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Linha de Pesquisa em Paleontologia Aplicada

DISSERTAÇÃO DE MESTRADO

FLORA FÓSSIL DOS NÍVEIS DE BENTONITA DA FORMAÇÃO
CAMPOS NOVOS (OLIGOCENO SUPERIOR) BACIA DE BOA
VISTA, PB, BRASIL.

Guilherme Artur Paniz

Orientadora: Prof^a. Dra. Tânia Lindner Dutra (PPGEO-UNISINOS)

São Leopoldo, fevereiro de 2015.

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A dissertação de Mestrado

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(OLIGOCENO SUPERIOR) BACIA DE BOA VISTA, PB, BRASIL.**

Apresentada por **Guilherme Artur Paniz**

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“Nos mesmos rios entramos e não entramos, somos e não somos.”

Heráclito de Éfeso

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RESUMO

O final do Oligoceno foi um momento crítico para a evolução das angiospermas, com o estabelecimento da vegetação moderna e o predomínio das pastagens. Foi um período de importantes eventos geológicos, como a elevação dos Andes permitindo a ligação com a América Central e modificando a fitogeografia. Uma nova associação fóssil é apresentada e descrita para as camadas de folhelho bentonítico da Formação Campos Novos, cuja datação $^{40}\text{Ar}/^{39}\text{Ar}$ geocronológica indica o final do Oligoceno. Esta unidade é parte da sequência deposicional que preencheu a Bacia de Boa Vista, uma pequena bacia *pull-apart* localizada no Nordeste do Brasil e situada sobre um embasamento Pré-Cambriano e afetada por eventos tectônicos e magmáticos. A taoflora é composta exclusivamente por angiospermas e está representada por folhas, folíolos, frutos e fragmentos de uma flor e de uma provável monocotiledônea. Entre os taxa identificados, predominam os da família Fabaceae seguida por Lauraceae, Annonaceae, Burseraceae, Anacardiaceae, Myrtaceae e Malvaceae. Dominam os tamanhos microfilicos com margens inteiras e venação broquidódroma, indicando clima tropical quente sazonal ou com períodos de restrição hídrica. Comparações feitas com outras assembleias Cenozoicas do Brasil e das Américas sugerem uma proximidade com as depositadas entre o Eoceno e Oligoceno da parte central do Brasil, e com aquelas do final do Oligoceno do Norte do Brasil e da região do Caribe. Isto sugere uma retração das floras tropicais das altas latitudes para latitudes mais baixas no final do Oligoceno, ligada, provavelmente, ao aquecimento ocorrido no final do período. Análogos modernos mostram uma flora mista de componentes da floresta Amazônica, Cerrado e Floresta Atlântica, ou um ecótono onde a maioria apresenta comportamento pioneiro. A flora fóssil de Boa Vista apresenta-se como potencial datadora para registros do final do Paleógeno do Brasil.

ABSTRACT

The end of Oligocene was a critical time for angiosperm evolution, with the definitive establishment of modern vegetation and grass-dominated landscapes. It was also a time marked by important geological events, with the first signs of the Andean uplift that led to closure of the Central America seaways and the resulting phytogeographic results. In the present article a new association of fossil plant imprints is described from a bentonitic shale interval of the Campos Novos Formation, for which $^{40}\text{Ar}/^{39}\text{Ar}$ geochronological dating has indicated a Late Oligocene age. This unit is part of the depositional sequence of the Boa Vista Basin, a small pull-apart basin in northeastern Brazil, established over a Pre-Cambrian basement and affected by tectonic and magmatic impacts. This taphoflora consists exclusively of angiosperm morphotypes, which are represented by leaves, leaflets, legume fruits (with a new genus *Albisiocarpum* proposed), a fragmentary flower, and one specimen from a probable monocot. Among these taxa, the Fabaceae-related forms stand out for their abundance (48% of representativeness), followed by Lauraceae (with a new species, *Nectandra bonavistensis*), Annonaceae, Burseraceae, Anacardiaceae, Myrtaceae, and Malvaceae. The dominant microphyllic leaves, with entire margins and brochidodromous venation, support the presence of a warm tropical climate, yet with times of more stressing conditions (seasonal or with hydric restriction). Comparisons made with other Cenozoic floral assemblages from Brazil and neighboring areas suggest the closest relations with Middle Eocene-Oligocene deposits from central and SE Brazil, and with assemblages preserved in Late Oligocene deposits from northern Brazil and the Caribbean region. This suggests a retraction of the tropical floras from higher to lower latitudes throughout the Oligocene, also probably linked to the short interval of climatic amelioration that occurred at the end of the period. Modern analogs show a mixed flora of Amazonian, Cerrado, and Atlantic Forest components, or an ecotone, with most of these displaying pioneer behavior. This fossil flora from the Boa Vista basin shows the potential for building a well-dated record for the fossil floras that precede the end of the Paleogene in Brazil.

1. INTRODUÇÃO

Restos de plantas são os fósseis mais comuns nas bacias interiores do Brasil durante o Cenozoico, ocorrem no Amazonas e Acre (Berry 1937; Machado et al. 2012), Pará (Duarte, 1967, 2004), Ceará (Duarte e Nogueira, 1980), Paraíba (Duarte e Vasconcelos 1980), Bahia (Hollick e Berry 1924), Minas Gerais (Dolianiti, 1949; Duarte, 1958; Duarte e Mello Filha 1980; Castro-Fernandes et al. 2013; Bernardes-de-Oliveira et al., 2014) e São Paulo (Duarte e Mandarim-de-Lacerda, 1989a; Fittipaldi et al., 1989; Veiga, 2009; Dos Santos e Bernardes de Oliveira, 2013; Biagolini et al. 2013).

A Bacia de Boa Vista (BBV) no Estado da Paraíba, se distingue por uma flora preservada em níveis de bentonita, cuja granulometria muito fina favoreceu a boa preservação, com impressões foliares que exibem caracteres da venação de mais alta ordem. A geologia da bacia foi bem estudada e conhecida devido à exploração da bentonita que proporcionou a identificação do material fossilizado. Trata-se de uma pequena bacia *pull-apart* preenchida por uma sequência vulcâno-sedimentar. O conteúdo fossilífero está localizado na Formação Campos Novos, e dados absolutos de idade obtidos permitiram recentemente precisar a idade da formação como tendo sido depositada entre 25.6+-0.4 e 24.9+-0.1 Ma, final do Oligoceno, (Souza et al., 2013).

O final do Oligoceno é caracterizado pelo primeiro intervalo de calor registrado para o Cenozoico, após um longo intervalo de climas frios que se estabeleceram ao final do Eoceno (Zachos et al., 2001). Os macrofósseis vegetais são uma boa ferramenta para estudo do paleoclima, uma vez que a vegetação responde às condições climáticas com adaptações fisionômicas e mudança na sua composição (e.g. Gray, 1879; Bailey and Sinnott, 1916; Dolph and Dilcher, 1979; Wolfe, 1995; Upchurch and Wolfe, 1997; Wilf, 1997; Spicer et al., 2004).

Distintas metodologias podem ser aplicadas no estudo de paleoclimas através de assembleias fosseis. Algumas necessitam um grande volume de dados e uma boa preservação do material, como o método da identificação do análogo moderno mais relacionado (MacGinitie, 1953; Mosbrugger and Utescher, 1997; Taylor et al., 2009), e o método da fisionomia e arquitetura foliar (CLAMP, Wolfe, 1995; Wolfe et al., 1998). Pode-se utilizar métodos mais simples, porém menos precisos, como o estudo do tipo de margem e tamanho foliar (Uhl et al., 2003; Royer and Wilf, 2006; Dutra, 2007).

Esta dissertação apresenta o estudo da tafoflora ocorrente nos níveis de bentonita da Formação Campos Novos, e os resultados são apresentados em formato de artigo, em anexo. Foram identificados 24 elementos distintos, e são apresentados 23 taxa, identificados a partir de impressões foliares, frutos e uma flor, incluindo uma nova espécie. A exceção de um fragmento atribuído à monocotiledoneae, todos os demais taxa são de dicotiledoneae, com predomínio da família Fabaceae com 48% dos taxa. Levando em consideração o análogo moderno, a flora é principalmente neotropical, e através da fisionomia foliar suporta um clima tropical quente, sazonal ou com longos períodos de restrição hídrica.

2. OBJETIVOS DA DISSERTAÇÃO

- Analisar os componentes da flora buscando sua reconstituição e comparação com outras tafofloras conhecidas no registro;
- Avaliar a associação faciológica dos restos de flora, visando a reconstituição do contexto ambiental de seu crescimento;
- Buscar os elementos (arquitetura foliar e seus análogos modernos) que determinaram seu crescimento, diante dos parâmetros geológicos propostos para a gênese da bacia e aqueles que regionalmente condicionavam o clima;
- Comparar os diferentes depósitos do Cenozóico brasileiro e meso-americano, como inferência para o estabelecimento das rotas de dispersão e do comportamento ecológico da tafoflora da Formação Campos Novos;
- Avaliar o uso da tafoflora estudada como parâmetro de idade para outras deposições cenozoicas do Brasil.

3. MATERIAIS E MÉTODOS

O material de estudo, identificado inicialmente por geólogos da CPRM de Recife, coordenados pela Dra. Cleide Moura, foi posteriormente ampliado a partir de duas novas coletas realizadas entre 2011 e 2012, em expedições conjuntas CPRM-LaViGæa. As amostras estão tombadas na coleção do Laboratório de História da Vida e da Terra (LaViGæa), do Programa de Pós-Graduação em Geologia (PPGEO), da Universidade do Vale do Rio dos Sinos (UNISINOS). Compõem-se de 201 amostras, que no perfil de detalhe realizado mostraram ser provenientes dos

níveis mais basais das camadas de bentonita aflorantes na mina de Juá II, sob as coordenadas geográficas 7°21'S, 36°12'W e 7°20'S, 36°10'W.

As amostras foram imediatamente enroladas em papel filme após a coleta para evitar rachaduras e perda de informações (Barboni *et al.*, 2008), pois se trata de material altamente higroscópico. Em laboratório foram selecionadas as amostras com impressões de folhas ou de outras partes vegetativas, e posteriormente a separação em morfotipos.

Para o estudo foi utilizado microscópio estereoscópico Olympus SZH com câmara clara acoplada, onde os fósseis foram analisados e desenhados para buscar caracteres morfológicos e arquiteturais das folhas (forma, tipo de margem, ápice e base, venação, medidas de comprimento e largura) que permitam precisar sua inserção taxonômica. As medidas lineares foram obtidas com paquímetro analógico e os ângulos com transferidor. O material foi fotografado com câmera Canon EOS digital em posição ortogonal, e preferivelmente sob iluminação natural, em alguns casos foi utilizada luz fria.

Em gabinete foi realizado o levantamento de outras assembleias fósseis nas bacias cenozoicas da América tropical, e o levantamento de biomas modernos de composição análoga, visando correlações, inferências ambientais e paleoclimáticas.

O material estudado foi comparado com táxons fósseis e atuais. Os elementos fisionômicos presentes na lâmina foliar são descritos a partir dos parâmetros propostos por Ellis *et al.* (2009). Na classificação sistemática foram utilizadas as classificações filogenéticas propostas pelo APG III (2009). As análises de agrupamento entre as diferentes bacias foram feitas no software Past utilizando o índice de similaridade de Jaccard, Hammer *et al.* (2001).

4. BACIA DE BOA VISTA

4.1. Contexto Geológico

A Bacia de Boa Vista (BBV) é uma pequena bacia (cerca de 65 km²) de orientação NW-SE, situada cerca de 12 km ao sul da cidade de Boa Vista e a sudoeste de Campina Grande, no Estado da Paraíba (Fig. 1), na região conhecida como Cariris Velho.

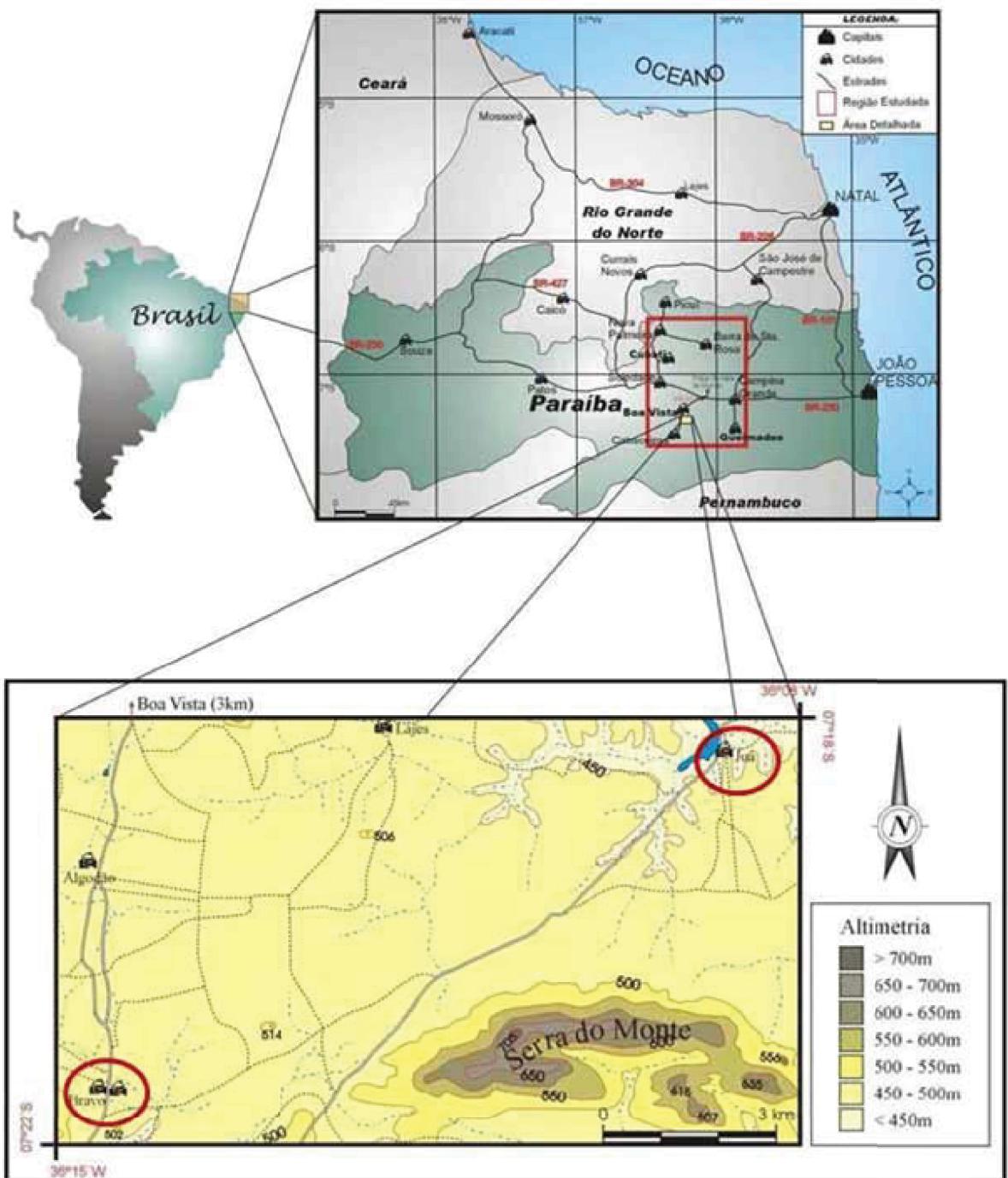


Figura 1. Localização e vias de acesso à Bacia de Boa Vista e das minas que contém as camadas com fósseis (modificado de Dias, 2004).

No contexto geológico regional, a bacia se insere na região de “Domínio da Zona Transversal” (DZT) da Província Borborema, entre os lineamentos Patos e Pernambuco (Fig. 2), onde se encaixa na faixa dobrada do terreno Alto Pajeú (Bizzi *et al.*, 2003; Petta e Barbosa, 2003; Souza *et al.*, 2005). Estruturalmente corresponde a um hemi-graben (feição resultante de apenas uma falha, que leva ao basculamento de um bloco e a uma depressão inclinada), preenchido por depósitos vulcânicos-sedimentares (Srivastava, 2005), por esta razão é classificada como bacia *pull-apart*.

4.2. Província Borborema

A Província da Borborema ocupa uma área de aproximadamente 380.000 km², coincidindo com o cinturão do Nordeste, originado durante o Ciclo Brasiliano. É limitada pelas Províncias de São Francisco e de Parnaíba, e a leste, pelas bacias costeiras e da margem continental (Almeida *et al.*, 1981). Conforme Mabessone (2002), a Província de Borborema é composta de um retalho de diferentes litologias separadas por falhas e lineamentos importantes.

A Província da Borborema constitui a parte mais ocidental em território brasileiro de uma unidade tectônica bem maior, que abrange os cráticos Oeste-Africano, Amazônico e São Francisco-Congo, representada na África pelas províncias Oeste e Leste-Nigeriano, Camarões e, possivelmente, Touareg. Ao longo de seus limites com os cráticos adjacentes, existem zonas de extensão em que se desenvolveram bacias intracratônicas e sedimentares (atualmente com depósitos metamorfizados), limitadas por falhas, em geral transcorrentes, que foram ativas durante sucessivos períodos tectônicos desde o Ciclo Brasiliano, e que resultaram em uma certa superposição dos seus pacotes sedimentares, Mabessone (2002). Dois destes falhamentos-lineamentos, Pernambuco e Patos ou Paraíba, com direção leste-oeste, destacam-se entre muitos outros existentes, diagonais à costa brasileira, que originaram terrenos distintos, e com diferentes idades (Figs. 2 e 3).

4.3. Bacia de Boa Vista

A Bacia de Boa Vista resulta do tectonismo pós-abertura do Atlântico Sul (Souza *et al.*, 2013). Sua geometria é caracterizada por um hemi-graben com depocentro que coincide

com o sopé da Serra do Monte (Fig. 4), e deposição controlada pela reativação da zona de cisalhamento homônima (Souza *et al.*, 2005; Lages *et al.*, 2008).

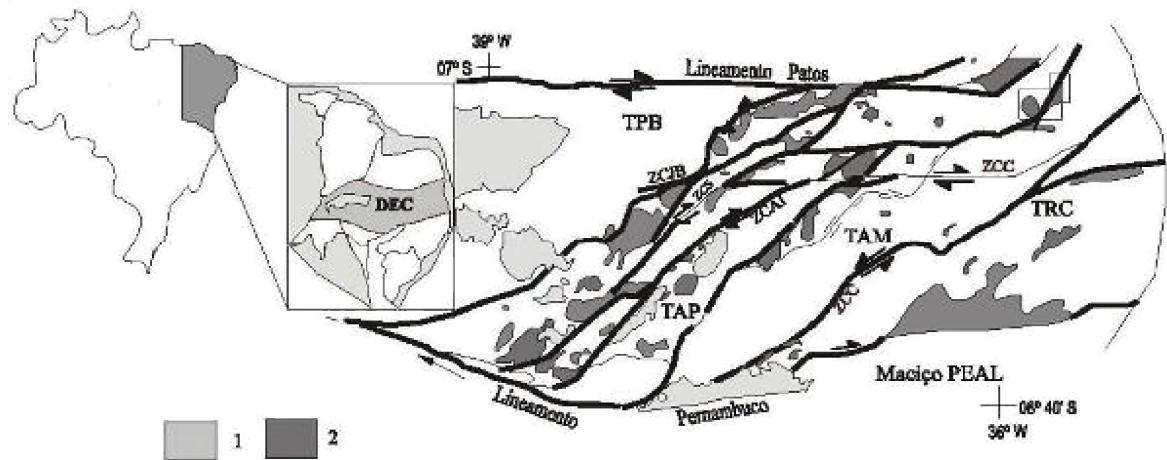


Figura 2 – Mapa geológico simplificado dos terrenos e Granitóides Brasilianos do Domínio Estrutural Central (DEC) da Província Borborema. 1. Coberturas Fanerozóicas; 2. Granitóides Brasilianos; TPB – Terreno Piancó-Alto Brígida; TAP – Terreno Alto Pajeú; TAM – Terreno Alto Moxotó; TRC – Terreno Rio Capibaribe; ZCJB – Zona de Cisalhamento Jesus Belém; ZCAI – Zona de Cisalhamento Afogados da Ingazeira; ZCC – Zona de Cisalhamento de Coxixola (Almeida *et al.*, 2002).

Para Souza *et al.* (2013) os limites da bacia são grosseiramente delimitados por duas falhas principais, uma normal ($N240^{\circ}$ -striking fault), a sul, com a unidade plutônica da Serra do Monte, e uma transcorrente (*dextral transcurrent*) a norte, orientada a $N290^{\circ}$. Estes faltamentos permitiram a extrusão de grandes volumes de lavas basálticas e a formação de edifícios vulcânicos. Segundo os mesmos autores, a extensão regional da bacia está provavelmente relacionada com a reativação de uma zona de cisalhamento em escala continental, embora os mecanismos que condicionaram sua extensão e reativação sejam ainda indeterminados. Uma das possibilidades apontadas seria o aumento da compressão na margem do Pacífico da América do Sul que pode ter sido transformado em um movimento transcorrente na zona continental de Patos e Pernambuco, resultando na extensão tectônica que originou as bacias de Cubati e Boa Vista. Outro possível mecanismo seria o alargamento da Província Borborema como resultado de um movimento de espalhamento diferencial e falha transformante ao longo da cadeia meso-atlântica.

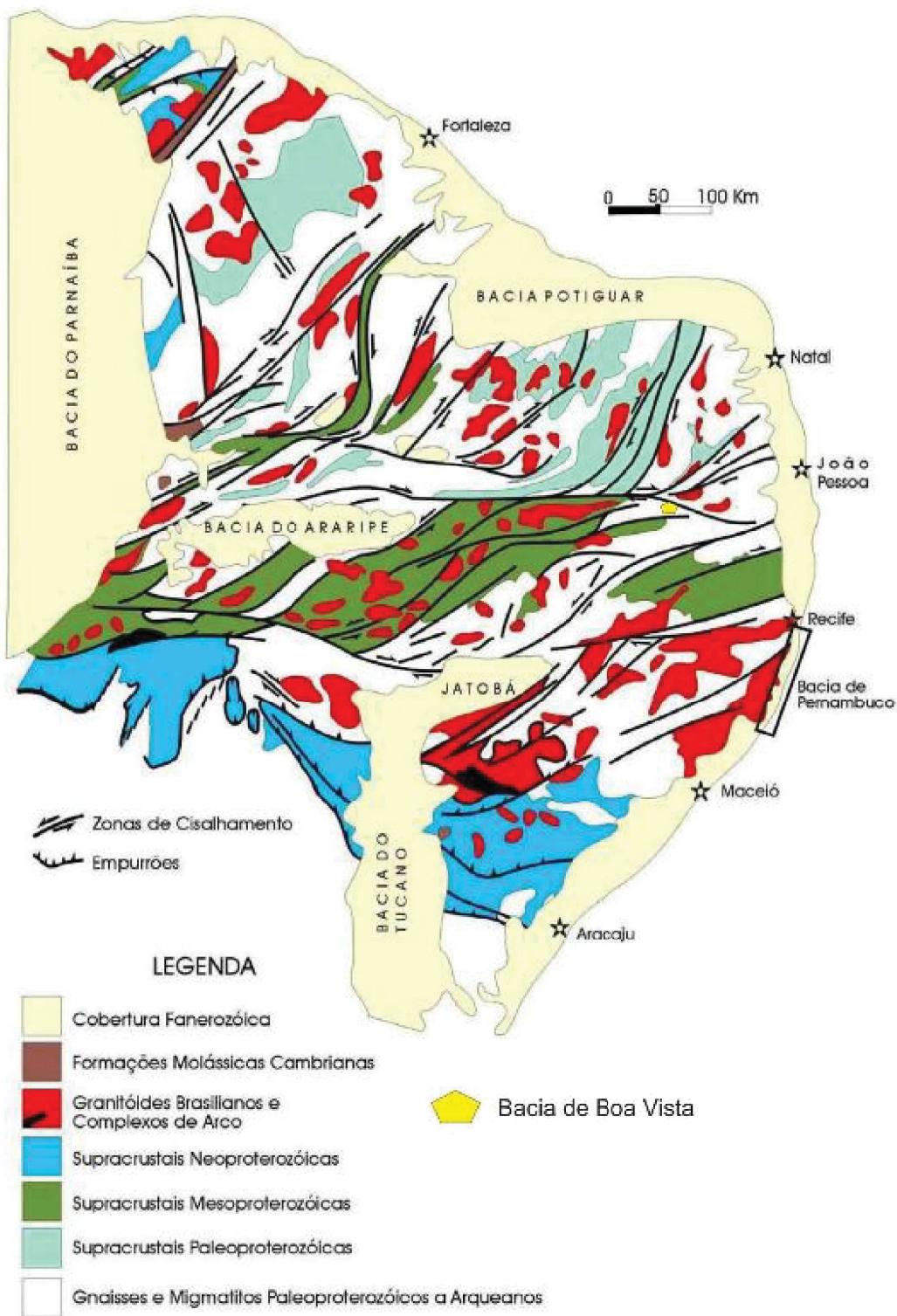


Figura 3 – Arcabouço tectono-estratigráfico da Província Borborema, seus limites e a disposição das bacias sedimentares pós-Brasiliense (modificado de Nascimento, 2003).

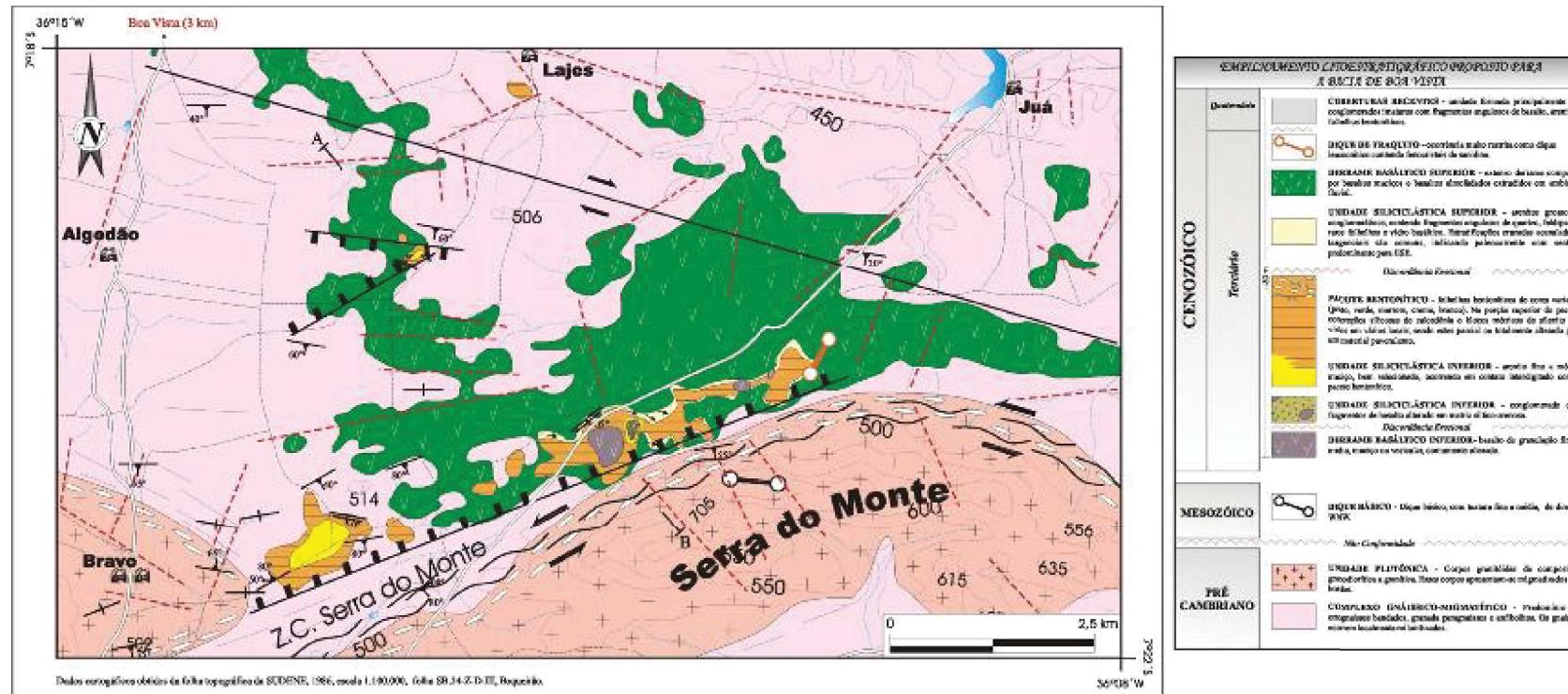


Figura 4 - Mapa geológico da BBV (modificado de Dias, 2004).

A datação dos basaltos revela pulsos de vulcanismos ocorridos entre 27 e 12 Ma e coincidentes com a formação das bacias de Boa Vista e Cubati, com uma ativação maior entre 27-22Ma. O relaxamento do estresse continental permitiu a acomodação dos corpos magmáticos ao longo das falhas do embasamento.

Em termos deposicionais, o preenchimento da bacia compreende uma sucessão grancrescente, com cerca de 35 metros de espessura, composta por folhelhos bentoníticos (ocasionalmente com restos de lenho silicificados e/ou intercalações de camadas centimétricas de basalto), siltitos, arenitos e conglomerados (também contendo lenhos), recoberta por derrames basálticos a olivina, tufos e lapilli (Gopinath *et al.*, 1981). As camadas sedimentares são limitadas inferior e superiormente por derrames basálticos. A presença de numerosos diques levou Petta e Barbosa (2003) a sugerir que o derrame superior de lavas originou-se por um vulcanismo de fissura.

Para Souza *et al.* (2005), três unidades principais compõem a deposição na Bacia de Boa Vista (Fig. 5): i) uma inferior, com 1 a 5 m de espessura, representada por basaltos vesiculares a olivina, frequentemente alterado e com amígdalas de carbonato e zeolita; ii) uma intermediária e mais expressiva, composta por uma camada basal de bentonita (4 a 30 m dependendo das exposições nas distintas minas), seguida de arenitos (1,4 a 5 m de espessura). Nestas camadas ocorrem restos de lenhos e pequenos caules de dimensões métricas a decimétricas e, nas camadas de bentonita, as impressões de folhas; iii) uma superior, igualmente composta por basaltos a olivina, com 1,5 a 6 m de espessura e cerca de 10 km².

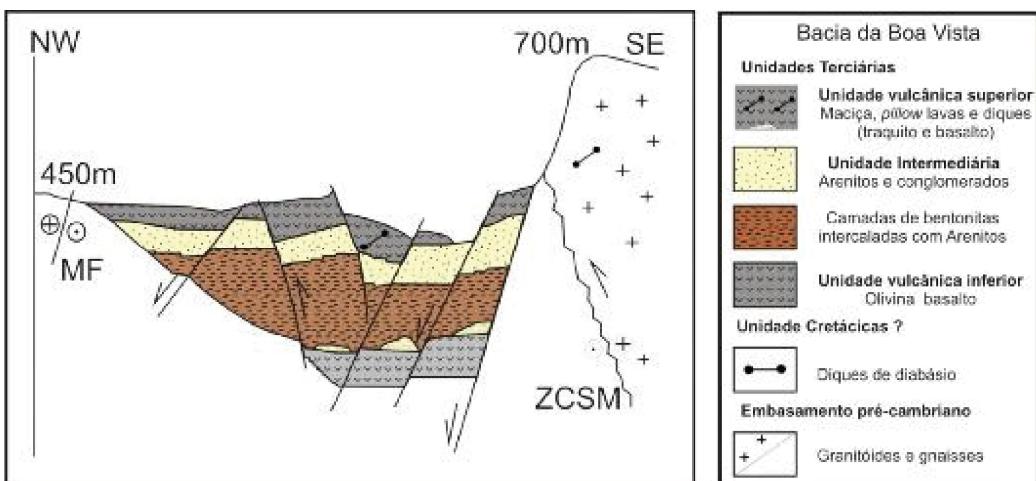


Figura 5. Seção esquemática da BBV e as três unidades litoestratigráficas propostas (Souza *et al.*, 2005).

Diversos autores que trabalharam na bacia atribuíram uma gênese lacustre ou de planície de inundação para a unidade intermediária e a individualizaram na Formação Campos Novos (Fig. 6), à época datada como correspondente ao limite entre o Oligoceno inferior e superior (Srivastava, 2005; Lages *et al.*, 2008; Lages e Marinho, 2012; Souza *et al.*, 2013).

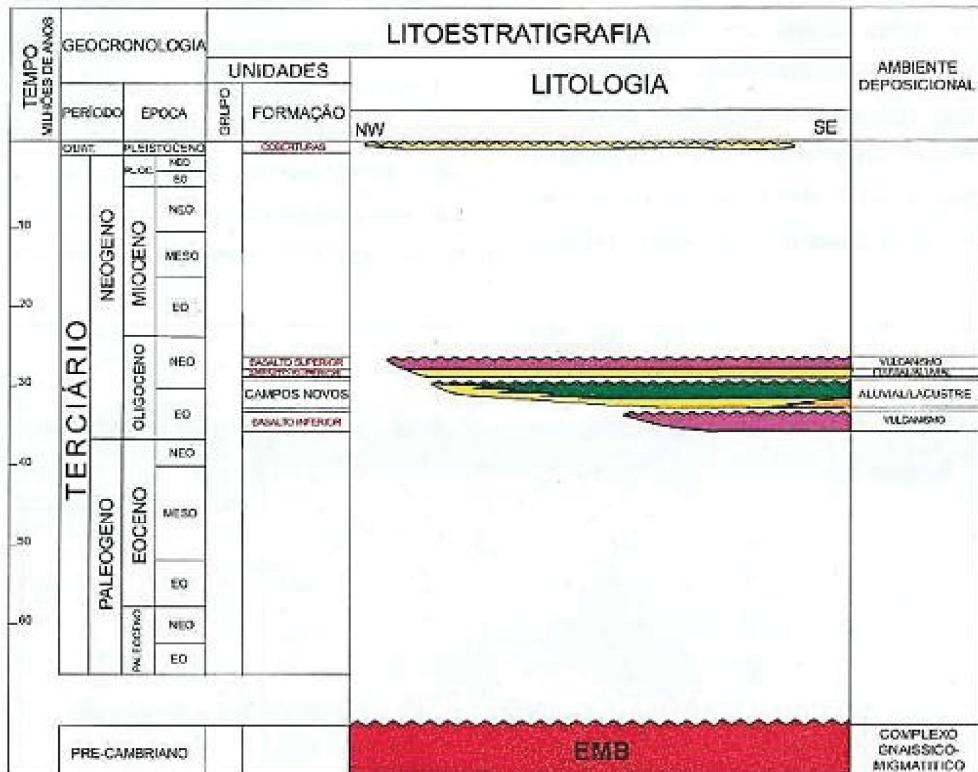


Figura 6. - Carta estratigráfica simplificada da BBV (modificado de Srivastava, 2005).

A Formação Campos Novos (FCN) foi definida por Holder Neto e Silva (1974), e é caracterizada pela presença de arenitos localmente silicificados e argilitos bentoníticos, compartilhados com outros ocorrentes na região de Cubati (Bacia de Cubati), Pedra Lavrada e Boa Vista (PB), também portadoras de vulcanismo do tipo fissural e que originou basaltos e olivina basaltos amidaloides.

No caso da região de Boa Vista (PB), a gênese flúvio-lacustre é atestada pela presença de laminações planoparalelas nas argilitos, sobrepostas e truncadas por arenitos conglomeráticos, arenitos arcoseanos bem selecionados, subangulosos e de granulação média a fina, com estratificações cruzadas tangenciais. Os conglomerados e arenitos médios a grossos, depositados de modo erosivo sobre os argilitos sugerem sua origem a partir de leque aluviais e canais (Lages *et al.*, 2008).

A correlação regional dos depósitos das bacias de Boa Vista e Cubati, as relações de campo, as características petrográficas, e os dados geocronológicos permitiram propor uma origem em áreas fora dos limites das bacias para os materiais piroclásticos e determinar a idade da Formação Campos Novos. Dados de $^{40}\text{Ar}/^{39}\text{Ar}$ para os níveis basálticos da base na BBV, forneceram uma idade de $25,6 \pm 0,4$ Ma e, para os basaltos de topo os métodos de K/Ca e $^{40}\text{Ar}/^{39}\text{Ar}$ não apresentaram diferença significativa, indicando idades de $22,2 \pm 0,2$ Ma. Na Bacia de Cubati, apenas as lavas superiores foram datadas, indicando uma idade de $24,9 \pm 0,1$ Ma, que sugere intervalo entre 25-24 Ma e 22 Ma, para a deposição das argilas bentoníticas (Souza *et al.*, 2013).

4.4. Gênese da bentonita e suas feições deposicionais na BBV

Bentonita é o nome genérico para argilominerais do grupo das esmectitas (normalmente montmorilonita), de grande plasticidade e resultantes da alteração de cinzas vulcânicas, independente da sua origem ou ocorrência. Em contato com a água seu volume aumenta expressivamente (razão do cuidado que se deve ter na coleta dos restos fósseis) e forma-se um fluido viscoso que a torna útil para vários usos. Por estas propriedades é utilizada em distintas aplicações, como liga, selador, absorvente e lubrificante (Murray, 2005). Na indústria é empregada como aglomerante em areias de fundição, na produção de cerâmicas, na pelotização de minério de ferro, perfuração de poços de petróleo, captação de água, indústria química e farmacêutica, e como clarificante (Silva, 2013).

Os depósitos de bentonita são gerados a partir da alteração de materiais piroclásticos (Gopinath *et al.*, 1981, 1988, 2008; Petta e Barbosa, 2003; Souza *et al.*, 2005). No caso da BBV, formaram-se pela devitrificação em corpos de água dulcícolas e a partir da acumulação de produtos intemperizados dos basaltos. A riqueza em magnésio e a pequena quantidade de sílica favorece o processo de alteração (Gopinath *et al.*, 1988). Na BBV, os depósitos de argila bentonítica ocorrem e são lavrados hoje em cerca de oito pequenas sub-bacias que se alinham leste-oeste ao longo de cerca de 10 km (Figs. 1 e 4). As estruturas sedimentares e as cores das bentonitas variam nas diferentes minas, algumas com cores claras e homogêneas e outras de coloração cinza, marrom, verde e branca (Gopinath *et al.*, 1981; Souza *et al.*, 2005).

Na área da Mina Juá II (Fig. 7 e 8), com cerca de 200 m de cava e de onde provém a maior parte dos restos de planta que serão objeto do estudo, os argilitos mostram espessura variável (entre 1 m e 5 m), graças às ondulações da paleosuperfície do embasamento. Nesta

mina, as camadas basais são compostas por basaltos, de contato brusco com os argilitos, em geral alterados, de cor cinza-esverdeada e que afloram nas bordas da sub-bacia. Na Mina Bravo, com profundidade de 35 m, as intercalações entre os argilitos bentoníticos e os sedimentos epiclásticos (conglomerados, arenitos e siltitos), de geometria lenticular, afloram a oeste. A espessura da sucessão alcança cerca de 10 m (Gopinath *et al.*, 1981).



Figura 7. Vista geral dos níveis de bentonita, sobrepostos por areias com estratificação cruzada e conglomerados, da Mina Juá.

4.5. Paleoambiente

A sequência vulcano-sedimentar da BBV tem sido interpretada como originada em um ambiente continental e flúvio-lacustre por seu conteúdo em arenitos, argilitos bentoníticos, derrames basálticos e tufos lapilíticos que preencheram paleodepressões do embasamento e ao longo das zonas de fraqueza (Gopinath *et al.*, 1988; Petta e Barbosa, 2003; Souza *et al.*, 2005). Esta condição é apoiada pela ausência de qualquer evidência de fósseis marinhos, a presença dos lenhos e folhas, e as feições deposicionais dos arenitos e conglomerados (leques aluviais), que atestam o contexto fluvial. Para Gopinath *et al.* (1988), ainda, a deposição continental é apoiada pelas características mineralógicas e químicas observadas nas

bentonitas. Na mina Bravo, para reforçar esta interpretação, foram identificados lenhos em posição de vida.

Souza *et al.* (2005) argumenta que a presença de lavas em almofada (*pillow*) apoia sua extrusão em um ambiente subaquoso e lacustre, como proposto por Petta e Barbosa (2003). Os autores ainda distinguem os dois derrames de lavas em almofada, as da base mais fragmentadas e/ ou brechadas, e as superiores, maciças. A fina granulação dos derrames maciços e do interior das almofadas comprova o rápido resfriamento.

Dias (2004) propôs um modelo esquemático para a sedimentação da bacia (fig. 9). Primeiramente o vulcanismo fissural seguido por deposição de conglomerados com fragmentos de basalto e arenitos médio a finos evidenciando deltas desaguando em um lago de nível freático baixo. O segundo estágio é caracterizado pelo aumento da profundidade do lago e consequentemente aumento da deposição de material argiloso originário de vulcanismo. Neste momento são formados os argilitos bentoníticos com gradação de cores, mais claros na base, evidenciando o aumento da profundidade do lago. No terceiro momento há a diminuição do nível do lago e aumento do aporte fluvial com arenitos grossos apresentando estratificações. Por fim o derrame basáltico cobrindo a as unidades sedimentares.

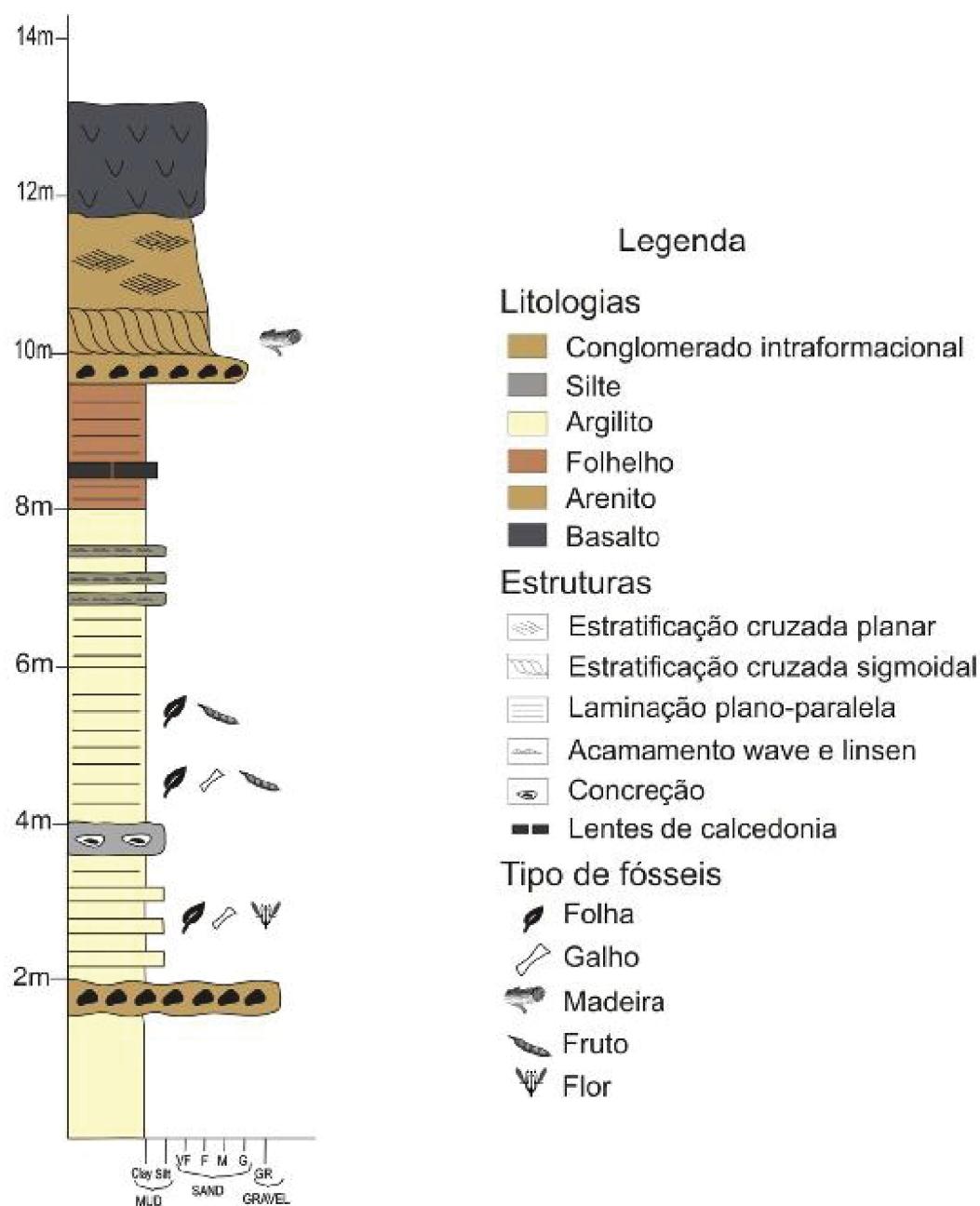


Fig. 8 – Perfil da Mina Juá na sessão que expõem os níveis de bentonita.

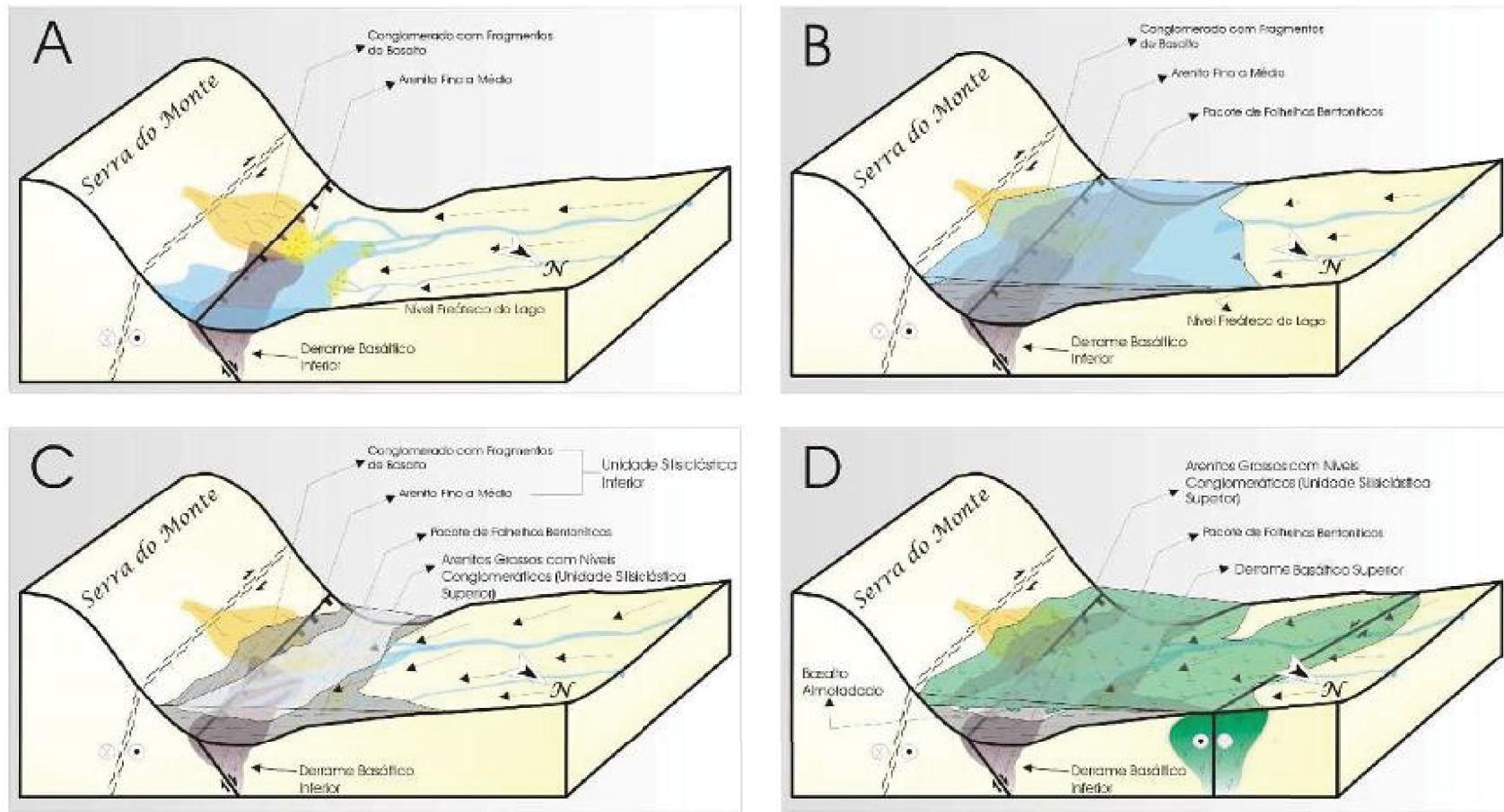


Figura. 9. Modelos esquemáticos e estágios evolutivos do vulcanismo e sedimentação da BBV (Dias, 2004).

5. FÓSSEIS DE PLANTAS, PALEOCLIMA E PALEOAMBIENTE

5.1. Vegetação como informadora climática

O termo paleoclima tem sido usado pelos paleobotânicos para referir as condições de temperatura e umidade que condicionaram a presença pretérita dos biomas vegetais (Dolph e Dilcher, 1979). Sua influência é de caráter regional e o modelo se embasa na observação de que modernamente, junto com os tipos de solo, é o fator primário determinante na distribuição dos vegetais terrestres, refletindo-se em sua forma e modo de crescimento (Iannuzzi e Vieira, 2005).

Para Margalef (1983), a alta sensibilidade das plantas ao ambiente as torna verdadeiros ecótipos (onde morfologia e hábitat são relacionados). Sua plasticidade genética permite que rapidamente modifiquem suas características e muitas adotem estratégias oportunistas (*r*), aumentando a taxa de natalidade e mortalidade, a resistência e a adaptabilidade, maximizando os processos reprodutivos.

Na avaliação dos paleoclimas pode ser utilizada a associação dos restos fósseis como um todo, na busca de recuperar a composição da comunidade pretérita original, a forma e a estrutura das folhas individualmente (a arquitetura foliar de Hickey, 1973; Hickey e Wolfe, 1975), ou ainda os anéis de crescimento dos lenhos, capazes de informar sobre a sazonalidade do clima ou a disponibilidade de água no solo (Alves *et al.* 2005).

Os elementos fisionômicos presentes na lâmina foliar permitem inferir sua adaptação ao clima através dos seguintes aspectos arquiteturais:

- 1. Identificação do análogo moderno mais relacionado.** Baseia-se na procura da forma viva (*nearest living relatives-NRL*) que exibe relações genéticas ou de morfologia que melhor se adequam aquelas presentes no registro e, a partir daí, na verificação de suas adaptações ecológicas modernas. Embora tenha recebido críticas dadas as mudanças de geografia e clima e os processos evolutivos (Wing *et al.*, 2009; Little *et al.*, 2010), é um método amplamente utilizado, especialmente em floras do Cenozóico, onde muitos análogos ainda crescem nos ambientes modernos e portanto, podem ser testados (MacGinitie, 1953; Dolph e Dilcher, 1979; Wolfe, 1995; Mosbrugger and Utescher, 1997; Stranks e England, 1997; Wolfe *et al.* 1998; Wilf *et al.*, 1998; Wilf, 2008; Taylor *et al.*, 2009). Peppe *et al.* (2011), demonstraram que com a inclusão de características

foliares funcionalmente ligadas ao clima, é possível obter dados ainda mais precisos sobre o clima pretérito. Para as reconstituições paleoclimáticas deve ser possível dispor de três tipos básicos de informação: a) a presença entre os fósseis de formas capazes de ser associadas a tipos modernos; b) que existam formas vivas proximamente relacionadas e que sua autoecologia seja bem compreendida; c) que as comunidades florísticas que contêm as formas vivas relacionadas ainda estejam presentes no planeta (Fig. 10). Para fazer esta avaliação foi proposto pioneiramente por Wolfe (1995) o *Climate-Leaf Analysis Multivariate Program* (CLAMP), um método de análise que leva em conta que os diferentes condicionantes do meio podem interagir para produzir certos tipos de morfologia foliar. A complexa obtenção dos dados e a necessidade de pelo menos 29 caracteres foliares para cada táxon presente na associação, têm dificultado o uso do CLAMP e favorecido metodologias mais simples, como a proposta por Wilf (1997) de que sejam avaliados, sem grandes prejuízos às inferências climáticas, o tipo de margem e o tamanho da folha.

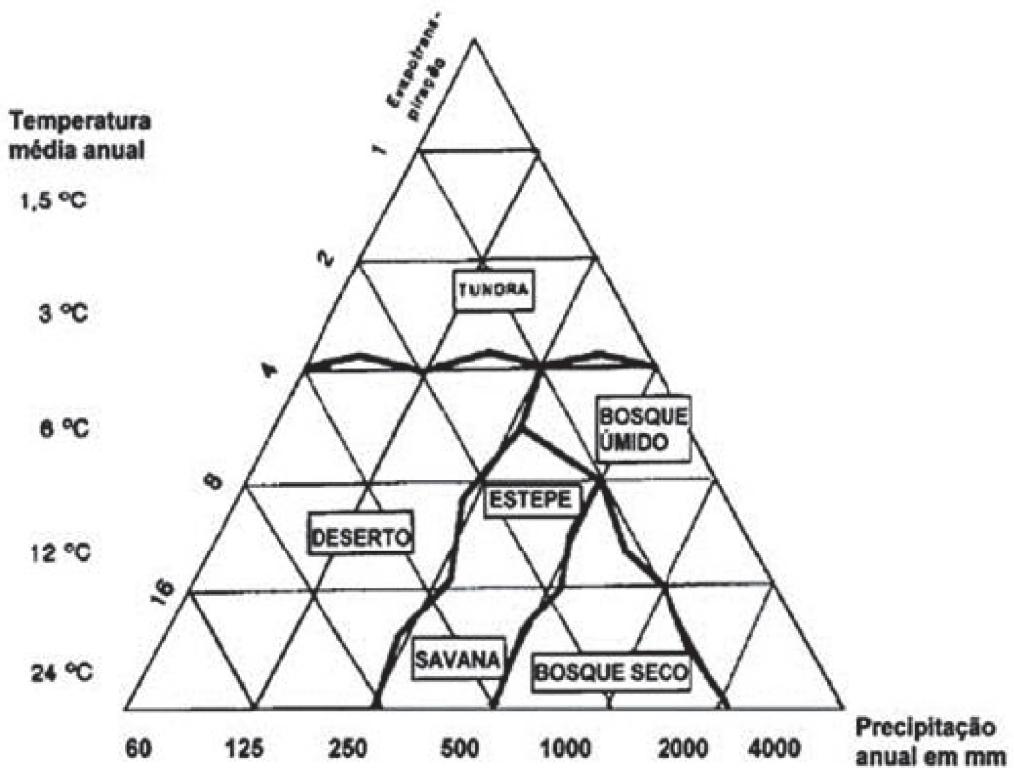


Figura 10 – Distribuição dos principais biomas vegetais em relação à temperatura e precipitação (de Margalef, 1980).

2. **Fisionomia foliar.** Método táxon-independente, que utiliza caracteres morfológicos das folhas que compõem o conjunto da tafocenose (de modo análogo ao estudo de uma serapilheira ou folhedo moderno) para estimar o paleoclima. Oito caracteres fisionômicos são tidos como correlacionáveis ao clima: a) o tamanho da folha (expresso pela sua área); b) o tipo de margem da folha (se lisa, denteada, lobada); c) a presença de ápices pronunciadamente agudos (*drip-tips*); d) a organização (composta x simples); e) o padrão principal de venação; f) a densidade de venação; g) textura; e, h) a forma da base. Contabilizados e comparados estes parâmetros para o conjunto da associação fóssil, é possível avaliar a presença de períodos de seca ou frio (ou de déficit de água no solo), paleolatitude e temperatura (Fig. 11). A correlação entre área foliar e a média anual de precipitação, e do tipo de margem foliar com a da temperatura foi usada por Wilf *et al.* (1998) para a avaliação das mudanças climáticas no limite Paleoceno-Eoceno nos Estados Unidos e norte da África;
3. **Padrão de venação.** Neste aspecto é avaliada a presença de tipos mais complexos (densos) da rede de veias, em especial nas de ordem mais alta, associados à textura da folha e à forma das células. Uma rede condutora mais ampla sugere um maior rendimento fotossintético, já que amplia a condutividade hidráulica que permite a água chegar às células do mesófilo e ser transmitida ao estômato, ampliando a taxa de fotossíntese (Brodrribb *et al.*, 2007). Experimentos demonstraram que nas coníferas, cuja estrutura condutora é composta por traqueídeos (menos condutivos), as espécies que possuem folhas com uma única veia média necessitam assumir formas foliares mais afiladas para garantir a condutância e a vida em ambientes com menor umidade ou mais iluminados. As angiospermas por outro lado, dotadas de vasos e folhas melhor condutoras, são por isto, mais hábeis neste processo (Brodrribb *et al.*, 2005). Assim, a posição das veias tem grande influência na eficiência hidráulica das folhas e as plantas que evoluíram para padrões complexos de venação alcançaram maior rendimento fotossintético (Peppe *et al.*, 2011).

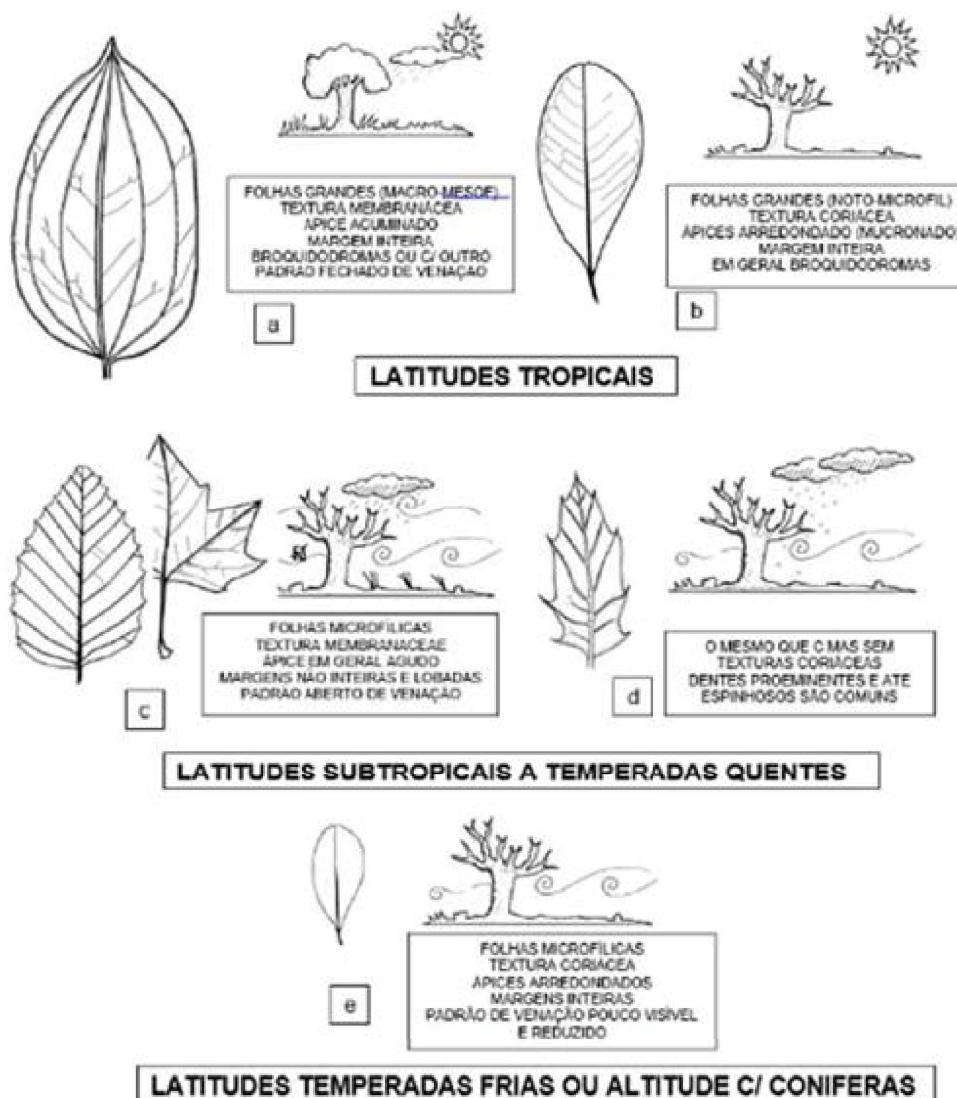


Figura 11 - Diferentes fisionomias foliares e suas relações com os parâmetros ambientais. **a.** Quente e úmido; **b.** Quente e seco; **c.** Frio e úmido; **d.** Frio estacional (estação de chuva); **e.** Frio seco. Retirado de Alves *et al.* (2005).

A avaliação das condições ambientais e do clima a partir de fitotafocenoses compostas por folhas, em relação à de outros fósseis vegetais, como os lenhos e assembleias polínicas (mais transportados pela água e vento a grandes distâncias), costumam ser mais vantajosas. Minimamente transportadas (hipoautóctones ou parautóctones) são uma excelente ferramenta para as reconstituições locais (Alves *et al.*, 2005). Além disto, costumam representar acumulações quase instantâneas ou representativas de curtos períodos de tempo (Burnham, 1993).

É importante salientar, no entanto, que a utilização da arquitetura ou fisionomia foliar na avaliação do clima pretérito envolve aspectos que tem sido questionados nos últimos anos. O CLAMP, por exemplo, não premia um estudo mais detalhado dos biomas do Hemisfério Sul. Estudos em vegetações modernas tem demonstrado que alguns modelos propostos não são adequados, como por exemplo, quando se trabalha com floras tropicais, ou com grupos de planta cujas folhas mostram grande variação de morfologia (e.g. *Acacia*), enquanto outras, como Lauraceae e Myrtaceae, mantém padrões homogêneos independente das variações do clima (Hickey e Wolfe, 1975; Gregory-Wodzicki, 2000; Burnham *et al.* 2001; Greenwood *et al.* 2004). Segundo Little *et al.* (2010), para que os resultados sejam confiáveis, é necessário um trabalho paleoecológico de detalhe e com amostras coletadas com um controle estratigráfico cuidadoso.

5.2.Clima do Cenozoico (limite Neógeno-Paleógeno)

Durante o Cenozoico ocorreram grandes mudanças na configuração dos continentes e no clima global (figura 12). O clima da Terra esfriou fortemente nos últimos 50 Ma. após o pico de calor do Eoceno Inicial, Pearson e Palmer (1999).

Zachos *et al.* (2001), ao estudarem as variações do clima ao longo do Cenozoico, destacaram três principais anomalias caracterizadas por variações extremas da temperatura global, ocorridas há 55, 34 e 23 Ma. A mais proeminente delas refere-se ao pico de calor (*Greenhouse*) que caracterizou o final do Paleoceno e início do Eoceno (*Paleocene–Eocene Thermal Maximum* ou PETM). As temperaturas elevadas produziram uma ampliação da faixa tropical do globo e fortes precipitações, patrocinando o crescimento de florestas subtropicais a temperadas úmidas e a diversificação de muitos grupos de mamíferos, mesmo nas latitudes acima de 60°S e N (Dutra, 2004; Wing *et al.*, 2005; Gingerich, 2006; Reguero *et al.* 2013). Este intervalo foi ainda marcado por um aumento na produtividade marinha e da deposição de carbono orgânico (Speijer *et al.*, 2012).

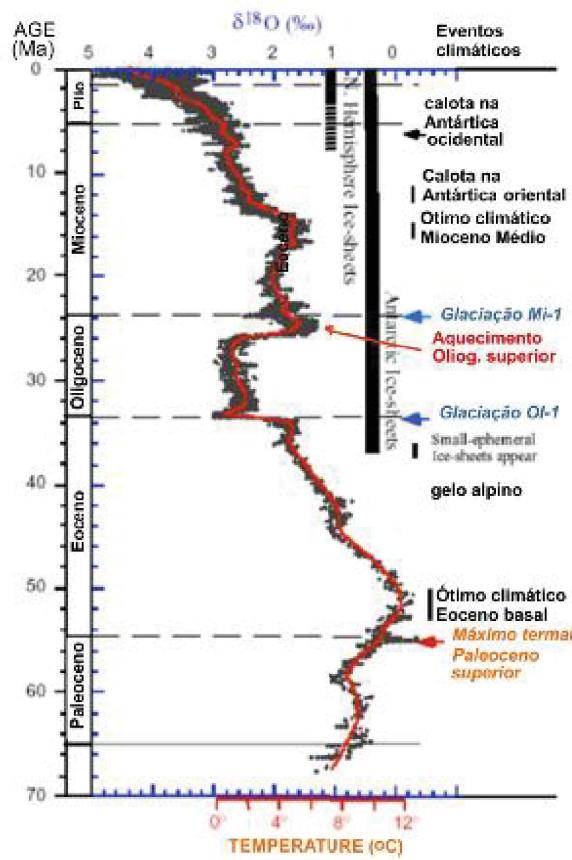


Figura 12 - Variação do clima global durante o Cenozoico (temperatura da água do mar), obtidos a partir de isótopos de $\delta^{18}\text{O}$ (modificado de Zachos *et al.*, 2001).

As alterações do clima que se seguiram, por outro lado, caracterizaram-se por períodos de quedas pronunciadas e gradativas na temperatura (*ice-house*). A primeira delas, no limite Eocene-Oligocene e com duração de cerca de 400 Ky, provocou o aparecimento nas áreas marginais da Antártica, até então vegetadas por florestas subtropicais a temperadas quentes (Reguero *et al.*, 2013), das primeiras evidências de gelo alpino e será seguida de novos intervalos de frio até a chegada do gelo ao nível do mar (Birkenmajer *et al.*, 2005). A reorganização do sistema clima/oceano daí decorrente provocou uma ampla mudança na distribuição dos sedimentos biogênicos marinhos, aumento da fertilidade nos oceanos, e aumento dos limites da zona de compensação dos carbonatos nos fundos marinhos e das comunidades florísticas nos continentes (Francis *et al.*, 2009). O segundo pico de resfriamento coincide com o limite Oligocene/Mioceno, mas não teve a mesma expressão e duração (200 Ky) do anterior e foi precedido por um intervalo de calor no final do Oligocene final. A partir daí, uma série de intervalos de frio menos expressivos levam à queda gradativa e global da

temperatura e à formação de calotas de gelo no Ártico e Antártica, há cerca de 5 Ma (limite Mioceno-Plioceno).

Estes eventos afetaram a vida do globo, acelerando as taxas de *turnover*, graças a eventos de extinção-especiação de certos grupos da biota. A curva de O¹⁸ e as razões Magnésio/Cálcio (Mg/Ca) atestam estes processos mostrando um aumento de sua porcentagem nas faunas bentônicas marinhas (Lear *et al.*, 2000).

Nos ambientes sub-aéreos das porções do globo menos afetadas pela glaciação (como no hemisfério oposto àquele onde há mais gelo, como foi o caso do Hemisfério Sul no Mioceno, quando o gelo cobriu grande parte do Hemisfério Norte), o efeito da glaciação costuma refletir em fases de aridez nas latitudes médias e aumento da umidade nas latitudes tropicais (Willis e McElwain, 2002). Zachos *et al.* (2001) propuseram que no limite Eoceno-Oligoceno (~34 Ma) o gelo alcançava áreas 50% maiores que a atual e o clima experimentou uma queda na temperatura global de cerca de 4°C. O frio persistira até perto do final do Oligoceno (26-27 Ma), sugerindo que este intervalo de tempo caracterizou-se por baixas temperaturas até pouco antes de seu final, quando uma tendência ao aquecimento reduziu o gelo do Ártico e se manteria até a parte média do Mioceno (~15 Ma – Ótimo Climático do Mioceno Médio), quando voltaria a esfriar. A resposta da vegetação a estes processos foi à restrição das floras tropicais à faixa equatorial e uma expansão das floras temperadas para as baixas latitudes (Willis e McElwain, 2002). Pelo menos seis distintos biomas são reconhecidos para o Oligoceno, cujas diferenças resultam de variações na temperatura e umidade (Figura 13).

5.3. Vegetação

Após o máximo climático do Eoceno, o esfriamento global alterou a distribuição da vegetação. A faixa de vegetação tropical que era extensa restringiu-se à região equatorial, a partir do Oligoceno.

Um pico de diversidade ocorreu no Eoceno médio. A partir deste ponto começa a declinar até o início do Oligoceno, onde se tornou estável até a transição Oligoceno/Mioceno, quando declinou novamente (Jaramillo *et al.*, 2006).

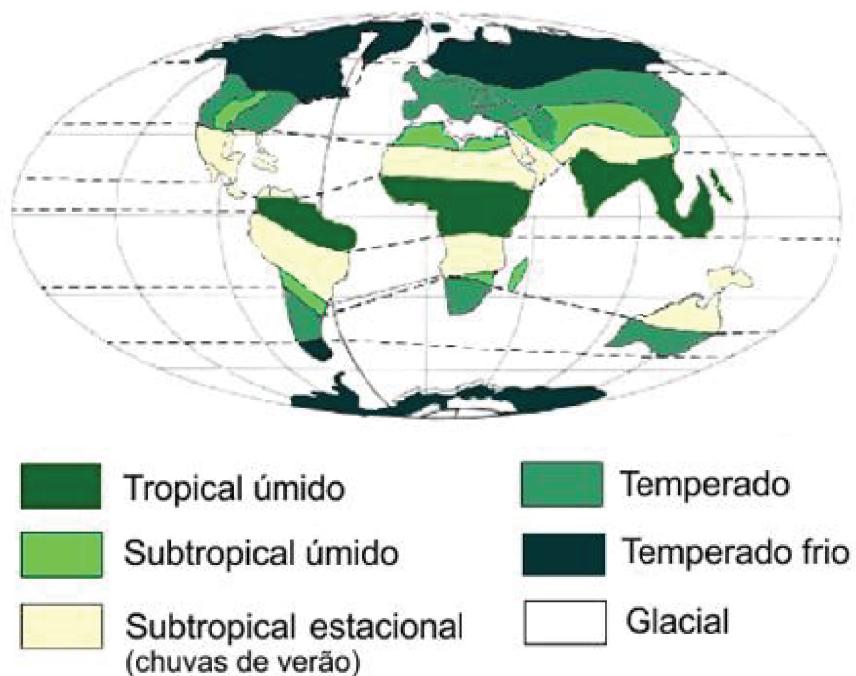


Figura 13 - Distribuição dos biomas vegetais durante o Oligoceno, segundo Willis e McElwain, (2002).

O número de distintas formações vegetais adaptadas à aridez, que hoje ocorrem exclusivamente em regiões de clima árido, tornam-se gradualmente mais reconhecidas nos registros fósseis a partir do Eoceno superior (~47 Ma) em diante. Ao menos 32 famílias que atualmente possuem um ou mais taxons adaptados a climas e habitats de aridez extrema ou sazonal evoluíram entre o Eoceno e o Plioceno (~55-5 Ma). O Oligoceno (23,8-33,7 M.a.) é o intervalo com o maior surgimento destas famílias, num total de 11 (Willis e McElwain, 2002),

Jaramillo *et al.* (2006), estudando a diversidade da flora do Neotrópico no Cenozoico, mostrou que a correspondência entre os padrões de diversidade e a curva de temperatura global sugerem uma relação de causa. O provável motivo da diversidade da vegetação do Eoceno médio está ligada ao fato de a vegetação tropical ter se expandido até áreas ocupadas pela moderna vegetação temperada. Grandes regiões podem suportar mais espécies, aumentando a diversidade local e regional pela redução do risco de extinção e aumento dos nichos e oportunidades.

Levando em conta a distribuição dos biomas proposta por Willis e McElwain (2002), a Bacia de Boa Vista situava-se numa zona de transição entre a faixa de clima tropical úmido e

a de condições subtropicais estacionais com verões úmidos. Estes autores afirmam que há pouca evidência que indique a exata composição ou localização das florestas tropicais durante o Oligoceno, mas que sua composição devia se assemelhar àquelas do Paleoceno e do Eoceno, com domínio de angiospermas perenes, de folhas grandes e margem inteiras, frequentemente com *drip tips*. Mas teriam uma distribuição latitudinal mais restrita e seriam compostas predominantemente por Elaeocarpaceae, Burseraceae, Sapindaceae, Euphorbiaceae e Fabaceae. A restrição latitudinal de sua distribuição se deve ao avanço do bioma subtropical com verão úmido (floresta paratropical) em direção ao Equador.

Para Scotese (2001) as coberturas de gelo foram exclusivas do Polo Sul durante o Oligoceno, o que provocou a expansão das florestas temperadas quentes pelo norte da Eurásia e América do Norte.

No Brasil, biomas subtropicais com eudicotiledôneas perenifolias, lianas, palmeiras, coníferas (araucariáceas e podocarpáceas), fetos arborescentes e herbáceos, até então exclusivos das latitudes mais altas da Argentina, avançam pelo sul e sudeste do Brasil, chegando a áreas mais setentrionais (Castro-Fernandes *et al.*, 2013). O documentário desta ocorrência é atestado no registro nas bacias do Estado do Rio de Janeiro (Macacu, Casa de Pedra, Resende), especialmente na Formação Itatiaia, São Paulo (Bonfim, Tanque, Taubaté), na Formação Tremembé e Itaquacetuba, e Minas Gerais (Aiuruoca, Fonseca e Gandarela), mantendo-se nestas regiões, com pequenas variações, até o presente (Fig. 10 e Tabela 1).

5.4. Levantamento das bacias fossilíferas brasileiras

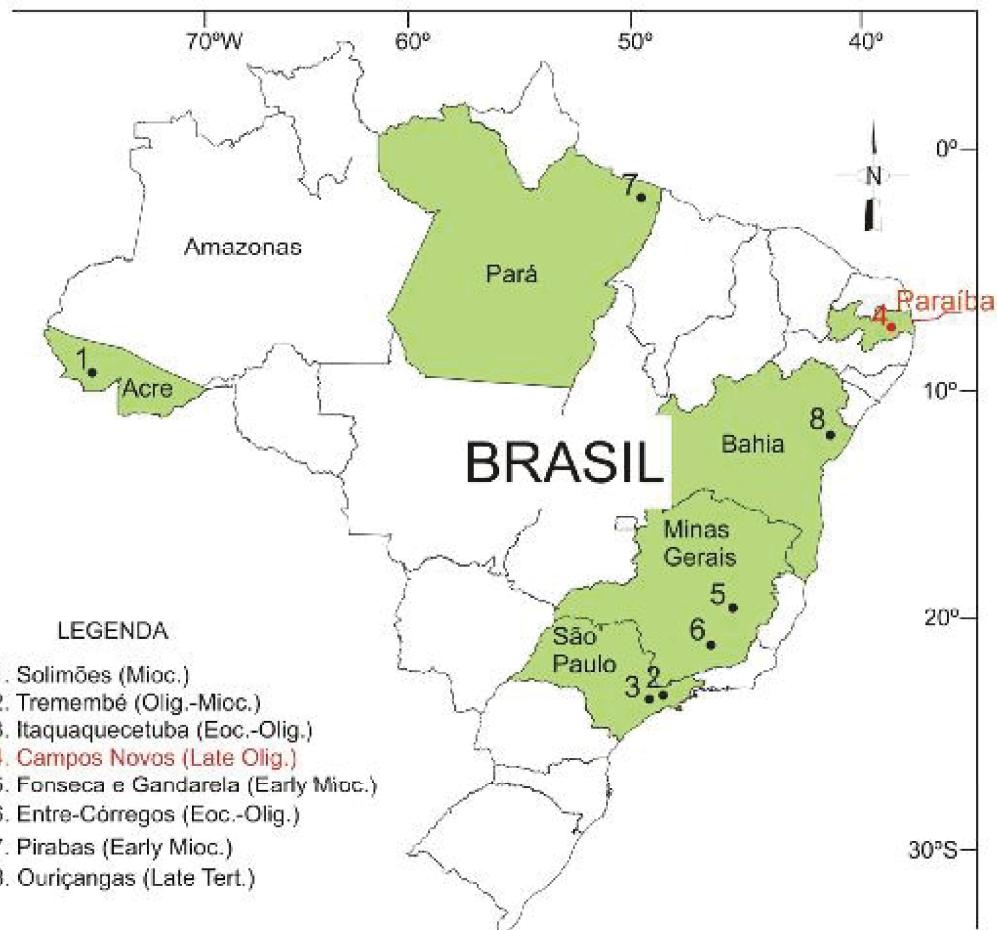


Figura 14— Mapa de localização das bacias interiores do Cenozóico no Brasil, onde fósseis de planta foram identificados, unidades geológicas presente e idade proposta para os níveis com fitotafoflora.

Levantamento das bacias fossilíferas estudadas: Bernardes-de-Oliveira *et al.* (2002), Berry (1937), Biagolini (2012), Biagolini *et al.* (2013), Castro-Fernandes (2011), Castro-Fernandes *et al.* (2013), Dolianiti (1948), Duarte (1956), Duarte (1958), Duarte (1967), Duarte (1985), Duarte (2004), Duarte e Mello-Filha (1980), Duarte e Rezende-Martins (1983), Duarte e Rezende-Martins (1985), Duarte e Mandarim-de-Lacerda (1987), Duarte e Mandarim-de-Lacerda (1989)a, Duarte e Mandarim-de-Lacerda (1989)b, Duarte e Mandarim-de-Lacerda (1992), Fanton *et al.* (2012), Fittipaldi (2002), Fittipaldi *et al.* (1989), Franco-Delgado e Bernardes-de-Oliveira (2004), Hollick e Berry (1924), Mello *et al.* (2000), Veiga (2009).

6. RESULTADOS (os resultados da dissertação estão expressos no artigo em anexo)

Resumo do tema abordado:

ANGIOSPERMS FROM THE BENTONITIC SHALES OF CAMPOS NOVOS FORMATION (LATE OLIGOCENE), BOA VISTA BASIN, STATE OF PARAÍBA, BRAZIL.

O artigo comunica o estudo do material fóssil referente a restos de folha, identificados nos níveis de bentonita da Formação Campos Novos. São abordadas sua taxonomia, fisionomia foliar e suas afinidades com floras fósseis conhecidas para o Cenozóico das bacias tropicais e com floras modernas análogas, visando avaliar sua resposta ao clima proposto para o final do Oligoceno, intervalo atribuído à sucessão estudada.

Como resultados são apresentados 24 taxas, incluindo uma nova espécie, pertencentes a 7 famílias botânicas. A comparação com a vegetação atual demonstra uma flora dominada por componentes amazônicos, somados aos do Cerrado e Caatinga, e formada por componentes arbóreos, cujo comportamento sucessional é predominante pioneiro. As características fisionômicas indicam clima tropical com seca sazonal ou prolongada. A comparação com outras assembleias apresentou maior proximidade com aquelas do Eoceno médio a Oligoceno inferior do centro do Brasil, refletindo, possivelmente sua dispersão (ou retração) para os trópicos.

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ANEXO

Artigo submetido

**ANGIOSPERMS FROM THE BENTONITIC SHALES OF THE CAMPOS NOVOS
FORMATION (LATE OLIGOCENE), BOA VISTA BASIN, STATE OF PARAÍBA,
BRAZIL**

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Abstract

The end of Oligocene was a critical time for angiosperm evolution, characterizing the establishment of modern vegetation and the appearing of grass-dominated landscapes. It was also marked by important geological events, with the first signs of the Andean uplift and closure of the Central America seaways. A new association of fossil plant imprints is described to the bentonitic shales of Campos Novos Formation, NE Brazil, for which $^{40}\text{Ar}/^{39}\text{Ar}$ geochronological data indicates a Late Oligocene age. Compound part of the deposition from Boa Vista Basin, a small intracratonic depression established over a Pre-Cambrian basement, and affected by tectonic and magmatic events in the Cenozoic. The angiosperm remains are composed by vegetative and fertile foliage impressions, dominated by Fabaceae representatives, and allows describe a new legume (*Leguminocarpum paraibensis* sp. nov.) and a laurophyllic leaf impression linked to the Lauraceae (*Nectandra bonavistensis* sp. nov.). The leaf physiognomy give support to a tropical climate, yet locally marked by moments of stress, probably due to the reactivation of volcanic activity or more dry periods. The comparison with other Cenozoic floras from Brazil shows a next relation with those preserved to the Eocene-Oligocene of SE regions, and still with that from the Oligocene-Miocene from North Brazil to Mexico. It suggests a retraction of tropical floras from high to lower latitudes throughout the Oligocene. The fossil assemblage mixed elements nowadays dispersed in Brazil (Amazon and Atlantic rainforests, *Cerrado* and *Caatinga*), and yet in Caribbe and México, most displaying a pioneer behavior. The well-dated plant fossil assemblage from the Boa Vista Basin allows enjoy its potential to the correlations and paleoenvironmental reconstructions, and to check the impact over vegetation of the allo- and autocyclic events.

Key words: angiosperms, tropical flora, intracratonic basin, Boa Vista Basin, Oligocene, paleoclimate, NE Brazil

1. Introduction

The first records of tropical floras date from the beginning of the Cenozoic (Moore, 2008; Wing et al., 2009). At that time, the first elements that today characterize the tropics are found at higher latitudes, reflecting the warm global temperatures and the new oceanic

regions created by the breakup of Gondwana and later Andean uplift (Gayó et al., 2005; Osborne and Beerling, 2006, Jaramillo, 2012). Only in the end of the Paleogene the tropical landscapes assume their modern physiognomy, after survive from a long time of successive drops in global temperatures (Burnham and Johnson, 2004; Fine et al., 2014).

In the Americas the fossil record of ancient tropical rainforests attests to the presence of a broad Equatorial belt extending from the southern United States, Mexico, and Mesoamerica (Berry, 1916; 1924; 1930; 1937a; 1937b; 1939a; Calvillo-Canadell and Cevallos-Ferriz, 2005; see also Supplementary File) to northern South America (Berry, 1917; 1919; 1921; 1922a; 1939b; 1945). At the end of Paleocene and until the Middle Eocene, some of them still lives in Patagonia (Berry 1925, 1937c, 1938; Romero, 1978; Hinojosa and Villagrán, 1997; Prámparo et al. 2007; Brea et al., 2008; Iglesias et al., 2011; Pujana et al., 2011; Martínez, 2013; Caviglia and Zamalloa, 2014), and northern Antarctic Peninsula (Zastawniak, 1994; Dutra, 2004; Cantrill and Poole, 2012; Reguero et al. 2013).

The paleobotanical record in Brazil shows a similar scenario, with deposits dispersed across an extensive area and also attesting the effect of the climatic changes after the end of Eocene (see also Supplementary Files). Plant fossils has been registered in Amazonas and Acre (Berry 1937b; Machado et al. 2012), Pará (Duarte, 1967, 2004), Ceará (Duarte and Nogueira, 1980), Paraíba (Duarte and Vasconcelos 1980), Bahia (Hollick and Berry 1924), Minas Gerais (Dolianiti, 1949; Duarte, 1958; Duarte and Mello Filha 1980; Castro-Fernandes et al. 2013; Bernardes-de-Oliveira et al., 2014) and São Paulo (Duarte and Mandarim-de-Lacerda, 1989; Fittipaldi et al., 1989; Veiga, 2009; Dos Santos and Bernardes de Oliveira, 2013; Biagolini et al. 2013). More restricted, microfloras are known to the Cenozoic of Brazil in the north (Colinvaux et al., 1999; Silva-Caminha et al., 2010; Jaramillo et al., 2010; Nogueira et al., 2013), southeastern (Lima and Salard-Cheboldaeff, 1981; Lima et al., 1991; Garcia et al., 2007), and on the continental slope (e.g. Regali et al., 1974; Tokutake et al., 2010).

Following the global Paleocene-Eocene Thermal Maximum (PETM), the gradual decrease in temperatures becomes more visible, with a first peak seen at the beginning of the Oligocene (Zachos et al., 2001; Liu et al., 2009). The results include an increase in aridity and the retraction of vegetation to low and/or more favorable latitudes (Royer et al., 2001; Willis and McElwain, 2002; Wing et al., 2009; Fine et al., 2014). However, one interruption in this

trend occurs at the end of the Oligocene, marked by the Late Oligocene Warming event (Larsson et al., 2010; Paul et al., 2010).

At the same time, many allocyclic changes affected the northern and northeastern Brazil. These coincide with the rapid exhumation of the Merida Andes (Kohn et al., 1984) due to the initial Andean uplift and the proximity of North and South America, which probably influenced the reactivation of deep Precambrian shear zones and created new reliefs (Gentry, 1982; Higgs, R., 1993; Hoorn et al., 2010; Sousa et al., 2013).

Fossil plant assemblages are a good tool for gaining and understanding of the past climatic and geographical changes, since they are an independent terrestrial proxy used to test the data obtained from marine faunas. Plants grow in environments where conditions are more variable and contrasting, and vegetation responds to climatic requirements rapidly by changes in its composition, physiognomy, and biome distribution (e.g. Gray, 1879; Bailey and Sinnott, 1916; Dolph and Dilcher, 1979; Wolfe, 1995; Upchurch and Wolfe, 1997; Spicer et al., 2004).

Various distinct methodologies have been applied in the evaluation of paleoclimates using fossil leaf assemblages. Some of these approaches require more extensive amounts of data and are most appropriate for better-preserved leaf impressions, such as the Nearest Living Relatives method (NLR, MacGinitie, 1953; Mosbrugger and Utescher, 1997), or the evaluation of climate relations using leaf architecture (CLAMP, clamp.ibcas.ac.cn/Clampset2.html; Wolfe, 1993, 1995; Spicer et al., 2004). A simpler method (but with lower accuracy) can allow for good general results and take in account the main features of the leaf, e.g., size and margin type (Uhl et al., 2003; Royer and Wilf, 2006; Dutra, 2007). Moreover, the inverse relationship between atmospheric CO₂ and stomatal index allows paleo-CO₂ concentrations in the atmosphere to be inferred, yet for this the presence of leaf compressions is required (Royer, 2001; Royer et al., 2002; Kerp, 2002). Uhl and Mosbrugger (1999) have also proposed that wet climates can be inferred from evaluation of venation density.

It is more difficult to rely upon macrofloral assemblages when the focus is that of determining the age of deposits, especially in those composed of angiosperms and in Cenozoic successions. Rare new elements that could be using for this purpose appear after the Paleogene and most assemblages are composed of isolated debris, without organic connections or preserved cuticles, making more precise taxonomic assignments difficult, a

problem magnified if considered the known plasticity of leaves to ecological constraints (Givnish, 2002).

Taking all of this into account, the possibility of comparing a new taphoflora with those previous known, and the availability of radiometric age data, allows better results in relation to age and environmental inferences.

The new plant fossil assemblage discussed comes from a bentonite mudstone interval exposed near Boa Vista County, State of Paraíba, northeastern Brazil (Fig. 1A). The preserved plant remains are dominated by isolate impressions of leaves and leaflets, and also include impressions of twigs, fruits, and a partially preserved small flower. The aim of this study has been to evaluate the taxonomic affinities and composition of the assemblage looking by its relation to climate and with other Neotropical biomes from the end of the Paleogene.

The isolated condition of the Boa Vista Basin (BVB) and its location in a tropical area, today subject to intense aridity, make this plant community useful in the evaluation of many biological and geological processes, favored by its good age control. Furthermore, information from the paleobotanical record remains scarce in relation to the effects of distinct, critical global events that mark the end of the Oligocene, the moment considered to the establishment of modern vegetation distribution (Hinojosa and Villagrán, 1997; Osborne and Beerling, 2006).

2. Location and Geological Context

The bentonitic shales that contains the vegetative and reproductive plant structures is exposed in various outcrops opened up in the mineral resource exploitation in the surroundings of Boa Vista and Cubati areas (geographic coordinates 7° 20' to 7° 21' S and 36° 10' to 36° 16' W), central-eastern portion of State of Paraíba, NE Brazil (Fig. 1B). However, the well-preserved and abundant materials come from the Juá II mine (Fig. 1).

In the exposed section the basal olivine basalts are absent and the profile initiates with the fossiliferous mudstones. In the monotonous laminated succession the unique variation is the distinct colors ranging from pale-orange, green to gray, brown, and pale-brown, and some intercalations of chalcedony nodules and rare silty layers (Fig. 2). The deposits were proposed to be deposited in a shallow lake due to some intercalations with paleosoils (Srivastava, 2005;

Lages et al., 2008; Moura et al., 2008; Lages and Marinho, 2012). They give way to erosive coarse-grained sandstones (sometimes intercalated with conglomerate sandstones), characterized by tangential cross bedding and channeled stratification, assigned to a braided fluvial system (Souza et al., 2005; Lages and Marinho, 2012). Big fossil wood logs were found in these layers. Petta and Barbosa (2003) relate the genesis of the bentonitic shales with subaerial volcanic emissions of gas and ash that precipitated into the shallow lakes.

Since its discovery, distinct studies on the origins and geological constraints of the Boa Vista Basin have been published (Holder Neto and Silva, 1974; Silva et al., 2003; Petta and Barbosa, 2003; Dias, 2004; Souza et al., 2005; 2013). In those works the tectonic influence over the deposits was confirmed, as well as the infilling of the basin by a clastic (and volcanoclastic) continental succession of the Campos Novos Formation (Holder Neto & Silva, 1974). In more regional context, the Boa Vista Basin is inserted into the Borborema Province, from the northeastern fold belt developed during the Neoproterozoic Brasiliano cycle, and controlled by two main lineaments (Patos and Pernambuco), a structural control also observed in other Mesozoic-Cenozoic basins from northeastern Brazil. High-temperature, continental-scale amalgamated shear zones and subsequent reactivations controlled the tectonic evolution of the basins in the area since the Palaeozoic (Souza et al., 2013).

The stressing tectonic processes resulted in the half-graben (5 x 15 km) that contains the deposits (Fig. 1C). Two distinct lava flows controls the sedimentary succession, the basal one composed by vesicular olivine basalts and that in the top, by pillow lavas (Fig. 1B). To Saadi (1993) and Souza et al. (2013), the continental successions accumulated in the northeast basins of Brazil during the Neogene, more than reflects the extensional movements of the open Atlantic, and reflects the subduction ones linked to Andean Cordillera.

Previous studies have proposed a variety of ages for deposition of the Boa Vista Basin, including the possibility that Upper Cretaceous and Eocene deposits could be present (Roesner et al. 2004). The more recent $^{40}\text{Ar}/^{39}\text{Ar}$ geochronological data was obtained by Souza et al. (2013). It dates the lower volcanism like occurring between 27.3 ± 0.8 and 25.4 ± 1.3 Ma, and the upper one, at 22.0 ± 0.2 Ma. From those results, the age of the sedimentary sequence with the plant remains was considered to an interval between 25.6 ± 0.4 to 24.9 ± 0.1 Ma, and allows correlate the lithologies from Boa Vista Basin with those from the neighboring Cubati Basin. The nature of the basalts indicates a regional reactivation of the volcanism in the northeastern tip of Brazil, involving both extensional and compressional forces (Souza et al., 2013; Motoki et al., 2012).

3. Materials and Methods

The analyzed plant fossils were obtained in collects made during the work developed in Boa Vista Basin by geologists from the Brazilian Geological Survey (CPRM), and from two subsequent field works (2011 and 2012) made, involving the CPRM and LaViGaea (UNISINOS) team. The 201 analyzed samples are stored in the LaViGaea under the labels ULVG and CPRM-CM. They were obtained in the basal-middle part of the bentonitic interval at the Jua II mine, where the fossils occur mainly in three levels (considered here as lower, middle, and upper, Fig. 2). During fieldwork the samples were kept wrapped in PVC plastic for at least two weeks to prevent overly rapid drying of the mud-composed materials (Barboni et al., 2008). As mentioned above, the assemblage includes isolated leaves and leaflets, twig impressions, legumes and other fruits, and a partially preserved flower. They occurs indistinctly distributed along the profile, with the exception of the flower, exclusive from the basal one (Fig. 2).

In the taxonomic work the leaf impressions were analyzed and graphically represented using an Olympus SZH stereomicroscope with a camera lucida, then photographed with a Canon EOS digital camera. To enhance the contrast and visualizing, cross-polarized light, close-up filters, and inclined light angles were used. The angiosperm leaf imprints were described following Ellis et al. (2009), sometimes complemented (e.g. vein course, use of intramarginal vein) with Hickey (1973). For determining taxonomic affinities comparisons were made with previous fossil materials described, in published studies nominated above, and in the proper literature (e.g. Hickey and Wolfe, 1975; Stewart and Rothwell, 1993; Taylor et al., 2009). Taking in account the relatively young age of the fossiliferous beds, the insertion into high clades follows the APG III (2009) parameters. The rules for lower-order ranking follow the proposals of ICBN (McNeill et al., 2012).

Comparisons with extant plants took place by looking for analogous foliar architecture and reproductive structures in physical (IAC Herbarium, Instituto Anchietano de Pesquisas; Foliar-Herbarium from LaViGaea; UFP Herbarium, Universidade Federal de Pernambuco) and virtual herbaria (Kew Herbarium Catalogue [<http://apps.kew.org/herbcat/navigator.do>]; Neotropical Herbarium Specimens [<http://fm1.fieldmuseum.org/vrrc>]; REFLORA, Brazil [<http://floradobrasil.jbrj.gov.br>]).

Additionally, a Q-mode cluster analysis was made using PAST© 3.x (version 3.05, 2015) software (Hammer et al., 2001), searching for the affinities between the BVB forms and those preserved in other known tropical American assemblages of assumed Eocene to Miocene ages (for data of fossil occurrences see Supplementary Files). The recommendation of Utescher and Mosbrugger (2007) to include only floras with a diversity of fossil taxa ≥ 10 was followed. The Jaccard Similarity Coefficient was chosen for producing the dendograms, with Cophenetic Correlation values over 0.8 obtained.

4. Results

The plant impressions preserved in the Campos Novos Formation shows to be composed only by angiosperms, represented by morphogenera that is included between the magnoliids and eudicots. One small fragment of a stem (not figured), however, attest a relation with the monocot by the preservation of a nodal zone and longitudinal parallel grooves (ULVG 9017). The fruits (legumes) and the partially preserved flower identified shows an exclusive relation with the Fabaceae and are discussed bellow with the leaf impressions related to this Family.

4.1. Systematic Paleobotany

MAGNOLIID

Order Laurales Berchtold & Presl

Family Lauraceae Jussieu

Genus *Nectandra* Rol. ex Rottb.

Type species: *Nectandra sanguinea* Rol. ex Rottb. (typ. cons.)

Nectandra bonavistensis sp. nov.

(Fig. 3A-D)

Holotype. ULVG 8990a-8990b

Paratypes. ULVG 9015a-9015b; ULVG 9031a-9013b; ULVG 9120; ULVG 10733a/10733b.

Occurrence: In pale-brown / pale-yellowish brown middle levels from the Juá II Mine.

Etymology. The specific epithet alludes to the basin (and region) where the fossils were preserved.

Diagnosis. Notophylllic coriaceous leaves with entire margin, obovate and symmetrical in form, base convex. Stout and straight pinnate primary venation, delicate brochidodromous secondaries with arcuate upward course, originating exmedially a series of successive loops. Alternate percurrent and forked tertiaries meeting the opposite ones in a regular disposition on the intercostal area forming a sinuous (zig-zag) line. Epimedial tertiaries ending at the margin.

Description. Part and counterpart of an obovate, notophylllic and symmetric leaf impression (8.5 cm long, 4 cm wide), with entire margin. Petiole and apex not preserved and base convex (basal angle 90°). Primary vein straight, thick at the origin (2.5 mm) and clearly visible along its course (1.4 mm at the base and narrowing to 1 mm wide). Ten fine secondaries (0.3 mm wide), opposite, inserted at broad and uniform angles (55°), also regularly spaced, and with a curved course. They exmedially produce a set of successive loops. One or two anomalous secondaries (convex or bifurcated) could be present. Percurrent tertiary veins normally alternate, leave the secondaries at right angles and with a sinuous course, reaching the opposite alternate tertiary vein and forming a sinuous line that crosses the intercostal area between the secondaries. Epimedial tertiaries present and convex. Fourth-order venation not preserved or visible.

Comparisons. The morphological characters described (brochidodromous venation, stout primaries and regularly spaced and curved secondaries, with uniform angles of divergence) relates this leaf imprints to the “laurophyllous” architecture, common to Lauraceae and other angiosperm families. Among the modern comparatives evaluated for tropical areas from Brazil, a next similarity is shown with *Nectandra* representatives, and between them, many common features are present in *N. cissiflora* Ness (Fig. 3D), by the broad obovate leaf, weak brochidodromous secondaries, some with an anomalous ones, and the zig-zag course formed in the tertiary mesh. However, a new specific epithet is proposed taking into account the antiquity of the analyzed morphotype.

The trees of *N. cissiflora* grows today in forests from Brazil, Mesoamerica and Mexico (Burger and van der Werff, 1990; Parr et al., 2014). In the previously knowing taphofloras, species of *Nectandra* was recorded from Eocene-Oligocene levels of SE Brazil, in São Paulo Basin (Fittipaldi et al., 1989; Biagolini et al. 2013) and Minas Gerais (Castro-Fernandes et al., 2013; Bernardes-de Oliveira et al., 2014), but in the preserved materials there are no comparable forms. The *Nectandra* sp. described to Entre-Corregos Formation (Franco-Delgado et al., 2004), exhibits alternate secondaries and numerous external loops, distinct from *N. bonavistensis* sp. nov.

Remarks. Extant forms of *Nectandra* occurs in the Atlantic and Amazon rainforests and in *Cerrado* to Brazil. They grow as part of the riparian and *terra firme* vegetation and are able to withstand seasonally dry climates (Lorenzi, 2002; Carvalho, 2002; 2003; REFLORA, 2015).

Nectandra cf. *N. lanceolata* Nees

(Fig. 3 E-H)

Material: ULVG 9049a-9049b, ULVG 10723

Occurrence: In the pale-orange basal levels from the Juá II Mine.

Description. Well-preserved oblong microphylllic leaf, slight asymmetric, 8.4 cm long and 2.6 cm wide. Margin entire, slight undulation, with acute and decurrent base (angle of 87°), apex not preserved. A thick (1.8 mm) and long (8.6 mm) petiole gives way to a thick primary vein, which lose gauge distally (from 1.2 mm to 0.5 mm). The six preserved weak brochidodromous secondary veins exhibit a curved upward course and acute angles of divergence (45° to 51°), and are more widely spaced in the middle and apical parts. A clearly visible tertiary pattern shows alternate percurrent intercostal veins and numerous epimedial ones diverging at right angles. Quaternary and quinqueinary vein fabric irregular reticulate.

Comparison. The elongated leaf with entire and undulate margins, thick petiole, and curved pattern of the secondaries, approximates the present morphotype to the one found in the extant species *N. lanceolata* (Fig. 3H), wide distributed in Brazil, northern Argentina, Paraguay, and

Bolivia (Zanon et al., 2009; Parr et al., 2014). However, the absence of the apex in the fossil, considered acuminate in the modern species, inhibits a more precise affinity. In the weak and curved brochidodromous venation shares some affinity with *N. megapotamica* (Zanon et al., 2009) and *Endlicheria paniculata* (Spreng.) J.F. Macbr, despite the latter have a lower number of secondaries with many external loops, and a still weaker tertiaries. The same features differentiates the form described here from the extant *Ocotea nectandrifolia* Mez from South Brazil.

Remarks. *N. lanceolata* grows preferentially in everwet to seasonal areas (riparian forest, subjected to periodic flooding) of the south and central part of the Brazil (Lorenzi, 2002; Carvalho, 2002; 2003). However, is the only species of the genus that also survive in the *Cerrado* (Zanon et al., 2009). Forms with leaves similar to *N. lanceolata* are well-distributed throughout the fossil record from Brazil and Mexico (see Supplementary files) and in South America, occurs in areas located at higher latitudes during the Eocene, for example the species *N. patagonica* Berry and *N. prolifica* from Rio Turbio, Argentina (Berry, 1925, 1928, 1937, 1938; Romero and Arguijo, 1981). After the end of Oligocene their fossils indicate a restriction to more tropical areas, which is maintained until today.

Nectandra and other related leaf imprints of Lauraceae was important in the fossil record of all Americas. Species of *Nectandra* were detected since Mexico, by all Mesoamerica (especially at Tehuantepec Isthmus deposits, Oaxaca) and in northern South America in the Neogene (Berry, 1921a, 1922a, 1922b). It is incentivate by the new land bridges created between North and South America with the falling sea level caused by the first stressing tectonism at Andean Range (Antonelli et al., 2009; Hoorn et al., 2010). Additionally, related forms growed in Antarctica Peninsula, Patagonia and central Chile due to the favorable climate existing during the Cretaceous and Paleogene (Engelhardt, 1895; Berry, 1938; Romero, 1978; Zastawniak, 1994; Cantrill and Nichols, 1996; Dutra, 2004; Gayó et al., 2005; Cantrill and Poole, 2012).

Leaves and wood related with Lauraceae, accompanied by flowers and fruits, also occur during the Cretaceous-Paleogene, in both Laurasia and Gondwana (Menéndez, 1972; Herendeen et al., 1999; Eklund, 2000; Poole et al. 2000; Renner, 2005), however some of them have some dubious aspects about a real affinity. Hickey and Wolfe (1975) and Rohwer (2000), call the attention to the difficult of discriminate between Myrtaceae and Lauraceae related forms (at generic and specific level) in fossil assemblages composed of laurophylllic

leaves. Many forms linked to the family, like *Ocotea*, *Nectandra*, *Endlicheria*, and *Pleurothyrium*, for example, exhibit similar foliar features and brochidodromous venation that is yet common among other angiosperms.

Phylogenetic analysis estimates an age to crown group of Lauraceae of 61 Ma (Michalak et al., 2010), younger than that showed by the fossil record, taking in account that laurophyllous leaves have been recorded since the beginning of the Cretaceous in Australia (Dettmann et al., 2009) and, like commented herein, in Antarctic Peninsula. The carbonized *Potomacanthus lobatus* flower described by von Balthazar et al. (2007) for the Early Cretaceous (Albian) of the United States is also related with the family. The modern presence of *Beilschmiedia* and *Nectandra* in Africa and Mesoamerica is a good argument in favor of an origin of the group already in the end of the Mesozoic, and about the influence of Gondwana regions on the evolution of the family.

Modern Lauraceae diversity is concentrate in Southeast Asia and South America, and comprises evergreen or rarely deciduous shrubs to tall trees, with only one herbaceous parasite included. The family is abundant in the tropics and subtropics, making it an important paleoclimatic indicator (Burger and van der Werff, 1990; Rohwer, 1993).

Order Magnoliales Bromhead

Family Annonaceae Jussieu

Tribe Annonoideae Rafinesque

Genus *Annona* L. (1753)

Type species: *Annona muricata* L

Annona sp.

(Fig. 3I)

Material: ULVG 9069a-9069b; ULVG 8997; ULVG 9001a-9001b; ULVG 9006a-9006b; ULVG 9008a-9008b; ULVG 9009a-9009b; ULVG 9018; ULVG 9024a-9024b; ULVG 9028a-9028b; ULVG 9088; ULVG 8989a-8989b; ULVG 10784; CPRM-CM 0236 F.

Occurrence: In pale-orange to pale brown/ pale yellowish middle levels from the Juá II Mine.

Description. Partially preserved impressions of an oblong and apparently coriaceous microphylllic leaf, with entire margin. The lamina is approximately 4.4 cm long and 2.4 cm wide on average (L: W ratio around 2:1). The low relief of the primary venation and the weak secondaries suggests preservation of the abaxial face of the leaf. The base is rounded and has a broad angle (170°). The thick petiole (1.6 mm) gives way to a pinnate primary vein (0.5 mm in width), with sub-opposite inserted brochidodromous secondaries (0.25 mm wide), more widely spaced at mid-leaf, diverging in regular angles of ~51°. Intersecondaries present, reaching >50% of the extension of the secondaries. Tertiary venation alternate percurrent, with a slightly sinuous course and disposed in acute angles in relation to the secondaries. Epimedial tertiaries are present, diverging from the primary at right angles. Quaternary veins with an irregular polygonal reticulate pattern.

Comparisons. The morphological characters, including the rounded base, thick petiole, weak brochidodromous secondaries, presence of intersecondaries and epimedial tertiaries, and the type of the fourth-order venation are similar to those present in some extant forms of the genus *Annona*. Although the small size, the general disposition of the venation also approximates from the form illustrate by Berry (1921a) to “*Anona*” *costaricana* Berry, from Costa Rica Tertiary levels. However, the absence of more complete materials prevents the assignment to a more specific affinity. The marked heterophyly (Franco-Delgado and Bernardes-de Oliveira, 2004), with adult caducifolious leaves been more elongated and with well-organized venation than the younger ones, normally actinodromous in venation, ampliates the difficulties.

Remarks. Morphotypes related to *Annona* occur in Paleocene assemblages from Colombia and Egypt and in the Eocene of Argentina (Raven and Axelrod, 1974). In Brazil, the oldest records dated from Eocene, with *Annona* (and *Oxandra*) been identified in basins from Minas Gerais. Three new species were described to Fonseca Formation (Eocene) by Duarte (1958) and a form exhibiting an uncommon actinodromous venation were record to the late Eocene-early Oligocene Entre-Córregos Formation (Franco-Delgado and Bernardes-de-Oliveira, 2004; Castro-Fernandes et al., 2013).

Pirie and Doyle (2012) have estimated an age between 98 and 86 Ma for the diversification of the crown group of Annonaceae, although secure fossil records are only

recorded in the end of Cretaceous, represented by seeds and pollen grains from the Maastrichtian of Nigeria and Colombia (Chesters, 1955; Sole de Porta, 1971). Except for the record of a flower from the Coniacian of Japan (Takahashi et al., 2008), the global record indicates an origin for the family in Gondwana, as proposed by Raven and Axelrod (1974).

Today the Annonaceae have a pantropical distribution, been represented by deciduous or evergreen shrubs, trees, and rarely woody vines. This has been considered as one of the most diverse families of the magnoliid clade and an important component of lowland rainforests (Gentry, 1993), with its abundance varying according to temperature and rainfall (Punyasena et al., 2008). Nevertheless, modern *Annona* species are almost exclusively found in tropical and subtropical South and Central America, with few endemic species from tropical Africa (Berry, 1919a; Pinto et al. 2005).

EUDICOTS

Order Fabales Bromhead 1838

Family Fabaceae Lindley 1836

Subfamily Caesalpinoideae D C 1825

Tribe Cercideae Brønn

Genus *Bauhinia* Lineu

Type species: *Bauhinia divaricata* L.

Bauhinia cf. *B. unguifolia* L.

(Fig. 4A-C)

Material. ULVG 8725

Occurrence. Pale-orange basal to middle levels of bentonitic shales at the Juá II Mine.

Description. Partially preserved impression of a notophylllic leaf (apex absent and lateral sides of base partially preserved), with probable actinodromous venation and six clearly visible primary veins (0.5 to 0.6 mm wide at divergence point). Primary veins with a large gauge (1 mm), apically attenuate, originating from a wide and thick petiole (3 mm in length, 1 mm wide), with a pulvinus (2 mm wide). Primaries diverge from the petiole at acute angles (25° - 30°). Between the sets of primaries a tertiary mesh unites the primary veins in an arcuate, slightly sinuous and percurrent course, with right angles of divergence. Fourth-order veins also percurrent (regular polygonal reticulate), and fifth-order forming areoles (three to four sides) with FVEs unbranched or 1-branched.

Comparisons. In the fault of a comparative form described in the comrable fossil record analyzed, is here proposed an affinity with the modern species of *Bauhinia*. Between then *B. ungulata*, divide the nearly straight primaries with acute angles of divergence, no visible secondaries, and the percurrent pattern of the tertiaries. The lack of a preserved apex difficult more precise affinities, but the strong actinodromous primaries and the absence of a mucron, approximate the fossil to the modern species.

It is important to observe however that at specific level, this morphotype shares similar features with the modern *B. variegata* L., from China and India (Wang et al., 2014).

Remarks. Two other forms of *Bauhinia* were described to South America: *Bauhinia* aff. *B. divaricata* from the Eocene-Oligocene Itaquaquecetuba Formation, Brazil (Biagolini et al., 2013), and *B. potosiana* Berry from Potosí, Bolivia, and Ecuador (Berry, 1939b; 1945), but exhibiting very distinct characters.

The extant *B. ungulata* is a shrub or small deciduous tree that grows in Mesoamerica and South America (Parr et al., 2014). In Brazil this species is broadly dispersed, growing in *Cerrado* and in the Atlantic and Amazon rainforests, where is adapted to gallery forests and *terra firme*, been common in disturbed areas affected by anthropogenic influence (REFLORA, 2015). In the same area where the here studied fossils were found, at semi-arid *Caatinga*, today grows the threatened species *B. cheilantha* (Bong.) Steud, and in all *Caatinga* biome, *Bauhinia* is a characteristic genus (Silva et al., 2004).

Bauhinia sp. 1

(Fig. 4D-E)

Material. CPRM-CM 021F, CPRM-CM 218F

Occurrence. In pale-orange and grayish-orange basal and middle levels of bentonitic shale, Juá II Mine.

Description: Partial impression of a double-lobed leaf with entire margin (6.5 cm long, 4.5 mm wide), apparently ovate in shape, notophylllic to mesophylllic in size. Apex, base, and part of the margin not preserved. Major venation actinodromous, with a midrib (*sensu* Van der Pijl, 1952), and three curved lateral veins per lobe, containing external and basal agrophic veins. These diverge from the pulvinus at angles of 35°, attenuating in gauge and curving apically to form loops that connect with the next admedial primary. Interior secondaries nearly opposite with a percurrent course that unites the main primary to the lateral ones. Exterior secondaries diverge from the lateral primaries at uniform and right angles and curve abruptly, forming festooned loops quadrangular in shape. Higher venation pattern regularly arranged with weak percurrent intercostal veins and opposite tertiaries, also diverging at right angles and forming 4-sided areoles. Veinlets not visible.

Comparisons. In the previous known taphofloras a form of *Bauhinia* (*Bauhinia aff. B. divaricata* L.) was identified in reworked mudstone blocks (included in a Pleistocene succession) originally linked to the Eocene-Oligocene Itaquaquecetuba Formation (Suguio et al. 2010; Biagolini et al., 2013). The associated morphotypes differ from those of the *Bauhinia* sp. 1 described here by the absence of the brochidodromous pattern of the major venation and by the more regular, sinuous, and percurrent tertiary pattern.

Compared to *Bauhcis moranii* n. sp. described from the Oligocene Coatzingo Formation (Pie de Vaca Formation) by Calvillo-Canadell and Cevallos-Ferriz (2002) from Puebla, Mexico, *Bauhinia* sp. 1 is distinct in terms of the form of the basal sector, the high number of primary veins per lobe, and the divergent secondaries, with intersecondaries. However, the two share the delicate character of the brochidodromous venation, with a broad angle of divergence.

Bilobed leaves with a basal and spaced actinodromous major venation (with external agraphics) that attenuates apically and forms broad loops (brochidodromous) connected with the next primary are common in many species of extant *Bauhinia*, e.g. *B. glabra* Jacq., *B. bauhinoides* (Mart.) J.F. Macbr., and *B. andrieuxii* Hemsl.. However, here the incomplete preservation prevents a preferential association to one of those species.

Bauhinia sp. 2

(Fig. 4F)

Material: ULVG 10770

Occurrence: In pale-orange basal levels from the Juá II Mine.

Description: A very incomplete and fragmented, probably micro-notophylllic leaf, with a well-developed pulvinus and thick petiole (6.8 mm in length, 1.2 mm to 1.8 mm wide). At least four straight actinodromous primaries diverge at acute angles (30° to 35°). Interior secondaries unite the primaries at right angles of divergence. In an associated fragment from the same sample it was possible to see rare and weak secondaries forming quadrangular loops that reach the margin.

Comparisons. The fossil impression is quite incomplete, but the presence of superimposed primaries, attested to by the combination of low and high reliefs, suggests the preservation of the folded lobes of a unique leaf. Thus despite the scarce preservation, a bilobate character of the leaf can be inferred. Furthermore, the presence of a thick pulvinate petiole indicates affinity with members of the *Circideae* tribe.

In the preserved characters the form described resembles the extant *B. bauhinoides*, which today grows in the *Caatinga* (white woodlands) and in savannah landscapes from *Pantanal* in central Brazil, where grows in gallery forests and riparian vegetation. The shared features include a common thick petiole, straight primaries, and lobes of small size. A coriaceous texture of the original leaf is inferred by the weakly visible secondaries.

The Cercideae tribe includes *Cercis* and *Bauhinia* that share similar morphological features. Given the absence of native forms of *Cercis* in South America and the partial

preservation of the leaf imprint, a preferable affinity between the herein described morphotypes with *Bauhinia* is proposed.

Based on phylogenetic analysis, Lavin *et al.* (2005) proposed a 34 Ma age for the appearing of the crown-group of Cercideae, which seems to be in accord with the proposed fossil record, where *Cercis*-related fruits found in Oligocene beds from Oregon are considered to be the oldest reliable evidence of the tribe (Manchester and Meyer, 1987). Meanwhile, the leaf impressions associated to *Cercis* from the Oligocene Florisan Formation, United States (MacGinitie, 1953), have a dubious pulvinus, which is considered a characteristic feature of the genus.

Bauhinia is the largest genus of the Cercideae and a pantropical taxon, initially considered a sister group of all other Fabaceae (Lavin *et al.*, 2005; Bell *et al.*, 2010). Recent studies, however, considered it to be an early offshoot in the Leguminosae (Käss & Wink, 1996; Bruneau *et al.*, 2001; Kajita *et al.*, 2001). In the fossil record the oldest forms of *Bauhinia* were related to leaves found in the Cretaceous of the United States, especially *B. cretacea* Newberry, from New Jersey (Berry, 1910). However, further studies made by Herendeen *et al.* (1992), determined that many of those forms deserve revision, since most of the *Bauhinia* leaves reported for the North American Cretaceous-Palaeogene are probably related to a dubious Magnolioaceae (*Liriophyllum*).

Bilobate leaves were recently found in levels extending from the Eocene to the mid-late Miocene on various continents, including from the Eocene-Oligocene in Brazil (Biagolini *et al.*, 2013). However, these leaves are in general poorly preserved and do not allow evaluation of the presence of the pulvinus or the basal actinodromous or acrodromous character of the main venation (Jacobs and Herendeen, 2004; Carpenter *et al.*, 2011; Böhme *et al.*, 2013). Cladistic analysis performed on the *Bauhcis moranii* form mentioned above from the Lower Oligocene Coatzingo Formation in Puebla, Mexico, suggests that this could represents a stage prior to the differentiation between *Cercis* and *Bauhinia* (Calvillo-Canadell and Cevallos-Ferriz, 2002). And, in a more recent work Wang *et al.* (2014) is proposed that the oldest reliable evidence of *Bauhinia* and *Bauhinia*-like foliage are provided by the Oligocene Ningming Formation, Guangxi, South China, with three species (*B. ningmingensis* sp. nov.; *B. cheniae* sp. nov. and *B. larsenii* (D.X. Zhang et Y. F. Chen) Qi Wang *et al.*). They also propose that the emergence of *Bauhinia* and *Cercis* must probably occurred within floras from the Eocene-Oligocene boundary in the mid-low latitudes. During the Oligocene and

Miocene the genus becomes more frequent, also appearing in India, Nepal, Thailand, and Ecuador, as well as in the Pliocene of Uganda (Wang et al. (2014).

Tribe Cassieae

Genus *Senna* Mill.

Type species: *Senna alexandrina* Mill.

Senna aff. *S. tapajozensis* (Ducke) H.S. Irwin & Barneby

(Fig. 4G-I)

Material: ULVG 8726a-8726b; ULVG 9060a-9060b

Occurrence: In the pale-orange basal levels at the Juá II Mine.

Description. Well-preserved obovate and entire marginated microphylllic leaflets, slightly asymmetrical, 3.6 cm long and 2.3 cm wide. The basal part partially preserved (85° basal angle) but petiole absent. The apex is mucronate and broad (150° angle). Thick and pinnate primary vein, attenuating along its slightly curved course (0.6 mm to 0.2 mm). Eight to nine generally opposite brochidodromous secondaries of thick gauge diverging from the primary at angles of 43° to 51° , forming an additional external loop near the margin. The basal pair of secondaries extends upward until the middle part of the lamina, with extra loops originating along their course. The space between secondaries gradually increases proximally (6.7 mm to 2.6 mm) whereas the angles diminish in relation to the primary. Intersecondary veins present, with a parallel and sinuous course, reaching more than >50% of the extension of the secondaries. The well-visible, opposite tertiaries, have a percurrent fabric and a straight to sinuous course, nearly parallel to the primary vein. These bifurcate (forked) to join with adjacent secondaries. Few exterior tertiaries looped.

Comparisons. Brochidodromous secondaries with addition of an external arch near the margin indicate affinity of this leaflet with those present in the genus *Senna*. In terms of the extant comparative species, it is very similar in terms of venation and general form to those

present in *S. tapajozensis* (Fig. 4I). Specifically, the common aspects include in the large gauge of the regular secondary and tertiary venation, the prominent intersecondaries with a sinuous course, the opposite arrangement in relation to secondaries, and the unique bifurcation. *S. tapajozensis* grows today in savannah open areas of Amazonia and central Brazil (REFLORA, 2015, Fig. 4I), been native from Peru and Bolivia (Parr et al., 2014, TROPICOS, 2015).

Remarks. The fossil evidences indicate that *Senna* dates from the Eocene (Herendeen et al., 1992), predating many legume genera. This is consistent with molecular data that suggest an origin in the Early Eocene. The major clades of *Senna* appeared during the mid-Eocene to early Oligocene and diversified during the early Oligocene to early Miocene (Marazzi and Sanderson, 2010). Fossil fruits of the genus were described from the Eocene of North America (Herendeen and Dilcher, 1990) and Mexico (*Senna sousae*, Calvillo Canadell and Cevallos-Ferriz, 2005).

The fossil record for *Senna* is scarce, probably due to its morphological similarity with *Chamaecrista* and *Cassia*, with which forms a monophyletic group. Some authors includes the three genera in *Cassia sensu lato* (Irwin and Barneby, 1982), but the real relationships between these three genera are not well-established (Marazzi et al., 2006).

Currently as a genus *Senna* is native to the tropics, but with a small number of species existing in temperate regions. Of the approximately 350 species currently ascribed to *Senna*, 80% occur on the American continent, while most of the remaining members are found in tropical Africa, Madagascar, and Australia, and with few species in southeastern Asia and the Pacific Islands. Its evolution and specialization proceeded primarily in two directions, either towards fewer and larger leaflets or more numerous and smaller ones (Irwin & Barneby, 1982). One remarkable feature of the genus was the appearance of the extrafloral nectaries (EFNs), a morphological novelty that could have played a role in its large-scale diversification through its interaction with insects (Marazzi et al. 2006).

Genus *Cassia* L.

Type species: *Cassia fistula*

Cassia aff. *C. wendtii* Britton

(Fig. 4J)

Material: ULVG 9100

Occurrence: pale-orange basal levels at Juá II Mine.

Description: Well-preserved elliptic microphylllic leaflet, slightly asymmetric, entire margin, 1.9 cm long and 0.9 cm wide. The base is rounded with an angle of 125° and contains a thick pulvinate petiole, 1.2 mm in gauge. The apex is rounded and with a broad angle (140°). The pinnate and thick primary vein attenuates along its slight curved course (0.4 mm to 0.2 mm). Weak and numerous (more than 15) brochidodromous secondaries diverge at acute angles (40° to 60°) from the main vein, maintaining a narrow irregular spacing. Intercostal tertiaries weakly visible, exterior ones looped, sometimes free ending at the margin.

Comparisons: The morphological character in the preserved leaflet indicates its affinity with the forms included in *Cassia* genus, mainly by the dense secondary framework. The next closest proximity to an extant species would be with *C. moschata* Kunth, where the small proximal leaflets are elliptical with an assymetric contour as is the case here, yet with rounded base and apex. In terms of the fossil record, the form discussed here shows great similarity with the leaflets associated with *C. wendtii* Britton by Berry (1917, Pl. 16, fig. 2-4), identified in the Neogene of Potosí, Bolivia. The common aspects in this case are the small size of the leaflets, the general disposition of the main venation, and the numerous brochidodromous and upwardly curvate secondaries.

Remarks. *Cassia* leaflets have been frequently reported in palaeobotanical works, although most of the morphotypes described deserve a revision in light of the new phylogenetic and taxonomic affinities proposed. As discussed herein, the distinction between *Cassia*, *Senna* and *Chamaecrista*, especially when its small leaflets is isolated found. Currently they are native of tropical regions.

Frodin (2004) has considered *Cassia* a “big” plant genus due to its broad modern occurrence. The modern species *C. moschata* grows in areas from Mexico to Brazil (Parr et al., 2014), making part of gallery forest from the Amazonian rainforest and *Cerrado* (sensu lato), as a deciduous element (REFLORA, 2015).

Subfamily Mimosoideae

Tribe Mimoseae

Genus *Dinizia* Ducke

Type species: *Dinizia excelsa* Ducke

Dinizia aff. *D. excelsa* Ducke

(Fig. 5A-C)

Material: ULVG 8728; ULVG 8735 ULVG 8736; CPRM-CM 0210F; CPRM-CM 0226 Fa/b; CPRM-CM 0227F

Occurrence: in the pale orange and grayish-orange levels, respectively from the basal and middle part of the bentonitic interval at the Juá II Mine.

Description: Well-preserved oblong microphylllic and asymmetric leaflet, 2.5 cm long and 1.3 cm wide, with entire margin. Base partially preserved (basal angle probably 135°), also asymmetric. Rounded apex (150° angle). Pinnate and stout primary vein (0.4 mm in the base) attenuating apically (0.1 mm wide). Seven to eight pairs of opposite to sub-opposite, clearly visible brochidodromous secondaries, diverging at acute angles from the primary (40° - 65°), irregularly arranged and forming clearly visible, elongate loops near the margin. Occasional intersecondary veins with parallel course are present, reaching 50% of the extension of subjacent secondaries. Well-visible tertiaries are opposite and percurrent, and sometimes transversely ramified on the intercostal area of the lamina, forming extra loops in addition to those from the secondaries at the margin.

Comparison. The proposed closest affinity with extant *D. excelsa* (Fig. 5C) is based on the asymmetrical character of the leaf and the number and irregular disposition of the secondaries and the external loops. In previously described fossils, *Dinizia* shares some similar features with *Duckeophyllum eocenicum* described by Herendeen and Dilcher (1990) to the Eocene-Oligocene of southeastern North America and also correlated by them to *D. excelsa*.

Otherwise, fossil records for this tribe are very rare, probably due to the in general small size of its leaflets.

Remarks. *Dinizia* is a monospecific genus and the most generalized and isolated in the Mimosaceae tribe, leading to the proposal that its divergence occurred very early in the evolution of the Mimosoideae (Herendeen and Dilcher, 1990; Mesquita et al., 2009).

D. excelsa is today a native and endemic emergent tree in the Amazon Forest, growing in muddy soils of the *terra firme* (non-flooded) woods (REFLORA, 2015). Its role in the successional stage is difficult to determine (atipic), from pioneering to late successional, due to its dormant seeds and affinity with light (Ferraz et al., 2004).

Genus *Parkia* R. Brown

Type Species. *Parkia biglobosa* R. Wight and G. Arnott

Parkia cf. *P. nitida* Miquel

(Fig. 5D)

Material: ULVG 9045a/9045b, ULVG 9047; ULVG 9102; ULVG 9499

Occurrence: Pale-orange basal levels from the Juá II Mine.

Description. Impression of an elongate leptophylllic to nanophylllic leaflet (9 mm long, 1.8 mm wide), coriaceous and with an asymmetric oblong/lanceolate form. Apex rounded (angle 180°). Base still asymmetric and with a broad angle, cuneate on acroscopic side, rounded on the basiscopic side. A thick pulvinate petiole gives way to a stout and straight primary vein (0.2 mm in gauge), slightly curved distally. The main veins are disposed in a particular pattern, with only one side supplied by a lateral “primary”, more slender, that leaves the base in a right course, parallel to the margin, and distally forming small loops. The secondaries are brochidodromous, with irregular courses that lead to irregular festooned branches and loops. One or two extra “anomalous” secondaries also leave the base and narrow apically.

Comparisons. Even in view of the scarce preservation of the present leaflets, which lack more diagnostic evidence of branch insertion and about the occurrence of petiolar glands, the

unique design of the venation and the asymmetric form incentive a preferential relations with the extant species *P. nitida*.

Remarks. *P. nitida* is now a native component of the flora of northern Brazil and the surrounding countries, influenced by the ever-wet and/or seasonal areas of Amazonia (Obermüller et al., 2011). Taking in account the similar features shared by many Mimosoidea leaflets, is not possible to rule out the similar leaflet features found in *Pseudopiptadenia psilostachya* (DC.) G. P. Lewis & M.P. de Lima, which besides the Amazon is the single species of the genus growing in Atlantic rainforest (REFLORA, 2015). Yet, curiously, the leaflets of the Asiatic type species *Albizia julibrissin* Durazz., exhibits the next most comparable features in terms of size and the asymmetric characters of the leaflets.

Forms of *Parkia* are found throughout the tropics, including Africa, Asia, and twenty species in the neotropics (Luckow and Hopkins, 1995). In Brazil it is a native component that extends throughout all north, northeast, and central-western regions, and into the southeastern coastal areas (State of Espírito Santo). In the Amazon rainforest and other Neotropical areas from South America they represent pioneering primary to secondary elements that grow on the *terra firme* environments, on well-drained mesophytic soils rior, or on the wet soils of flooded forests (REFLORA, 2015). Ecologically and in terms of the successional stages, *Parkia* behavior is very similar to that of *Dinizia*, with seeds that also have a good capacity to dormancy (Ferraz et al., 2004).

Tribe Ingeae

Genus *Inga* Mill.

Type species: *Inga guayaquilensis* G. Don

Inga aff. *I. marginata* Willd.

(Fig. 5E-G)

Material: ULVG 9022a/9022b, ULVG 8991

Occurrence: in the pale brown/pale yellowish brown upper levels at the Juá II Mine.

Description. A well-preserved oblong and microphylllic leaflet (7.1 cm long, 2.3 cm wide), with entire margin. Apex not preserved, cuneate base with acute basal angle (85°). Primary vein pinnate, 1.5 mm (base) to 0.4 mm (apex) in gauge. Eight to nine arcuate and delicate brochidodromous secondaries, sub-opposite, disposed at acute angles (51° - 55°) and irregularly spaced. Rare and irregular intersecondary veins reaching 50% of the extension of the secondaries, sometimes curving to connect with the precedent secondary vein. Percurrent epimedial tertiaries.

Comparisons. The general character (form, brochidodromous venation with irregular and spaced secondaries and percurrent epimedial tertiaries) approximates the fossil leaflet imprint from that included in the extant genus *Inga*, and the species *I. marginata*.

Remarks. *I. marginata* (Fig. 5G) has a large native range that extends from Costa Rica to northern Argentina (Parr et al., 2014). It is the most abundant species of the genus in Mesoamerica and South America. In Brazil it occurs in Amazonia, *Cerrado*, and Atlantic Forest, growing in gallery forest or on the solid ground of the *terra firme*, with pioneering behavior.

Inga representatives have been found in the fossil record since the Eocene of southeastern United States (Wilcox Formation), with leaflets and fruits (Berry, 1930), being one of the more common leaf remains in Oligocene and Miocene leaf assemblages from the tropical latitudes (Engelhardt, 1895; Berry, 1917, 1919; 1921; Calvillo-Canadell and Cevallos-Ferriz, 2005; see also Supplementary File). These records include a form described by Hollick and Berry (1924) from Bahia, Brazil, *Inga myrianthaefolia*.

Reproductive structures of Fabaceae

Leguminocarpum Dotzler 1937

(Fig 5H)

Material: ULVG 9016a-9016b

Occurrence. In the grayish-orange middle to upper levels of the Juá II Mine.

Description. The middle part of an apparently open legume, plane-compressed (preserved part 6.9 cm long, 1.8 cm wide), with constriction (the one well-preserved constriction is similar to that found in lomenta) and with a prominent margin (0.8 mm in gauge). Three circular chambers are visible, 9 mm in diameter, containing rounded seeds.

Remarks. The establishment of better affinities remains uncertain due to the partial preservation. However, in the Fabaceae, elongated fruits with many constrictions are common between the Mimosoideae (e.g. *Inga*, *Parapiptadenia*, *Acacia*). Similar fruits from the subfamily occurs in the Eocene and Oligocene levels from Mexico (see Supplementary files), and have been assigned to *Acacia* and *Inga* (Calvillo-Canadell and Cevallos-Ferriz, 2005).

Leguminocarpum paraibensis nov. sp.

(Fig. 5I)

Holotype. CPRM-CM 0228F

Occurrence: pale-orange basal levels at Juá II Mine.

Etymology. Referring to the State of Paraíba, where is located the studied basin and where today grows the analogous modern forms of Fabaceae (*Albizia* and *Bauhinia*), with similar legumes.

Diagnosis. Linear to oblong legume, plane-compressed, prominent suture accompanying the margin, one or two weak constriction and nearly six seeds.

Description: Legume broadly linear or oblong (8.9 cm long, 1.9 cm wide), flattened, margin straight in one side, convex in the other, with prominent sutures (0.8 mm in gauge). Acute base and obtuse or truncate apex. Six (7?) externally undulate areas weakly visible and elliptic in form corresponding to the seed chambers (7 mm wide, 5 mm long).

Comparisons. Plane-compressed oblong legumes, with thick and slightly curved sutures, elliptic seminal chambers and in general rounded apex are characteristic in both Mimosoidea and Caesalpinoidea (e.g. *Bauhinia*, a component of the herein studied community). A

preferential affinity, however, with the modern *Albizia* legume is based mainly in the absence of a mucron (characteristic in *Bauhinia*, but that could be broken in taphonomic process) and in the fruit dimensions. Between the modern representatives of the *Albizia* genus, most with a greater number of seeds, a next affinity is expressed with the Brazilian native form, *A. polyccephala* (Benth.) Killip ex Record, by the next fruit morphology, size, form and mainly, by the fewer number of seeds (3 to 7). Yet in *Bauhinia* normally the fruit is more elongate, sometimes more constricted, and also contains a higher number of seeds.

Remarks. The form described could represents a first record of probable *Albizia*-related fruit in Brazil. *Albizia* legumes, however, were identified in the Miocene (Duho Formation) of Korea, where is associated with rounded seeds of *A. bracteata* Dunn and *A. miokalkora* Hu & Chaney (Kim, 2005). Is important to note however, that very similar features is also present in the assigned to *Caesalpinia claibornensis* (subg. Mezoneuron), described by Herendeen and Dilcher (1990) to the Middle Eocene Clairborne Formation in Tennessee, USA. The North American form shows also thick sutures, signs of elongated seeds, and a similar size and width, varying only in the more rectangular chamber outlines and the bi-convex contour of the fruit (here right-convex).

Fossil woods related with *Albizia* have been identified in the Upper Miocene Chiquimil Formation from Argentina (*Paraalbizioxylon caccavariae* Martínez) and in Mexico (*P. cienense* Cevallo Ferriz and Barajas-Morales), and Europe (*P. nathorstii* Schuster and *P. hungaricum* Greguss), as shown the compiled and discussed data from Martínez (2013). Guinet et al. (1987) identified *Albizia* polyads in the Middle Eocene from Egypt, which until now has been the oldest record for the genus and indicates a zoocoric pollen dispersal for the Ingeae Tribe.

A. polyccephala grows today in the gallery forests of *Caatinga* (white woodlands), *Cerrado*, and in the Atlantic rainforest (REFLORA, 2015), been an endemic perennial tree from South America (Parr et al., 2014).

In the taxonomic insertion of the new species the use of *Leguminocarpum* Dotzler 1937, instead other names proposes (*Leguminosites*, Bowerbank 1840, *Leguminocarpum* (Goeppert) Göpp. ex Pálfalvy 1951, follows the proposal of Wang (2012) after discussed the fossil record and the distinct treatment of fossil legumes.

Imcomplete flower

(Fig. 5J)

Material: ULVG 9095; ULVG 10732a-10732b

Occurrence: In the pale-orange basal levels at the Juá II Mine.

Description: Impression of the laterally compressed basal part of a very fragmentary and small flower (preserved part 4 mm long), with only a triangular receptacle visible, enlarged apically and laterally to originate the sepals.

Remark. Zygomorphic flowers (Fig. 5K) are common in the subfamily Caesalpinoideae, a paraphyletic clade in the Fabaceae and one of first to diverge (Herendeen et al., 2003; Bruneau *et al.*, 2008). Due to the fragmentary remains of a probable gamopetalous flower, is only possible to propose an affinity with the Caesalpinoideae, or to a young Mimosoideae flower (Wang *et al.*, 2013). In the fossil record fruits of Fabaceae are relatively well-known, although evidence of flowers is more restricted. The few known materials refers to two mimosoid flowers from southeastern United States, *Protomimosoidea buchananensis*, from the Paleocene-Eocene (Crepel and Taylor, 1986) and the catkin *Eomimosoidea plumose* from Middle Eocene (Crepel and Dilcher, 1977). Crepel (1979) suggested that the flowers of *P. buchananensis* were wind pollinated. In Mexico, a *Hymenea* related flower has been detected in an amber-forming resin of Miocene age (Calvillo-Canadell *et al.*, 2010).

The presence of this incomplete and little flower, however, complete and confirm the important record of Fabaceae to the bentonitic shales of Boa Vista Basin.

The Fabaceae representatives have its most ancient record in Brazil dating from the today considered Middle Eocene Fonseca Formation (Dolianiti, 1948), where is represented by Caesalpinoideae and Papilionoideae (see Supplementary files). At the Eocene-Oligocene boundary they reappear in the São Paulo Basin (Itaquaquecetuba Formation), as Mimosoideae and Faboideae (Fittipaldi *et al.*, 1989; Biagolini *et al.*, 2013). A papillonoideae wood (*Zollernioxylon tinocoi* Mussa) was found in Miocene levels from Acre (Kloster *et al.*, 2012).

Similar extended temporal records exist for the well-known floras of the United States and Mexico, with the oldest legume fossils concentrated in the latter country and represented by the fruits identified in La Carroza Formation by Calvillo-Canadell and Cevallos-Ferriz (2005). A looking for the extensive fossil record here made to the family in tropical areas (Supplementary files), allows observe that the major record are concentrated between the Eocene to Miocene, like highlight by Martínez-Cabrera et al. (2006). From the Upper Cretaceous from United States comes what is considered its anciest record, represented by fossil woods (Herendeen et al., 1992).

In the Paleocene, vegetative and reproductive organs, important in evolutionary and taxonomic terms, appear on all continents. By the beginning of Eocene all of the three modern subfamilies are established, and reach an extensive diversification during the Middle Eocene. In Africa, the Mimosoideae were apparently more diverse, whereas the Caesalpinieae and Sophoreae dominated southeastern North America and England (Crapet and Taylor, 1986; Herendeen and Dilcher, 1992; Wing et al., 2009). In biological and environmental terms this evolutionary success seem to have resulted from the ability of Fabaceae to colonize disturbed habitats such as water courses and/or lake margins (Herendeen et al., 1992) and was also influenced by the contribution of pollination by bees (Crapet and Taylor, 1985).

In terms of phylogenetic analyses an age of c. 59 Ma was firstly proposed by Lavin et al. (2005) to the establishment of its crown group, with an estimated ages to the older caesalpinioid crown clades differing little from those suggested to the mimosoids and papilionoids. After, Bell et al. (2010) indicates distinct moments to the appearing of crow Fabaceae, in the interval of 77 to 47 Ma, in accord with was see bellow to the fossil record. The after using of the plastid matK gene sequences supports well-resolved subclades within the Leguminosae and attests to the monophyly of the entire family (excluding *Dinizia*). Meanwhile, Caesalpinoideae is paraphyletic and next to the mimosoids, that together forming a strongly supported clade and a sister group to the papilionoids (Wojciechowski et al., 2004). Lavin et al. (2005) additionally suggests that a couple of million years (1.0 to 2.5 Ma) distinguishes the mean ages of the legume stem and crown clades.

Order Myrtales Reichenbach

Family Myrtaceae Jussieu

Subfamily Myrtoideae Sweet

Tribe Myrteae Candolle

Subtribe Myrciinae O. Berg

Genus *Myrcia* DC. ex Guill.

Type species: *Myrcia bracteolaris* (Poir.) DC., 1828 (=*Myrcia fallax*)

Myrcia rostrataformis Hollick and Berry 1924

(Fig. 6A-D)

Material: ULVG 9048

Occurrence: In the pale-orange basal levels at the Juá II Mine

Description. Microphylllic ovate to elliptical leaf, 7.8 cm long and 2.8 cm wide (L:W ratio nearly 3:1), with entire margin, acuminate apex (angle of 25°) and a slight asymmetric and cuneate base (angle from 35-40°). Primary vein pinnate and curved, initially thick, attenuating upward (1.4 mm to 0.5 mm). Thin brochidodromous secondaries, sub-opposite to alternate disposition, diverging at angles of 70° and closely spaced. Loops quadrangular in form, rarely forking exmedially, their union forming an intramarginal vein. Fimbrial vein present and originating from loops of the exmedial tertiaries.

Comparisons: In the fossil record, except for their wider lamina, the Boa Vista specimens shares the same diagnostic features that characterizes *Myrcia rostrataformis*, originally described by Hollick & Berry (1924) to Ouricanguinhas, Bahia, Brazil ("Tertiary"). Also, Fittipaldi et al. (1989) described a similar *Myrcia* cf. *M. rostrataformis* from the Eocene-Oligocene Itaquaquecetuba Formation, São Paulo Basin. The uncertainty expressed in the latter study regarding the relations with Berry's impressions is due to the distinctly more elongate form of the lamina, similar to the herein described form, yet this may only reflect a distinct environmental response or its location in the tree.

M. diafana Duarte & Rezende-Martins described to Taubaté basin (Duarte and Rezende-Martins, 1985), presents a symmetrical form (more elongate) and an emarginated apex, distinct from the Boa Vista leaf imprints. The fossiliferous beds at the Taubaté basin was included in the Tremembé Formation, dated by its contents in mammals and pollen grains, to the boundary between Oligocene and Miocene (Marshall et al., 1986). Other impressions were associated to *Myrcia* by Duarte (1967) in levels of the Pirabas Formation (Miocene), State of Pará, but without descriptions provided.

The secondary loops forming intramarginal veins indicates the affinity with the Myrtales, at least here they are broader, like those seen in some pinnate Dillenidae (Hickey and Wolf, 1975). In the family Myrtaceae the acute apex, delicate venation, external loops in the secondaries and broad marginal areas are more common in the Myrciinae subtribe, and could occur in distinct modern genera, e.g. *Myrcia*, *Gomidesia*, and *Myrceugenia*. The scarce material referring to this morphotype makes assignment to a more precise affinity difficult, but by the apex and ovate/elliptic form, approximates from *Myrcia* variation, where elongate lamina and weak venation is characteristic of some endemic Brazilian species like *M. splendens* (Sw.) DC. and *M. brasiliensis* Kiaersk.

Remarks. The first record of *Myrcia* related forms, which would later achieve a great representativeness in North and South America, comes from the Late Cretaceous in the southeastern United States (Berry, 1916; 1919). However, Berry's leaves show morphologies very similar with those also found among the Lauraceae, so the affinities of these remains have been put into doubt. From the end of Paleocene onwards the genus expanded in number and diversity and its distribution was extended, along with other Myrtaceae, to areas of Patagonian and the Antarctic Peninsula (Engelhardt, 1895; Berry, 1922b; 1924; 1925; 1937c; 1938; Dutra, 2004; Panti, 2011; Iglesias et al., 2011). Another pulse of diversity marked the Early Miocene (Fiori, 1940; Anzótegui, 2000; Duarte, 2004).

Studies of DNA sequences suggest an origin of the Myrtaceae in Gondwana and for the tribe Myrtae an origin and diversification in Australia at the K-Paleogene boundary (Wilson, 2004). The tribe is today pantropical and includes Brazilian forms, the same occurring with *Myrcia* genus, today restricted to South and Mesoamerica (Sytsma et al. 2004; Biffin et al., 2010; González, 2011). In Brazil its species occurs mainly in the rainforests of central-west and southeastern parts of the country, but extends the south (in Araucaria forest)

and reaches Argentina and Uruguay. More rarely, they grow in areas of the *Cerrado* and in riparian vegetation and wet soils (Carvalho, 2003).

Calyptanthes Swarts 1788

Type species: *C. chytraculia* (L.) Sw. (typ. cons.)

Calyptanthes cf. *C. argilosa* Duarte & Rezende-Martins

(Fig. E-I)

Material. ULVG 9067a-9067b

Occurrence: In the pale-orange basal levels at the Juá II Mine

Description. Incomplete impression of a microphylllic leaf with well-preserved venation, showing an elliptical leaf with entire margin (4 cm long, 3 cm wide). Apex rounded but with a stunted central projection (angle of 70°), basal part not preserved. The main venation is pinnate brochidodromous with a straight and thick primary (0.2 to 0.6 mm) and with secondaries emerging at acute angles (30–50°), alternate to opposite and closely spaced. Forming quadrangular exmedial loops at the ends and with a clearly visible intramarginal vein that runs parallel to but distant from the margin. A few extramarginal loops weakly visible. Intersecondaries sometimes bifurcating at their origin and attenuating exmedially. These branches exmedially to reach the secondaries anywhere, but mainly at the loops that form the intramarginal. Tertiary veins admedially ramified, arranged at inconsistent angles. Fourth-order veins weakly visible and freely dichotomizing.

Comparison. The only previous records of *Calyptanthes* in Brazil refers to *C. argilosa*, found in levels now considered as Oligo-Miocene from the Piraçununga Formation at Vargem Grande do Sul, state of São Paulo (Duarte and Rezende-Martins, 1985), that shares common features with the Boa Vista basin leaf imprints, and *C. marahiaensis* Hollick and Berry, from Bahia (Hollick and Berry, 1924). The affinity with *C. argilosa* is expressed in the similar venation pattern, size, divergence angles of the secondaries and thick primary vein. However,

taking in account the partial preservation, the affinity is still dubious. Moreover, the general morphology described here is common to many modern Myrtaceae (abborded in the previous *M. rostriformis* comparisons), especially those in from Myrciinae, and in *Myrcia* (*ex-Gomidesia*) and *Psidium* genera. Nevertheless, the straight course of the intramarginal vein and the occasional bifurcation of the secondaries at their point of divergence from the primary are typical features of *Calyptanthes*.

Remarks. Records of *Calyptanthes* related leaf prints were known since the Eocene (*C. eocenica* Berry) and extends into the Oligocene from North to South America (Berry, 1916; 1918; 1921b; Hollick and Berry, 1924). It has also been recorded in the Dominican Republic (*C. dominguensis* Berry) and in Brazil, as mentioned *C. marahiaensis* Hollick and Berry. In the extant species similar morphologies are present in *C. clusiifolia* O. Berg, *C. lucida* Mart. ex DC., and *C. creba* McVaugh (Fig. 6H-I), which grows in Brazil from the north (Amazonas) to the southeast, in semi-deciduous forests and Cerrado, on *terra firme* or in flooded areas (REFLORA, 2015). Today *Calyptanthes* and the subtribe Myrciinae are distributed from Mexico to northern Argentina, with their greatest distribution in southeastern Brazil (Mori et al., 1993; Souza et al., 2007).

Representatives of the Myrtaceae family occurs since the end of the Cretaceous on Antarctic Peninsula (Zastawniak, 1994; Dutra, 2004) and in southernmost Argentina (Frenguelli, 1953; Menéndez, 1972; Passalia et al., 2001; Prámparo et al., 2007; Iglesias et al., 2011). In the Cenozoic they dispersed into many South American areas, been represented in most of the Cenozoic Brazilian basins (Hollick and Berry, 1924; Duarte 1967; 2004; Duarte and Mello-Filho, 1980; Duarte and Rezende-Martins, 1985; Fittipaldi et al., 1989; Machado et al., 2012), attesting the importance of the West Gondwana areas in the evolution of the family. Myrtaceae is also well represent in the microflora from the Late Cretaceous of Africa, Australia, and Southeast Asia. Nonetheless, some pollen grains assigned to the family are difficult to precise in its relations to the family (Thornhill and Macphail, 2012).

The commented record seems to be in accord with the findings of Sytsma et al. (2004) and Biffin et al. (2010), which proposed that the crown group of Myrtaceae dates from Cretaceous, yet with an origin in Australasian areas. However, a more complete analysis of the macro- and micro-assemblages seems to corroborate the proposition of Raven and Axelrod (1974), which points the West Gondwana areas to the initial diversification of the family.

It seems to be confirmed with the more recent molecular and paleontological study performed by Murillo-A. et al. (2012) with genus *Myrceugenia* and that includes a discussion on the biogeography of all Myrtaceae. They confirm a preferential place of origin in southern South America, where the family is represented by pollen grains of Campanian age (Prámparo et al., 2007). In the Paleocene they also appears in leaf and wood assemblages, with forms related to *Eugenia*, *Luma*, and *Myrcia*. The authors also proposed two centers of species diversity, central Chile and southeastern Brazil, which also seems to be valid to other austral angiosperms (Sapindaceae, Proteaceae, Myrtaceae, Malvaceae) and attested also by the distribution of *Araucaria* genus in South America and Antarctic Peninsula (Dutra and Stranz, 2003; Cantrill and Poole, 2012).

Yet, according to Murillo-A et al. (2012) the Myrtleae tribe must be older than proposed by Sytsma et al. (2004) and Biffin et al. (2010). Based on a great quantity of paleontological data and supported by the work of Hernández et al. (2005), Murillo-A et al. (2012) also points that the discontinuous Miocene distribution of Myrtaceae (Chile and South Brazil) resulted from the establishment of the Paranaense Sea. The late Miocene-early Pliocene definitive uplift of the Andes and the “Pampean Mountain Range” was, on the other hand, responsible for the arid diagonal that characterized Patagonia and the Atacama Desert (Hinojosa and Villagrán, 1997), as well as for the wet climatic conditions in central Chile and southeastern Brazil.

Order Sapindales

Family Burseraceae Kunth

Tribe Protieae Marchand

Genus *Protium* Burm.f.

Type species: *Protium javanicum* Burm. f.

Protium cf. *P. heptaphyllum* (Aubl.) Marchand 1873

(Fig. 7A-E)

Material: ULVG 9007a-9007b; ULVG 10761a-10761b

Occurrence: In the pale-orange (basal) and pale-brown/pale yellowish (middle to upper) levels from the Juá II Mine.

Description. Well-preserved (in fine details) elongate, oblong and microphylllic leaflet, slightly curved, 8 cm long and 2 cm wide (L:W ratio of 4:1), with a homogeneous width maintained along the lamina. Basal part not preserved. The margin is entire and the apex rounded, with a broad angle of 100°. A thick primary vein (0.35 mm - 0.6 mm), with curved course supports numerous brochidodromous secondaries (13-14) of 0.2-0.3 mm width. The secondaries are sub-opposite (basal part) to alternate (distally) arranged, more widely spaced in the middle portion of the leaflet than at the ends. These diverge from the main vein at marked right and varied angles (65° to 90°). Intersecondary veins have a zig-zag course, bifurcating exmedially, each branch curved upward to meet the next secondary arc. Intercostal tertiaries present and alternate, percurrent, with sinuous course, diverging at right angles to the secondaries, sometimes meeting the primary vein (epimedial tertiaries). Looped exterior tertiaries present, one of them bigger, located between the arcs of the secondaries. Fourth-order veins with regular courses, sometimes forming areoles, or freely ending veinlets (FEVs) with two branches and simple terminals. Well-developed areolations with 4-5 sides.

Comparison. The morphology and venation features described, e.g. large and elongate leaflets, with parallel margins, highlighted venation, brochidodromous secondaries diverging at nearly right angles and with elongate exmedial loops, the presence of intersecondaries, and the percurrent tertiaries, link this morphotype to forms included in the genus *Protium*, which is already known to show great variation in leaf morphology (Swart, 1942). However, within their representatives, the present features are most closely matched in *P. heptaphyllum* (Fig. 7D-E).

Remarks. Modern forms of *P. heptaphyllum* grow today in *Cerrado* and in areas of the Atlantic and Amazon rainforests. This latter area has been considered as its center of diversity and it is where *Protium* is today one of the most common genera (Aguilar-Sierra and Melhem, 1998). Using bayesian fossil-calibrated analyses, Fine et al. (2014) dated the Protieae stem in nearly 55 Ma. These same authors called attention to the influence of Andean uplift and the union of South and North America on Neotropical floras and used biogeographic analyses to reconstruct the initial late Oligocene/early Miocene radiation of Neotropical Protieae in

Amazonia, as well as subsequent occurrence of *Protium* (Miocene) in the Caribbean, Guianas, and Paraguay. They nevertheless emphasize the habitat specialization of *Protium* to the white sand or flooded soils common in Amazonia. Species of *Protium* have also been shown to be adapted to other distinct types of vegetation, like gallery forests, *Cerrado* and *Restinga*, and to soils that could experience hydric deficiency (Daly *et al.*, 2012).

Protium cf. *P. rhynchophyllum* (Rusby) D.C. Daly

(Fig. 7F-G)

Material. ULVG 9042, ULVG 9051a-9051b,

Occurrence: In the pale-orange basal levels from the Juá II Mine.

Description: Impression of part and counterpart from the abaxial side of an elliptical microphylllic leaflet, 2.4 cm wide and 5.5 cm long, asymmetric, with entire margin. Thick petiole (1.5 mm wide, 6 mm long) that loses gauge apically. Basal part of the lamina also asymmetric, angle of 120°, apex not preserved. Primary vein pinnate, 0.3 mm – 0.9 mm in gauge. Brochidodromous secondaries, opposite (basal part) to alternate (distally) arranged, uniform spacing and diverging in broad (73°) to distally acute angles (45°), more curved on one of the sides of the leaflet. Occasionally these form one to three extra distal arches of secondary gauge. Rare intersecondaries, of sinuous course and exmedially bifurcated. Intercostal tertiaries mostly percurrent and epimedial ones with parallel distal course. The exterior tertiaries and the fourth-order venation are poorly visible or absent.

Comparisons. The general characteristics (form, asymmetric base, thick petiole, brochidodromous venation) one more time approximates the present morphotype to that found in the variation of *Protium*. Also, between the extant species analyzed share elements with *P. rhynchophyllum* (Fig. 7H), in the form and regular distribution of the brochidodromous secondaries, varied external loops, rare intersecondaries, and mostly percurrent tertiaries. However, the size of the leaflet is only half as large in the fossil impression as in the extant form, which together with the blunt apex seems to reflect a local adaptation to lower moisture. The free ending of exterior tertiaries is also a characteristic of the extant species but is not

apparent in the fossil leaflet. Those aspects and the low relief of the high order venation distinguish this morphotype from the previous one described.

Remarks. Today *P. rhynchophyllum* is exclusive from the *terra firme* environments in near all states (Acre, Roraima, Amazonas, and Mato Grosso) covered by the Amazon rainforest, where is arboreal element (Obermüller et al., 2011; REFLORA, 2015).

The two forms here discussed to the Campos Novos Formation are the first record to the genus to Brazil. However, recently Chambers and Poinar Jr. (2013) described a fossil flower of *Protium callianthum* to mid-Tertiary ambers from Dominican Republic.

The monophyletic Protieae tribe is one of the most important Neotropical tree lineages in terms of diversity and abundance, considered a sister group of Bursereae (Fine et al., 2014). The stem age inferred by fossil-calibrated data points to an origin at the end of the Paleocene or Early Eocene in tropical North America. Indeed, the Protieae's oldest fossil comes from the London Clays, dated at 50–56 Ma, and the next younger one (44 Ma) comes from Oregon (North America), consisting of a fossil endocarp that closely resembles Protieae (Manchester, 1994).

Weeks et al. (2005), also working with molecular data and fossil evidence, suggest a vicariant Laurasian origin for the Burseraceae, and a secondary dispersal to southern-hemisphere continents. This coincides with the records from the Eocene of England, Austria, Czechoslovakia, India, and Sumatra. In the neotropics the Burseraceae are found in the same time interval in Venezuela and Mexico (Calvillo-Canadell et al., 2013) as well as in the Oligocene of Mexico (Martínez-Cabrera et al., 2006).

At the end of the Oligocene members of the crown group split between the paleotropics and neotropics where diversification occurred after the mid Miocene (Fine et al., 2014). Once again an influence of Andean Range is observed, associated with the approach and collision of North and South America and the arriving of colder climates that resulted in the retraction of the high-latitude tropical forests towards the equator (Zachos et al., 2001; Willis and McElwain 2002; Fine et al., 2014). This fall in temperatures led the two original lineages of the Protieae to move in direction of the low latitudes of North America, with one lineage dispersing to the Old World tropics and another towards South America (Daly et al., 2012). Into the Miocene the establishment of dispersion routes becomes more difficult, e.g. those between South America and Africa, and Central America. According to Fine et al.

(2014) this could have occurred at least in three separate times between 5 and 10 million years ago. Today the Burseraceae is a cosmopolitan Neotropical family, occurring in Mexico, South and Central America, Africa and Asia, where it is largely represented by the *Protium* genus (Daly et al., 2012).

Family Anacardiaceae R. Brown, nom. cons.

Tribe Anacardioideae Takhtajan

Genus *Anacardium* L.

Type species: *A. occidentale* L.

Anacardium cf. *A. occidentale* L.

(Fig. 8A-B)

Material: CPRM-CM 0223Fa/0223Fb

Occurrence. In the pale-orange basal to middle levels from the Juá II Mine.

Description: Well-preserved but incomplete microphylllic leaf impression, probably oblong, and with entire margin (4.8 cm long, 2.6 cm wide). The pinnate primary vein, 0.6 mm – 0.2 mm in gauge, contains eight sub-opposite pairs of brochidodromous secondaries, regularly spaced, which diverges at broad angles (60°-70°) and present external loops. Few intersecondaries present, with more than 50% of the extension in relation to the next secondaries. The tertiaries are percurrent and alternate disposed, meeting between the secondary mesh forming a zig-zag, transversely aligned in relation to the midrib. Fourth-order veins irregular reticulate and arranged in well-developed areolations.

Comparisons. The present morphology with regularly spaced brochidodromous secondaries containing external loops, and the alternate percurrent tertiaries make the leaf imprints from Boa Vista Basin very similar to the leaves of the extant species *A. occidentale* L. (Fig. 8C).

Remarks. *A. occidentale* (Caju) originates from Central and South America (Parr et al., 2014). In Brazil its origin is indicated within the same northeast areas where the studied fossils were detected and since today grows in the *Caatinga* (sensu stricto) biome. The species is also found in the *Cerrado* sensu lato, in coastal areas with well-drained soils (*Restinga*),

and in open areas of Amazon rainforest (REFLORA, 2015), reflecting a well-adapted condition to hydric stress in the soil. It is now commercially cultivated in semi-arid tropical areas for harvesting of its nuts (cashews).

In the Brazilian fossil record, the Anacardiaceae related morphotypes were scarce, known by a fruit (*Anacardites brasiliensis*) and a leaflet (*Spondias*) reported by Hollick and Berry (1924) from Ouricanguinhos, Bahia. Dolianitti (1948) described a new species of *Rhus* (*Rhus toxicodendroides*) from the Miocene Juruá River basin in Acre. Pleistocene woods of *Astronioxylon mainieri* Suguio and Mussa (prolaby rework from older levels) were described from São Paulo Basin (Suguio and Mussa, 1978), and leaf impressions of *Astronium faxilifolium* Scott ex Spreng, were identified in the Quaternary levels of Catalão, Goiás (Silva, 2013). One more time the herein described leaf represents a first record to the genus in Brazil, significative taking in account its today grow in the same area.

Anacardiaceae related fossils have been reported in levels so old than Cretaceous in Chile (Menéndez, 1972) and to the Paleocene-Eocene, in Antarctic Peninsula (Dutra, 2004). They are also abundant in Oligocene and Miocene levels from the Isthmus of Tatuapé (Oaxaca) Mexico, and in Peru, and Venezuela (See Supplementary Files). Currently the family includes nearly 600 tropical species, more rare in temperate areas (Martínez-Millán and Cevallos-Ferriz, 2005). Estimated ages for the Anacardiaceae crown group, phylogenetically considered to be a sister group of the Burseraceae, have been estimated as 72.7, 65.2, and 54.8 Ma by Muellner et al. (2007).

Order Malvales Berchtold & J. Presl

Family Malvaceae Jussieu, nom. cons.

Tribe Grewioideae Hochreutiner

Genus *Luehea* (Mart.) Stuntz

Type species: *Luehea speciosa* Willd.

Luehea cf. *L. paniculata* Mart. & Zucc.

(Fig. 8D-F)

Material: ULVG 9002a, 9002b

Occurrence: In the pale-brown and pale-yellowish brown upper levels from the Juá II Mine.

Description. Impression of part and counterpart of a microphylllic, membranaceous leaf, with a slightly curved lamina, 5.2 cm long and 2.1 cm wide. Margins, base, apex, and petiole not preserved. The vein framework is made up of three basal actinodromic primaries, the central one more visible (0.7 mm wide), containing upwardly curved external secondaries (agrophic veins) that diverge at angles of 45°–65° and which appear to end at the margin (serrate?). The lateral primaries reach 2/3 of the leaf length. Intercostal secondaries also actinodromous, with an exmedial sinuous course, a few of them occasionally diverging from the central primary, mainly in the middle and upper part of the lamina, at angles of 40°. Epimedial tertiaries, opposite to alternate inserted and with a straight course, covering the intercostal areas, transversally disposed (broad angles in relation to the primaries). External comb-like veins percurrent and with variable concave-convex course. Quaternary veins also percurrent and diverging in right angles.

Comparison. The actinodromous pattern of the venation, with three main curved primary veins, that ends in the lateral margin of the lamina, containing agrophic veins, are common in many Malvaceae and both *Luehea* and *Lueheopsis*. The presence of teeth, common in *Luehea*, is impossible to evaluate due to unpreserved marginal characters, and but is inferred here by the irregular character of the lamina contours in the impressions. Taking in account the other morphological features, a possible affinity with *Luhea paniculata* Mart. & Zucc. is proposed (Fig. 8F), mainly based on the size and open disposition of the main venation, with long lateral primaries. In the fossil record from Brazil only the *L. divaricatidormis* Fitipaldi discussed below, from the Oligocene of São Paulo, shows a superficial resemblance to the for described here.

Luehea related leaf imprints are a common element in the Brazilian fossil record. The most ancient one refers to a better-preserved impression of a large rounded leaf, with serrate margin and many agrophic veins ending at the tooth apex, assigned to the Fonseca Formation deposits in Minas Gerais (today considered Eocene-Oligocene in age), and to the species *Luhea roxoi* Dolianiti (Dolianiti, 1949). To the Paleogene, the record ampliates with the species found in early Oligocene levels from São Paulo (Tremembé Formation), southeastern

Brazil, *L. nervaperta* Duarte and Mandarim-Lacerda. However, the morphotype described have weak and short primaries broadly disposed (Duarte and Mandarim-Lacerda (1989), distinct features in relation to the here described leaves. Two other forms were found to the Itaquaquecetuba Formation, *Luhea* sp. (Biagolini et al., 2013) and the commented *L. divaricatiformis* (Fittipaldi et al., 1989). The latter has broad and big leaves with serrate margins and a venation similar to that in the Boa Vista materials, but is too incomplete to allow comparisons. At any rate, call the attention to the smaller sizes of leaves in Oligocene materials when compared with those from the Eocene.

Remarks.

Luehea was also record from Ecuador and assigned to a new species “*Luehea*” *tertiaria* (today invalidated by the wrong generic epithet), described by Engelhardt (1895), which was compare to the extant *L. speciosa*. However, the obtuse angle of divergence and concave course of the epimedial tertiaries makes it distinct from the herein described form.

The extant *L. paniculata* shows pioneer behavior and a deciduous habit, growing along forest borders, independent of soil humidity. Its distribution has since been found from high to low-lying areas and is common in the *Cerrado* and *Caatinga*, where it grows among the riparian vegetation (REFLORA, 2015). In South America this species is distributed from Surinam to Uruguay and northern Argentina, where it inhabits the *Pampa* plains (Milward-de-Azevedo and Valente, 2005; Parr et al., 2014). In northeastern Brazil (Pernambuco) it can be found in the woodlands from the “Zona da Mata” and along coastal sandbanks (*Restinga*), where grows on the clay soils of the interdune body waters (Tschá et al., 2002).

Genus *Lueheopsis* Burret

Type species: *Lueheopsis duckeana* Burret

Lueheopsis cf. *L. hoehnei* Burret

(Fig. 8G)

Material: CPRM-CM 0232F

Occurrence: in the grayish-orange upper levels from the Juá II Mine

Description. Impression of a notophylllic ovate leaf with entire margin, 7.9 cm long and 4.2 cm wide (in the preserved portion). The base is rounded with an angle of 185°. Petiole and apex not preserved. Three main basal and delicate actinodromous veins originate (at angles of 55°) from the base and maintain a curved upward course. The central one is 0.6 mm wide, the laterals 0.7 mm. From these, and in the middle and apical sectors of the lamina, secondary veins diverge at angles of 45°. Also, numerous curved agrophic veins diverge from the basal part of lateral primaries. Opposite to sub-opposite percurrent epimedial tertiaries, with 3 mm spacing and straight course, diverge from the primaries at right angles.

Comparisons. The broader lamina and weak actinodromous venation (yet this could due to the preservation of the adaxial face), inserted at more open angles, distinguish this morphotype from the one previously described and associated to *Luehea*. In addition, entire margins are exclusive from *Lueheopsis* species. Among the modern *Lueheopsis*, the morphological characters described here are most closely shared with those present in the species *L. hoehnei* Burret (Fig. 8H) and *L. duckeana* Burret, both from Amazonia (the former also in the “Cerrado”). However, the elliptic form, slight asymmetry, and the general pattern of the venation in the first species is sharing with the leaf impression described here, the reason for the proposed affinity.

In the scarce fossil record to the genus in Brazil only two morphospecies are previously known. The first comes from the same Boa Vista Basin and was still associated to *Lueheopsis* (Wilberger et al., 2010) and the other was assigned to *Dicotylophyllum* sp. 6, by Dos Santos and Bernardes-de-Oliveira (2013, Figs, 6E-F) and still compared to the extant *Lueheopsis* genus. The last was identify to Neogene levels, near Rio Claro, state of São Paulo, and exhibits an entire margin and three primaries, as is the case with the new specimen discussed here, but it has a more acute base and the presence of agrophic veins is not mentioned.

Remarks. The worldwide fossil record for the genus is still scarce, with only three forms named up until now (*L. dissymetra* Langeron, *L. verisimilis* Langeron, and *L. vertieri* Marty) from France (van der Burgh, 2010).

Besides in Brazil (Lorenzi, 2002), the modern species *L. hoehnei* grows in tropical South America, from Bolivia to French Guiana (Parr et al., 2014; REFLORA, 2015). Gentry (1988) described *Lueheopsis* “*hoehnei*” as a dominant form in the swamp environments of

the Peruvian Amazon region, and another species, *L. burretiana* Ducke, is exclusive from Amazon rainforest (REFLORA, 2015).

The estimate age of the Malvaceae crown group has been evaluated at between 66 and 39 Ma (Bell et al., 2010). This is consistent with the fossil record, which shows a bi-hemispheric occurrence in the Maastrichtian, evidenced by pollen grains and fossil woods (Knowlton, 1919; APG III, 2009). During the Paleocene, pollen grains of *Tilia*, *Brownlowia*, and *Grewia* are still present (Muller, 1981), and since the Eocene distinct kinds of macrofossils (wood, leaves, fruits, and flowers) related with *Tilia* and *Grewia* are globally distributed (Taylor et al., 2009, Pigott, 2014).

Using sequence analysis based on morphological features and biogeographic data, Bayer et al. (1999) proposed a merging of Sterculiaceae, Tiliaceae, and Bombacaceae in the Malvaceae. Alverson et al. (1999), using a similar molecular analysis, recognized the monophyly of the group, yet also noted the still poorly understood character of the clade's internal structure. Based on the work of Bayer et al. (1999), those researchers also proposed a Pantropical Grewioideae clade to included *Luehea* and *Lueheopsis* (ex-Tiliaceae).

The more than 4500 species of modern Malvaceae have a mainly tropical distribution and shows affinities with humid soils (Kubitzki and Bayer, 2003; Burnham and Johnson, 2004).

Other materials

Dicotylophyllum sp. 1

(Fig. 8I)

Material: ULVG 9001; ULVG 9118a-9118b

Occurrence: in the pale-brown/pale-yellowish brown middle-upper levels from the Juá II Mine.

Description. Complete leaf or leaflet, obovate, microphylllic, with entire margin, 5.3 cm long and 2.4 cm wide. Obtuse base with broad angle (195°), acute apex (83°). Pinnate primary vein

with opposite brochidodromous secondaries of weak gauge and straight course, curving abruptly near the margin. These diverge at variables angles of 55° to 70°, and are irregularly spaced. Intersecondaries veins present.

Remarks. The general form and brochidodromous venation resemble those seen in extant forms of *Senna* (e.g. *S. corymbosa* (Lam.) H.S.Irwin & Barneby), but in the absence of an identifiable pulvinus and high venation orders, its apparent relation is uncertain. The presence of other leaf impressions related to *Senna* in the basal levels of the same expositon, but with too distinct features (a great number of secondaries and lower sizes), maintains the uncertainty.

Dicotylophyllum sp. 2

(Fig. 8J)

Material: CPRM-CM 022F; ULVG 9072

Description. Elliptical microphylllic leaf, margin entire, 3.3 cm long and 1.9 cm wide. Base with a broad angle (140°), acute apex (78°). Pinnate primary vein contains alternate weak brochidodromous secondary that diverges in acute angles. Percurrent tertiary veins.

Remarks. The weak preservation prevents more next affinities.

4.2. Statistical and Ecological analysis

The analysis performed using PAST software made use of the 24 distinct types of plant fossils identified from the Campos Novos Formation, 13 related to leaf impressions and 7 to leaflets (related to Fabaceae and Burseraceae). The two legume fruits, the partially preserved flower, and the fragmentary stem of a probable monocot were not considered. A summary of the taxonomic, physiognomic, and ecological analyses is seen in Figure 9. It shows that the assemblage is composed by dominant microphylllic leaves with brochidodromous venation patterns (representing Lauraceae, Annonaceae, Fabaceae,

Myrtaceae, Anacardiaceae and Burseraceae). Actinodromic and non entire margins are exclusive from the Malvaceae and of *Bauhinia* (Fabaceae) related forms.

The cluster analysis performed, in order to look for a preferable correlation of the Campos Novos taphocoenosis with other fossil assemblages from Brazil, northern South America, Mesoamerica, and Mexico (Fig. 10 and 11), shows that the closest similarity to the Boa Vista Basin flora (Campus Novos Formation) is with the Eocene-Oligocene Itaquaquecetuba Formation (Fittipaldi et al., 1989; Garcia et al., 2007), in the state of São Paulo. Both Campos Novos and Itaquaquecetuba formations floras, also share elements with other known taphoflora from southeastern Brazil (e.g. the Entre-Corregos and Fonseca formations), most dated from the Eocene-Oligocene or basal Oligocene. All of those basins also shares a genesis in a tectonic context (Santos et al., 1999). Secondarily, the analysis confirms affinities with the coetaneous Tremembé Formation, São Paulo, and a more distant relationship is expressed with deposits dated to the Early (Pirabas) and Late Miocene (Solimões Formation, Gross, 2011) from Northern Brazil (Fig. 10). In a more regional context, the BVB taphoflora is included in the clade of generic correlation with that preserved in levels of the same age that the here studied, at Oaxaca, Isthmus of Tehuantepec (Peres-Garcia et al., 2001) and those from Costa Rica (late Oligocene?) studied by Berry (1921a), as seen in Fig. 11.

5. Discussion and conclusions

The new late Oligocene plant assemblage studied to Boa Vista Basin shows to be composed by vegetative and fertile foliage impressions, mainly composed by leaves and leaflets and legume fruits. In the assemblage the Fabaceae-related forms stand out for their abundance, followed by Lauraceae, Annonaceae, Burseraceae, Anacardiaceae, Myrtaceae and Malvaceae, indicating an arboreal and pioneering vegetation, that mixing forms today dispersed in distinct biomes. They were preserved in a lacustrine or flood plain system installed in distinct parts of an isolate and small intracratonic basin, in a similar condition to others ones existing to the Cenozoic in Brazil. Its geological and environmental restrict condition and the comparisons with more regional constraints, combines several challenging aspects.

The end of Oligocene was characterized by a short interval of global warmer climate conditions, only comparable to that from the Middle Miocene (Zachos et al. 2011). In this context, the BVB assemblage represents a good proxy, yet in small scale, to accompany the vegetation behavior in relation to it and the coincident first exhumations that marks the Andes uplift. Additionally, the surrounding stressed area, with an active volcanism is in course, rarer in the other comparable basins, and must be the reason to some identity of the flora, with that nowadays growing under the Andes influence.

The analyzed data and ecological affinities of the area-restricted Boa Vista Basin taphoflora (NLR approach at generic level) indicates an early successional stage, made up of pioneering and mostly arboreal forms, represented by *Nectandra*, *Anacardium*, *Luehea*, *Inga*, *Protium*, *Dinizia*, and *Parkia* (Gandolfi et al. 1995; Ferraz et al., 2004; Utescher and Mosbrugger, 2007; REFLORA, 2015). A minor shrub component is informed by the Myrtaceae, *Bauhinia* and *Luehea*.

The low-latitude location of the basin maintained since the Oligocene (Schettino and Scottese, 2001) guarantees also a favorable condition to the comparisons between fossil and extant floras in the region. Looking to its physiognomy and taking only in account the leaf components (since small laminas characterizes leaflets), the microphylllic to notophylllic character of the leaf imprints (Fig. 9A), may reflect or a restriction in atmospheric moisture or, hydric deficiency in the soils. For other side, the close venation and entire margins supports the warm climate (Wolfe, 1995; Dutra, 2007; Wing et al., 2009). Taking in account that dry soils are not expected in the fluvial and deltaic context informed by the associated facies, restrictions in atmospheric humidity, yet lower than that today exists in the area, seems to be the main parameter affecting the wood vegetation.

Such kind of environmental conditions is similar to that influence the vegetation from South Mexico in the end of Oligocene (Perez-Garcia et al., 2012), characterized by the first appearing of seasonally dry tropics, it stimulates the vegetation heterogeneity and the coexistence of species typical of moist habitats, with those clearly adapted to xeric conditions, similar to that expressed by the BVB paleocommunity.

Additionally, the significant presence of the Fabaceae (and Burseraceae), known today by their well-adapted behaviour and capacity for recolonizing disturbed areas (including seed dormancy, such as in the Amazonian *Dinizia*), confirms the unstable soils produced by the

cyclic reactivations of the fluvial systems and the volcanic events. It is also informed by the presence of some taxa, like *Parkia*, *Protium*, *Nectandra* and *Calyptranthes* that supports periodic flooding. Those aspects and the absence of drip tips in the fossil leaves (today present, for example, in *Protium*), attests a more broad condition of low atmospheric humidity. The presence of *Bauhinia*, *Luehea*, *Anacardium* and *Albizia*, today still present in the *Caatinga*, attests the arid conditions, at least seasonally distributed.

However, and contradictorily, the majority of the modern analogous of the fossil community, grows today in the Amazon biome (Fig. 9F), yet adapted to more well-drained soils from *terra firme* areas (to references, see above the remarks to each taxa). And the minor components today found in *Cerrado*, *Caatinga* and *Pantanal*, are specialized to open herbaceous or shrubby biomes, where occupies the riparian or gallery forest. The few that also are common with Central America areas, confirms its Neotropical appeal, but also characterize the “seasonally dry” climate conditions.

The disjunctive paleovegetation of Boa Vista Basin community could also be useful in ecological and biogeographical terms, in terms of represents an ecotone (Lloyd et al., 2000), or by its stochastic character (Van der Maarel, 1990). The first ecological approach seems to be more reasonable taking in account the unstable condition of the soils. On the other hand, given its isolated conditions (like in other Cenozoic basins in Brazil), the application of the refuge concept cannot be discarded. Overall, the role of the Fabaceae, Anacardiceae, Myrtaceae, and Annonaceae in colonizing areas in a regeneration stage (Herendeen et al., 1992), strengthen these inferences and make difficult to select a preferable option among one of those ecological contexts. The tectonically induced area that generates the basin (Souza et al., 2005; 2013) also promotes the appearance of new ecological niches and coincides with a moment knowing by a peak in diversity for most of the taxa here detected (e.g. *Annona*, *Albizia*, and other Fabaceae).

The similarity detected between the BVB assemblage with those from the Eocene-Oligocene boundary in southeastern Brazil (Fig. 10), separated by nearly 10 million years, also indicates that during this time interval a retract from the vegetation from high to lower latitudes occurs, answering the gradual post-Eocene drop in global temperatures.

Like proposed by Fine et al. (1014) the transitional mixed floras, with a discontinuous distribution in small and protected basins and suffering cyclical variances, could have allowed

these to function as seed banks that, when ceased the instability, promotes the expansion of the vegetation. Such kind of process could explain the presence in the Boa Vista taphoflora, of analogous today found in distinct biomes. Similar conditions were proposed to the birth of Amazon rainforest, when the Middle Miocene reversal of the flow in the putative paleo-Orinoco River occurs (Hoorn et al., 2010).

The survey made with areas where similar taxa grow today in the north of South America and Central America (Fig. 11), shows that its near relatives are mainly present in the vegetation of Caribbe and Gulf of Mexico, which also attests the role of the active tectonism and uplift of Andes and that this events began still before the end of Paleogene, instead only in Miocene, like proposed by Bacon et al. (2013).

In terms of biostratigraphy, the floras preserved in the small basins formed from the Middle Paleogene onwards in Brazil, by its isolate conditions, are not so useful. Additionally, nearly all angiosperms families were well established after the Oligocene, which prevents the discernment of age-diagnostic taxa. But if analyzed in relation of the community composition and its environmental appeals, the appearing of more dry-resistant elements or of signals of grasslands expansion (Barreda and Palazzi, 2007), could date the limit between Paleogene and Neogene. It is visible also when we accompany the distribution and affinities with more regional floras. Like commented above and is expressed by the cluster analysis from figures 10 and 11, the next relations to Campos Novos Formation flora are expressed in the fossil floras with similar age or that which corresponds to the boundary between Oligocene and Miocene, with the only exception of the Mexican Coatzingo Formation, that was controlled by more arid conditions and exhibits influence from Northern taxa (Martínez-Cabrera and Cevallos-Ferriz, 2008).

In all those aspects, the absolute ages obtained in the geological researches at Boa Vista basin (e.g. Souza et al. 2013) were critical, and make the studied flora a good proxy for the correlations. The data here collected, either from its paleobotanical approach or from the analysis of associated lithologies, attest its importance in the discussions about the comparative role of auto- and allocyclic processes and the answer of vegetation to geological and environmental events.

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Figure captions

Fig. 1. **A.** Location of Paraiba state in northeastern Brazil and the Boa Vista region; **B.** Geological constraints and distribution of main lithologies at the Boa Vista Basin (BVB) and the location of studied outcrop at Juá II Mine (star). Modified from Geological Map of Boqueirão (from Lages and Marinho, 2012); **C.** Transversal section of the half-graben and fault system conditioning the BVB deposition (from Souza et al., 2005).

Fig. 2. **A.** Geological section of the Juá II Mine and the three plant fossil levels studied here in the bentonitic shales. Fossil wood logs were also detected in the upper sandstones; **B.** General view of the exposure from Juá II Mine and the fossiliferous interval (marked).

Fig. 3. **A-D.** *Nectandra bonavistensis* sp. nov. (ULVG 8990a-8990b): in A and B, part and counterpart of the partially preserved leaf; in C, drawing highlighting the venation pattern, the distal successive loops in the secondaries and the percurrent zig-zag course of the tertiaries; in D, leaf of the extant *Nectandra cissiflora* Ness; **E-H.** *Nectandra* cf. *N. lanceolata* Nees (ULVG 9049a-9049b) with the well-visible primary and the apically curvate course of the secondaries; in G, quaternary and quinquenary pattern with irregular reticulate fabric; in H, leaf of the extant *N. lanceolata*; **I.** *Annona* sp. (ULVG 9069a), highlight the rounded base, thick primary vein and weak secondaries. Scale bars: A-F and H-I = 1 cm; G = 0.5 cm.

Fig. 4. **A-C.** *Bauhinia* cf. *B. unguifolia* L. (ULVG 8725): in A, the apparently actinodromous venation and thick petiole (pulvinate); B, well developed mesh of tertiary veins, with 3-4 sided areoles and the unbranched or 1- branched FEVs; in C, a leaf of extant *B. unguifolia* (photo from Parr et al., 2014); **D-E.** *Bauhinia* sp. 1, part and counterpart from a half of the leaflet and its three arcuate actinodromous primaries (CPRM-CM 218F); **F.** *Bauhinia* sp. 2 (ULVG 10770) and the straight primaries. Folded lobes are suggested by the superimposition of ventral and dorsal venation impressions; **G-I.** *Senna* aff. *S. tapajozensis* (Ducke) H.S. Irwin & Barneby, obovate and asymmetric leaflet, with clearly visible brochidodromous secondaries and percurrent tertiaries. In G (ULVG 8726a) and H (ULVG 9060a); in I, the leaflet of extant *S. tapajozensis* (photo from Parr et al., 2014); **J.** *Cassia* aff. *C. wendtii* Britton

(ULVG 9100) leaflet, highlight the pulvinate petiole and numerous brochidodromous secondaries, narrow and irregularly spaced. Scale bars: A, C-J = 1 cm; B = 0.5 cm.

Fig. 5. A-C. *Dinizia* aff. *D. excelsa* Ducke (CPRM-Cm 0226), part and counterpart, showing the well-visible main vein, with irregularly spaced brochidodromous secondaries; in C, clarified leaflet of a extant *D. excelsa*, native of the Amazonian rainforest (from Herendeen and Dilcher, 1990); **D.** *Parkia* cf. *P. nitida* Miquel, leaflet (ULVG 9045a); **E-G.** *Inga* aff. *I. marginata* Willd (ULVG 9022a), in F, the drawing of the main features; in G, the leaflet of the extant *I. marginata* (photo from Parr et al., 2014); **H.** *Leguminocarpum* Dotzler 1938 (ULVG 9016a); **I.** *Leguminocarpum paraibensis* sp. nov. (CPRM-CM 0228F), legume fruit, with a plane-compressed and linear form, prominent marginal suture, one or two constrictions, and the elongate seeds; **J-K.** a very incomplete flower preserving part of the receptacle (ULVG 9095); in K, a comparable zygomorphic flower of *Cassia excelsa* (figured by Martius, 1824), today included in *Senna spectabilis* var. *excelsa* (Schrad.) H.S. Irwin & Barneby. Scale bars: A-C, E-I = 1 cm; D and K = 0.5 cm, J = 0.2 cm.

Fig. 6 A-D. *Myrcia rostrataformis* Hollick and Berry (ULVG 9048), in B and C, details of the intramarginal and fimbrial veins; **E-G.** *Calyptranthes* cf. *C. argilosa* Duarte & Rezende-Martins (ULVG 9067a): in F, drawing of leaf showing the tertiary mesh; in G, a detail of the intramarginal and fimbrial veins disposition; **H-I.** *Calyptranthes creba* McVaugh, detail of the admedially ramified tertiary and fimbrial veins in the extant *C. creba*, today growing at Amazonian rainforest and *Cerrado* (photo from Parr et al., 2014); in I, general aspect of *C. creba*. Scale bars: A-B, D-F, I = 1 cm; C, G and H = 0.5 cm.

Fig. 7. A-D: *Protium* cf. *P. heptaphyllum* (Aubl.) Marchand. In A-B (ULVG 10761a), and in C (ULVG 9007a); D shows the leaflet of extant *P. heptaphyllum*, today found in diversified biomes from rainforests and *Cerrado*, Brazil (photo from Parr et al., 2004); **F-H.** *Protium* cf. *P. rhynchophyllum* (Rusby) D.C. Daly (ULVG 9051a): in G, detail of the regularly disposed brochidodromous secondary veins, with distinct exmedial loops; **H.** a leaflet from extant *P. rhynchophyllum* (Photo from Parr et al. 2014). Scale bars: 1 cm.

Fig. 8. A-C: *Anacardium* cf. *A. occidentale* L. (CPRM-CM 0223Fa): in B, the attenuate exmedial loop of the secondaries and the zig-zag line formed by tertiary bifurcations meeting in intercostal areas, in C, leaf detail of the extant *A. occidentale* L., today growing in *Caatinga*, NE Brazil, and the well-developed areolation, 4-5 sides. The exterior loop formed exmedially between the main secondary loops is visible (photo from Parr et al., 2014); D-F: *Luehea* cf. *L. paniculata* Mart. & Zucc (ULVG 9002a). In E, a detail of the few secondaries that diverges from the main primary, only in middle-apical part of the lamina; in F, leaf of the extant *L. paniculata* (photo from Parr et al., 2014); G-H: *Lueheopsis* cf. *L. hoehnei* Burret (CPRM-CM 0232F), showing the broad leaf. In H, leaf from *L. hoehnei*, today growing in Amazon rainforest and *Cerrado* (photo from Parr et al., 2014); I. *Dicotylophyllum* sp. 1 (ULVG 9118a), with affinities with the extant forms of *Senna* Mill.; J. *Dicotylophyllum* sp. 2 (CPRM-CM 022F). Scale bars: A and D, F-J = 1 cm; B-C and E = 0.5 cm.

Fig. 9. Graphic to foliar physiognomy, representativeness and biome data analysis for the Campos Novos Formation assemblage. In those referring to biomes and forest types, the ecological affinities were taken from each single taxa.

Fig. 10. Dendrogram obtained to the leaf morphogenera similarity between the Campos Novos assemblage (Boa Vista Basin) and other Cenozoic Brazilian taphofloras (see Supplementary File 1, to the data).

Fig. 11. Results from cluster analysis in the evaluation of leaf morphogenera similarity between Campos Novos Formation and other Neotropical taphofloras from northwestern South America, Mesoamerica and South Mexico (data in Supplementary Files 2).

Supplementary file 1: Basins and age data of the knowing record of leaves and wood in Cenozoic levels from Brazil (references in the text). Family insertion is that from the original works.

Supplementary file 2. Cenozoic angiosperm record (leaves, fruits and wood) to the Mesoamerica and northern South America deposits and the proposed ages (references in the text). Family insertion is that from the original works.

Figure 1

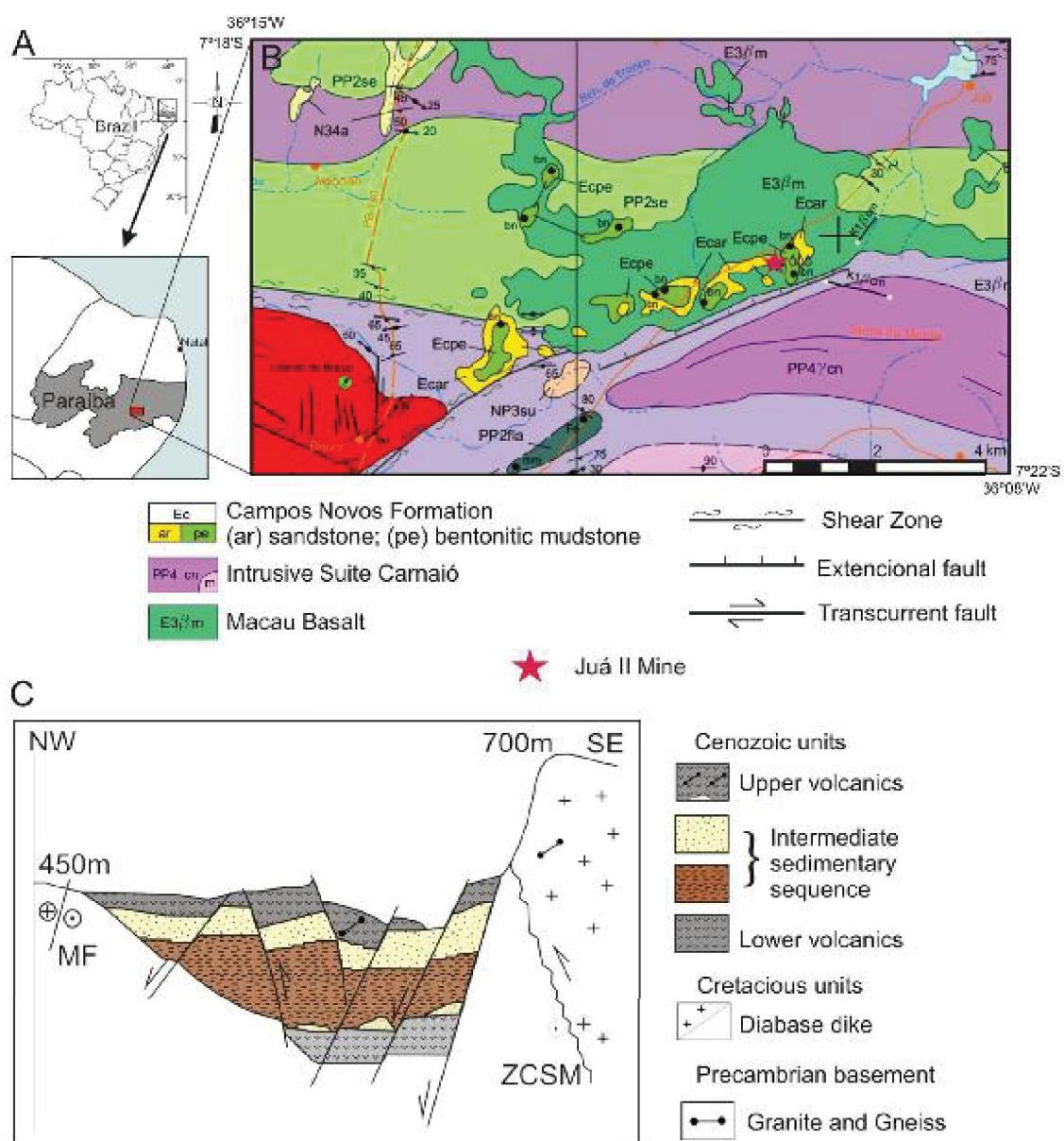


Figure 2

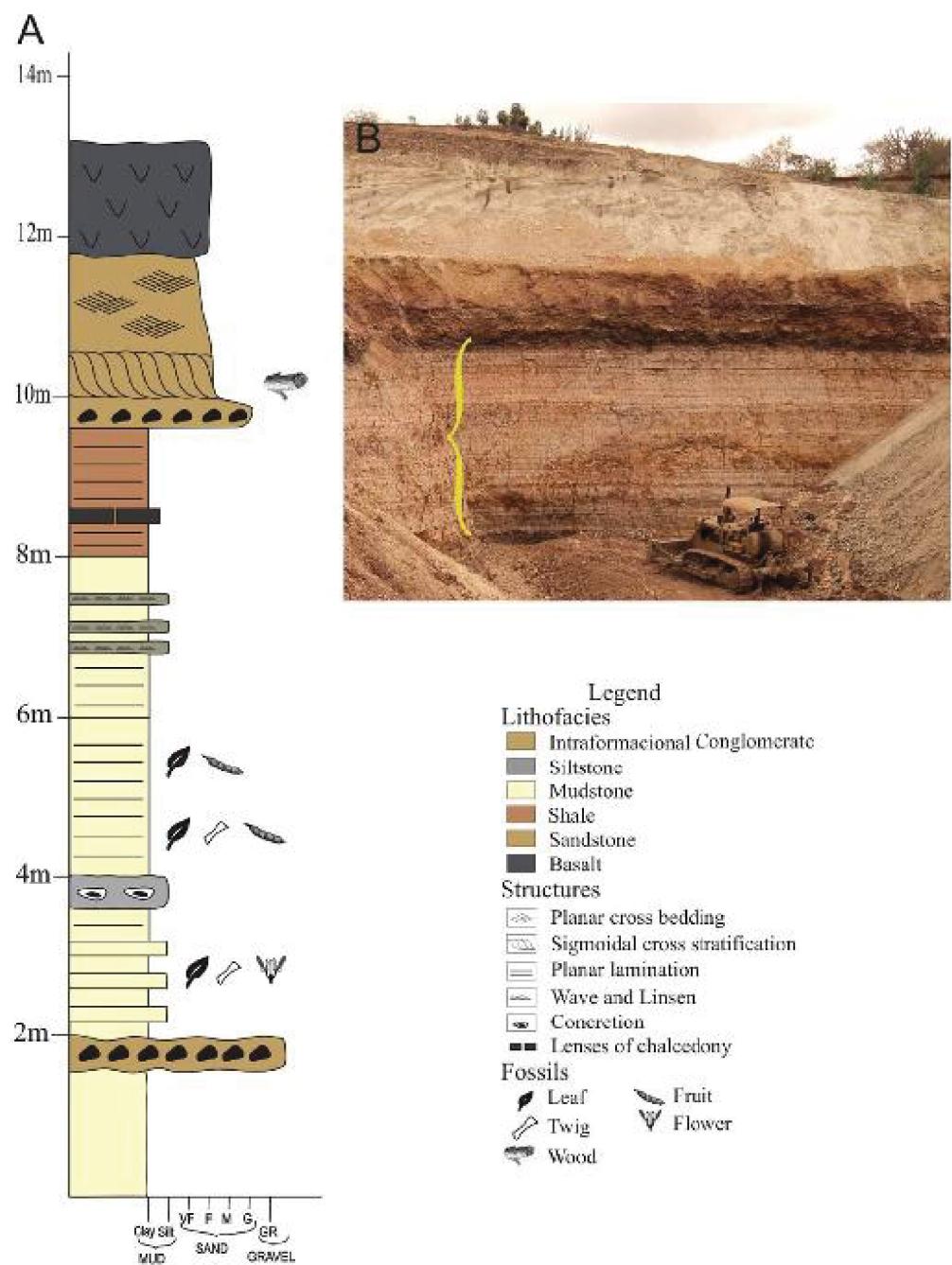


Figure 3

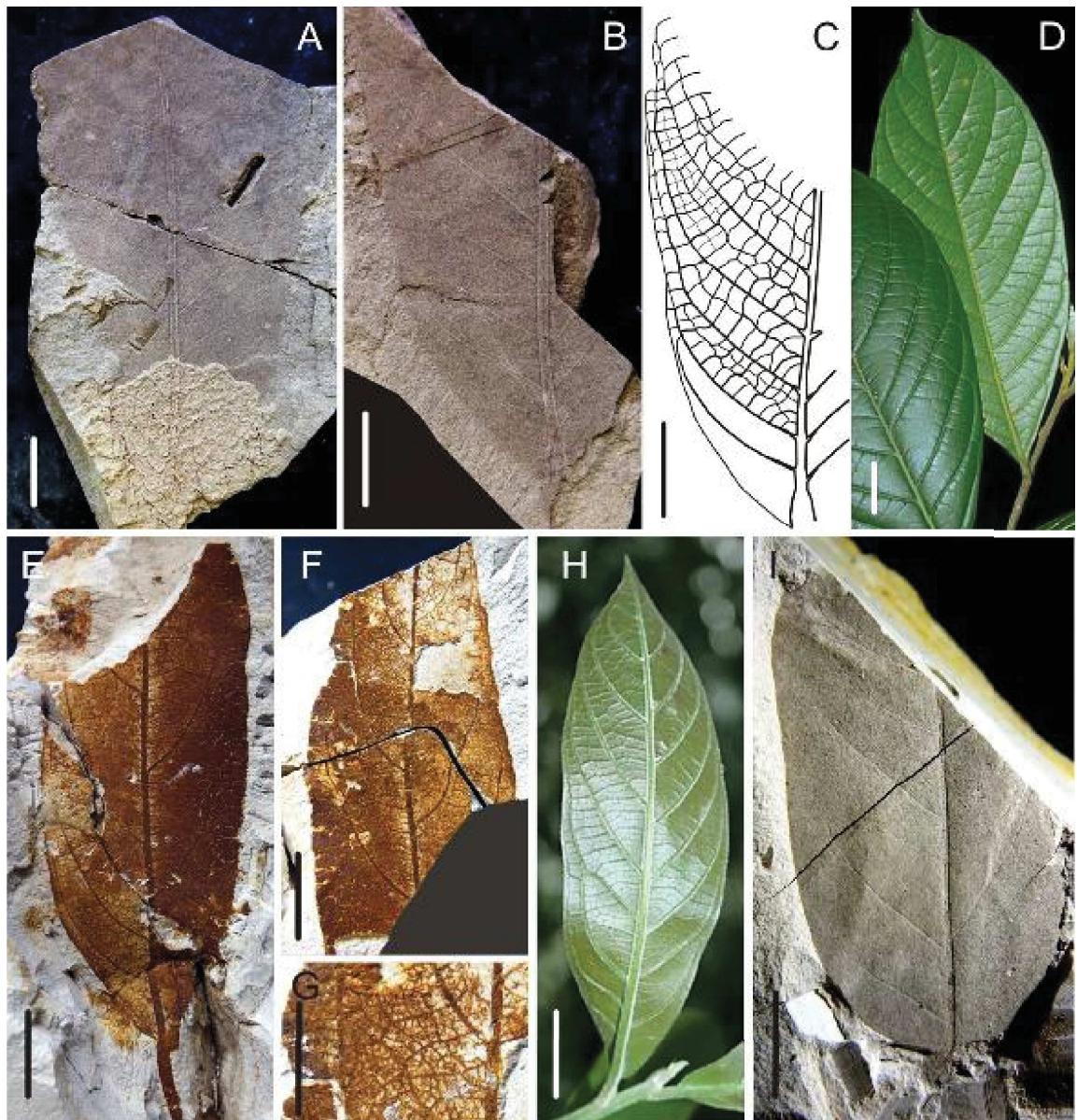


Figure 4

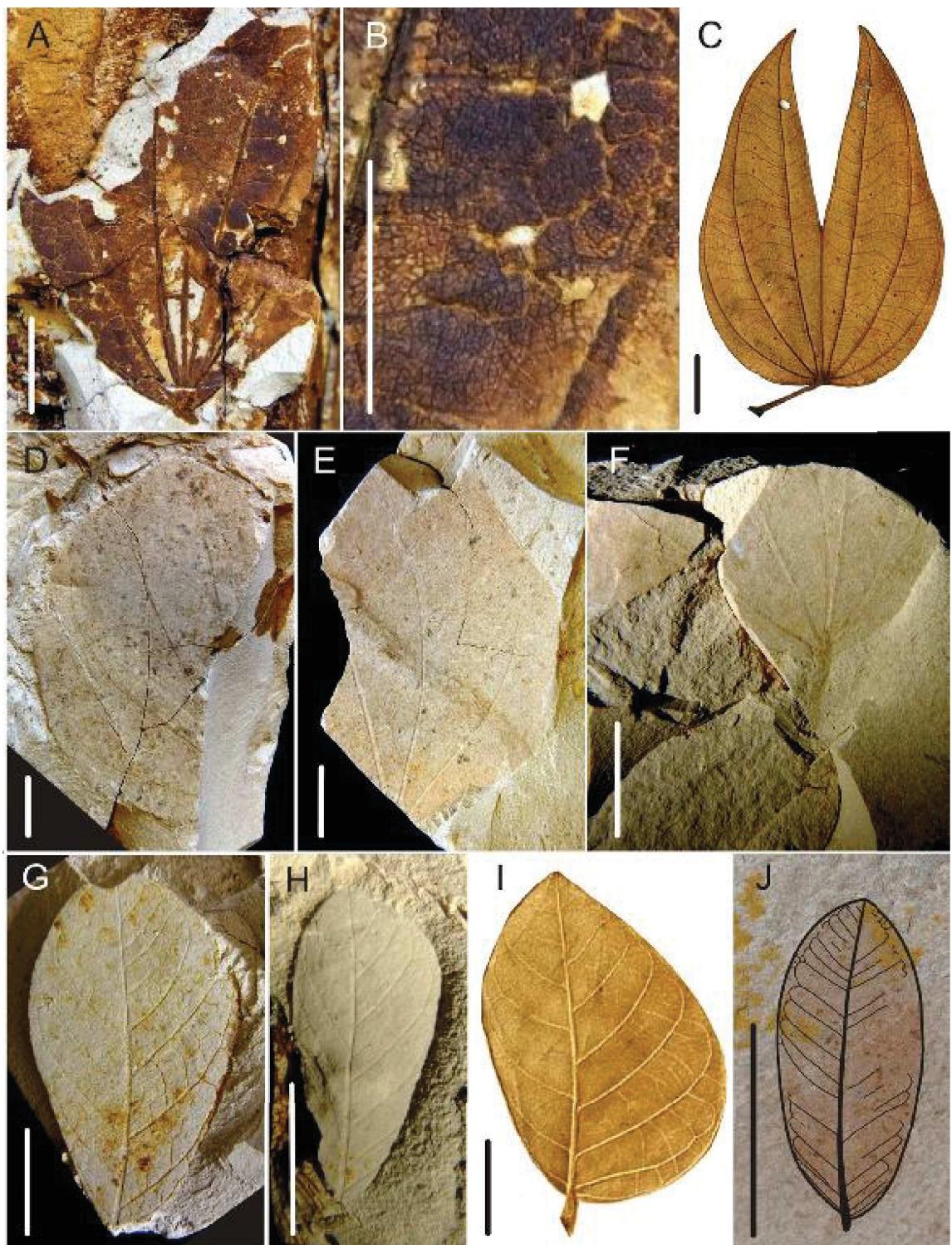


Figure 5

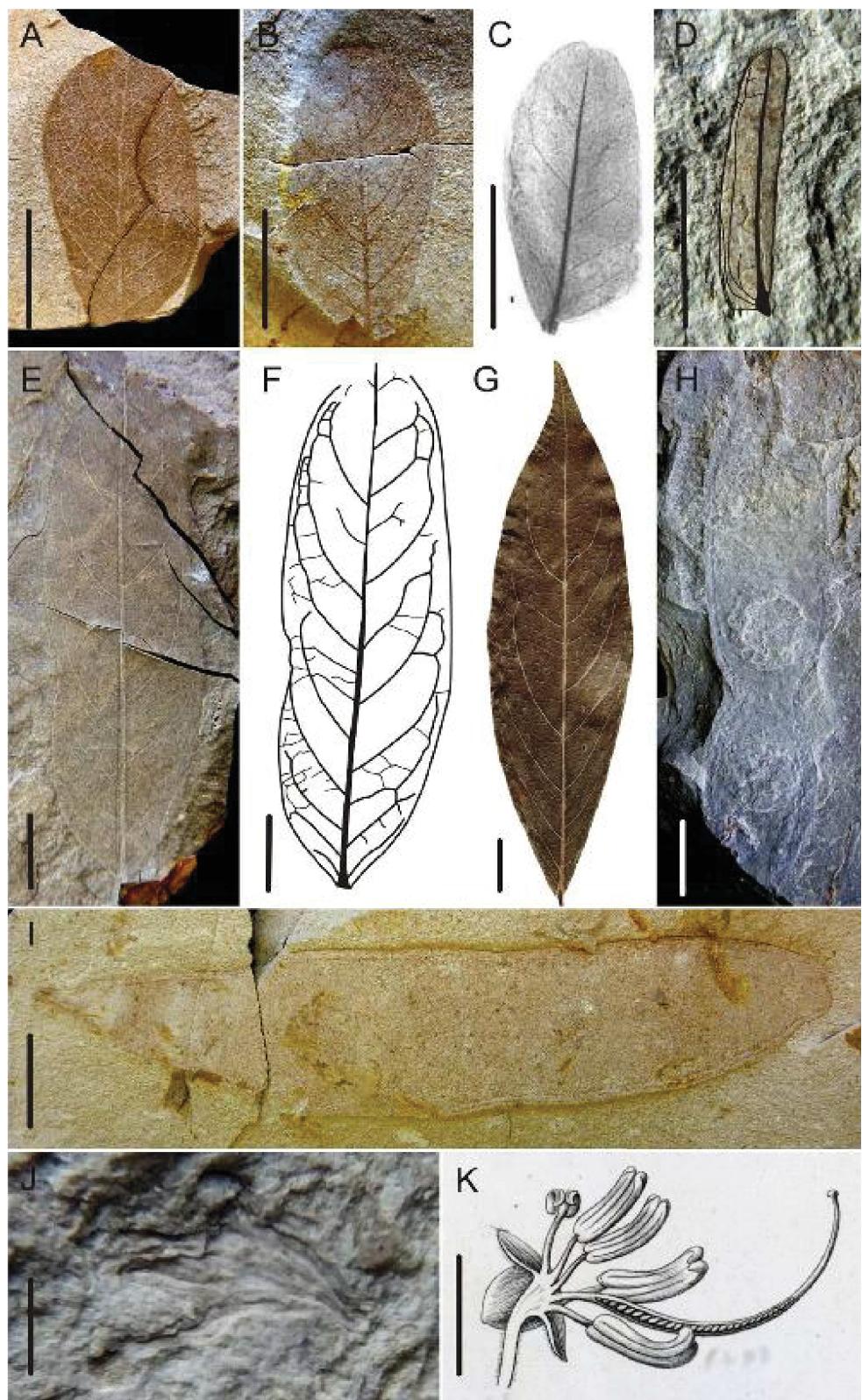


Figure 6

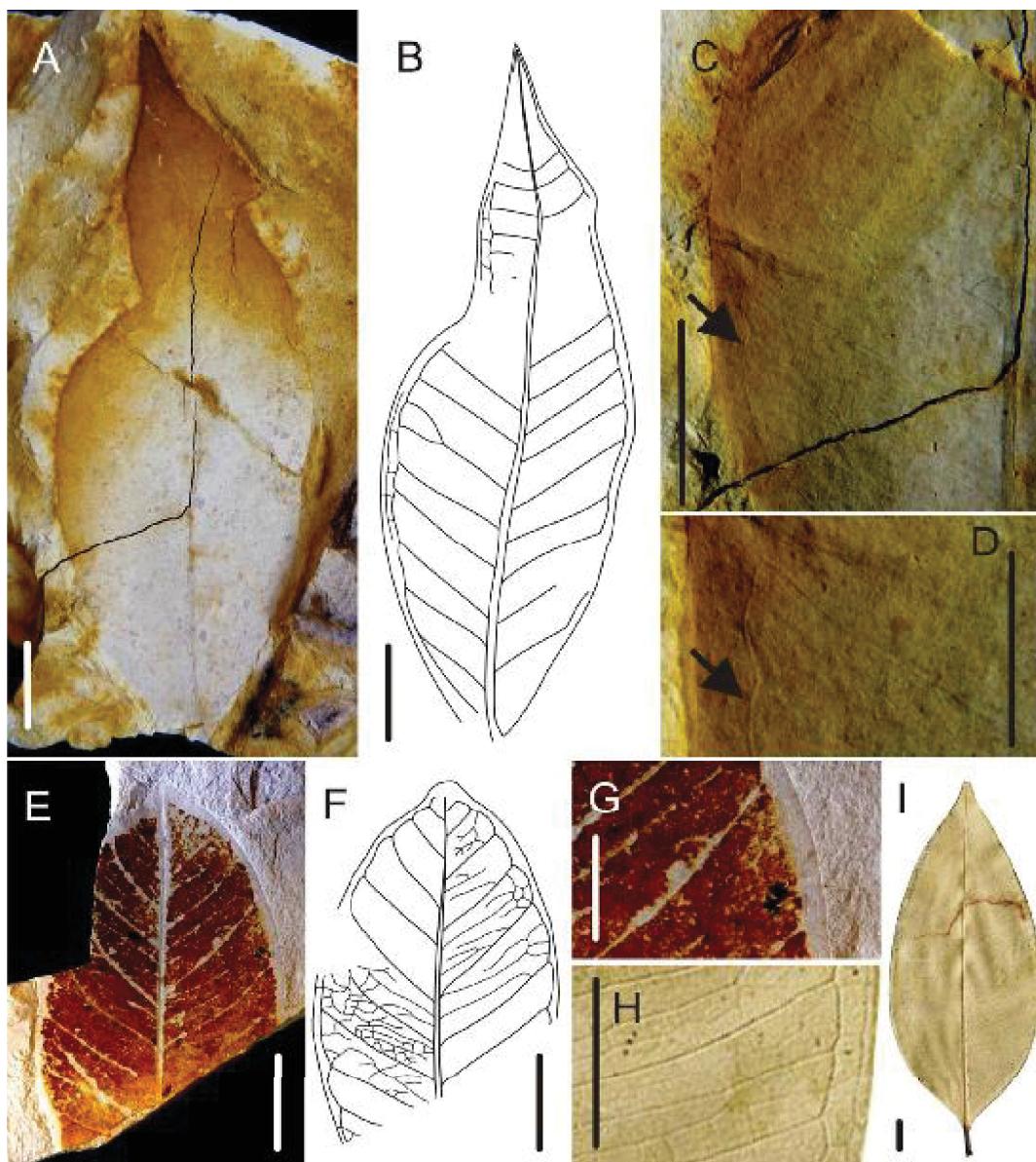


Figure 7

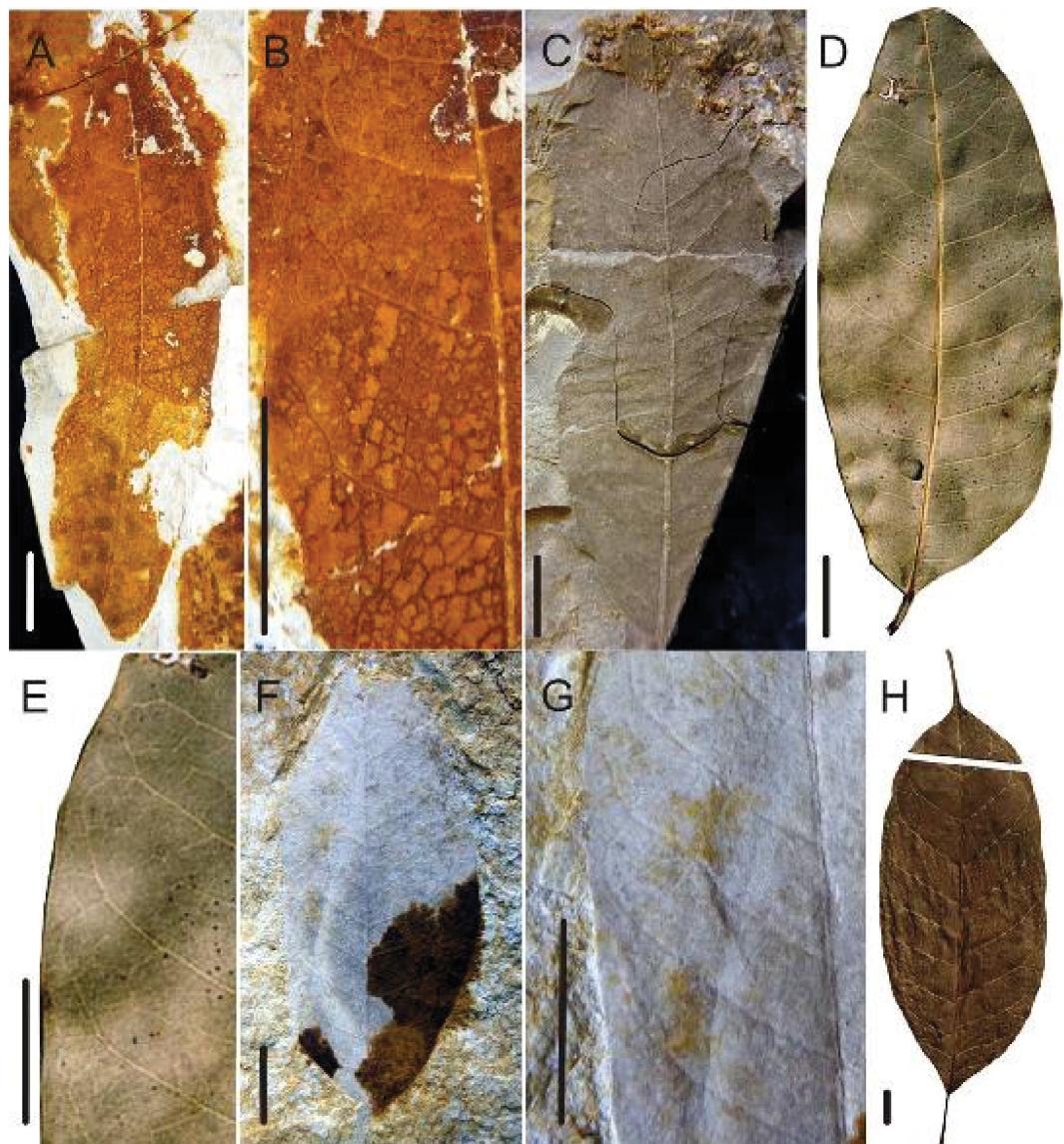


Figure 8

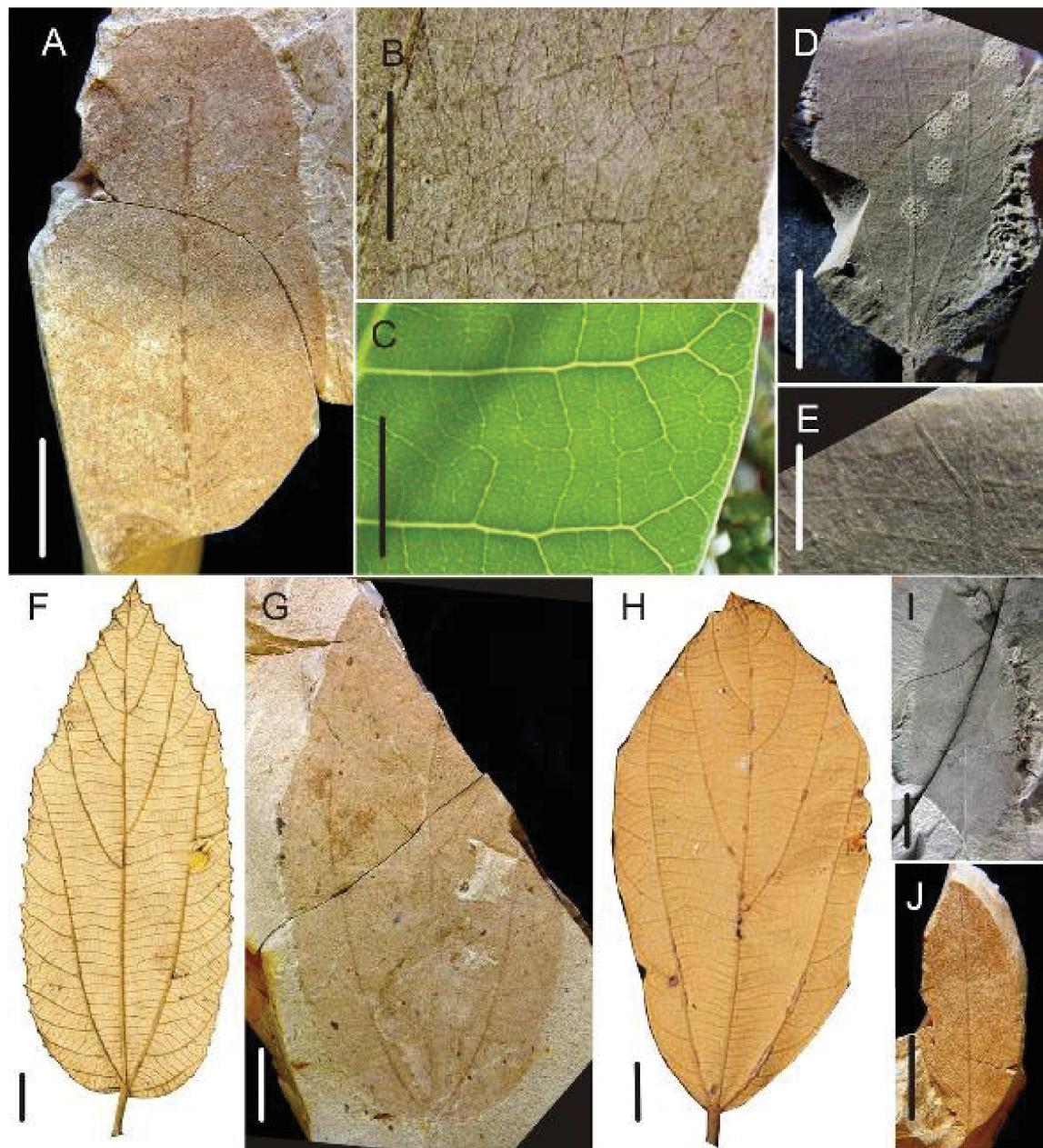


Figure 9

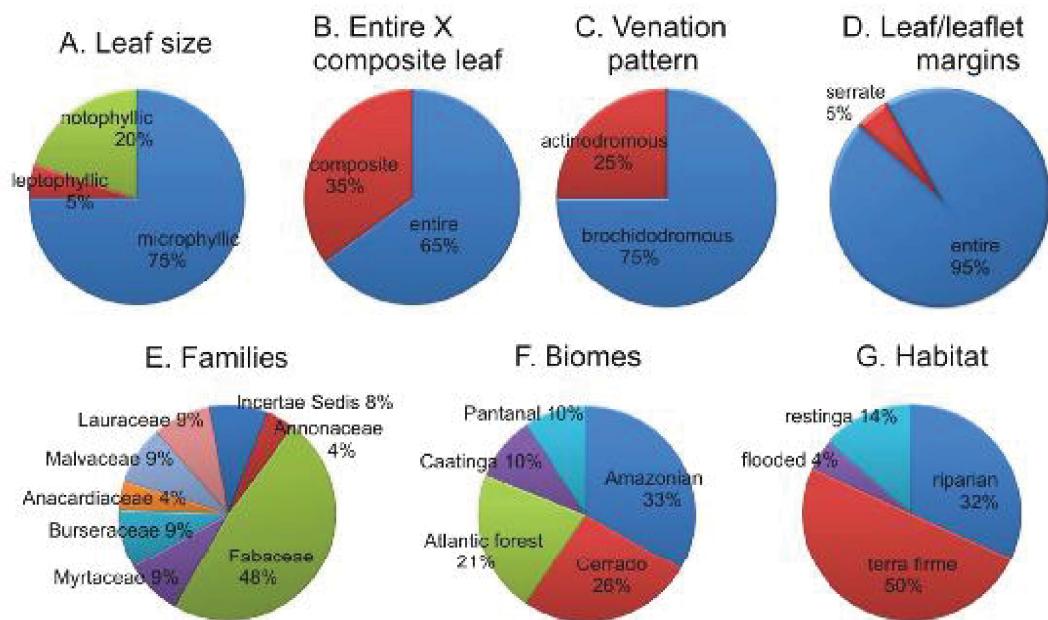


Figure 10

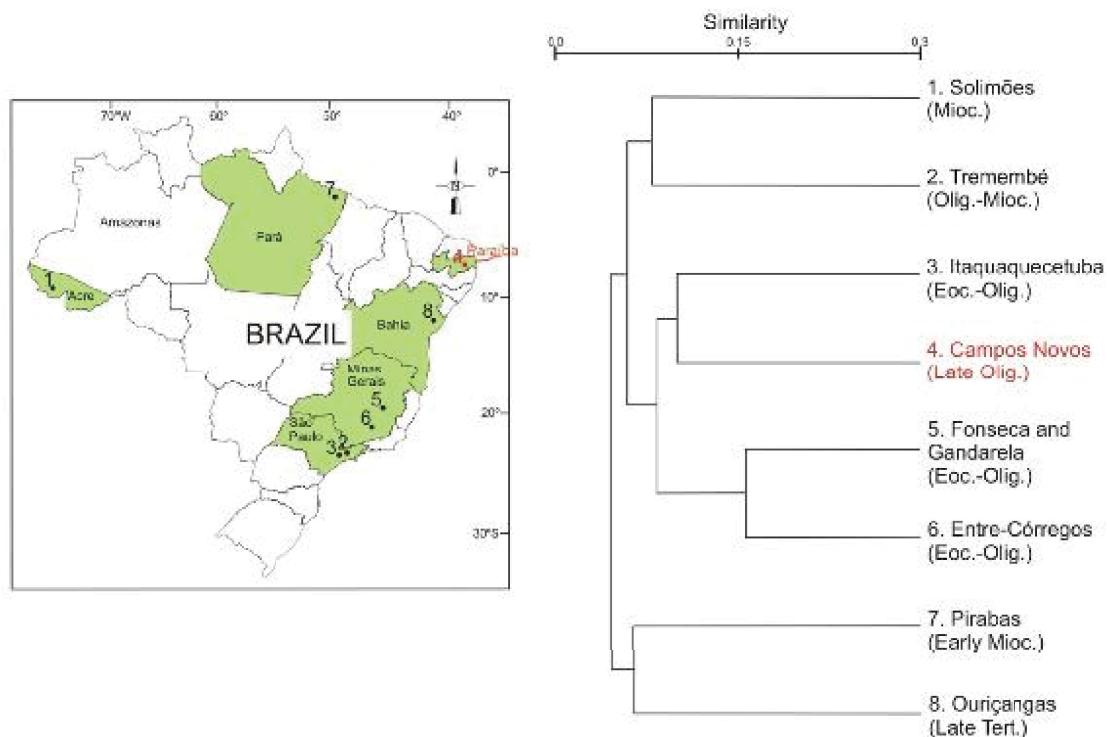


Figure 11

