Parkia* was established in this region during the Miocene. The estimated ages for the Paleotropical clade (crown age 8.28 Ma, Fig. 3) are too young to support any hypothesis involving continental disjunction, since the initial division between these continents occurred c. 100 Ma, although with supposed later connections (Morley, 2003). This suggests that long-distance dispersion provides the most plausible explanation for this disjunction, and the timing, in the Miocene, accords with the estimated time of divergence proposed by Lavin et al. (2004) for most intra- and trans-continental dispersions of crown groups in the legumes.

The diversification of lineages in the Indo-Pacific corresponds to the region's tectonic and climatic history. The time of diversification we found is consistent with the Himalayan uplift acceleration, derived from the India-Asia continental collision (Hall, 2002, 2009, 2012; Hu, et al. 2017), and with the intermittent glaciations that followed the glaciation at the Oligocene-Miocene boundary (Zachos et al., 2001). Records of pollen from the Middle Miocene indicate a high and humid climate and expansion of the tropical forest in these newly formed islands (Morley, 1998). Land bridges connected some areas, including New Guinea, Indochina, Sumatra, Java and Borneo. During the last glacial maximum (LGM) in the Plio-

Pleistocene, sea level was approximately 120 m lower than today, resulting in complete exposure of the Sunda Shelf and allowing migration between the Asian continent and Borneo (Miller et al., 2005). Rapid rates of rising or falling sea levels on the gradual incline of the Sunda Shelf would have exaggerated patterns of shoreline erosion, sedimentation, soil accumulation processes, and development of plant and animal communities (Hanebuth and Stattegger, 2004; Page et al., 2004). These events combined may have shaped the dispersion and diversification of *Parkia* lineages in this region. The occurrence of endemic species in New Guinea and the Solomon Islands (*P. versteeghii*) and on islands in the Pacific *P. parrii* Horne ex Baker (Fiji), *P. parvifoliola* (Palau), and *P. korom* Kanehiro (Ponape) implies a series of possibly recent oceanic dispersal events, but our sampling of these species precludes drawing conclusions of the origins or sequence.

Fewer species occur in Africa and Madagascar compared to tropical America and the Indo-Pacific region. In view of the relatively recent radiation of the African lineage (2.55–3.76 Ma), one possible explanation is that there has been insufficient time since *Parkia* arrived on the African continent for significant diversification there. Other possible explanations for the paucity of species are the lower availability of niches in Africa or higher extinction rates, preventing the accumulation of species. A similar pattern was found in the genus *Mimosa* (Simon et al., 2011). Most groups of plants with pantropical distributions have lower diversity in tropical Africa compared to South America and Southeast Asia (Richards, 1973; Couvreur, 2015). This difference is traditionally attributed to a combination of a smaller area of tropical forest, drought and fire regimes and forest contractions due to fluctuations in the climate (Parmentier et al., 2007; Couvreur, 2015; Terborgh et al., 2016). Another possible reason suggested by Terborgh et al. (2016) is megafaunal herding on the African continent that has established a landscape with more grasses and herbs than woody trees (Bakker et al., 2016; Malhi et al., 2016). In addition, Africa has been geomorphologically stable for the last

40 Ma, which might explain the lower diversity in this area (Potts and Behrensmeyer, 1992).

Although the species of the Indo-Pacific seem older than those of Africa, this does not mean that the dispersion of the Neotropics was necessarily to the Indo-Pacific and not to Africa. Several studies suggest that the transoceanic dispersion between South America and Africa is the hypothesis that best explains the pantropical distribution of some current taxa (Dick et al., 2003; Renner, 2004). A probable explanation for the recent ages of African lineages would be that the immediate ancestors of current African species are extinct.

For groups of legumes with similar disjunct distributions and sister groups in Africa-Madagascar and the Neotropics (Lavin and Luckow, 1993; Lavin et al., 2000, 2004; Thulin et al., 2004; Haston et al., 2005; Schrire et al., 2005), the boreotropical hypothesis has been proposed. This supposes that some lineages used to be more widespread in the northern hemisphere, occupying terrestrial connections between North America and Europe during the Eocene or early Oligocene (Wolfe, 1975; Lavin and Luckow, 1993; Schrire et al., 2003). However, the estimated younger ages for the disjunction between Paleotropical and Neotropical *Parkia* lineages and the possible South American ancestor for the Paleotropical clade does not support a boreotropical explanation for the distribution of the genus. Instead, long-distance oceanic dispersal, which has been proposed to explain various intercontinental disjunctions in many groups of legumes and other plants (for example, Lavin et al., 2004; Renner, 2004; Givnish et al., 2004, 2011 ; Denk et al., 2015), is the most likely explanation for the current distribution of *Parkia*.

5. Conclusions

Our study comprises the first molecular phylogeny of *Parkia*. Chloroplast and nuclear DNA data support the monophyly of the genus but the results of our Bayesian analysis are not fully aligned with any of the proposed sectional classifications. The results of the ML analysis are in line with the sectional arrangement. In our study, geography appears as the main predictor of the phylogenetic structure. The divergence time estimates and ancestral area reconstruction suggest a Neotropical origin for *Parkia* and a crown age of 18.49 Ma. Dispersal from the Neotropics to the Paleotropics explains its pantropical distribution, with greater radiation in the Neotropics, no doubt influenced by various biotic and abiotic factors, including geological history.

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Supplementary Material

Appendix A1. Voucher specimens for DNA sequences using in this study.

Figure S1. Maximum Likelihood tree and phylogram derived from the PhyML analysis.

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Appendix A1. Voucher specimens for DNA sequences used in this study. For each entry in the following list, the species name and author, collection locality, collector's name and number for the voucher, herbarium acronym, and GenBank accession numbers are reported. Superscripts before GenBank accession numbers indicate sequences: ^{1}*matK*, ^{2}*trnL*, ^{3}*psbA-trnH*, ^{4}*rps16-trnQ* and ^{5}ITS/18S/26S.

Anadenanthera colubrina (Vell.) Brenan.: Unknown locality, *Pennington 845* (E), ^{1}AF521813, ^{2}AF522947, –, –, ^{5}JQ910930.

Anadenanthera peregrina (L.) Speg.: Unknown locality, *Miller 1615*, ^{1}EU812046, ^{2}EU440022, ^{3}EU811982, –, –.

Lachesiodendron viridiflorum (Kunth) P.G.Ribeiro, L.P.Queiroz & Luckow: Mexico, *Hughes 1681* (FHO), ^{1}KT364173, ^{2}KT364001, –, –, ^{5}KT364066.

Microlobius foetidus (Jacq.) M.Sousa & G.Andrade: Unknown locality, *Macqueen 432* (FHO), ^{1}AF521842, ^{2}AF278506, –, ^{4}AF524979, ^{5}AF458783.

Mimosa candollei R.Grether: Bolivia, *Hughes 2324* (FHO), ^{1}KT364211, ^{2}KT363988, –, –, ^{5}KT364050.

Mimosa pigra L.: Bolivia, *Hughes 2414* (FHO), ^{1}KT364213, ^{2}KT363994, –, –, ^{5}KT364060.

Parapiptadenia excelsa (Griseb.) Burkart: Bolivia, *Hughes 2425* (FHO), ^{1}KT364160, ^{2}KT363996, –, –, ^{5}KT364062.

Parapiptadenia rigida (Benth.) Brenan: Unknown locality, *Silva 1890* (BH), ^{1}AF521849, ^{2}AF278505, –, –, –.

Piptadenia adiantoides (Spreng.) Macbr.: Brazil, *Simon 726* (FHO), ^{1}KT364158, ^{2}KT363998, –, –, ^{5}KT364064.

Piptadenia gonoacantha (Mart.) J.F.Macbr.: Bolivia, *Simon 735* (FHO), –, ^{2}FJ982238, –, –, ^{5}KT364065.

Pityrocarpa moniliformis (Benth.) Luckow & R.W.Jobson: Brazil, *Way 2449* (K), ^{1}KT364162, ^{2}KT364002, –, –, ^{5}KT364067.

Pseudopiptadenia contorta (DC.) G.P.Lewis & M.P.Lima: Unknown locality, *Queiroz 15507* (CEN), ^{1}KT364155, ^{2}KT364005, –, –, –.

Pseudopiptadenia psilostachya (DC.) Benth.: Unknown locality, *Simon 1245* (CEN), ^{1}KT364170, ^{2}KT364006, –, –, ^{5}KT364070.

Stryphnodendron adstringens (Mart.) Coville: Unknown locality, *Scalon 260* (ESA), ^{1}KT364188, ^{2}KT364010, –, –, ^{5}KT364074.

Stryphnodendron gracile Her. & Rizz: Unknown locality, *Scalon 458* (ESA), ^{1}KT364177, ^{2}KT364019, –, –, ^{5}KT364080.

Stryphnodendron pulcherrimum (Willd.) Hochr.: Brazil, *Queiroz 15487* (HUEFS), ^{1}KT364205, ^{2}KT364043, –, –, ^{5}MG001281.

Parkia bahiae H.C.Hopkins: Brazil, Bahia, *Amorim 8574* (CEPEC), ^{2}KX388312, ^{3}KX388277, ^{4}KU844157. Brazil, Bahia, *Queiroz 15699* (HUEFS), ^{1}KY046204,

Parkia barnebyana H.C.Hopkins: Brazil, Amazonas, *M.J.G. Hopkins 1902* (INPA), ^{2}KX388313, ^{3}KX388278, ^{4}KU844164.

Parkia bicolor A.Chev.: Ghana, *Ameka 233* (K), ^{3}KX388279, ^{4}KU844174.

Parkia biglandulosa Wight & Arn.: Unknown locality, *Banana Tree Nursey* (BH), ^{1}AF521850, ^{2}AF278498.

Parkia biglobosa (Jacq.) R.Br.: Burkina Faso, *Teklehaima 219* (K), ^{2}KX388315, ^{3}KX388280, ^{4}KU844173. Senegal, *SENp4-I-2* (Herbarium unknown) –,^{2}HM489999, ^{3}HM489995, –, –.

Parkia cachimboensis H.C.Hopkins. Brazil, Pará, Belém, *Hopkins & Hopkins 3907* (INPA), ^{3}KX388281, ^{4}KU844158.

Parkia decussata Ducke: Brazil, Amazonas, Manaus, *Oliveira 93* (INPA), ^{2}KX388315, ^{3}KX388282, ^{4}KU844156. Brazil, Amazonas, Manaus, *Oliveira 117* (INPA), ^{2}KX388316, ^{3}KX388283, ^{4}KU844139. Brazil, Amazonas, Manaus, *Oliveira 118* (INPA), ^{2}KX388317, ^{3}KX388284, ^{4}KU844139.

Parkia discolor Spruce ex Benth.: Brazil, Amazonas, Manaus, *Oliveira 51* (INPA), ^{2}KX388320, ^{3}KX388287, ^{4}KX388341. Brazil, Amazonas, Manaus, *Oliveira 94* (INPA), ^{2}KX388318, ^{3}KU844170, ^{4}KX388285. Brazil, Amazonas, Manaus, *Oliveira 96* (INPA), ^{2}KX388319, ^{3}KX388286, ^{4}KX388342.

Parkia filicoidea Oliv.: Kenya, *Robertson 7287* (K), ^{2}KX388321, ^{3}KX388288, ^{4}KU844176.

Parkia gigantocarpa Ducke: Brazil, Pará, Bélem, Cult. at Museu Paraense Emílio Goeldi, Leaves sampled by *M.J.G.Hopkins*, without voucher, ^{2}KX388322, ^{3}KX388289, ^{4}KU844171.

Parkia igneiflora Ducke: Brazil, Amazonas, Manaus, *Oliveira 95* (INPA), ^{3}KX388290, ^{4}KU844169. Brazil, Amazonas, Manaus, *Oliveira 96* (INPA), ^{3}KX388291, ^{4}KX388340. Brazil, Amazonas, Manaus, *Oliveira 115* (INPA).

Parkia leiophylla Kurz: Thailand, *Hansen 12705* (K). Unknown Locality, *Niyomdham 549* (E), [1]KY046207, –, –, –, –.

Parkia lutea H.C.Hopkins: Brazil, Amazonas, Maués, *Zarucchi 2930* (INPA), [3]KX388292, [4]KU844167.

Parkia madagascariensis R.Vig.: Madagascar, *Du Puy M556* (K), [2]KX388323, [3]KX388293, [4]KU844175.

Parkia multijuga Benth.: Brazil, Amazonas, Manaus, *Oliveira 75* (INPA). Brazil, Amazonas, Manaus, *Oliveira 86* (INPA), [2]KX388306, [3]KX388270, [4]KU844162. Brazil, Amazonas, Manaus, *Oliveira 87* (INPA), [2]KX388307, [3]KX388271, [4]KX388332.

Parkia nitida Miq.: Brazil, Amazonas, Manaus, *Oliveira 74* (INPA), [2]KX388324, [3]KX388294, [4]KU844168. Brazil, Amazonas, Manaus, *Oliveira 111* (INPA), [2]KX388325, [3]KX388295, [4]KU844141. Brazil, Amazonas, Manaus, *Oliveira 112* (INPA), [2]KX388326, [3]KX388296, [4]KU844142.

Parkia panurensis Benth. ex H.C.Hopkins: Brazil, Roraima, Rorainópolis, *Oliveira 83* (INPA), [3]KX388297, [4]KU844165. Brazil, Amazonas, Manaus, *Oliveira 113* (INPA). Brazil, Amazonas, Manaus, *Oliveira 114* (INPA)

Parkia paraensis Ducke: Brazil, Amazonas, Cult. at Instituto Nacional de Pesquisas da Amazônia, *M.J.G. Hopkins* 2421(INPA).

Parkia parvifoliola Hosok.: Micronesia, Palau, *Costion 489* (K).

Parkia paya H.C.Hopkins: Malaysia, Borneo, *Bruning S12025* (K).

Parkia pendula (Willd.) Benth. ex Walp.: Brazil, Roraima, Rorainópolis, *Oliveira 70* (INPA),[2]KX388309, [3]KX388274, [4]KU844159. Brazil, Rondônia, *Costa 122B* (INPA), [3]KX388276, [4]KX388335. Brazil, Pernambuco, Recife, *Klein s.n.* (INPA).

Parkia platycephala Benth.: Brazil, Maranhão, Chapadinha, *Chaves s.n.* (UFMA), [2]KX388308, [3]KX388273, [4]KU844160.

Parkia reticulata Ducke: Brazil, Pará, *Mehlig 605* (INPA), [2]KX388327, [3]KX388299, [4]KU844166.

Parkia singularis Miq.: Brunei, *Kalata et al. BRUN 15032* (K). Indonesia, *Argent et al. 9624* (K). Malaysia, *Bray FRI 11787* (K).

Parkia speciosa Hassk.: Malaysia, Borneo, *Lee S.55725* (K). Philippines, Palawan, *Podzorski S.M.H.I.770* (K). Singapore, Cult. at Singapore Bot. Gard., *Sng SING-MS 82* (K), [2]KX388328, [3]KX388300, [4]KU844172.

Parkia sumatrana Miq.: Unknown locality, *Murphy 349* (E), [1]KY046214, –, –, –, –.

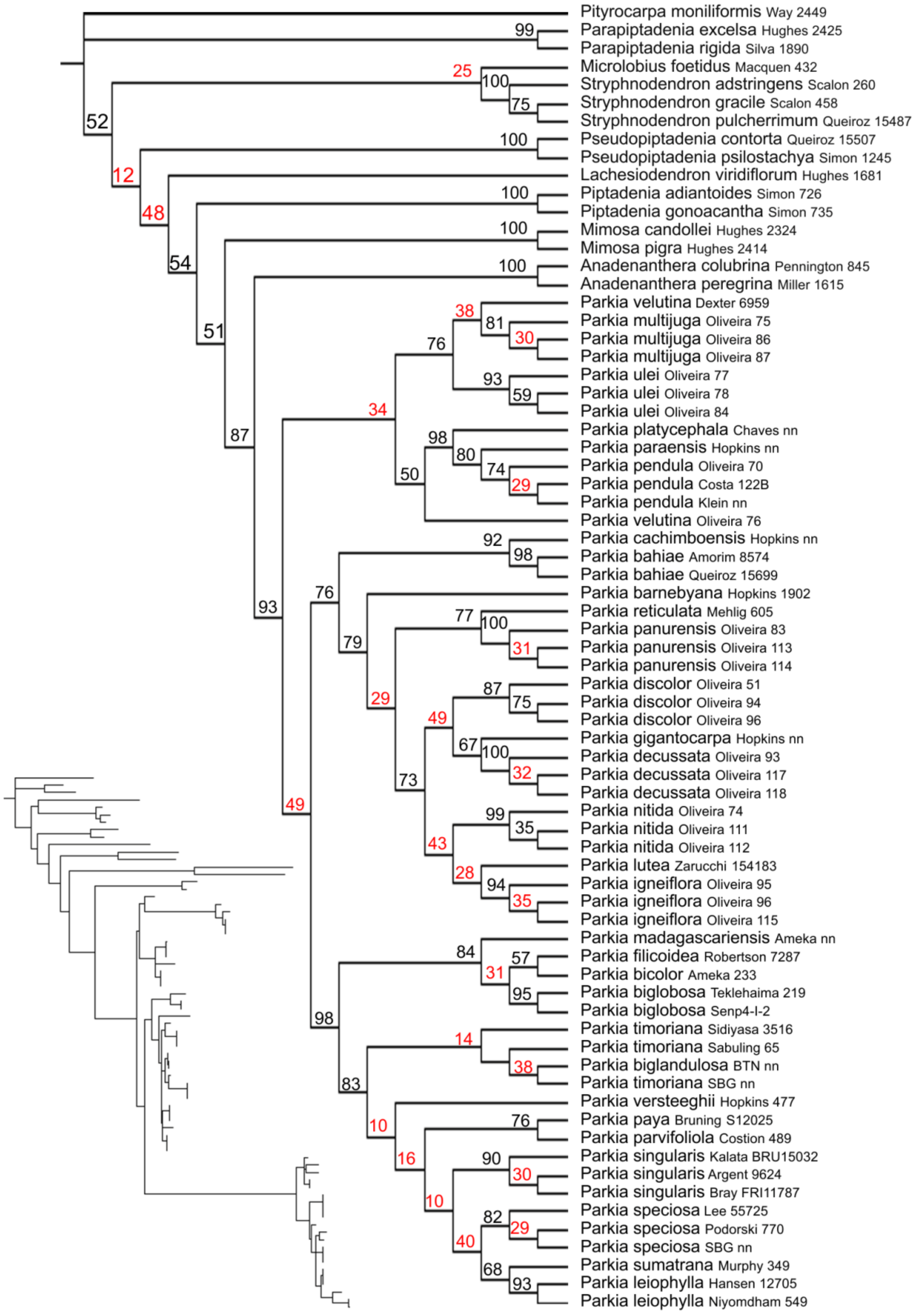
Parkia timoriana (DC.) Merr.: Indonesia, Borneo, *Sidiyasa 3516* (K). Singapore, Cult. at Singapore Bot. Gard., *Sng SING-MS 83* (K), ^{2}KX388329, ^{3}KX388301, ^{4}KU844177. Malaysia, *Sabuling 65* (K).

Parkia ulei (Harms) Kuhlm.: Brazil, Roraima, Rorainópolis, *Oliveira 77* (INPA). Brazil, Roraima, Rorainópolis, *Oliveira 78* (INPA), ^{2}KU388330, ^{3}KX388265, ^{4}KU844163. Brazil, Roraima, Rorainópolis, *Oliveira 84* (INPA), ^{2}KX388303, ^{3}KX388266, ^{4}KX388331.

Parkia velutina Benoist: Brazil, Amazonas, Manaus, *Dexter 6959* (E), ^{1}KY046084, –, –, –, –. Brazil, Amazonas, Manaus, *Oliveira 76* (INPA), ^{2}KX388305, ^{3}KX388269, ^{4}KU844161.

Parkia versteeghii Merr. & L.M.Perry: Papua New Guinea, *H.C. Hopkins 477* (K).

Figure S1. Maximum Likelihood tree and phylogram derived from the PhyML analysis based on DNA sequences of the *matK*, *trnL*, *psbA-trnH* and *rps16-trnQ* noncoding plastid loci and ITS/18S/26S nuclear region, showing the relationships among 30 species of *Parkia* and 16 outgroups. Numbers are bootstrap values (BS).



Highlights

- Detailed molecular phylogeny of *Parkia*
- Strong geographical phylogenetic signal in all clades
- Origin of the genus in Amazonia
- Long-distance dispersal to Paleotropics

Author Statement

Lorena Conceição Oliveira: Conceptualisation, Investigation, Formal Analysis, Data Curation, Writing – Original Draft, Visualisation. **Doriane Picanço Rodrigues**: Writing – Review and Editing, Supervision. **Helen C. Fortune Hopkins**: Data Curation, Writing – Review and Editing. **Gwilym Peter Lewis**: Data Curation, Writing – Review and Editing. **Michael John Gilbert Hopkins**: Conceptualisation, Data Curation, Writing – Review and Editing.

Capítulo 2

Evolution of the capitulum morphology and pollination systems in *Parkia* (Leguminosae, Caesalpinioideae, mimosoid clade)

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Abstract

Pollination systems often reflect adaptations to specific groups of pollinators, being indicative of specialized evolution and have been important in the diversification of angiosperms. Here, we study the evolution of pollination systems in the pantropical genus *Parkia*, which comprises 35 species of trees distributed largely in forests in South and Central America, Africa, Madagascar and the Indo-Pacific. The flowers are grouped into capitula that are composed of one, two, or three distinct morphological types, and are principally pollinated either by insects or by bats. We used a dated phylogeny based on combined chloroplast and nuclear DNA data to reconstruct the ancestral state of the capitulum and hence infer the ancestral pollination syndrome to reveal the direction and lability of the floral characters associated with pollination. Our results indicate that the ancestral capitulum in the genus had three flower types, a morphology today associated with bat pollination, and that in one clade, the number of flower types was reduced to two (capitulum also bat pollinated) or one (insect pollinated). Thus, entomophily, as seen in some Neotropical species of *Parkia*, is derived from a bat pollinated ancestor.

Keywords: chiropterophily, entomophily, evolution, Fabaceae, legumes

1. Introduction

Pollination systems involving animals are characterized as a set of floral attributes with convergent adaptations that often reflect features of specific groups of pollinators and these adaptations have been important in the diversification of angiosperms (Faegri & van der Pijl, 1966, Rech & Brito, 2012; Ashworth et al., 2015). A floral morphology that allows a better fit between the flower and the pollinator's body can generate greater reproductive success (Kay, Whittall & Hodges, 2006). Therefore, floral characteristics tend to be shaped by those more effective pollinators (Fenster et al., 2015). The floral specialization involving adaptations to new pollinators is intriguing because it causes changes in the ecological niche, being potentially linked to reproductive isolation, and can directly affect speciation (Armbruster, Lee & Baldwin, 2010; Rosas-Guerrero, Quesada & Armbruster, 2011; Willmer, 2011; van der Niet & Johnson, 2012).

The concepts of direction and lability of character transitions are frequently studied in floral evolution (Pérez, Arroyo, Medel & Hershkovitz, 2006; Whittall & Hodges, 2007; Tripp & Manos, 2008; Brito, Fendrich, Smidt, Varassin & Goldenberg, 2016). A common hypothesis is that specialized pollination systems are generally derived and generalized pollination systems are more likely to be ancestral (Ollerton et al., 2009, 2015; Rosas-Guerrero et al., 2014). Highly specialized floral attributes, such as those seen in many chiropterophilous flowers, allow a precise adjustment with morphology of the pollinator, thus restricting pollination to a single functional group (Muchhala & Thomson, 2010). Such a morphological restriction makes it difficult for other functional groups of visitors to act as pollinators, and thereby exercises selective pressure on the morphology (Ollerton, Killick, Lamborn, Watts & Whiston, 2007; Ollerton, Winfree & Tarrant, 2011; Ashworth et al., 2015).

Chiropterophily has been considered an evolutionary “dead-end”, which means that it can rarely be replaced by another pollination system (Tripp & Manos, 2008; Muchhala &

Thomson, 2010; Gómez et al., 2014). The reverse transition route from entomophily or ornithophily to chiropterophily is a more common evolutionary event (Tripp & Manos, 2008; Muchhala & Thomson, 2010), due to the fact that many plants pollinated by bats have a probable ancestor pollinated by bees, moths or birds (Rosas-Guerrero et al., 2014; Vogel, 1969b).

Parkia is a pantropical genus with approximately 35 tree species that show high regional endemicity, occurring in the tropical forests and savannas of South and Central America, Africa, Madagascar and the Indo-Pacific region. Most species, in both Old and New Worlds, are known or predicted to be pollinated by bats. Chiropterophily in pantropical genera is very rare, and apart from *Parkia*, it is known only in *Mucuna* (Leguminosae) , a genus largely of climbers that contains chiropterophilous and ornithophilous species, as well as a few in which non-volant mammals are significant flower visitors (Fleming et al., 2009). The pantropical distribution of *Mucuna* is attributed to long distance dispersal (Moura et al., 2016), presumably involving floating seeds. The genus appears to have originated in tropical Asia and achieved its wide distribution through numerous dispersal events, including ones to the New World at c. 12 and 6 Ma (Moura et al., 2016).Although largely Neotropical, the tree genus *Ceiba* (Malvaceae) contains a single amphi-Atlantic, bat pollinated species, *C. pentandra* (L.) Gartn., which is native in the New World and west tropical Africa, and introduced elsewhere in the tropics, including Asia. Its amphi-Atlantic distribution is also the result of recent long distance dispersal (Dick et al., 2007). The rarity of genera that are contain chiropterophilous species in both the Old and New Worlds means that *Parkia* provides a unique example in which to examine the evolution of bat-pollination in a pantropical genus of trees.

The monophyly of *Parkia* has been supported both by morphological (Luckow & Hopkins, 1995) and molecular data (Oliveira, 2015). Its species have flowers grouped into capitula, which are arranged in panicles. Each capitulum is composed of many small, tubular flowers inserted on a receptacle with a globular or ellipsoid apex, and each is composed of up to three functional types of flowers: fertile, nectar-secreting and staminodial. These are arranged in different ways to produce three different capitular morphologies, and the structure of the capitulum is the basis for the current infrageneric classification of the genus, which recognises three taxonomic sections (Hopkins, 1986) whose characters are summarized in Table 1.

Table 1. Characters of the three taxonomic sections of *Parkia*.

	Taxonomic section		
	Parkia	*Platyparkia*	*Sphaeroparkia*
Characters			
Number of species	c. 29	3	3
Distribution	Pantropical	Neotropical	Neotropical
Shape and structure of capitula	Clavate or biglobose; composed of apical fertile flowers, intermediate nectar-secreting flowers, and basal sterile flowers with staminodia	Oblate; composed of basal fertile flowers and apical nectar-secreting flowers	Spherical; composed of only fertile flowers
Pollinators	Pteropodidae bats in Paleotropics; Phyllostomidae bats in Neotropics	Phyllostomidae bats	Insects

Entomophily in *Parkia* occurs in three species that have capitula composed entirely of fertile flowers. The capitula are smaller than in the chiropterophilous species, they are red or yellow-cream in colour and they produce no, or very little, nectar (Hopkins 1984; Chaves, 2015). The pollinating agents include diurnal and nocturnal bees (Fig. 1E), and possibly microcoleoptera and Thysanoptera in one species (Hopkins, 1984; Hopkins et al., 2000; Chaves, 2015).

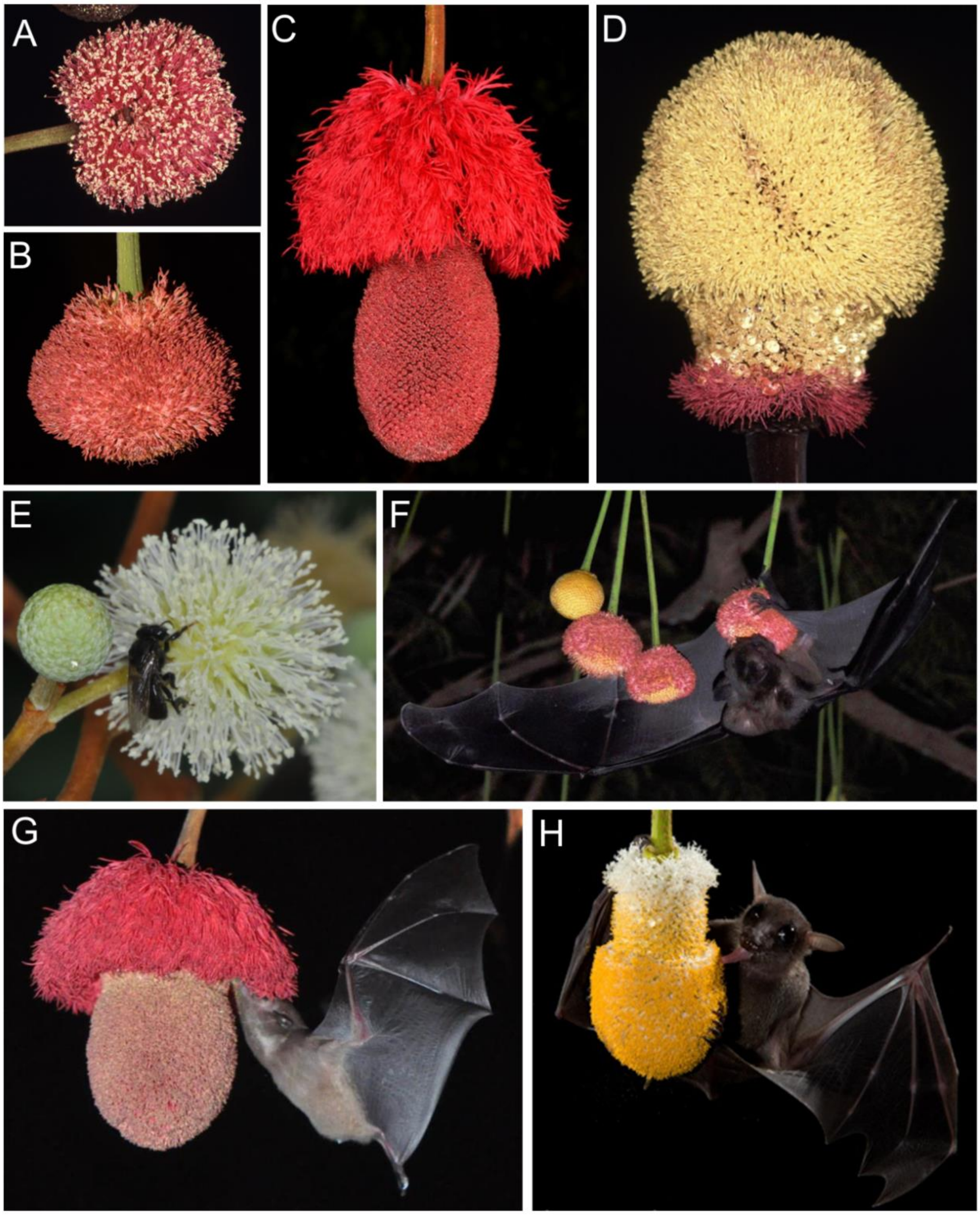

Figure 1. A-D Morphology of capitula in *Parkia* (Leguminosae, Caesalpinioideae, mimosoid clade): **(A)** *P. velutina*, spherical capitulum comprised only of fertile flowers; **(B)** *P. pendula*, oblate capitulum with fertile flowers in the middle and basal portion and nectar-secreting flowers at the apex (note visible nectar droplets); **(C)** *P. igneiflora*, capitulum with fertile flowers forming a ball at the apex, nectar-secreting flowers in the middle portion (beneath the fringe and therefore not visible) and staminodial flowers at the base, their staminodes forming a fringe; **(D)** *P. decussata* with short staminodes not forming a fringe. **E-H** Pollinators in *Parkia*: **(E)** *Trigona* sp. bees at *P. ulei*; **(F)** *Phyllostomus* sp. at *P. pendula*; **(G)** *Phyllostomus* sp. at *P. igneiflora*; **(H)** *Eonycteris spelaea* (Pteropodidae) at *P. speciosa*. Photographs: A, D & F by Michael Hopkins; B & C by

Francisco Farroñay; F & G by Luiz Melo; H by Merlin Tuttle.

In contrast, the chiropterophilous species have larger capitula and dedicated nectar-secreting flowers, which produce large amounts of nectar (5-12 ml per night), with a high concentrations of sugar (e.g. Piechowski, 2007). The capitula are generally held free from the foliage, in some cases on long compound inflorescence axes (up to 6 m), which project beyond the crown. The flowers reach anthesis in late afternoon, and have, yellowish-cream, yellow or red coloration, and strong, distinctive odours (Hopkins, 1998).

Entomophily in the genus occurs only in the Neotropics (except for cases of primarily chiropterophilous species that are pollinated by bees in the absence of bats, e.g. Lassen, Ræbild, Hansen, Brødsgaard & Eriksen, 2012). Chiropterophily as the primary mode of pollination occurs in both Neotropical and paleotropical species. In the Neotropics, the bat pollinators are species of Phyllostomidae (Fig. 1F and 1G), and in the Paleotropics, they belong to the family Pteropodidae (Fig. 1H) (e.g. Baker & Harris, 1957; Vogel, 1968; Hopkins, 1983, 1984, 1986, 1998; Grünmeier, 1990; Singaravelan, Raja & Marimuthu, 2007; Bumrungsri, Harbit, Benzie, Carmouche, Sridith & Racey, 2008; Piechowski, Dotterl & Gottsberger, 2010; Vololona, Ramavovololona, Lalarivoniaina & Goodman, 2020). The two families of bats are only distantly related to each other, being in different sub-orders, suggesting that the evolutionary path to chiropterophily was different in the Old and New Worlds.

The number of species of plants pollinated by bats is at least four times higher in the Neotropics than the Paleotropics (von Helversen, 1993). This has been explained by the presence in the New World of many highly specialized nectar feeding bats, most of them belonging to the subfamily Glossophaginae (Phyllostomidae) (von Helversen, 1993; Tschapka & Dressler, 2002). These species have undergone morphological, physiological and behavioural changes as adaptations to feeding on nectar, often involving the ability to hover at flowers, and the possession of very long and specialized tongues, elongated rostra and reduced dentition (von Helversen, 1993; Tschapka & Dressler, 2002), all of which allow them to exploit flowers with tubular morphologies that exclude other, less specialised bats. These less specialised Neotropical nectar feeding bats are either primarily frugivorous or insectivorous and include members of the genera *Artibeus*, *Carollia*, *Phyllostomus* and *Sturnira* (von Helversen, 1993; Tschapka & Dressler, 2002; von Helversen & Winter, 2003). When flower-visiting, these bats typically land on flowers that offer easy access to large quantities of nectar.

In the Paleotropics, Pteropodidae, also known as Old World fruit bats, have an almost exclusively plant based diet (Fleming, 1986, 1993). Many species that visit flowers also consume fruit and lack specialized adaptations for nectar feeding and so can be classified as "opportunistic visitors to flowers" (Tschapka & Dressler, 2002). However, other species, especially amongst the smaller taxa, are specialised nectarivores, including *Megaloglossus woermanni* Pagenstecher, which is a pollinator of *Parkia bicolor* in Africa (Grünmeier, 1990) and *Eonycteris spelaea* Dobson, which is an important pollinator for several *Parkia* species in SE Asia (Bumrungsri, Harbit, Benzie, Carmouche, Sridith & Racey, 2008). Chiropterophilous species of *Parkia* are principally pollinated by Pteropodidae in the Old World and by non-Glossophaginae Phyllostomidae in the New World.

The presence of both entomophilous and chiropterophilous syndromes in *Parkia* allows us to examine changes in morphology and pollination systems within a phylogenetic and biogeographic context. In this study, phylogenetic and biogeographic data are combined with morphological data to understand the evolution of capitular morphology and pollination systems in *Parkia*. We test hypotheses about the origins of the two main pollination systems and comment on lability and directionality in pollination-related character transitions.

2. Materials and methods

A species tree was reconstructed for 30 of the 35 species currently recognised in *Parkia* and 16 outgroups, using the multilocus data set and we estimated the lineage divergence times using the uncorrelated lognormal relaxed clock Bayesian method in BEAST v.2 (Bouckaert et al., 2014), assuming a general time-reversible model, with invariable sites and among-site rate heterogeneity (GTR+I+Γ). Markov Chain Monte Carlo simulations (MCMC) were performed for two runs of 10,000,000 generations, recording the tree parameters every 1000th generation. Tracer v.1.6 (Rambaut and Drummond, 2009) was used to check if sample sizes and estimated values (ESS) were >200, and the results were assessed to have reached stationarity and convergence. Data from multiple runs were combined after exclusion of burn-in trees. A maximum clade credibility (MCC) tree was calculated in TreeAnnotator v.1.8.0 (Drummond and Rambaut, 2010). The MCC tree with 95% highest posterior density (HPD) was visualized in FigTree v.1.4.2 (Rambaut, 2014). The divergence between them was estimated to have occurred in the Middle Eocene because the crown node of the Piptadenia group was constrained to 45 Ma using the fossil pollen "Q" (Simon et al., 2009). Voucher information, taxon author, and GenBank accession numbers of all sequences used in this study are provided in Appendix A1.

Ancestral character state reconstruction analysis was used to investigate the evolution of the types of capitula identified in *Parkia* under a maximum parsimony criterion using the package Mesquite v. 3.5 (Maddison & Maddison, 2018). We performed the analysis without outgroups and the character state coding was done as follows: (0) capitula spherical, composed of only fertile flowers; (1) capitula oblate, with both fertile and nectar-secreting flowers, and (2) capitula biglobose to clavate, with fertile, nectar-secreting and staminodial flowers. Pollination syndrome coding was done as follows: (0) entomophily and (1) chiropterophily. The information on the character states for morphology and pollination systems was compiled from the literature (including Baker & Harris, 1957; Vogel, 1968; Hopkins 1983, 1984, 1986, 1994, 2000a & b; Grünmeier, 1990; Hopkins, Hopkins & Sothers, 2000; Fischer, 2000; Singaravelan, Raja & Marimuthu, 2007; Bumrungsri, Harbit, Benzie, Carmouche, Sridith & Racey, 2008; Chaves, 2015;; Piechowski, Dotterl & Gottsberger, 2010; Vololona, Ramavovololona, Lalarivoniaina & Goodman, 2020) and observations in the herbarium.

3. Results

The reconstruction of ancestral character states for the morphology of the capitula and the pollination systems are presented in Figure 2. Our analysis indicates that the ancestral species of the genus (at 18.49 Ma with 95% highest posterior density (HPD) of 11.95–26.17 Ma) had capitula with three types of flowers (Fig.1C). This state is conserved in all the paleotropical species and in the most species rich Neotropical lineage (clade 3), which together constitute the paraphyletic section *Parkia*. The paleotropical species form a monophyletic clade, with two subclades (Indo-Pacific and Africa-Madagascar, clade 4 and 5, respectively) that have a divergence node at 8.28 Ma (95% HPD 5.66–14.39 Ma). The spherical capitulum formed only by flowers (Fig. 1A), therefore being the probable derived, it occurs in the three species corresponding to the section *Sphaeroparkia*, recovered in the clade, with an age of divergence of approximately 5.96 Ma (HPD 2.11–10.4 Ma). The three species with capitula composed of two types of flowers (Fig. 1B), was recovered from clade 2 with an age of divergence of approximately 3.05 Ma (HPD 1.11–5.12 Ma), corresponding to the section *Platyparkia*. The clade containing sections *Platyparkia* and *Sphaeroparkia* diverged from sect. *Parkia* at 12.89 Ma (95% HPD 5.66–14.39 Ma), and subsequently diverged from each other at 9.79 Ma (95% HPD 5.66–14.39 Ma).

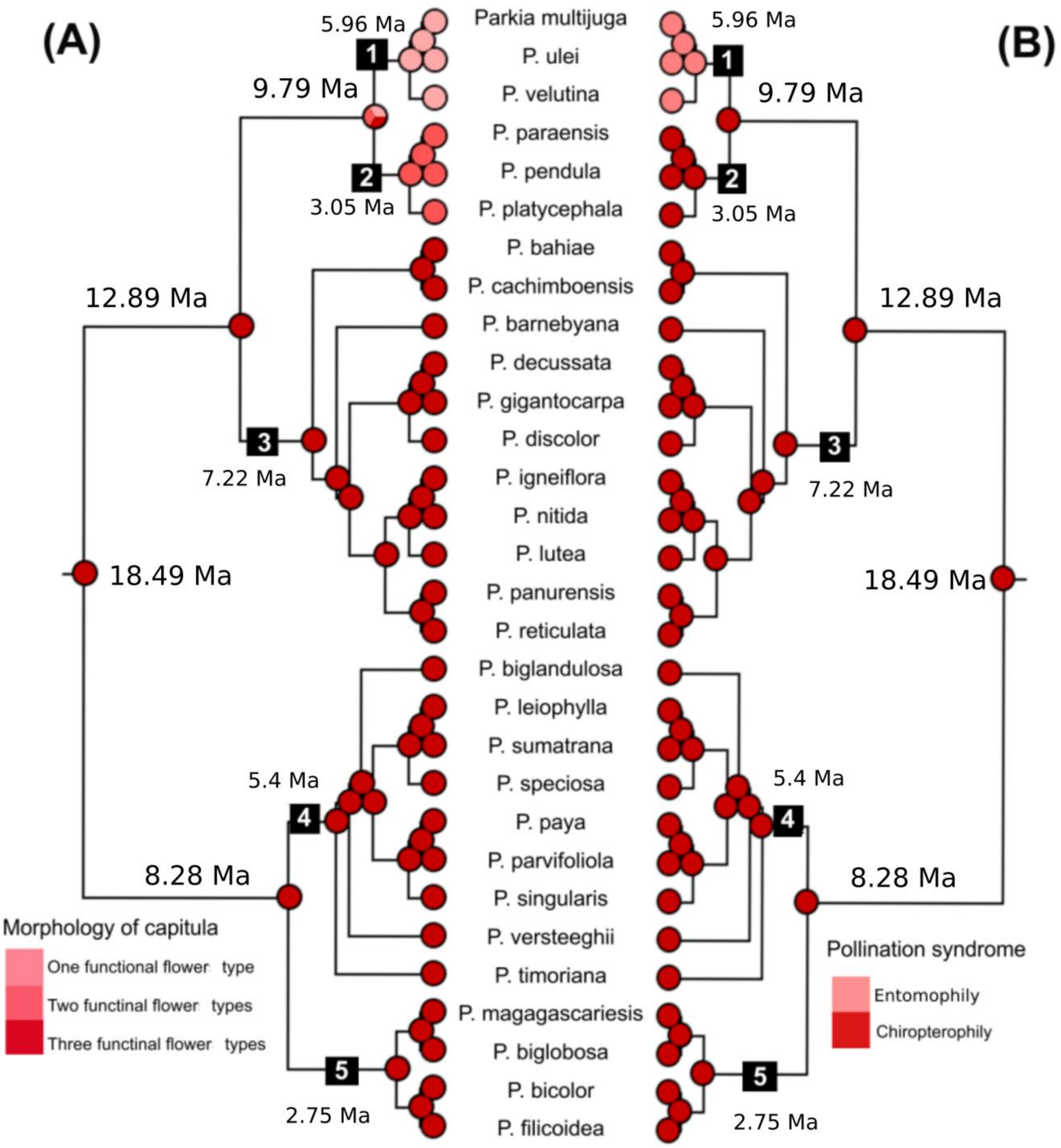

Figure 2. Character optimizations onto a 50% majority-rule Bayesian tree showing the evolution of **(A)** types of capitula and **(B)** syndrome pollination in *Parkia*. Numbers are divergence time estimation in Beast. Ma = Millions years ago.

The Chiropterophily is recovered as ancestral pollination syndrome, first appears independently in two Neotropical lineages, and in paleotropical lineages of the genus (clade 4 and 5). Entomophily is monophyletic, and probably the derived syndrome in *Parkia* and it appears in a subclade that corresponds to the section *Sphaeroparkia*. The Chronogram tree of

Parkia derived from divergence time estimation in Beast is available in Suplementary Material Figure S1.

4. Discussion

The latest common ancestor of extant *Parkia* species had capitula with three types of flowers (Fig. 1C), this condition was present in the crown node of the genus of approximately 18 Ma. In all extant species of *Parkia*, in both the Neotropics and Paleotropics, capitula with three flower types are associated with pollination by bats.

The diversification of bats in the Neotropics probably occurred during the Miocene (Jones, Bininda-Emonds & Gittleman, 2005; Teeling et al., 2005; Fleming, Geiselman & Kress, 2009; Datzmann, von Helversen, & Mayer, 2010; Rojas, Vale, Ferrero, & Navarro 2011, 2012; Almeida, Giannini, & Simmons, 2016; Rojas, Warsi, & Dávalos, 2016). Phyllostomidae bats diversified at the end of the Middle Miocene Climatic Optimum (15–20 Ma) by when most genera had appeared (Arita, Vargas-Barón, & Villalobos, 2014; Rojas, Warsi, & Dávalos, 2016; Datzmann, von Helversen, & Mayer, 2010; Rojas, Vale, Ferrero, & Navarro, 2011, 2012). Jones et al. (2005) detected two significant changes in the rate of diversification in Phyllostomidae in the Chiroptera supertree (Jones et al., 2002) and suggested a relationship between this diversification events and the rate of diversification in flowering plants.

Pteropodidae are older than Phyllostomidae, dating from approximately 39 Ma (Teeling et al., 2005). Some lineages of fruit bats from the Indo-Pacific region date from the Oligocene at approximately 31 Ma, with diversification events from the Miocene to the Pleistocene (Almeida, Giannini, DeSalle, & Simmons, 2009; Almeida, Gianini & Simmons, 2016). Recent phylogenetic studies indicate that Pteropodidae probably repeatedly colonized Africa from Asian ancestors (Almeida, Giannini, & Simmons, 2016). Estimates of divergence dates suggest that these events occurred in different periods and that although local diversification appears to have started in the late Miocene, the more extensive diversification that produced the modern fauna occurred much later, in the Pleistocene (Cunha, Giannini, & Simmons, 2016). The diversification dates for Phyllostomidae and Pteropodidae are consistent with the confidence intervals for the time of diversification of *Parkia* in the Neotropics and Paleotropics. Thus bat-pollination is likely to be the ancestral condition in the lineage of the genus, dating back to at least 18 Ma.

Chiropterophily probably not is an evolutionary "dead-end" in *Parkia*. The entomophily is probably the ancestral condition, and during the evolution of the genre there was at least a change from chiropterophily to entomophily. Rejecting, the hypothesis that specialized pollination systems are derived from generalized systems.

In *Parkia*, changes between the capitulum of entomophilous species for capitulum of chiropterophilous species is the presence of flowers specialized in the production of large quantities of nectar, and staminodes (except in the capitula of *Parkia paraensis*, *P. pendula* and *P. platycephala*). *Parkia velutina*, *P. multijuga* and *P. ulei* although differ slightly in the characters associated with entomophily, such as size, colour and smell of the capitula, in general, present capitula with less specialized structure compared to those pollinated by bats.

Capitula composed of a single flower type are found in the three entomophilous species (Clade 1, sect. *Sphaeroparkia*), and this condition is derived from an ancestor that was bat pollinated, and had capitula composed of three types of flower. These three species, previously considered to be a paraphyletic ancestral group (Luckow and Hopkins, 1995), can now be interpreted as a derived monophyletic clade with derived pollination syndromes. Although all three species in sect. *Sphaeroparkia* appear to be entomophilous, they have different floral visitors. The pale yellow flowered *Parkia ulei* is the only diurnal species in the genus, and is pollinated by diurnal bees (Hopkins 1986; Chaves, 2015). The red flowered, nocturnal, *P. velutina* is visited by nocturnal bees of the genus *Megalopta* (Hopkins, Hopkins & Sothers, 2000). The pollination of the nocturnal, yellow flowered, *P. multijuga* is still enigmatic, the principal visitors being nocturnal microcoleoptera and Thysanoptera (Chaves, 2015). This diversity of syndromes suggests diversification after the loss of bat-pollination, although some characteristics from chiropterophily have been retained, such as nocturnal anthesis in *P. velutina* and *P. multijuga*.

Capitula composed of two types of flower, found in the three species that form clade 2 (sect. *Platyparkia*), also represent a condition derived from a three-flowered ancestor. However, they retain a bat pollination syndrome, and are (largely) pollinated by the same species of Phyllostomidae as clades 3, 4 and 5, but they have a radically different capitular morphology with the nectar-producing flowers apical and the fertile flowers basal. Since clade 2 is sister to clade 1, possibly their ancestors retained bat pollination during a radical morphological shift in the position of the flower types, or possibly they passed through a one-flower type phase, and evolved bat-pollination secondarily from this, perhaps insect-pollinated, condition.

The capitula evolution in *Parkia* may have been directional. Changes in morphology were concomitant with the change in pollinators. Floral specialization has been discussed under the concept of pollination syndromes (Faegri and van der Pijl, 1966; Fenster et al., 2004). Pollination syndromes are sets of floral traits associated with attraction, and reflect adaptations to a specific pollinator or to a functional group of pollinators (Fenster et al., 2004). Several studies support the theory that syndromes reflect pollination by specific animal groups (Schemske & Bradshaw 1999; Hargreaves et al. 2004; Machado & Vogel 2004; Wilson et al. 2004; SanMartin-Gajardo & Sazima 2005; Muchhala 2006; Pauw 2006; Whittall & Hodges 2007; Tripp & Manos, 2008).

5. Conclusions

Despite considerable differentiation in inflorescence morphology and pollination syndromes, the genus is clearly monophyletic, and the ancestral condition is bat pollination. There was (probably) a single dispersal event after the evolution of bat pollination, and the bat pollinated syndrome was preserved when the dispersed species encountered an ecosystem which included flower-visiting bats capable of pollinating its flowers, despite these bats being only distantly related to the group with which it originally evolved its pollination syndrome. The most likely direction of the long distance dispersal event was from the New to the Old World. Entomophily in three species is a derived condition.

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Appendix A1. Voucher specimens for DNA sequences used in this study. For each entry in the following list, the species name and author, collection locality, collector's name and number for the voucher, herbarium acronym, and GenBank accession numbers are reported. Superscripts before GenBank accession numbers indicate sequences: ^{1}*matK*, ^{2}*trnL*, ^{3}*psbA-trnH*, ^{4}*rps16-trnQ* and ^{5}ITS/18S/26S.

Anadenanthera colubrina (Vell.) Brenan.: Unknown locality, *Pennington 845* (E), ^{1}AF521813, ^{2}AF522947, –, –, ^{5}JQ910930.

Anadenanthera peregrina (L.) Speg.: Unknown locality, *Miller 1615*, ^{1}EU812046, ^{2}EU440022, ^{3}EU811982, –, –.

Lachesiodendron viridiflorum (Kunth) P.G.Ribeiro, L.P.Queiroz & Luckow: Mexico, *Hughes 1681* (FHO), ^{1}KT364173, ^{2}KT364001, –, –, ^{5}KT364066.

Microlobius foetidus (Jacq.) M.Sousa & G.Andrade: Unknown locality, *Macqueen 432*

Mimosa candollei R.Grether: Bolivia, *Hughes 2324* (FHO), ^{1}KT364211, ^{2}KT363988, –, –, ^{5}KT364050.

Mimosa pigra L.: Bolivia, *Hughes 2414* (FHO), ^{1}KT364213, ^{2}KT363994, –, –, ^{5}KT364060.

Parapiptadenia excelsa (Griseb.) Burkart: Bolivia, *Hughes 2425* (FHO), ^{1}KT364160, ^{2}KT363996, –, –, ^{5}KT364062.

Parapiptadenia rigida (Benth.) Brenan: Unknown locality, *Silva 1890* (BH), ^{1}AF521849, ^{2}AF278505, –, –, –.

Piptadenia adiantoides (Spreng.) Macbr.: Brazil, *Simon 726* (FHO), ^{1}KT364158, ^{2}KT363998, –, –, ^{5}KT364064.

Piptadenia gonoacantha (Mart.) J.F.Macbr.: Bolivia, *Simon 735* (FHO), –, ^{2}FJ982238, –, –, ^{5}KT364065.

Pityrocarpa moniliformis (Benth.) Luckow & R.W.Jobson: Brazil, *Way 2449* (K), ^{1}KT364162, ^{2}KT364002, –, –, ^{5}KT364067.

Pseudopiptadenia contorta (DC.) G.P.Lewis & M.P.Lima: Unknown locality, *Queiroz 15507* (CEN), ^{1}KT364155, ^{2}KT364005, –, –, –.

Pseudopiptadenia psilostachya (DC.) Benth.: Unknown locality, *Simon 1245* (CEN), ^{1}KT364170, ^{2}KT364006, –, –, ^{5}KT364070.

Stryphnodendron adstringens (Mart.) Coville: Unknown locality, *Scalon 260* (ESA), ^{1}KT364188, ^{2}KT364010, –, –, ^{5}KT364074.

Stryphnodendron gracile Her. & Rizz: Unknown locality, *Scalon 458* (ESA), ^{1}KT364177, ^{2}KT364019, –, –, ^{5}KT364080.

Stryphnodendron pulcherrimum (Willd.) Hochr.: Brazil, *Queiroz 15487* (HUEFS), ^{1}KT364205, ^{2}KT364043, –, –, ^{5}MG001281.

Parkia bahiae H.C.Hopkins: Brazil, Bahia, *Amorim 8574* (CEPEC), ^{2}KX388312, ^{3}KX388277, ^{4}KU844157. Brazil, Bahia, *Queiroz 15699* (HUEFS), ^{1}KY046204,

Parkia barnebyana H.C.Hopkins: Brazil, Amazonas, *M.J.G. Hopkins 1902* (INPA), ^{2}KX388313, ^{3}KX388278, ^{4}KU844164.

Parkia bicolor A.Chev.: Ghana, *Ameka 233* (K), ^{3}KX388279, ^{4}KU844174.

Parkia biglandulosa Wight & Arn.: Unknown locality, *Banana Tree Nursey* (BH), ^{1}AF521850, ^{2}AF278498.

Parkia biglobosa (Jacq.) R.Br.: Burkina Faso, *Teklehaima 219* (K), ^{2}KX388315, ^{3}KX388280, ^{4}KU844173. Senegal, *SENp4-I-2* (Herbarium unknown) –,^{2}HM489999, ^{3}HM489995, –, –.

Parkia cachimboensis H.C.Hopkins. Brazil, Pará, Belém, *Hopkins & Hopkins 3907* (INPA), [3]KX388281, [4]KU844158.

Parkia decussata Ducke: Brazil, Amazonas, Manaus, *Oliveira 93* (INPA), [2]KX388315, [3]KX388282, [4]KU844156. Brazil, Amazonas, Manaus, *Oliveira 117* (INPA), [2]KX388316, [3]KX388283, [4]KU844139. Brazil, Amazonas, Manaus, *Oliveira 118* (INPA), [2]KX388317, [3]KX388284, [4]KU844139.

Parkia discolor Spruce ex Benth.: Brazil, Amazonas, Manaus, *Oliveira 51* (INPA), [2]KX388320, [3]KX388287, [4]KX388341. Brazil, Amazonas, Manaus, *Oliveira 94* (INPA), [2]KX388318, [3]KU844170, [4]KX388285. Brazil, Amazonas, Manaus, *Oliveira 96* (INPA), [2]KX388319, [3]KX388286, [4]KX388342.

Parkia filicoidea Oliv.: Kenya, *Robertson 7287* (K), [2]KX388321, [3]KX388288, [4]KU844176.

Parkia gigantocarpa Ducke: Brazil, Pará, Bélem, Cult. at Museu Paraense Emílio Goeldi, Leaves sampled by *M.J.G.Hopkins*, without voucher, [2]KX388322, [3]KX388289, [4]KU844171.

Parkia igneiflora Ducke: Brazil, Amazonas, Manaus, *Oliveira 95* (INPA), [3]KX388290, [4]KU844169. Brazil, Amazonas, Manaus, *Oliveira 96* (INPA), [3]KX388291, [4]KX388340. Brazil, Amazonas, Manaus, *Oliveira 115* (INPA).

Parkia leiophylla Kurz: Thailand, *Hansen 12705* (K). Unknown Locality, *Niyomdham 549* (E), [1]KY046207, –, –, –, –.

Parkia lutea H.C.Hopkins: Brazil, Amazonas, Maués, *Zarucchi 2930* (INPA), [3]KX388292, [4]KU844167

Parkia madagascariensis R.Vig.: Madagascar, *Du Puy M556* (K), [2]KX388323, [3]KX388293, [4]KU844175.

Parkia multijuga Benth.: Brazil, Amazonas, Manaus, *Oliveira 75* (INPA). Brazil, Amazonas, Manaus, *Oliveira 86* (INPA), [2]KX388306, [3]KX388270, [4]KU844162. Brazil, Amazonas, Manaus, *Oliveira 87* (INPA), [2]KX388307, [3]KX388271, [4]KX388332.

Parkia nitida Miq.: Brazil, Amazonas, Manaus, *Oliveira 74* (INPA), [2]KX388324, [3]KX388294, [4]KU844168. Brazil, Amazonas, Manaus, *Oliveira 111* (INPA), [2]KX388325, [3]KX388295, [4]KU844141. Brazil, Amazonas, Manaus, *Oliveira 112* (INPA), [2]KX388326, [3]KX388296, [4]KU844142.

Parkia panurensis Benth. ex H.C.Hopkins: Brazil, Roraima, Rorainópolis, *Oliveira 83* (INPA), [3]KX388297, [4]KU844165. Brazil, Amazonas, Manaus, *Oliveira 113* (INPA). Brazil, Amazonas, Manaus, *Oliveira 114* (INPA)

Parkia paraensis Ducke: Brazil, Amazonas, Cult. at Instituto Nacional de Pesquisas da Amazônia, *M.J.G. Hopkins* 2421(INPA).

Parkia parvifoliola Hosok.: Micronesia, Palau, *Costion 489* (K).

Parkia paya H.C.Hopkins: Malaysia, Borneo, *Bruning S12025* (K).

Parkia pendula (Willd.) Benth. ex Walp.: Brazil, Roraima, Rorainópolis, *Oliveira 70* (INPA),[2]KX388309, [3]KX388274, [4]KU844159. Brazil, Rondônia, *Costa 122B* (INPA), [3]KX388276, [4]KX388335. Brazil, Pernambuco, Recife, *Klein s.n.* (INPA).

Parkia platycephala Benth.: Brazil, Maranhão, Chapadinha, *Chaves s.n.* (UFMA), [2]KX388308, [3]KX388273, [4]KU844160.

Parkia reticulata Ducke: Brazil, Pará, *Mehlig 605* (INPA), [2]KX388327, [3]KX388299, [4]KU844166.

Parkia singularis Miq.: Brunei, *Kalata et al. BRUN 15032* (K). Indonesia, *Argent et al. 9624* (K). Malaysia, *Bray FRI 11787* (K).

Parkia speciosa Hassk.: Malaysia, Borneo, *Lee S.55725* (K). Philippines, Palawan, *Podzorski S.M.H.I.770* (K). Singapore, Cult. at Singapore Bot. Gard., *Sng SING-MS 82* (K), [2]KX388328, [3]KX388300, [4]KU844172.

Parkia sumatrana Miq.: Unknown locality, *Murphy 349* (E), [1]KY046214, –, –, –, –.

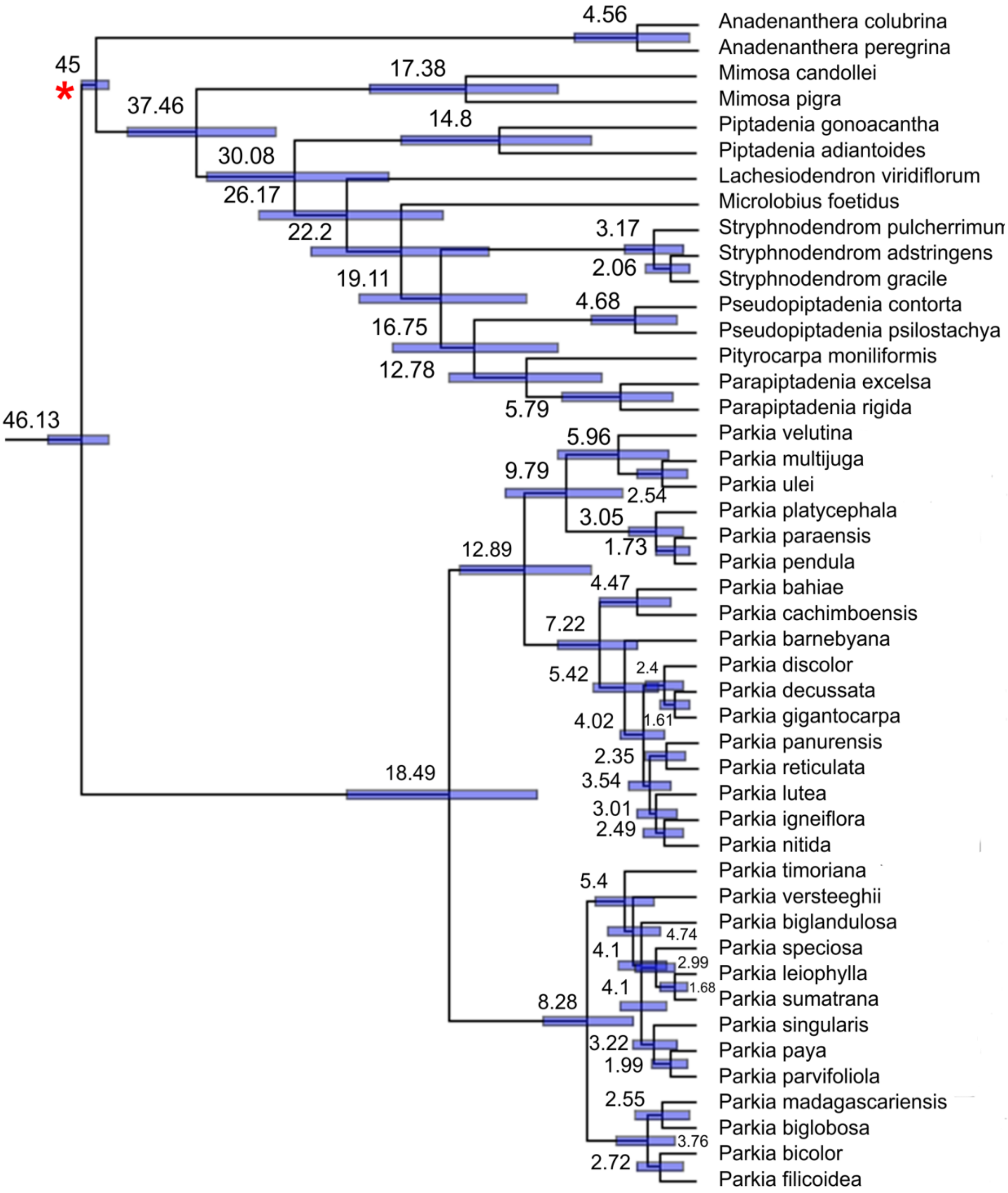
Parkia timoriana (DC.) Merr.: Indonesia, Borneo, *Sidiyasa 3516* (K). Singapore, Cult. at Singapore Bot. Gard., *Sng SING-MS 83* (K), [2]KX388329, [3]KX388301, [4]KU844177. Malaysia, *Sabuling 65* (K).

Parkia ulei (Harms) Kuhlm.: Brazil, Roraima, Rorainópolis, *Oliveira 77* (INPA). Brazil, Roraima, Rorainópolis, *Oliveira 78* (INPA), [2]KU388330, [3]KX388265, [4]KU844163. Brazil, Roraima, Rorainópolis, *Oliveira 84* (INPA), [2]KX388303, [3]KX388266, [4]KX388331.

Parkia velutina Benoist: Brazil, Amazonas, Manaus, *Dexter 6959* (E), [1]KY046084, –, –, –, –. Brazil, Amazonas, Manaus, *Oliveira 76* (INPA), [2]KX388305, [3]KX388269, [4]KU844161.

Parkia versteeghii Merr. & L.M.Perry: Papua New Guinea, *H.C. Hopkins 477* (K).

Figure S1. Chronogram tree of *Parkia* derived from divergence time estimation in Beast. Asterisk refers to the calibration point. Shaded blue horizontal bars show the 95% highest posterior densities (HPD) of the divergence times.



Considerações Finais

Nosso estudo compreende a primeira filogenia molecular de *Parkia*. Os dados de cloroplasto e DNA nuclear suportam a monofilia do gênero, embora nossos resultados da análise bayesiana não estão totalmente alinhados com nenhuma das classificações seccionais propostas para o gênero, os resultados da análise de ML estão alinhados com o arranjo secional proposto por Hopkins (1986). A geografia aparece como o principal preditor da estrutura filogenética em nossas análises. As estimativas do tempo de divergência e a reconstrução da área ancestral sugerem uma origem neotropical para *Parkia* há aproximadamente 18,49 Ma. Durante a história evolutiva do gênero houve pelo menos um evento de dispersão para os paleotrópicos. A radiação pelos neotrópicos promoveu maior especiação comparada a região paleotropical, sem dúvida influenciada por vários fatores bióticos e abióticos, incluindo a história geológica.

Quanto à evolução das duas síndromes de polinização, observadas no gênero, a condição ancestral é a polinização por morcegos. Houve (provavelmente) um único evento de dispersão após a evolução da polinização por morcegos, e a síndrome polinizada por morcegos foi preservada quando as espécies dispersas encontraram um ecossistema que incluía morcegos visitantes de flores, capazes de polinizar suas flores. A entomofilia em três espécies é uma condição derivada. O capítulo com estrutura formada por três tipos de flores é ancestral, os demais tipos de capítulos, formado por dois tipos de flores e o composto inteiramente por flores férteis foram recuperados como derivados.